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Franck Trolliet

Dispersion des graines zoochores et régénération de la forêt tropicale humide face aux activités anthropiques dans une mosaïque de forêts-savanes en République Démocratique du Congo

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Animal-mediated seed dispersal and tropical rainforest regeneration in the face of anthropogenic activities in a forest-savanna mosaic in Democratic Republic of the Congo

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Département de Biologie, Ecologie, Evolution Unité de Biologie du Comportement

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Sous la supervision d'Alain Hambuckers

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A ma famille, Jantje et Jules

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Résumé

Les patrons de biodiversité dans les forêts tropicales humides résultent d'interactions complexes à l'échelle de la communauté, tels que la dispersion des graines par les animaux. Les activités anthropiques (chasse, perte et fragmentation des forêts, etc.) perturbent ces processus écologiques et menacent ainsi le maintien de la diversité à l'échelle de la communauté végétale. Néanmoins, le niveau de résilience des processus impliqués dans la régénération forestière dans les paysages perturbés demeure incertain. La présente thèse vise à comprendre comment les services de dispersion des graines assurés par les grands frugivores ainsi que leur rôle fonctionnel dans la régénération des plantes sont affectés dans un paysage influencé par les activités anthropiques. Nous avons mené un travail de terrain dans une mosaïque de forêts-savanes en République Démocratique du Congo, un paysage ayant une structure spatiale fragmentée et qui abrite des activiés anthropiques (chasse, agriculture itinérante sur brûlis).

Premièrement, nous avons examiné les services de dispersion des graines assurés par un grand primate menacé, le bonobo (*Pan paniscus*). Les bonobos dispersent une majorité de grandes graines que peu d'autres frugivores peuvent disperser, qui incluent de nombreuses espèces sciaphiles. Ce frugivore assure des services capitaux dans la mosaïque et joue probablement un rôle fonctionnel clé dans la régénération des forêts matures.

Dans le Chapitre 2, nous nous sommes concentrés sur le processus de dispersion des graines d'une espèce d'arbre à grandes graines, *Staudtia kamerunensis* (Myristicaceae). Nous avons trouvé que la pression de chasse, la couverture forestière et la disponibilité en fruits influençaient le niveau d'activité du présumé principal disperseur, le calao à cuisses blanches (*Bycanistes albotibialis*), déterminant ainsi le pourcentage de dispersion des graines.

Dans le Chapitre 3, nous avons exploré l'influence de deux taxons majeurs de frugivores, les primates et les calaos, sur la génération de foyer de recrutement de plantules. Nous avons montré que *S. kamerunensis* agissait comme un foyer de régénération, et que les calaos jouaient un rôle clé dans ce système, lequel a probablement un rôle structurant dans les forêts afrotropicales. Aussi, nous avons vu que la densité de plantules dispersées par les calaos était positivement associée à la quantité de forêt dans le paysage.

Finalement, nous avons pu clarifier le niveau de redondance fonctionnelle des primates, des calaos et des éléphants dans le recrutement de plantules zoochores. Nous avons montré que le niveau de redondance entre ces taxons dépendait de la variable considérée. Plus particulièrement, les primates jouent un rôle clé dans le maintien de la richesse spécifique, alors que les éléphants et les calaos ont un rôle plus marqué pour la régénération d'espèces à grandes graines. Aussi, nous avons montré que les variables de sol expliquaient jusqu'à 17 % de la variation dans la communauté de plantules.

Généralement, nous avons conclu que les grands frugivores jouent un rôle fonctionnel unique et primordial grâce à leur capacité à disperser des grandes graines, et que les calaos semblent aussi très importants de par leur grande mobilité. Ces taxons assurent certainement le maintien de forêts matures et diversifiées et lient le processus de régénération au travers du paysage. Cependant, la chasse et la déforestation menacent ces frugivores clés, le processus de régénération forestière, et le maintien des forêts tropicales humides et des services associés.

Abstract

Patterns of biodiversity in tropical rain forests result from complex interactions at the community level such as animal-mediated seed dispersal. Anthropogenic activities (bushmeat hunting, forest loss and fragmentation, etc.) disrupt these ecological interactions and threaten the maintenance of diversity at the community-level. However, the level of resilience of the processes involved in forest regeneration in disturbed landscapes remain unclear. This thesis aims at understanding how the seed dispersal services provided by large frugivores and their functional role in plant regeneration are affected in a landscape influenced by human activities.

We conducted field work in a forest-savanna mosaic in Democratic Republic of the Congo, a landscape that has a fragmented spatial structure and house anthropogenic activities (hunting, slash-and-burn agriculture).

Firstly, we explored the seed dispersal services provided by a large endangered primate, the bonobo (*Pan paniscus*). Bonobos dispersed a majority of large-seeded plants that few other frugivores can disperse, among which numerous were shade-bearer species. This frugivore provide critical services in the mosaic and probably plays a key functional role for the regeneration of mature forests.

In Chapter 2, we focused on the seed dispersal process of a large-seeded tree species, *Staudtia kamerunensis* (Myristicaceae). We showed that hunting pressure, forest cover and fruit availability influenced the activity level of its presumed main disperser, the white-thighed hornbill (*Bycanistes albotibialis*), thereby determining percentages of seed dispersal.

In Chapter 3, we explored the influence of two major taxa of frugivores, primates and hornbills, on the generation of recruitment foci of animal-dispersed seedlings. We found that *S. kamerunensis* acted as a recruitment foci and that hornbills played a key role in this system, which is believed to have a structuring role in Afrotropical forests. Also, we found that the density of hornbill-dispersed seedlings was positively associated with the amount of forest cover in the landscape.

Finally, we could disentangle the level of functional redundancy among primates, hornbills, and elephants for seedling recruitment. We showed that the level of functional redundancy among those taxa depended on the variable considered. More particularly, primates appeared to play a key role for the maintenance of species richness, while elephants and hornbills had a stronger role for the regeneration of plant species with large seeds. Also, we found that soil variables explained up to 17% of the variation in the seedling community, which put into perspective the relative importance of biotic and abiotic processes.

Overall, we concluded that large frugivores play a unique and critical functional role thanks to their capacity to disperse large seeds. Similarly, hornbills appear very important because of their great mobility. Together, those taxa most probably ensure the maintenance of diverse and mature forests and link the regeneration process between disconnected areas in the landscape. Yet, hunting and deforestation threaten these key frugivores, ecological functioning and the maintenance of diverse tropical forests and its associated services.

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Introduction générale

Les forêts tropicales humides, qui s'étendent de part et d'autre de l'équateur, entre le tropique du Capricorne et le tropique du Cancer, représentent 44 % de l'étendue des forêts dans le monde (Fig. 0-1). Si le bassin Amazonien abrite le plus grand bloc et recouvre 40 % de l'Amérique du Sud, le bassin du Congo arrive, lui, en 2ème position avec ses 200 millions d'hectares de forêt (de Wasseige et al. 2012), ce qui représente près d'un tiers de la superficie totale des forêts tropicales de la planète. La République Démocratique du Congo prend une place particulière puisqu'elle abrite à elle seule 60 % des forêts du bassin, soit plus de la moitié des forêts du continent Africain (Mayaux et al. 2013).

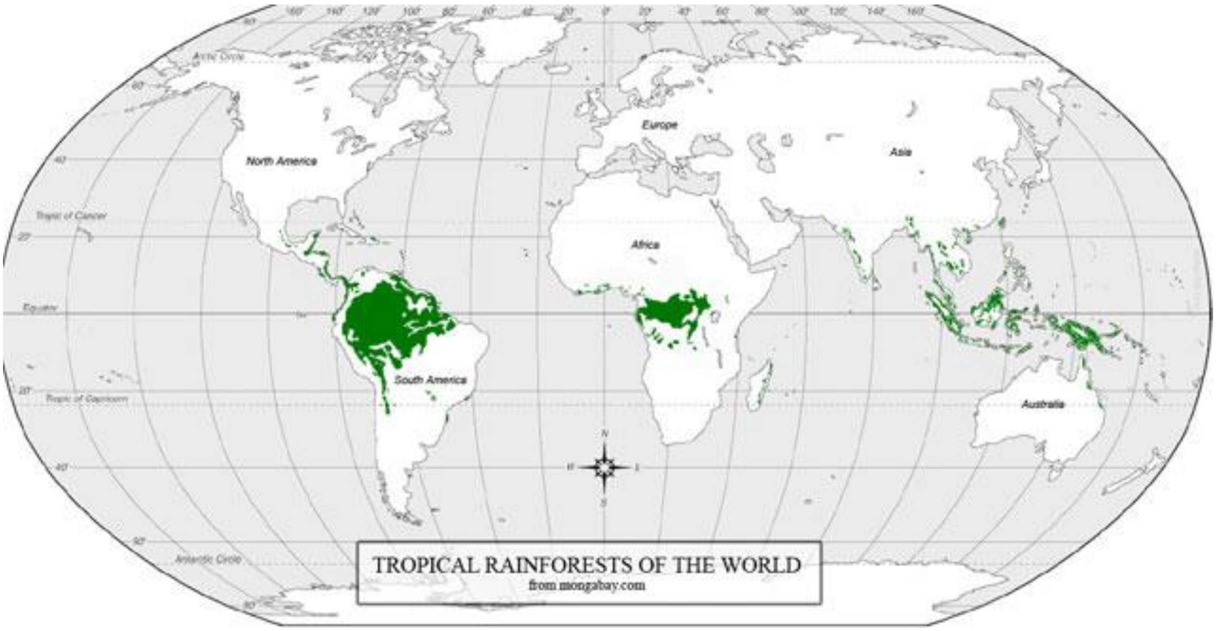


Fig. 0-1. Distribution des forêts tropicales humides de la planète.

Les forêts tropicales humides: un recueil de biodiversité et de services

Les écosystèmes forestiers tropicaux ne recouvrent que 13 % des terres émergées (FAO 2010), mais abritent plus de la moitié de la biodiversité de la planète. Cette diversité biologique particulièrement importante fût rapportée dès la fin du 15$^{\text{ème}}$ siècle lors de l'arrivée des explorateurs européens au Nouveau Monde. Durant les siècles qui suivirent, de nombreux explorateurs-naturalistes ont décrit une multitude de nouvelles espèces animales et végétales provenant d'Asie, d'Afrique, et d'Amérique, mais la richesse extraordinaire des forêts tropicales continue aujourd'hui de nous étonner. Premièrement, car de nouvelles espèces sont régulièrement découvertes, mais aussi car nous ne connaissons pas précisément le nombre d'espèces qui existent, et les estimations suggèrent qu'une grande proportion d'entre elles restent à découvrir (Morell 1996). Par exemple, des estimations récentes suggèrent qu'il existe entre 40 000 et 53 000 espèces d'arbres dans l'ensemble des forêts tropicales (Slik et al. 2015) alors que l'on en dénombre que 1166 dans l'ensemble des forêts tempérées de l'hémisphère Nord (Latham and Ricklefs 1993). Ainsi, les forêts tropicales humides sont considérées comme les communautés terrestres les plus diversifiées de la planète (Myers 1984). Plusieurs auteurs ont mis en évidence l'augmentation graduelle de la richesse biologique vers les basses latitudes (e.g. Darwin 1859, Fischer 1960, Pianka 1966) et de nombreuses hypothèses furent proposées afin d'expliquer ce patron global (Pianka 1978, Terborgh 1985, Stevens 1989), parmi lesquelles la productivité primaire, la température, les facteurs historiques tel que le conservatisme de niche, etc. semblent aujourd'hui les plus admises (Gaston 2000, Brown 2014). Néanmoins, ces différentes théories ne sont pas mutuellement exclusives et il ne semble toujours pas y avoir de consensus général quant aux raisons de cette forte diversité biologique sous les Tropiques. Cette problématique demeure dès lors un des thèmes de recherche essentiels en écologie et en biogéographie (Gaston 2000, Hillebrand 2004, Weir and Schluter 2007, Brown 2014).

Les forêts tropicales fournissent de nombreux services écosystémiques aux populations humaines, que ce soit de manière directe ou indirecte. En effet, plusieurs dizaines de millions de familles dans le monde sont largement tributaires d'une multitude de biens et services provenant de ces écosystèmes. Il est estimé que la survie de 60 millions de personnes en Afrique rurale dépend des ressources naturelles des forêts (Mayaux et al. 2013). Entre autres, le bois joue quotidiennement un rôle fondamental dans la construction de maisons et comme source d'énergie. En Afrique sub-saharienne, il remplit plus de 80 % des besoins et représente donc la principale source d'énergie domestique (Tutu and Akol 2009). En plus des ressources ligneuses, toute une série de produits forestiers non-ligneux (PFNL) tels que les fruits, les champignons, les plantes médicinales, etc. directement extraits des forêts sont d'une importance capitale pour le bien-être quotidien de nombreux ménages (Fig. 0-2). En particulier, la viande de brousse et le poisson sont cruciaux car ils représentent la principale source de protéine dans les zones rurales (Nasi et al. 2011). La grande majorité des populations humaines du bassin du Congo dépend aussi des forêts pour l'agriculture itinérante sur brûlis. Cette technique traditionnelle consiste à défricher annuellement une nouvelle parcelle de forêt et à brûler la biomasse abattue afin de rendre la terre plus fertile et de la cultiver. Après quelques années la parcelle est abandonnée à la friche pour que puisse se reconstituer la biomasse végétale (Fig. 0-2). Les forêts tropicales fournissent aussi des services culturels aux populations humaines tels que les activités traditionnelles (protection des esprits des anciens, lieux sacrées pour les cérémonies d'initiations et culturelles, cimetières forestiers etc.) (Aveling 2008). Dans certains cas, la participation à des activités touristiques peut constituer une source de revenus.

Fig. 0-2. Ressources forestières utilisées par les populations humaines. En haut à gauche: cueillette de champignons en forêt tropicale; en haut à droite : parcelle d'agriculture sur brûlis; en bas à droite : poissons péchés par un agent de sécurité (R.D.C, © F. Trolliet) ; en bas à gauche : animaux forestiers chassés pour leur consommation (Gabon, © P.-M. Forget).

Ces écosystèmes fournissent aussi des biens et services à l'échelle globale et profitent aux populations humaines sur l'ensemble de la planète. Un des exemples les plus connus est l'extraction du bois et son export vers les pays Occidentaux pour la construction et la fabrication de mobilier et de plancher. A titre indicatif, entre 27 et 53 millions de mètres cubes de bois sont extraits des forêts brésiliennes chaque année (Asner et al. 2005). De manière globale, le marché du bois tropical à une valeur annuel de 11,2 milliard de dollars (ITTO 2007). En Afrique Centrale, l'exploitation forestière industrielle est une activité en grande expansion avec des concessions qui couvrent désormais plus de 30 % de l'étendue des forêts de la région (Laporte et al. 2007). Par ailleurs, les forêts tropicales jouent un rôle clé dans la régulation du climat mondial car elles emmagasinent plusieurs centaines de milliards de tonnes de carbone (Laurance 1999a, Canadell et al. 2007). Plus particulièrement, les forêts afro-tropicales stockent plus de 90 % du carbone émis dans l'ensemble des écosystèmes terrestres du continent (Mayaux et al. 2013). Elles permettent aussi l'atténuation des inondations. Ces quelques exemples ne sont qu'un aperçu de l'importance globale de ces écosystèmes et des nombreuses utilisations de leurs ressources par l'homme. Cependant, ils nous permettent déjà de comprendre que la diversité des espèces animales et végétales qui les composent joue un rôle primordial dans la survie et le bien-être de très nombreux foyers aux quatre coins de la planète. Ainsi, la pérennité de ces services ne pourra être assurée que par la mise en œuvre d'une bonne gestion des écosystèmes forestiers tropicaux et la conservation des espèces qui la composent.

La biodiversité s'organise en communautés extrêmement complexes au sein desquelles de nombreuses interactions inter-espèces et processus écologiques permettent son maintien. Plus particulièrement, les interactions mutualistes plantes-animaux (pollinisation, dispersion des graines), et antagonistes (herbivorie, granivorie) influencent largement les capacités de régénération de nombreuses espèces de plantes, et ont un impact profond sur l'organisation des communautés végétales (Wang and Smith 2002). Il importe donc de s'intéresser à la dynamique des processus écologiques, et aux mécanismes qui permettent le maintien de la richesse en espèces et de la coexistence de ses espèces (Stevens et al. 2003, Safi et al. 2011). Par conséquent, dans le but de mieux comprendre les mécanismes fondamentaux du fonctionnement et de l'organisation spatiale de la biodiversité, et donc, de nous permettre de conserver efficacement ces écosystèmes et les biens et services associés, il parait capital de ne pas se contenter de simples indices de richesses, mais de considérer aussi les interactions inter-espèces qui caractérisent les communautés.

Interactions plantes-animaux et régénération des plantes

Au contraire des animaux qui sont mobiles, aptes à se déplacer pour échapper aux prédateurs, à chercher de la nourriture et des partenaires pour se reproduire, les plantes sont des organismes immobiles et fixés, donc largement dépendant des conditions environnementales locales dans lesquelles elles se trouvent. Les graines, contenant les embryons fertilisés, représentent un lien fondamental entre les plantes adultes et leur progéniture, et leur dispersion à l'écart des arbres parents assure la mobilité des plantes. Ce processus est considéré comme ayant une profonde influence sur la structure de la végétation (Wang and Smith 2002). La dispersion des graines peut apporter différents avantages aux plantes (Howe and Smallwood 1982, Wenny 2001). Un premier avantage est que les graines dispersées peuvent coloniser des nouveaux habitats. Cette hypothèse, dite de la colonisation, est particulièrement valable lorsque l'environnement est hétérogène. Par exemple, lorsque certains habitats sont perturbés ou ouverts, une dispersion efficace vers ces zones confère des capacités d'établissement élevées car l'habitat est peu sélectif. Une deuxième hypothèse, dite de la dispersion dirigée, suggère que les graines de certaines espèces soient disproportionnellement déposées dans des habitats où leur probabilité de survie et d'établissement seraient particulièrement élevées. Ainsi, des adaptations particulières des fruits et des graines pourraient permettre une bonne dispersion vers de tels sites. Finalement, le troisième avantage, qui concerne probablement le plus grand nombre d'espèces, serait qu'en étant dispersées à l'écart des arbres parents, les graines échapperaient à un risque de mortalité plus élevé à proximité de ceux-ci, là où il y a une plus grande densité de graines conspécifiques. Les graines non-dispersées qui s'accumulent aux pieds des arbres parents, aussi bien que les arbres parents eux-mêmes, attirent des ennemis spécialisés tels que des insectes, des champignons ou des bactéries (Mangan et al. 2010). Ces ennemis spécifiques augmenteraient le risque de mortalité *per capita*, lorsque la densité des graines ou de plantules augmente. Inversement, les graines dispersées à l'écart de ces zones connaîtraient une probabilité de mortalité moins élevés et seraient dès lors avantagées.

Cette dernière hypothèse est le fondement théorique du modèle de Janzen-Connell (Janzen 1970, Connell 1971) qui prédit que la probabilité de survie des graines et d'établissement des plantules augmente en fonction de la distance par rapport aux arbres parents (Fig. 0-3). On parle de processus de mortalité dépendant de la densité car la densité des graines et des plantules et donc la mortalité diminue avec la distance des arbres parents. Alors que les ennemis généralistes des graines et des plantules égalisent les abondances de survivants des différentes espèces en détruisant majoritairement les graines et plantules des espèces les plus abondantes, les ennemis spécialistes limitent les taux de recrutement en fonction des densités de graines et de plantules. Le modèle de Janzen-Connell permet de prédire que ces phénomènes tendent d'une part à favoriser la colonisation d'espèces dispersées, et particulièrement les espèces rares, et d'autre part à limiter le recrutement d'espèces abondantes, ce qui au final tend à maintenir une grande diversité végétale (Schupp 1992, Wright 2002, Terborgh 2012).

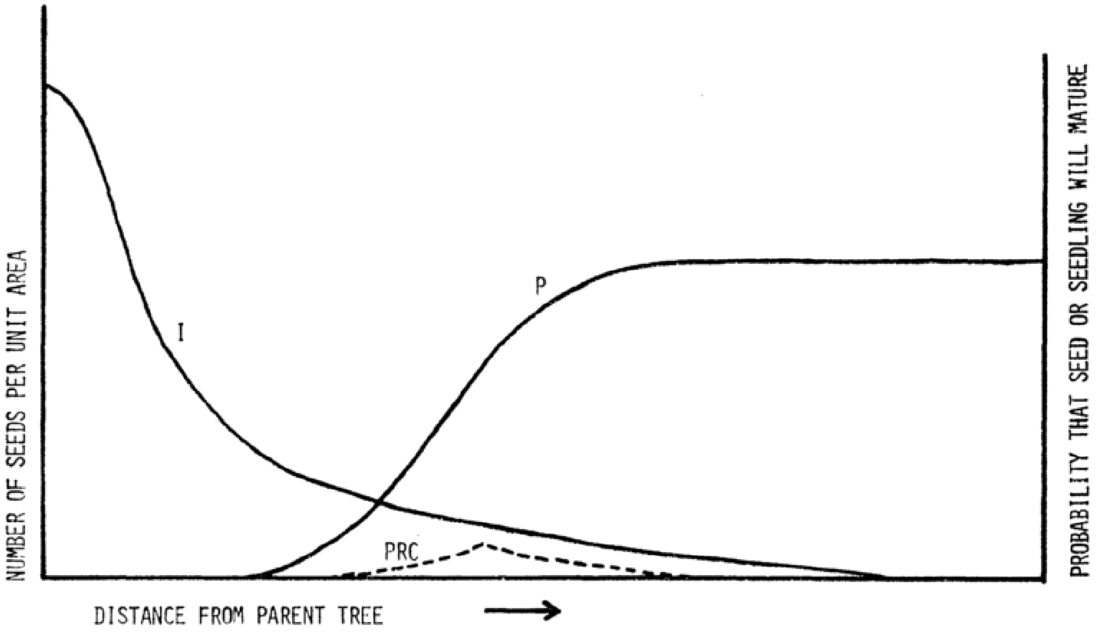
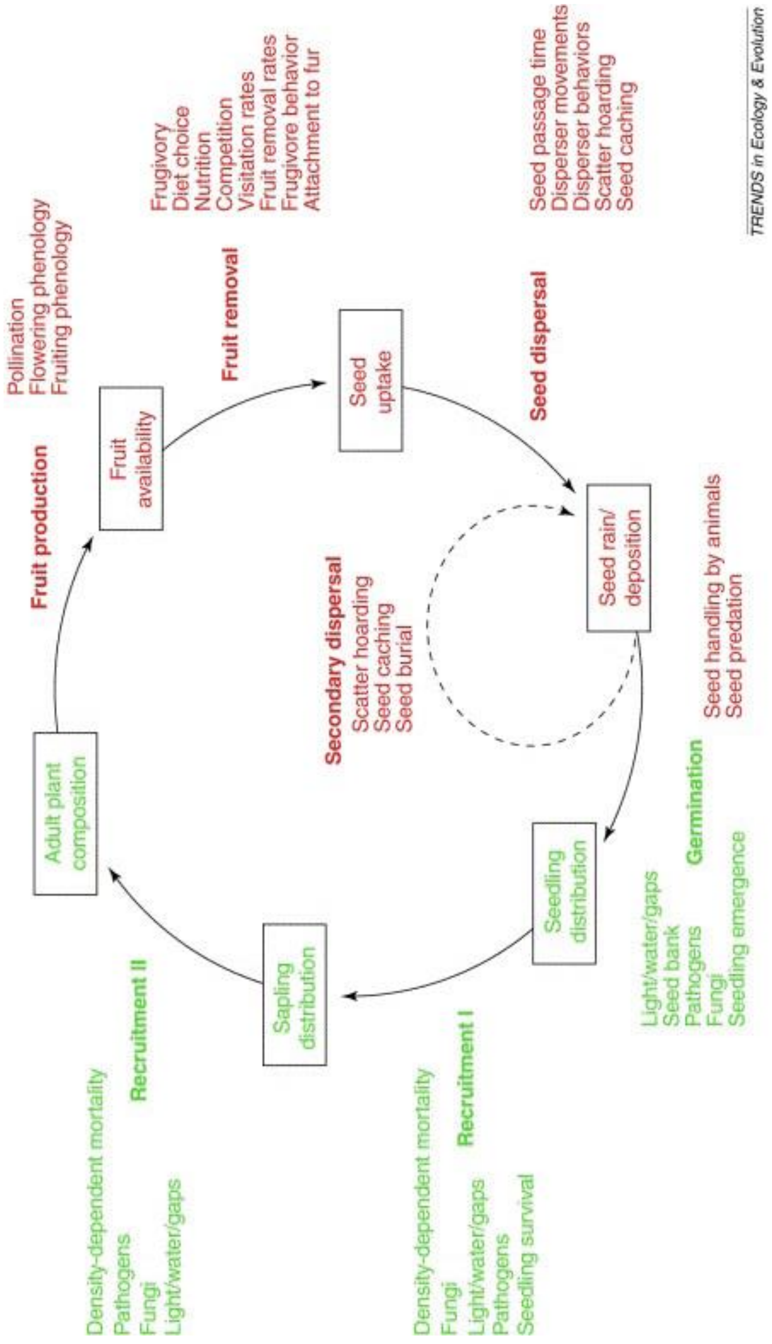


Fig. 0-3. Représentation graphique du modèle de Janzen-Connell (Janzen 1970, Connell 1971) illustrant la probabilité de maturation d'une graine ou plantule en fonction de la distance par rapport à l'arbre parent. Le nombre de graines par unité de surface (I) diminue rapidement en fonction de la distance par rapport à l'arbre parent, mais la probabilité (P) qu'une graine ou plantule échappe aux prédateurs avant sa maturation augmente. La différence entre ces deux courbes produit une courbe de recrutement de la population (PRC). Extrait de Janzen (1970).

Cependant, bien que les organismes limitant les capacités de survie et de recrutement des plantes aient un rôle important dans les patrons de biodiversité que l'on observe en forêt tropicale, ils n'en sont pas les seuls responsables. En effet, les frugivores constituent un groupe fonctionnel incroyablement important dans les écosystèmes forestiers tropicaux où ils peuvent représenter jusqu'à 85 % de la biomasse animale (Estrada et al. 1993) et regroupent de nombreuses espèces de mammifères et d'oiseaux. Plus particulièrement, ils sont impliqués dans des interactions mutualistes avec les plantes : il est estimé qu'entre 75 % et 85 % des espèces de plantes tropicales ont des fruits ayant un mode de dispersion dit zoochore, soit nécessitant l'action d'animaux pour prélever et disséminer leurs graines (Howe & Smallwood 1982, Beaune et al., 2013). Alors que certaines espèces de plantes ont des fruits et des graines dont la morphologie est spécialisée pour être dispersées par la plante elle-même (par le biais d'une ouverture explosive, autochorie), le vent (anémochorie), la gravité (barochorie), ou plus rarement l'eau (hydrochorie), la grande majorité des espèces tropicales est engagée dans des relations mutualistes de dispersion avec des frugivores. Ces derniers sont en effet attirés par les plantes zoochores qui arborent des fruits charnus ou des graines arillées. Les parties charnues des fruits ou les arilles agissent alors comme récompenses énergétiques. Pendant leur alimentation, les frugivores vont, selon l'espèce, la taille des graines, et le degré d'attachement de la partie charnue à la graine, soit ingérer les graines puis les déféquer après transit dans le tube digestif (nous parlons alors d'endozoochorie), soit stocker les graines dans des poches jugales ou dans un gésier afin de les transporter pour une consommation ultérieure, puis les recracher (nous parlons dans ce cas de stomatochorie). Au cours de leur alimentation à partir des fruits de différentes plantes, et suite à leurs déplacements dans leur habitat, les frugivores participent donc activement à l'enlèvement des graines et à leur dispersion à distance des plantes adultes. Ils aident ainsi les plantes à bénéficier des avantages décris précédemment, en plus d'assurer un brassage génétique au sein de la population (Fig. 0-4). Cette double composante fruits-frugivores définit ainsi cette interaction mutualiste qui profite aussi bien aux frugivores qu'aux espèces de plantes zoochores et permet le maintien de populations et de communautés diverses.



TRENDS in Ecology & Evolution

Fig. 0-4. Boucle de dispersion des graines représentée selon les deux principales approches pour étudier la dispersion des graines zoochores. L'une consiste à s'intéresser à la dispersion des graines telle qu'elle se produit dans la nature (dans le sens des flèches) et concerne généralement des travaux qui s'intéressent aux patrons et processus repris en rouge sur la figure. L'autre approche consiste à examiner les conséquences du processus de dispersion des graines et concerne des travaux qui s'intéressent aux patrons et processus repris en vert. (Wang and Smith 2002)

Les espèces de plantes zoochores s'organisent plus particulièrement selon différents syndromes de dispersion. Ces syndromes sont définis d'une part en fonction de la couleur et de la morphologie des fruits, et d'autre part en fonction des taxons de frugivores et/ou de granivores qui sont particulièrement attirés par ces différentes caractéristiques et qui vont donc se tourner vers certains types de fruits. Ainsi, Gautier-Hion *et al.* (1985) ont décrit un syndrome oiseaux-primates, qui regroupent des fruits à graines arillées ou des baies et drupes de couleurs vives à endocarpe succulent et à graines non-protégées, puis un syndrome ruminants-rongeurs-éléphants, caractérisé par des grosses drupes de couleur terne à mésocarpe plutôt sec et fibreux, contenant des graines bien protégées par un endocarpe coriace. Poulsen *et al.* (2002) ont par ailleurs observé que les primates avaient tendance à se nourrir de fruits marron et verts, alors que les calaos préféraient des fruits rouges et violets.

De plus, les différents fruits peuvent avoir des tailles de graine très variables, allant de quelques millimètres à près de 10 centimètres de long (Fig. 0-5). La taille des graines est un facteur important qui détermine leurs probabilités d'être ingérées et dispersées par les frugivores. Ainsi, les plantes ayant des petites graines (quelques millimètres de diamètre) peuvent être dispersées par des assemblages de frugivores diversifiés, incluant des espèces de petite taille. Ces frugivores ont donc des fonctions écologiques potentiellement redondantes, c'est-à-dire qu'ils assurent un service de dispersion de graines similaire vis-à-vis de ces plantes, ce qui peut augmenter la résilience de la plante face aux perturbations (Dennis et al. 2007). A l'inverse, plus les graines sont grandes, plus leur dispersion dépend de grands frugivores, eux moins nombreux. Ces grands frugivores, tels que par exemple les éléphants, les primates, les grands oiseaux (calaos, toucans), les tapirs, ont un rôle plus particulier au sein des communautés car ils sont capables de disperser des espèces à grosses graines que les plus petits frugivores ne peuvent disperser. Par exemple, les éléphants de forêts africains (*Loxodonta cyclotis*) sont les seuls animaux à assurer la dispersion des graines exceptionnellement grosses de *Balanites wilsoniana* (8,8 cm x 4,7 cm) (Chapman et al. 1992b). Certaines plantes ayant un syndrome dit « mégafaunal », ont ainsi évolué en produisant des fruits et des graines de taille particulièrement importante pour attirer les méga-herbivores, soit des herbivores ≥ 1000 kg (Janzen and Martin 1982, Campos-Arceiz and Blake 2011, Malhi et al. 2016).

Fig. 0-5. Gradient de taille de graines récoltées en forêt tropicale en R.D.C. La graine la plus en bas provient d'*Irvingia gabonensis* (Irvingiaceae), une espèce d'arbre dont les graines mesurent environ 60 mm de long et sont dispersées intactes par les éléphants. La graine tout en haut mesure seulement 3 mm de long (© F.T.).

Les communautés tropicales sont composées de nombreux agents biotiques impliqués dans des interactions mutualistes relativement peu spécialisées (Schleuning et al. 2012), formant ainsi des réseaux asymétriques (dans lesquels les espèces sont peu dépendantes les unes des autres), qui facilitent la coexistence d'espèces et le maintien d'une grande biodiversité (Bascompte et al. 2006). Par ailleurs, les interactions mutualistes de dispersion des graines s'organisent selon des syndromes de dispersion qui limitent la redondance fonctionnelle des différents taxons de frugivores (Clark et al. 2001, Poulsen et al. 2002) et accroît leur importance spécifique dans les processus de régénération des plantes à l'échelle de la communauté. Les comportements alimentaires (choix des espèces au cours du temps, quantités ingérées, traitement des graines, etc.) et d'utilisation de l'espace (taille des domaines vitaux, taux de mouvements pendant le transit intestinal) de ces différents taxons de frugivores peut largement déterminer les capacités de survie et de germination des graines, et de recrutement des jeunes plantules (Schupp et al. 2010). Par conséquent, l'assemblage de la communauté de frugivores est une variable cruciale qui influence la composition et la structure des nouvelles cohortes de plantes. A l'inverse, le maintien des populations de frugivores est étroitement dépendent de la présence de nombreuses espèces de plantes qui fournissent leurs ressources alimentaires. Le tableau 0-1 reprend le nombre d'espèces consommées par différents taxons de frugivores dans les forêts afro-tropicales.

Tableau 0-1. Nombre d'espèces de plantes consommées par les principaux taxons de frugivores dans les forêts afro-tropicales.

Taxon	Espèce (nom latin)	Nb d'espèces consommées	Référence
Calaos	*Ceratogymna atrata*, *Bycanistes cylindricus*, *B. fistulator*	59	Whitney *et al.* 1998
Eléphants	*Loxodonta cyclotis*	147	Theuerkauf *et al.* 2000
Gorilles	*Gorilla gorilla*	180	Rogers *et al.* 2004
Chimpanzés	*Pan troglodytes*	116	Head *et al.* 2011
Bonobos	*Pan paniscus*	91	Beaune et al., 2013
Primates (communauté)	*Lophocebus albigena*, *Cercopithecus* spp., *Colobus guereza*, *P. troglodytes*, *G. gorilla*	125	Poulsen *et al.* 2001
Singes (communauté)	*Cercopithecus* spp., *Procolobus* spp., *Cercocebus atys*	75	Koné *et al.* 2008

En définitive, nous avons là un type de communauté écologique très complexe dont la résilience dépend du maintien des interactions entre de nombreux agents biotiques, et dont la dynamique est aussi influencée par l'homme. Comme nous l'avons vu précédemment, les populations humaines exploitent les ressources animales et végétales forestières et peuvent donc influencer les équilibres existant entre ces agents. Il apparait dès lors primordial d'intégrer l'homme comme composante à part entière de ses systèmes afin de mieux comprendre son influence sur le fonctionnement de la régénération forestière, et ainsi de pouvoir mieux conserver la biodiversité et les services écosystémiques qui y sont associés.

Devenir des forêts tropicales dans l'Anthropocène

Bien que les populations humaines aient vécu à proximité des forêts tropicales et exploité leurs ressources durant des dizaines de milliers d'années, l'impact que l'homme exerce actuellement sur son environnement, et en particulier dans les régions tropicales, est de loin plus néfaste. Différents auteurs proposent désormais de définir l'Anthropocène comme une période géologique caractérisée par l'impact global des activités anthropiques sur les écosystèmes terrestres (Dirzo et al. 2014, Malhi et al. 2014, 2016). Une des raisons principales de cette augmentation des activités anthropiques est la très forte croissance de la population humaine mondiale. Celle-ci est passée de 2,5 à près de 7,5 milliards d'habitants entre 1950 et 2015 (Fig. 0-6), et cette augmentation s'est faite particulièrement ressentir sur le continent africain, en particulier dans plusieurs pays du bassin du Congo (Fig. 0-7). Par exemple, la population humaine de la R.D.C. a connu une augmentation de plus de 100 % entre 1999 et 2013. Avec près de la moitié de sa population ayant moins de 14 ans, ce pays connait aujourd'hui une des croissances démographiques des plus élevés de la planète (2,5 %, contre 0,1 % en Europe (USCB 2016)).

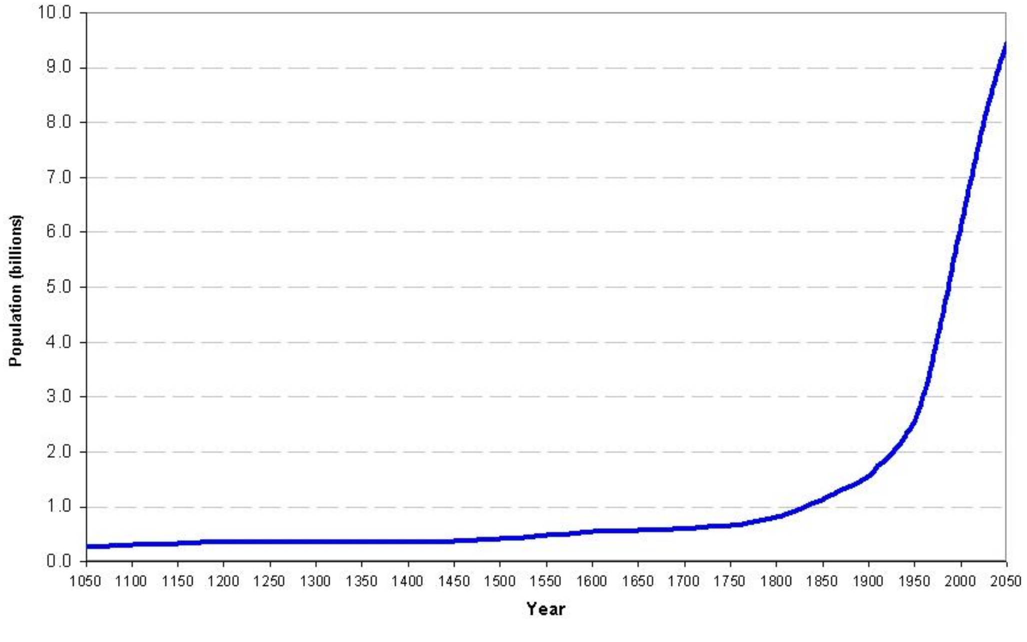
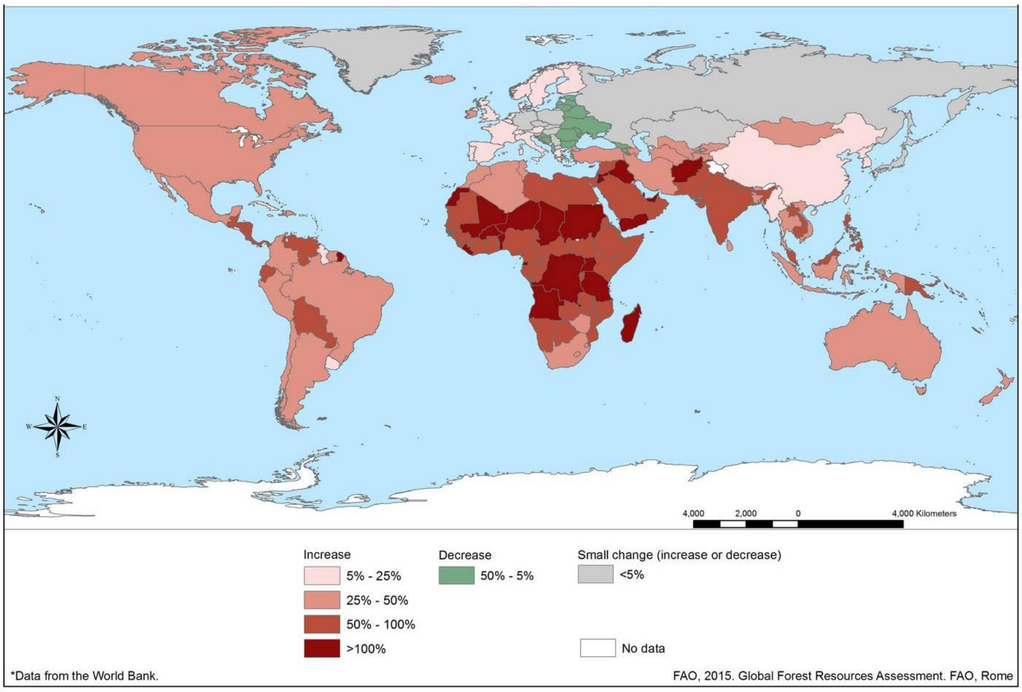


Fig. 0-6. Accroissement de la population humaine mondiale (en milliard) entre 1050 et 2050 (Données: US Census Bureau, International Programs; image: DSS Research).

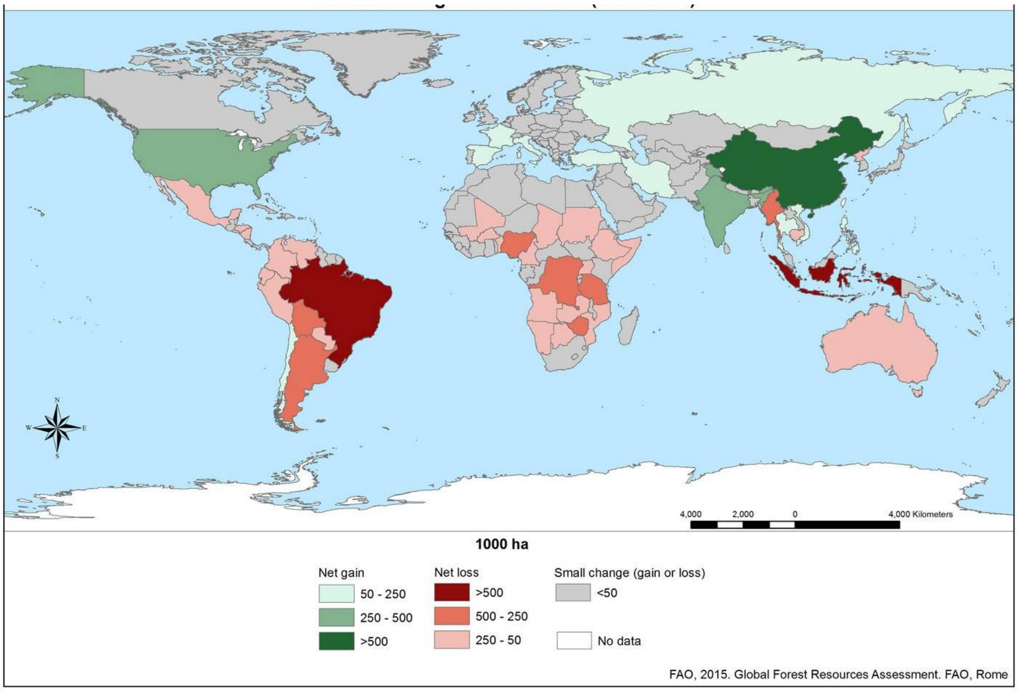


*Data from the World Bank.

FAO, 2015. Global Forest Resources Assessment. FAO, Rome

Fig. 0-7. Taux de changement de la population humaine par pays entre 1999 et 2013. L'Afrique est le continent connaissant la plus forte augmentation, dont la RDC, avec 50-100 % d'augmentation de sa population.

Cette population grandissante est sans aucun doute synonyme d'un accroissement de la demande des ressources naturelles forestières et donc des pressions sur l'environnement (Mayaux et al. 2013). La déforestation est une des pressions majeures actuelles dans les régions tropicales (Fig. 0-8). Celle-ci est majoritairement causée par l'expansion de l'agriculture et l'extraction du bois, aussi bien à échelle locale, par les agriculteurs traditionnels, qu'à échelle régionale, par les compagnies industrielles (Geist and Lambin 2002, Gibbs et al. 2010, Mayaux et al. 2013, Laurance 2015). Ces activités sont indirectement facilitées par de nombreux facteurs sous-jacents souvent bien présents dans les pays en développement : institutions gouvernementales faibles, politique environnementale peu développée, libéralisation commerciale et industrialisation croissante (Laurance 1999b, 2015). Ainsi, il est estimé que 21 millions d'hectares de forêt tropicale, soit 1,2 % de toutes les forêts tropicales de la planète, sont convertis (détruits ou exploités) chaque année (Laurance 1999b). Cette perte d'habitat est intimement associée à la fragmentation, qui se définie par l'apparition de fragments de forêts dont la taille et l'isolement augmentent au fur et à mesure que l'habitat disparait. Il est aujourd'hui largement reconnu que ces modifications de l'habitat ont un impact négatif sur les communautés animales en diminuant leur abondance (Anderson *et al.* 2007, Arroyo-Rodríguez & Dias 2009, Laurance, *et al.* 2008) et leur diversité (Estrada and Coates-Estrada 1996, Turner 1996, Brooks et al. 2002, Bierregaard et al. 2008, Laurance et al. 2008b, Ahumada et al. 2011, Bregman et al. 2014, Haddad et al. 2015). Par ailleurs, ce morcèlement de la structure spatiale de l'habitat forestier peut affecter le comportement d'un grand nombre d'espèces animales en diminuant leurs mouvements au sein et entre les fragments de forêt (Develey and Stouffer 2001, Bierregaard et al. 2008, Blake et al. 2008). Ces modifications de l'habitat ont des effets en cascade sur les interactions entre les niveaux trophiques tels que la dispersion des graines zoochores, et influencent par conséquent la régénération des forêts. Plusieurs études ont ainsi mis en évidence que l'isolement et la diminution de la taille des fragments de forêt diminuent le nombre de graines dispersées (Wright and Duber 2001, Cordeiro and Howe 2003, Kirika et al. 2008), en particulier pour les espèces ayant des graines de grande taille (Cramer et al. 2007), et affectent par conséquent les capacités de régénération de plantes zoochores (Benitez-Malvido 1998, Cordeiro and Howe 2001, 2003, Wright and Duber 2001, Melo et al. 2010).



FAO, 2015. Global Forest Resources Assessment. FAO, Rome

Fig. 0-8. Changement de couverture forestière annuel par pays entre 1999 et 2015. Les régions tropicales sont les plus touchées par la déforestation, et en particulier le Brésil et l'Indonésie. La RDC perd entre 250 000 et 500 000 ha de forêt par an.

Mis à part la déforestation qui influence directement les habitats, une autre menace, plus difficilement observable, mais toute aussi sérieuse et répandue, perturbe les écosystèmes tropicaux. Comme présenté au début de cette introduction, les populations humaines qui vivent sous les tropiques dépendent étroitement des animaux sauvages comme sources de protéines (Nasi et al. 2011). Ainsi, la chasse est une activité importante pour de nombreux foyers et représente aujourd'hui l'une des principales menaces qui affecte les communautés animales (Laurance *et al.* 2008, Kümpel *et al.* 2008, Laurance *et al.* 2012, Dirzo *et al.* 2014, Trail 2007, Poulsen *et al.* 2011). Celle-ci est d'autant plus sérieuse que la démographie humaine, la demande croissante de viande dans les centres urbains, et l'accès plus facile à des armes technologiquement plus avancées et efficaces qu'autrefois accentuent le taux d'extraction des animaux des forêts (Fa et al. 2002). On estime que 4,9 millions de tonnes de viande de brousse sont consommées chaque année dans le bassin du Congo (Fa et al. 2002). Généralement, les chasseurs ciblent préférentiellement les espèces de grandes tailles (Fa et al. 2005, Nasi et al. 2011), lesquelles ont des faibles taux de reproduction, sont moins abondantes et sont donc plus vulnérables aux perturbations (Robinson and Redford 1986, Nasi et al. 2011). Or, comme nous l’avons vu, ces espèces sont particulièrement importantes pour la dispersion des grosses graines.

La défaunation (c-à-d le processus de diminution des populations et de disparition d’espèces animales) est donc une menace ayant une grande portée écologique car elle peut indirectement affecter la dynamique des interactions inter-espèces. Redford (1992) a introduit le concept de « forêts vides », forêts où la végétation apparait intacte mais où de nombreuses espèces animales sont localement éteintes. Il prévenait ainsi du risque de croire qu’une forêt est en bonne santé en ne considérant seulement que sa végétation luxuriante. Au cours des vingt dernières années, de nombreuses études ont mis en évidence les conséquences néfastes de la défaunation sur l’efficacité de la dispersion des graines de plantes zoochores (Wright et al. 2000, Forget and Jansen 2007, Wang et al. 2007, Brodie et al. 2009a, Holbrook and Loiselle 2009, Markl et al. 2012, Boissier et al. 2014, Naniwadekar et al. 2015). De manière générale, il apparait que les interactions fruits-frugivores et les proportions de graines dispersées diminuent lorsque les populations de frugivores sont affaiblies, et particulièrement pour les graines de grandes tailles qui dépendent d’assemblages de disperseurs moins diversifiés et plus sensibles. Plusieurs travaux ont aussi exploré les effets en cascade sur la régénération de plantes, aussi bien à l’échelle spécifique que sur l’ensemble de la communauté végétale (Wright and Duber 2001, Bleher and Böhning-Gaese 2001, Muller-Landau 2007, Nuñez-Iturri and Howe 2007, Stoner et al. 2007, Wright et al. 2007, Nuñez-Iturri et al. 2008, Terborgh et al. 2008, Lermyte and Forget 2009, Vanthomme et al. 2010, Effiom et al. 2013, Harrison et al. 2013). De manière générale, la chasse affecte la régénération de la forêt en faisant diminuer l’abondance et la diversité d’espèces dispersées par les animaux, surtout pour les espèces à grandes graines (Terborgh et al. 2008, Vanthomme et al. 2010, Effiom et al. 2013, Harrison et al. 2013), en faisant augmenter leur aggrégation (Harrison et al. 2013), et en favorisant la régénération d’espèces dispersées abiotiquement (Wright et al. 2007, Terborgh et al. 2008, Effiom et al. 2013). A l’inverse, Wright *et al.* (2007) ont montré que la chasse peut aussi affecter les granivores et indirectement limiter la pression de prédation et favoriser la régénération d’espèces à grandes graines. Wright & Duber (2001) ont par ailleurs détecté un accroissement du regroupement des plantules d’une espèce de palmier proche des pieds adultes dans des sites défaunés alors que cette tendance ne semble pas marquée à l’échelle de la communauté (Terborgh et al. 2008).

Malgré des résultats concordant, notre compréhension des conséquences à long terme des activités anthropiques sur les communautés végétales demeurent néanmoins fragmentaire et limitée. Une des raisons est que la destruction des habitats et la défaunation affectent différents groupes fonctionnels d’animaux (frugivores, granivores, herbivores) et altèrent directement les processus de granivorie et d’herbivorie. Les interactions inter-espèces sont complexes et il est aujourd’hui difficile de prédire comment la structure et la composition des forêts va évoluer. Par ailleurs, bien que des études suggèrent que les principaux taxons de grands frugivores (primates, grands oiseaux, élephants de forêt) ne sont pas écologiquement redondants en ce qui concerne la dispersion des graines (Poulsen et al. 2002, Blake et al. 2009), nous ne pouvons pas encore prédire avec précision de quelle manière ces taxons influencent la régénération forestière à l’échelle de la communauté. Une autre raison qui limite notre capacité à généraliser les résultats et de mieux comprendre le processus de régénération des écosystèmes forestiers tropicaux est le manque d’études dans certaines régions des tropiques (Cassey and Blackburn

2006). En particulier, il y a aujourd'hui un déséquilibre dans les efforts alloués à ces problématiques en défaveur des paléo-tropiques. Le manque d'études reproduisant les résultats obtenus dans les néo-tropiques est probablement dû aux connaissances requises pour pouvoir identifier les centaines d'espèces d'arbres présentes dans les forêts tropicales africaines et asiatiques, mais aussi aux efforts d'échantillonnage importants qui sont nécessaires pour bien décrire ces communautés. Compte tenu de la rapidité à laquelle les activités anthropiques affectent les forêts tropicales et de l'étendue géographique des zones concernées, il y a un besoin urgent de mieux comprendre les processus écologiques qui permettent le maintien de ces écosystèmes, leur réponse aux activités anthropiques, et de mettre en œuvre des systèmes de conservation ou de restauration. Dans cette perspective, des méthodes efficaces d'évaluation de la santé des forêts basées sur l'analyse de groupes indicateurs ont vu le jour. Par exemple, Lermyte & Forget (2009) puis Boissier *et al.* (2014) ont développé une méthode d'évaluation rapide du taux d'enlèvement de graines d'arbres zoochores. Nuñez-Iturri & Howe (2007) ont proposé d'étudier la communauté de plantules sous la couronne d'arbres particulièrement attractifs pour les frugivores, qui au cours de leurs visites répétées génèrent une pluie de graines particulièrement importante et diversifiée (nous parlons aussi de foyer de dispersion des graines (Slocum and Horvitz 2000, Wenny 2001, Clark et al. 2004)) et pourraient laisser une signature dans la communauté de plantules sous ses arbres, c'est-à-dire un foyer de recrutement. Ces méthodes maximiseraient ainsi les informations relatives à l'influence des frugivores sur ces processus et permettrait d'examiner efficacement les effets de perturbations en menant des études comparatives (Nuñez-Iturri and Howe 2007, Vanthomme et al. 2010). Néanmoins, des progrès majeurs pourraient être accomplis dans la compréhension de l'altération des forêts tropicales en explorant l'influence spécifiques de différents frugivores sur ces processus en disposant ces protocoles rapides à l'échelle des paysages.

De manière générale, les activités humaines qui causent des changements environnementaux sont généralement interdépendantes : elles surviennent rarement seules (Malhi et al. 2014). Par exemple, la croissance démographique entraîne l'intensification de la chasse et le raccourcissement de la rotation des cultures sur abattis-brûlis donc une dégradation de la couverture forestière, voire sa fragmentation. La fragmentation entraîne elle-même l'intensification de la chasse, car elle permet une progression plus aisée des chasseurs. Il y a donc généralement en même temps dégradation et fragmentation du couvert végétal, et réduction des populations animales. Dès lors, il devient difficile de trouver des sites sans cette co-dépendance et de pouvoir examiner les effets spécifiques de différentes activités anthropiques sur le fonctionnement des écosystèmes (Wright and Duber 2001, Galetti et al. 2006).

Objectifs et organisation de la thèse

La présente thèse a pu débuter grâce au financement d'un projet « BELSPO - Science for a Sustainable Development » qui était guidé par des objectifs spécifiques, en particulier de collecter des informations de terrain permettant le développement d'un modèle dynamique de végétation (CARAIB pour CARbon Assimilation In the Biosphere, voir par exemple Dury et al. 2011) et son couplage avec un modèle socio-économique multi-agents décrivant l'évolution de l'occupation du sol. En parallèle, nous avons pu fixer des objectifs plus fondamentaux dans l'optique de compléter les connaissances actuelles dans le domaine de l'écologie tropicale et des interactions plantes-animaux liées à la régénération forestière. Les données de terrain avaient aussi pour but de permettre le développement d'un module simulant la dispersion des graines zoochores pour le modèle dynamique de végétation.

Ainsi, nous avons dévelopé les objectifs de recherche fondamentaux d'après le contexte socio-écologique actuel présenté. Globalement, il semble que le niveau de résilience des processus impliqués dans la régénération forestière dans les paysages perturbés demeure incertain. L'objectif principal de cette thèse est donc de mieux comprendre comment les services de dispersion des graines assurés par les frugivores ainsi que leur rôle fonctionnel dans la régénération de la forêt sont affectés dans un paysage abritant des activités anthropiques.

Plus particulièrement, il apparaît tout d'abord capital d'avoir des connaissances plus précises sur la qualité des services de dispersion des graines assurés par des espèces rares qui demeurent dans des habitats anthropisés. Ceci est particulièrement important pour des grands frugivores tels que les grands singes qui sont susceptibles de jouer une fonction écologique importante en forêts tropicales (Chapman and Onderdonk 1998, Vidal et al. 2013, Petre et al. 2015). Ensuite, il serait important d'obtenir plus de données sur les effets des pressions humaines sur les capacités de dispersion des arbres zoochores qui dépendent des grands disperseurs. Ceci permettrait de mieux comprendre le niveau de résilience des systèmes mutualistes et de mettre en évidence les similarités et différences entre les différentes régions tropicales. Mis à part les interactions fruits-frugivores et le processus de dispersion des graines, il serait très pertinent d'approfondir nos connaissances sur l'influence des frugivores dans la régénération de la forêt *per se*. Ainsi, des données précises sur l'influence de la dispersion des graines zoochores dans l'organisation spatiale de la végétation seraient très intéressantes. En particulier, il serait judicieux de mettre en avant le rôle spécifique des principaux taxons de frugivores dans la création de foyers de recrutement sous des arbres zoochores. Finalement, nos connaissances concernant le niveau de redondance fonctionnelle des principaux taxons de frugivores et des conséquences de leur extirpation sur la régénération des forêts restent assez générales. Aussi, l'influence relative de la dispersion des graines et de processus abiotiques dans la composition des communautés végétales est méconnue. Il est donc aujourd'hui crucial d'approfondir ces deux problématiques dans le but de mieux anticiper les conséquences à long terme des pressions anthropiques sur le maintien de la biodiversité végétale.

Ces différents points de recherche forment donc le corps de cette thèse et adoptent des approchent complémentaires afin d'aborder le sujet de manière holistique. Cette thèse s'organise en quatre chapitres. Plus particulièrement, les différentes questions de recherches spécifiques qui guident ces chapitres sont les suivantes :

Ch. 1. Quel rôle joue le bonobo, une espèce de grand frugivore rare et menacée, dans la dispersion des graines au sein d’un paysage affecté par les activités anthropiques ?

Ch. 2. Comment la couverture forestière, la chasse et la disponibilité en fruits affectent-ils les capacités de dispersion d’une espèce d’arbre à grande graines, *Staudtia kamerunensis* (Myristicaceae) ?

Ch. 3. Est-ce que les arbres zoochores agissent comme foyers de recrutement via l’attraction de calaos et de primates ? Est-ce que la couverture forestière et la disponibilité en fruits dans le voisinage influencent ce patron spatial de régénération ?

Ch. 4. Est-ce que différents taxons de frugivores (calaos, primates et éléphants) ont un rôle fonctionnel redondant sur la composition des communautés de plantules zoochores ? Et, quelle est l’importance relative de la dispersion des graines et des paramètres du sol sur la régénération des plantes ?

Matériel et méthodes

La zone d’étude

La zone d’étude se situe dans l’ouest de la République Démocratique du Congo, autour de la station de recherche Malebo du WWF - R.D.C., dans la province du Bandundu (2°29’3.87” S, 16°30’4.16” E) (Fig. 0-9). La pluviométrie annuelle y est d’environ 1500 mm. La grande saison sèche s’étend de juin à août, puis est suivie par la grande saison des pluies de septembre à janvier, et finalement par, consécutivement, la petite saison des pluies et la petite saison sèche de janvier à mai. La zone d’étude est une mosaïque de forêts-savanes, un paysage caractérisé par un patchwork de forêts tropicales humides semi-sempervirentes et de savanes plus ou moins arborées. Le paysage est fortement fragmenté et caractérisé par un système de fragments et de couloirs forestiers de tailles et formes variables, et principalement associés au réseau hydrographique de rivières et ruisseaux. En tant qu’écosystème de transition, ou écotone, sa structure spatiale fragmentée est naturelle, mais néanmoins maintenue par des activités anthropiques. L’agriculture itinérante sur abattis-brûlis diminue le couvert forestier et l’élevage de bétail, avec ses régimes de feux annuels, restreint la recolonisation des savanes par les espèces de forêts. Nous avons mené la récolte des données dans une zone d’environ 30 x 20 km du paysage de mosaïque.

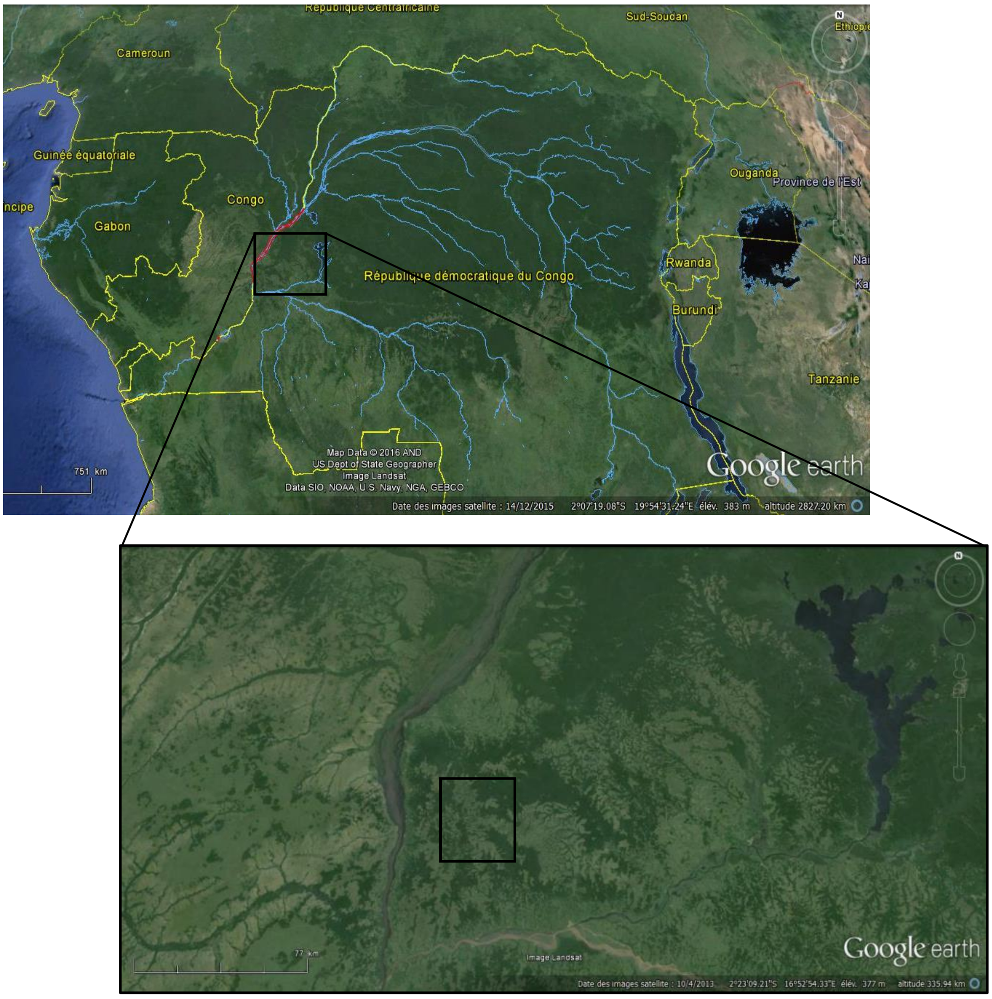


Fig. 0-9. Vue aérienne sur les plateaux Batékés et la mosaïque de forêts-savanes. L’encadré noir indique la localisation de la zone d’étude.

Les sites

Au sein de la zone de mosaïque le travail de terrain a été effectué dans cinq sites subissant des pressions humaines contrastées (Fig. 0-10, Tableau 0-2).

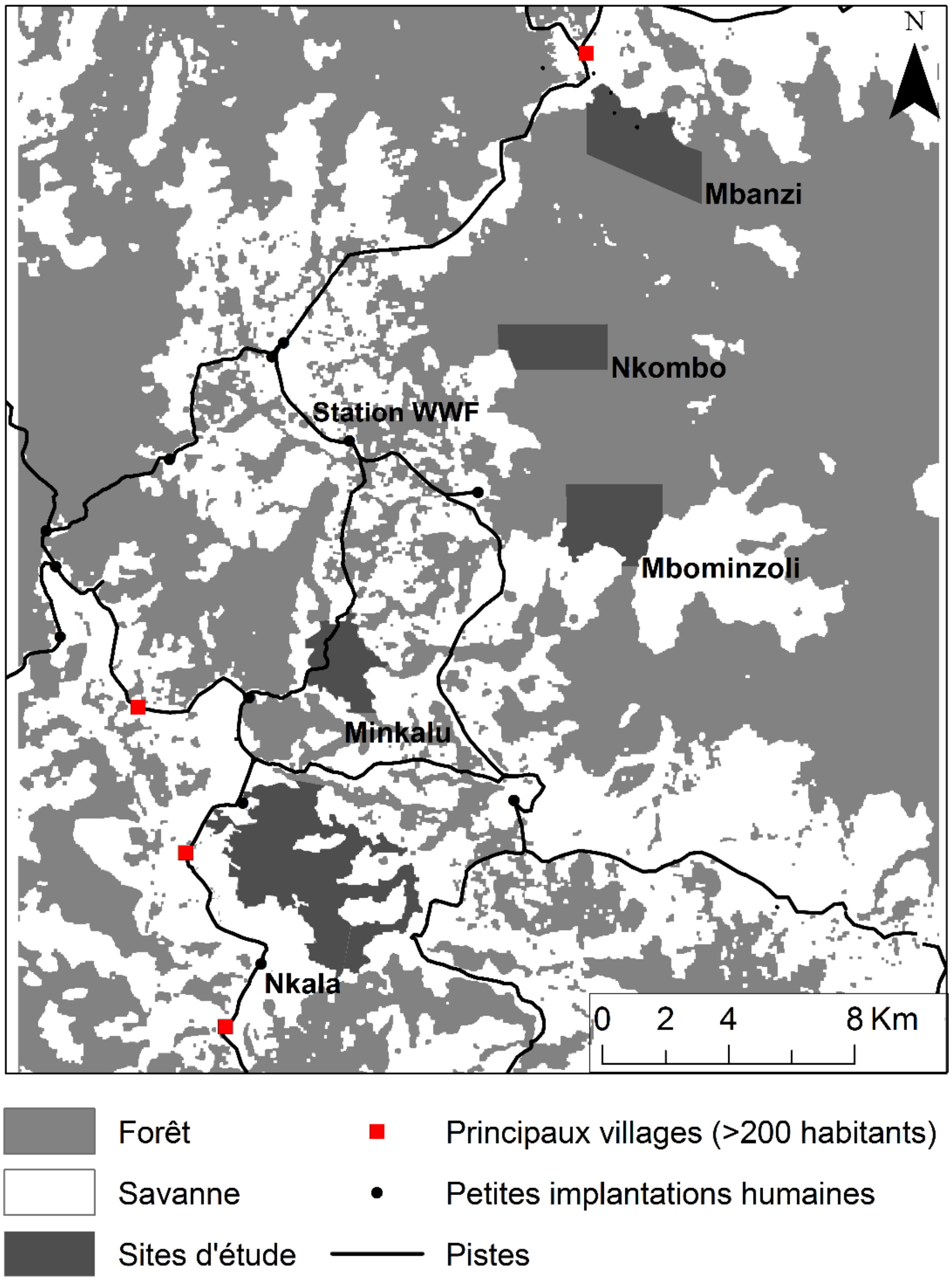


Fig. 0-10. Zone d'étude dans la mosaïque de forêts-savanes, avec les cinq sites forestiers sélectionnés pour le travail de terrain.

Trois sites, Mbanzi, Nkombo et Mbominzoli se situent dans un vaste bloc forestier de plus de 500 km². A l'échelle du paysage, une des caractéristiques principales de ces sites en ce qui concerne la communauté de frugivores, est la présence saisonnière d'un groupe d'éléphants de forêts (*Loxodonta cyclotis*). Grâce à la présence de la station de recherche du WWF, et d'une petite équipe de pisteurs (2 à 4 personnes) présente dans le village de Mbanzi dans le cadre du programme de suivis des éléphants, ces derniers ne sont pas chassés. Bien que j'aie pu attester de la présence d'éléphanteaux (Fig. 0-11) dans la forêt de Nkombo (à une dizaine de kilomètres de Mbanzi), cette population semble tout de même fragile et n'est pas activement protégée par des gardes forestiers. La taille de cette population ainsi que leur domaine vital et les caractéristiques de leurs mouvements saisonniers sont inconnus.

Fig. 0-11. Eléphants de forêt (*Loxodonta cyclotis*). Ces photos prisent par un piège photographique témoignent de la présence d'une femelle adulte et de son éléphanteau dans la forêt de Nkombo (© F.Trolliet).

Le village, ou « camp » Mbanzi fut originellement fondé, en 1982, comme camp de chasse. Il abrite aujourd'hui environ 600 personnes, dont de nombreux chasseurs, appartenant à diverses ethnies provenant des provinces du Bandundu (Batende, Basengele, Baboma, Bateke) et de l'Equateur (Mbumza, Ngombe, Mongo, Bangandu, Bangwandé, Topoké, Libinza). Cette diversité ethnique s'explique par les grandes forêts aux alentours qui ont attiré un nombre croissant de chasseurs depuis la fondation du village, et aussi par la présence d'une société d'exploitation forestière (SIFORCO) qui représente une des principales sources d'emplois dans la région. Le site forestier de Mbanzi est donc supposé connaître une forte pression de chasse.

Les sites Nkombo et Mbominzoli sont localisés plus à l'écart des principales implantations humaines et les pressions anthropiques y sont donc probablement plus limitées. Des groupes de chasseurs se rendent occasionnellement dans la forêt de Nkombo mais principalement lors d'occasions spéciales. Cette forêt n'est donc pas le lieu de chasse régulier des membres d'un village spécifique à proximité comme c'est le cas dans la forêt de Mbanzi. Le site de Mbominzoli se trouve à proximité d'une petite ferme à la limite géographique entre les groupes ethniques Boma et Téké, cette dernière pratiquant un tabou alimentaire et ne consommant pas de viande de bonobo. Ainsi, le groupe de bonobos qui occupe cette forêt n'est pas la cible des chasseurs. Ce site est donc unique car il abrite des éléphants et des bonobos, les deux plus grandes espèces de frugivores de la région. De part cette particularité, nous n'avons inclus ce site dans nos travaux qu'à partir de la deuxième partie de la thèse portant sur le rôle des grands frugivores sur la régénération forestière.

Les deux derniers sites, Minkalu et Nkala, se situent dans une partie de la mosaïque où la structure spatiale de l'habitat forestier est plus fragmentée. Ces sites se trouvent aussi dans la zone ethnique Téké, où les bonobos ne sont pas chassés. Le site Minkalu est un fragment de forêt de 4,6 km² qui appartient au terroir communautaire de Mpelu, un village peuplé d'environ 350 personnes. Cette forêt n'est pas le sujet de stratégie de conservation particulière et la chasse de subsistance y est autorisée et pratiquée par les villageois.

Le site Nkala est un fragment de forêt d'environ 17,5 km² qui appartient au terroir communautaire du village de Nkala, d'environ 200 habitants. Cette forêt est l'un des sites principaux où les ONG WWF-Congo (World Wide Fund) et MMT mènent leur programme d'habituation des bonobos, et elle détient par ailleurs le statut officiel de forêt communautaire. En accord avec la population locale, cette forêt est donc un espace consacré à la conservation des primates, la chasse des primates y est donc interdite, et généralement théoriquement limitée. Néanmoins, l'entrée de chasseurs provenant de villages extérieurs non partisans du programme de conservation en œuvre dans cette forêt est possible, et il n'est pas rare de trouver des pièges de type collet destinés à chasser des espèces de vertébrés terrestres tels que des rongeurs et des petites antilopes. Plus particulièrement, cette forêt est proche du village de Nkoo, plus au Sud, dont la population est sept fois plus importante que celle de Nkala (plus de 1400 personnes) et génère ainsi une demande en viande de brousse plus importante. La partie sud de la forêt connaîtrait donc une pression de chasse théoriquement plus importante que la partie nord, plus proche du village de Nkala et de la ferme pilote de l'ONG MMT (A. Serckx, communication personnelle). Dans le cadre du Chapitre 2, j'ai ainsi décidé de considérer ces deux zones de forêts comme deux sites différents : Nkala-Nord et Nkala-Sud.

Mises à part les spécificités énoncées concernant les populations de bonobos et d'éléphants, toutes les autres espèces de vertébrés frugivores et granivores sont chassés pour leur viande dans les différents sites (rongeurs, céphalophes, calaos, potamochères, primates, etc.). Les calaos, bien qu'ils ne soient pas la cible principales des chasseurs, sont de plus en plus chassés (Fig. 0-12) au fur et à mesure que les espèces de grands mammifères disparaissent (Trail 2007).

Fig. 0-12. Collection de becs de calaos stockés entre les villages de Nkala et de Nkoo. (© F.T.)

Tableau 0-2. Résumé des principales caractéristiques des sites d'études

Site	Programme de conservation/suivi de la faune	ONG impliquées	Distance en km au village le plus proche (nb d'habitants)	
Mbanzi	Suivis des éléphants	WWF	3,5 (600)	
Nkombo	Suivi des éléphants (jusqu'en 2013)	WWF	9,5 (600)	
Mbominzoli	Suivi des grands mammifères. Tabou traditionnel (pas de consommation de viande de bonobo)	MMT, Awely[a]	15,5 (600)	
Minkalu	Programme de conservation des bonobos. Tabou traditionnel (pas de consommation de viande de bonobo)	MMT, Awely[a], WWF	6,5 (350)	
Nkala	Programme de conservation des bonobos. Tabou traditionnel (pas de consommation de viande de bonobo). Espace de conservation communautaire	MMT, Awely[a], WWF	Nkala - Nord	2,8 (200)
			Nkala - Sud	4,5 (1400)

[a] L'ONG Awely a arreté ses activités dans la région en 2015.

Récolte des données

Organisation du travail de terrain

Le travail de récolte de données sur le terrain a été réalisé au cours de 6 missions qui se sont déroulées entre mai 2011 et juin 2015, sur une période totale de 14 mois. Une première mission préliminaire d'un mois et demi nous a permis de prendre connaissance de la zone d'étude de mosaïque de forêts-savanes au sud du paysage du Lac Tumba. L'objectif de cette mission était double. D'une part, il s'agissait d'évaluer les conditions logistiques et les infrastructures disponibles permettant de mener les futures missions de récolte de données et de mener à bien les objectifs de recherche. D'autre part, l'objectif était de repérer les espèces d'arbres à grandes graines candidates pour étudier le processus de dispersion des graines zoochores ainsi que les sites forestiers permettant de récolter ces données et d'étudier l'effet de pressions anthropiques. La récolte de données a débuté lors de la mission suivante qui s'est déroulée de mars à juillet 2012. Nous avons pu durant cette période récolter les données sur (i) les frugivores responsables de la dispersion des graines de *S. kamerunensis*, les taux de production et de dispersion des graines dans deux sites (Mbanzi et Nkombo), et (ii) débuter l'étude sur l'effet du transit intestinal des graines chez le bonobo sur leur potentiel de germination. Après cette mission, les pisteurs ont pu continuer la prise de données durant notre absence. La troisième mission, en janvier 2013, nous a permis de sélectionner trois autres sites d'études (Minkalu, Nkala-Nord et Nkala-Sud) afin d'augmenter le nombre de traitements expérimentaux (plus de variations de niveau de fragmentation et de pression de chasse) et le nombre d'arbres à échantillonner dans chacun des sites, afin d'augmenter la puissance des tests statistiques et de pouvoir prendre en compte l'effet de la production de fruits (fécondité) sur les taux de dispersion des graines. Nous avons installé des collecteurs à fruits sous la couronne de 34 arbres de *S. kamerunensis* afin d'obtenir les données sur les taux de dispersion dès le début de la saison de fructification suivante, soit en mai. Nous avons aussi pu suivre la germination des graines semées et semer des graines de nouvelles espèces. La mission suivante s'est déroulée entre juin et juillet 2013, soit durant le pic de fructification de *S. kamerunensis.* Cette mission nous a permis de récolter les données sur la production et la dispersion des graines de *S. kamerunensis*, ainsi que de mener les inventaires fauniques et de pression de chasse dans les cinq sites. Une mémorante, Kim Mathy, a pu durant cette mission m'aider dans la récolte des données de ces inventaires. Durant la cinquième mission entre mai et juin 2014, nous avons d'une part finalisé les inventaires fauniques dans les sites, et d'autre part mené une prospection de nouvelles espèces d'arbres candidates pour évaluer les taux de frugivorie et de dispersion des graines. C'est finalement lors de la dernière mission entre mars et mai 2015 que nous avons mené les inventaires sur la communauté de plantules dans l'ensemble des sites. Cette mission nous a permis aussi d'encadrer une mémorante, Alice Dauvrin, qui nous a aidé à récolter les données sur les fruits et graines non-consommés d'*Irvingia gabonensis*, *Klainedoxa gabonensis* (Irvingiaceae), et de *Xylopia staudtii* (Annonaceae) dans cinq sites (ces données n'ont pas été utilisées dans la présente thèse).

Inventaire de la faune et de la pression de chasse

Dans le cadre du programme de conservation des bonobos dans les forêts de Nkala et de Mpelu (incluant le site de Minkalu), Adeline Serckx a supervisé des inventaires le long de transects forestiers dans le but d'évaluer les densités de population de bonobos. Afin de fournir un effort d'échantillonnage suffisant pour estimer la densité avec une bonne précision, chaque transect a été espacé de 500 m (Serckx et al. 2014). Par ailleurs, ces travaux avaient aussi pour but d'examiner l'utilisation de l'habitat par les bonobos. Ces données ont été récoltées en 2011, 2012 et 2013, et utilisées dans le cadre du Chapitre 1. Dans le but de quantifier la pression de chasse et de caractériser la communauté faunique dans les différents sites dans le cadre des chapitres suivants, nous avons réutilisé les mêmes transects que ceux suivis par A. Serckx dans les sites Nkala et Minkalu afin de limiter l'impact de l'ouverture (coupe) des transects sur la végétation. Nous avons ensuite établis des transects dans les sites de Mbanzi et de Nkombo en suivant le même espacement de 500 m, mais en limitant leur longueur à 1 km. Ceci nous a permis de couvrir l'ensemble de la zone de forêt de chacun des deux sites afin de les caractériser convenablement sans pour autant augmenter le nombre total de kilomètres de transect (6 x1 km dans chaque site). Etant donné que la coupe de transects prend beaucoup de temps, nous avons préféré limiter la distance totale par site afin de privilégier les efforts alloués à l'échantillonnage *per se* plutôt qu'à la coupe et à l'entretien des transects. Par ailleurs, dans le but d'optimiser au maximum le temps passé en forêt et de mettre à profit les transits entre deux transects consécutifs, nous avons poursuivi les inventaires sur des transects REConnaissanCE (recce) (Fig. 0-13). Finalement, dans le cadre du programme de suivi des grands mammifères dans le site de Mbominzoli, un système de transect était déjà établi. Nous avons donc pu profiter de ces transects pour mener l'inventaire dans cette forêt.

Dans le cadre du Chapitre 2, l'échantillonnage total fût de 131 km, et dans le cadre des Chapitres 3 et 4, il fut de 170 km. Cette différence est due au fait que dans les deux derniers chapitres, le design expérimental inclut le site de Mbominzoli, et l'entièreté du site de Nkala, alors que dans le Chapitre 2, nous avons divisé le site de Nkala en deux pour considérer Nkala-Nord et Nkala-Sud. Ainsi, ces inventaires sur les transects et Recce nous ont permis de quantifier l'activité de chasse ainsi que la diversité et l'abondance des principales espèces animales susceptibles d'interagir avec des fruits charnus et des graines (frugivores, granivores, omnivores). Nous avons tenté de mener au maximum les inventaires aux périodes de plus fortes activités de la faune, soit entre 6h00-9h00 et 15h00-18h00 mais n'avons pas restreint les inventaires à ces périodes. Nous avons enregistré tous les indices directs et indirects de présence animale (fèces, traces de pas, cris, nids, terriers, observations visuelles) et d'activité de chasse (cartouches de fusil, coups de fusil, pièges, feux). Nous avons ensuite additionné tous les indices enregistré puis divisé par le nombre de kilomètres parcouru afin d'obtenir des Indices Kilométrique d'Abondance (IKA) dans le but de comparer les sites entre eux (Mathot & Doucet 2006, Vanthomme *et al.* 2010). Selon l'objectif de l'étude, des IKA peuvent être calculés pour différentes catégories : pression de chasse, primates, calaos, omnivores, granivores etc…

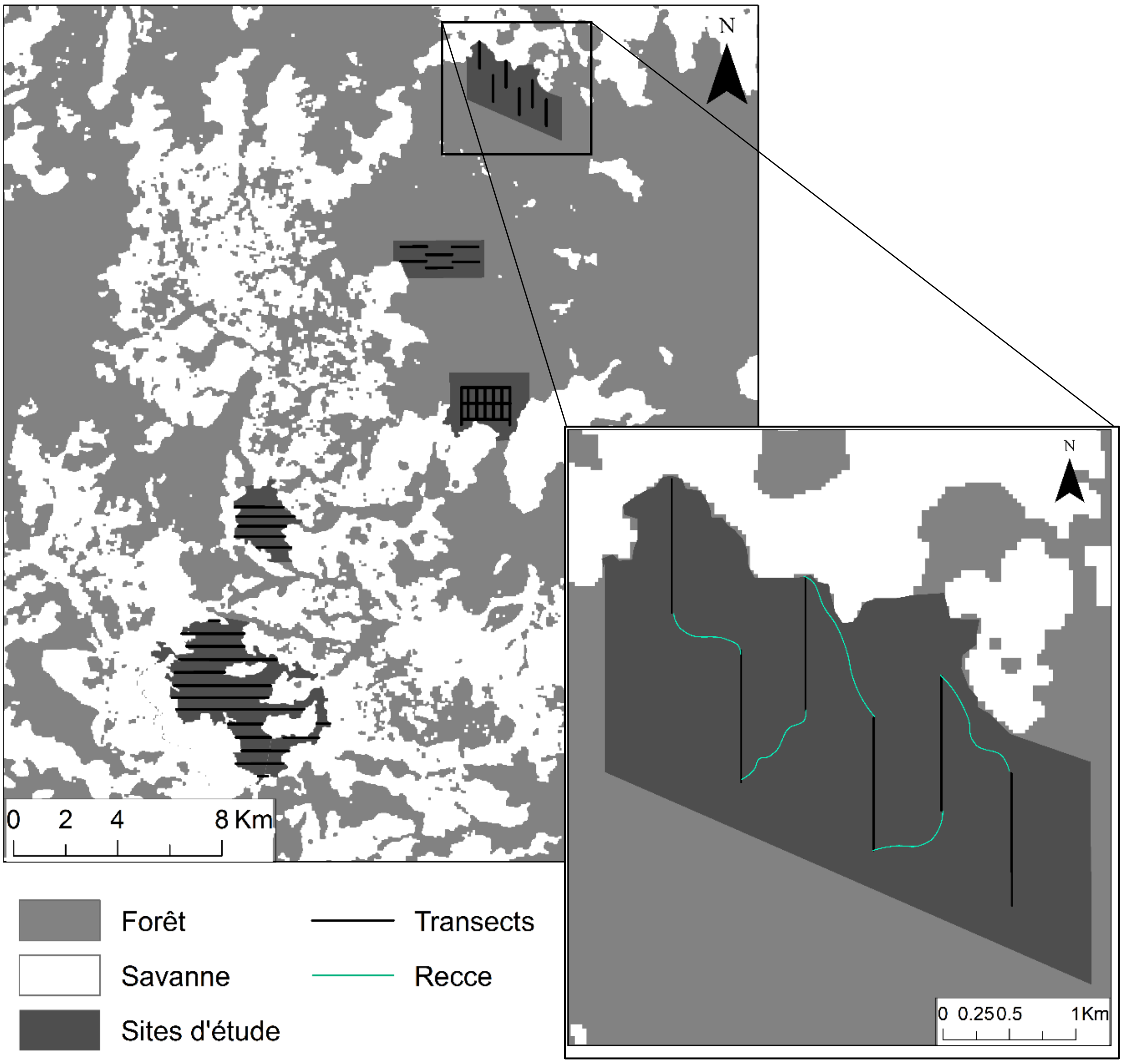


Fig. 0-13. Système de transects linéaires utilisé pour mener les inventaires fauniques dans chacun des cinq sites forestiers, avec un exemple de système de recce en complément.

Chapitre 1.

Ecosystem services provided by a large endangered primate in a forest-savanna mosaic landscape

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

Parmi les espèces de grands frugivores présents dans la mosaïque de forêt-savane, le bonobo est l'une des cibles prioritaires des ONGs de conservation. Par ailleurs il n'est pas chassé par les communautés locales dû à un tabou alimentaire traditionnel. Ainsi, certains groupes demeurent relativement bien protégés au travers de la mosaïque. Néanmoins, ces bonobos vivent à relative proximité des activités anthropiques, visitent et s'alimentent dans des habitats ouverts. Aussi, il est l'un des derniers frugivores capables de disperser des graines de grande taille. Ainsi, cette espèce a probablement un rôle unique dans la dispersion des graines et la régénération des plantes dans ce paysage particulier. Dans le premier chapitre, nous allons examiner les services de dispersion des graines assurés par ce grand primate menacé.

Among the large animal species present in the forest-savanna mosaic, the bonobo is one of the target priority of conservation NGOs. It is also not hunted by the local community thanks to a traditional eating taboo. Therefore, some groups are relatively well protected across the mosaic. Yet, those bonobos live in relative proximity to human activities, visit and forage in open habitats. They are also one the last frugivore remaining that is able to disperse large seeds. This species could thus have a unique role in seed dispersal and the regeneration of plants in this particular landscape. In the first chapter, we will investigate the seed dispersal services provided by this large endangered primate.

Résumé

Les paysages forestiers sont de plus en plus affectés par les activités anthropiques, mais le rôle de grands frugivores menacés en tant que disperseur de graines reste méconnu dans de tels écosystèmes. Dans cette étude, nous avons exploré le rôle d’un frugivore menacé, le bonobo (*Pan paniscus*), dans une mosaïque de forêts-savanes altérée en République Démocratique du Congo. Les groupes étudiés font partie d’un programme de conservation communautaire, mais vivent cependant à proximité d’activités humaines. Nous avons identifié les espèces dispersées grâce à l’analyse de fèces, puis les avons classées en guildes de régénération et en catégories de taille. Nous avons déterminé l’effet du transit intestinal sur la germination des graines, ainsi que l’utilisation de l’habitat par les bonobos. Les bonobos ont dispersé les graines intactes de 77 espèces, parmi lesquelles 80,8 % avaient de grosses graines (≥10 mm de long), que peu ou pas de frugivores sympatriques ne peuvent disperser. Ils ont dispersé une majorité (49 %) d’espèces sciaphiles, c’est-à-dire capables de s’établir dans des zones forestières avec une certaine pénombre, soit relativement âgées et donc peu perturbées. Le transit a eu un effet globalement positif sur la germination des graines. Les bonobos ont utilisé différents types d’habitats, bien qu’ils aient montré une préférence pour les sous-bois avec une quantité intermédiaire de lumière et dominés par une végétation ligneuse et herbacée. Ce patron de dispersion augmente probablement le succès de recrutement des espèces sciaphiles. Nous avons donc fait l’hypothèse que ces espèces bénéficient d’une dispersion dirigée par les bonobos. Cette espèce de frugivore menacée assure des services de dispersion uniques et joue probablement un rôle fonctionnel primordial pour la régénération des forêts à un stade de succession avancé dans ce paysage de mosaïque. Les plans de gestion devraient prêter une attention particulière au rôle des grands frugivores menacés dans les régions anthropisées car leur disparition pourrait empêcher la succession des forêts jusqu’à un stade climax.

Abstract

Forested landscapes are increasingly affected by human activities, but little is known about the role of large endangered frugivores as seed dispersers in such ecosystems. We investigated the role played by the bonobo (*Pan paniscus*) in a human-altered forest-savanna mosaic in Democratic Republic of the Congo. The studied groups are part of a community-based conservation programme but live at the interface with human activities. We identified dispersed species via faecal analysis, classified them into a regeneration guild and a seed size category, determined the effect of gut transit on seed germination, and the habitat use of bonobos. Bonobos dispersed intact seeds of 77 species, 80.8% of which were large-seeded (≥10 mm long), of which few can be dispersed by sympatric frugivores. They dispersed a majority (49%) of shade-bearers that thrive in forest understory with limited amount of light, all of which were large-seeded. Transit had an overall positive effect on seed germination. Bonobos used various habitat types, showing preferences for understory with intermediate light availability and dominated by woody or herbaceous vegetation. This dispersal pattern probably enhances recruitment of shade-bearers, and we thus hypothesised that those species benefited from directed dispersal by bonobos. This threatened frugivore provides unique dispersal services and likely plays a paramount functional role in the regeneration of late successional forests in this mosaic landscape. Management plans should pay particular attention to the role of large and rare frugivores in human-dominated regions as their disappearance could disrupt forest succession to a climax state.

Introduction

Forest communities are threatened by habitat loss and degradation, and increasing human population growth around the world (Haddad et al. 2015). Agricultural expansion (e.g. shifting slash-and-burn agriculture) and wood extraction create patches of secondary vegetation within primary forests, alter forest structure, and increase fragmentation (Norris et al. 2010, Mayaux et al. 2013). Forested landscapes have thus become dominated by forest–agriculture mosaics and percolated landscapes composed of vegetation at contrasting successional stages, including open and secondary habitats (Norris et al. 2010). In addition, bush-meat hunting depletes forests of their larger fauna, including ecologically important taxa such as frugivores (Fa et al. 2002, Vidal et al. 2013). Defaunation disrupts animal-mediated seed-dispersal, a crucial process for the regeneration of a large proportion of plant species (Markl et al. 2012, Kurten 2013), and can have long lasting effects by modifying the composition of forest communities (Vanthomme et al. 2010, Kurten 2013, Effiom et al. 2014).

Frugivores, especially large-bodied, are a key element of these mutualistic interactions with plants and thus play an invaluable role for forest resilience and conservation in the face of all the emerging threats (Vidal et al. 2013). Numerous populations of these large species inhabit non-optimal ecosystems with modified vegetation and spatio-temporal distributions of fruit resources (Lenz et al. 2011, Bregman et al. 2014, Arroyo-Rodríguez et al. 2015, Hockings et al. 2015, Lindsell et al. 2015), which can largely affect their degree of frugivory, habitat use, and the subsequent seed rain they generate. In addition, abiotic characteristics such as canopy openness can strongly limit the survival of seedling species with particular light requirements (Montgomery 2004). Ultimately, changes in these traits can have cascading effects on the seed-dispersal effectiveness of frugivores. Therefore, the level of resilience of forest communities increasingly depends on the ability of frugivores to maintain their ecosystem services in such changing environmental conditions (Lenz et al. 2011, Albert et al. 2014, Lindsell et al. 2015). Because seed-dispersal effectiveness is context-dependent (Schupp 2007), a thorough exploration of seed-dispersal services in degraded habitats is strongly needed for the implementation of effective landscape-scale conservation plans. Despite evidence that habitat alteration affects various components of seed dispersal of specific plant species, (Cf. Markl et al., 2012) few studies have evaluated seed-dispersal services from the perspective of dispersal agents in human-altered landscapes (but see Abedi-Lartey et al., 2016; Albert et al., 2014; Arroyo-Rodríguez et al., 2015; Lenz et al., 2011; Zhou et al., 2008). Many large-bodied frugivore populations are closely dependent on primary forests and rapidly disappear in human-dominated environments (Urquiza-Haas et al. 2009), whereas others show considerable ecological flexibility and maintain their seed-dispersal services in degraded areas (e.g., Albert et al., 2014; Arroyo-Rodríguez et al., 2015; Lenz et al., 2011). These disturbance-tolerant species that contribute effectively to the restoration of degraded forests are usually common and widespread such as cercopithecines and howler monkeys (Albert et al. 2014, Arroyo-Rodríguez et al. 2015), and hornbills (Lenz et al. 2011).

The bonobo, *Pan paniscus*, is a large endangered species that is endemic to the Democratic Republic of the Congo (D.R.C.) and preferentially uses primary mixed mature forests away from human presence in the Cuvette Centrale of the Congo Basin (White 1992, Reinartz et al.

2006), where they have been shown to be effective seed dispersers (Idani 1986, Tsuji et al. 2010, Beaune et al. 2013a). However, their behaviour in forest–savanna mosaics has only recently received more attention (Thompson 1997, Serckx et al. 2014). Those habitats are characterized by high food resource variation which is thought to drive bonobos to display a certain level of behavioural plasticity and to feed regularly on fallback species that grow in forest edges and disturbed areas (Serckx et al. 2014). Moreover, such ecosystems are very patchy and facilitate access to forest interior to subsistence hunters, which substantially threaten the large frugivore community (Fa et al. 2002). As a consequence, the locally protected bonobos remain the largest species in a vast area of this ecosystem, suggesting that dispersal of numerous large-seeded plants falls to this endangered animal. Such large-seeded species are the main representatives of late successional tropical forests (Foster 1986). Bonobos may thus provide unique seed-dispersal services and play a critical functional role in the forest-savanna mosaic, particularly for the maintenance of mature forests. However, the ecological role such endangered animal fulfil in impoverished and disturbed landscapes remain unexplored. In this study, we explored and compared seed dispersal services in bonobos and other sympatric frugivores discussing their respective role for forest regeneration. Additionally, we investigated functional traits (seed size, germination, regeneration guild, life form) of the dispersed plant species, and bonobo movement behaviour (i.e., seed-deposition sites) with regards to habitat preferences. Although this study focuses on a primate in a tropical region, the components that we discuss are relevant to other systems and human-modified regions.

Material & methods

Study area

The study took place in Democratic Republic of the Congo, close to the WWF-Malebo research station, in Bandundu province, (2°29'3.87S, 16°30'4.16E). The annual rainfall is between 1 500 and 1 600 mm, and mean daily temperature is approximately 25°C (Vancutsem et al. 2006). Two dry seasons occur from June to August and February to March, and two wet seasons occur from September to January and April to May. The site is situated in the western Congolian forest–savanna mosaic, a landscape composed of a mixture of tropical semi-evergreen lowland rain forests and savanna matrix, representing respectively, approximately 60 and 40% of the total area. The landscape is characterized by a system of forest patches and corridors of variable sizes and shapes (Fig. 1-1) mainly associated with the hydrographic network of small rivers. As a transitional ecosystem, or ecotone, its fragmented spatial structure is natural, yet maintained by anthropogenic activities. Shifting slash-and-burn agriculture encroaches on forest patches, and cattle ranching, with its associated yearly fire regimes, restricts colonization of forests. This landscape thus has a large ratio of forest-edge area to forest interior area, and a relatively high proportion of forests at early successional stages. A striking feature is the diversity of forest types, canopy openness and understory vegetation encountered within relatively limited distances. We conducted field work in a section of 200 km² (Fig. 1-1) where two groups of bonobos are part of a community-based conservation programme led by the WWF-DRC and Mbou-Mon-Tour NGOs. Since 2001, those NGOs have reinforced the application of an ancestral taboo that proscribes killing or eating bonobos. The local ethnic group therefore does not hunt them (Inogwabini et al. 2008).

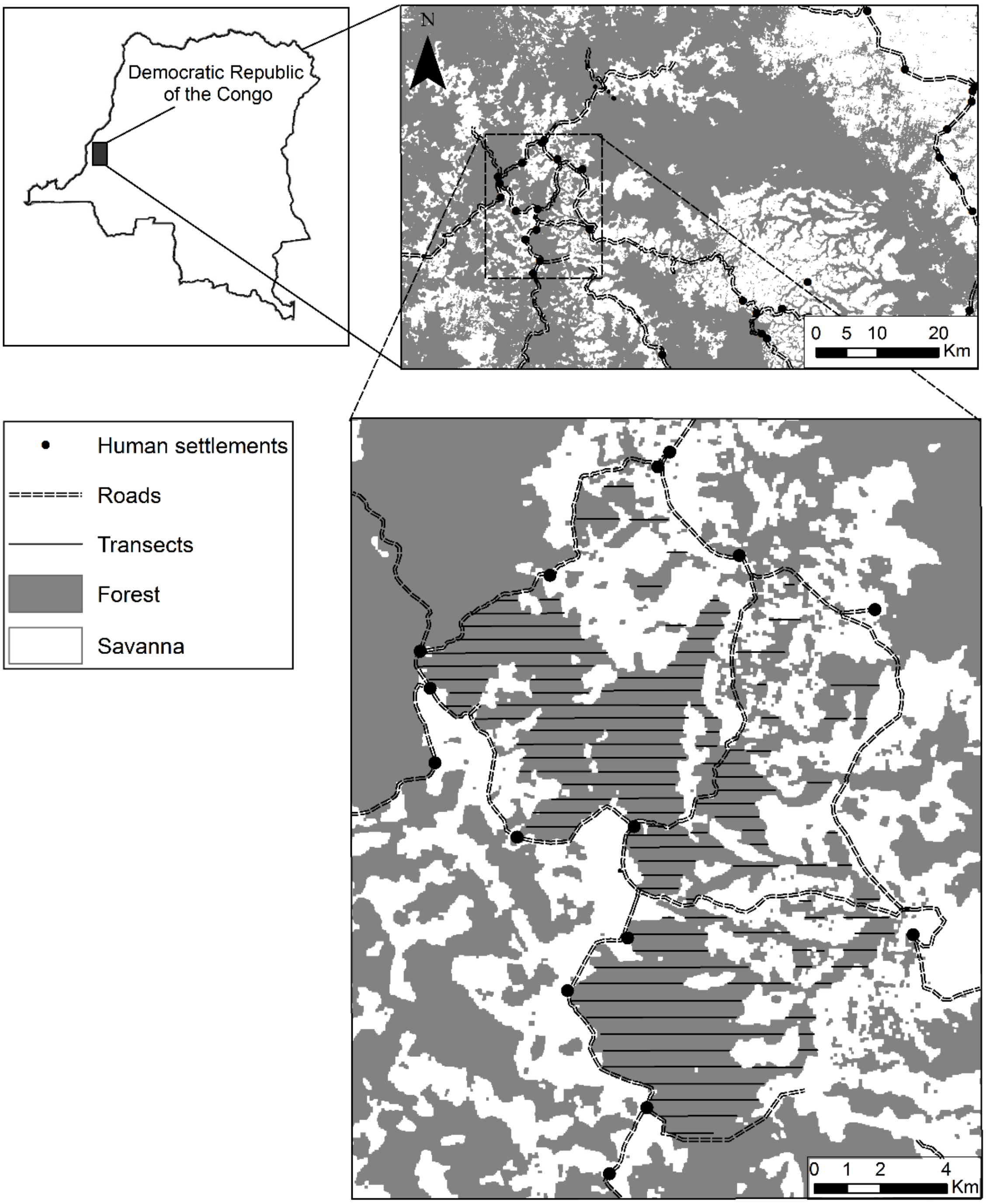


Fig. 1-1. The forest–savanna mosaic landscape in the Western Democratic Republic of the Congo, and the Nkala and Mpelu study site depicted by the system of line transects.

Frugivory and seed dispersal

Between May 2011 and June 2013, trackers of the WWF bonobo habituation programme regularly geolocated fresh nesting sites where they collected all fresh bonobo faeces found (N= 2 252). Each faecal sample (individual faeces) was gathered in a separate plastic bag and washed through a 1-mm mesh sieve to retrieve the seeds prior to their identification. We identified intact seeds (with no obvious sign of damage) with the aid of a reference collection established from fruiting plants identified by specialists. We kept seed samples to perform germination trials. To compare the frequencies of seed dispersal, we computed the percentage of faecal samples that contained at least one seed of each species. We sorted the seeds according to the two categories defined by Serckx et al. (2015). First, 'important species' were present in more than 50% of faecal samples for at least 1 month, and occurred in more than 10% of sampled days (McLennan 2013). Second, 'preferred species' were consumed disproportionately relative to their availability in the habitat (Marshall and Wrangham 2007). We evaluated species availability with the aid of a bimonthly monitoring of trees (N= 2 585) from species known to be consumed by bonobos or producing fleshy fruits. Further details can be found in Serckx et al. (2015). We also measured seed size (length and width) with a calliper. For the species that we did not measure, we gathered data from Amshoff et al. (1961) and Vivien and Faure (1985). We sorted seeds by length according to the following classes: small: <5 mm; medium: ≥5 to <10 mm; and large: ≥10 mm. In addition, we searched the literature for food species consumed and dispersed by other large frugivores species living in the area, i.e., primates (Lambert, 1999), and hornbills (Clark et al., 2001; Poulsen et al., 2002; Whitney et al., 1998), to assess the extent of seed dispersal redundancy.

Germination capacity

To test the effect of ingestion by bonobos on seed germination capacity, we conducted germination trials using dispersed and control seeds. We sowed dispersed seeds within two days after collection, and collected control seeds from several ripe fruits (as evaluated by humans) from several trees, avoiding fruits that showed signs of rot. We sowed a total of 1 986 seeds (963 control; 1 023 dispersed) of 16 species in a sterile cotton compress in individually labelled 9-cm diameter Petri dishes. The dishes were placed on a closed, predator-proof shelf in a shaded environment to prevent exposure to direct sunlight and seed desiccation. We checked each dish twice-weekly to record and remove any germinated seeds and to add water. We defined germination as the emergence of the radicle.

We analysed germination data with time-to-event analysis (Mcnair et al. 2012), and used the logrank test from the 'coxme' package (Therneau 2012) in R (R Development Core Team 2015, version 3.2.3) to compare data between the control and dispersed seeds. As all seeds were not sown at the same time, we considered the month at which each seed was sown as random term in order to account for the potential effect of seasonal variation in environmental conditions (temperature, humidity etc.) on seed germination. This test could not be run for two species (*Marantochloa leucantha and Pancovia laurentii*) that had too few germination events for control seeds, therefore we used the 'survival' package (Therneau and Lumley 2013) to perform the comparison. We then described the initial delay to germination (i.e., the time taken for the first seed to germinate), the speed of germination (the mean percentage germination per day), and the total percentage of germination (the proportion of seeds that ultimately germinated). We finally plotted Kaplan–Meier survival curves to illustrate these temporal patterns for (i) seeds from all species gathered together, and (ii) each species for which the statistical test has been conducted.

For three species (*Piptostigma fasciculatum*, *Grewia oligoneura*, *Megaphrynium macrostachyum*), no germination event was observed in either of the two treatments. We therefore did not perform any statistical test and considered that gut transit had a neutral effect for these species. However, our protocol might not have been effective at germinating these seeds, which could require other regimes of light and/or water to germinate.

Habitat use

We recorded indirect signs of bonobo activities as a surrogate for seed rain patterns. Because bonobos homogeneously disseminate seeds in their habitat (Beaune et al. 2015), and the mean interval between two consecutive defecations is relatively short (95 min, see Beaune et al. 2013), we hypothesized that defecation patterns were more or less random with regard to bonobo movements, and that in the long-term, seeds could be deposited in all habitat types visited. We surveyed a system of line transects for three consecutive years (2011–2013) to search for signs of bonobo activity (nests, food remains, footprints, vocalisations, direct encounters, faeces), (for further details, see Serckx et al., 2014). At each recorded location, we characterized the habitat type with two components: the understory vegetation and the amount of light at ground level. We described the dominant understory vegetation using one of the following categories: *open* (including burnt areas, fields, and fallows), *woody*, *liana*, *herbaceous* (Marantaceae and Zingiberaceae), and *Haumania* (referring to the Marantaceae species *Haumania liebrechtsiana*). This last category, together with the category *woody*, are known to positively influence bonobo's occurrence in forests (Reinartz et al. 2006). Overall, these categories depict where the main plant life forms (i.e., trees, lianas, herbs) can preferentially grow, even though they are not restricted to these sites. Secondly, we described canopy foliage to obtain a proxy for understory light availability at each location, which is a major environmental factor that influences seedling regeneration (Montgomery 2004). We recorded the presence or absence of foliage cover (1 or 0, respectively) at three height classes (2–10 m; 10–20 m; >20 m) to obtain a final score that represents one of four levels of foliage cover, hence, one of four levels of light available at ground level. These levels vary from 0 (foliage cover at the three height classes: high canopy cover and low light availability), to 1 (intermediate canopy cover, intermediate light availability), 2 (little canopy cover, high light availability), and 3 (no foliage cover at any height class, very high light availability). Our ultimate goal was to know whether some habitat types were used preferentially by bonobos (i.e., received disproportionally more seeds) with respect to their availability. To obtain the frequency distribution of habitat types in the forest, we systematically described habitats with the same two components every 25 m on a line transect system. We described a total of 6 269 locations. We finally compared the frequencies of signs of bonobos in the different habitat types with the availability of those habitat types with a G-test. Given that the occurrence of bonobo nests is biased towards food hotspots within this landscape (Serckx et al. 2016), we grouped signs of nesting (*Nesting*) separately from those of other activities occurring during the day (i.e., feeding and travelling; *Daily activities*). The observed nests were all night nests. We described a total of 1 488 locations where we encountered nests, and 389 locations where we found signs of *Daily activities*. We adjusted the p-values from the G-test for multiple comparisons with the Bonferroni correction.

Regeneration guild of the plant species

In order to evaluate the potential ecological match between plant species and the site where their seeds were deposited, we categorised each species to a regeneration guild according to shade tolerance *sensu* Hawthorne (1995), consisting of pioneer (P) (species with seedlings found in gaps only, and adults very rare in the forest understory), non-pioneer light-demanding (NPLD) (species with seedlings common in the understory, but adults need a gap to grow), and shade-bearer species (SB) (seedlings and adults are only found in the forest understory). The herb species in this study do not strictly belong to regeneration guilds, but have a more tolerant behaviour towards light regimes (Detchuvi 1996). Additionally, we reported the different life forms (tree, liana, herb).

Results

Frugivory and seed dispersal

Overall, bonobos dispersed intact seeds of 77 species, out of which nine could only be identified by their local name, and 27 could not be identified at all (Supplementary material Table 1-S1, Fig. 1-S2). Bonobos dispersed a mean of 2.3 species, a median of 2 species, and a maximum of nine species per faecal sample. Seed dispersal events were frequent, as 99.4% of all faecal samples contained at least one seed. The three most frequently dispersed species, *Musanga cecropioides*, *Aframomum* spp. and *Marantochloa leucantha*, were recorded in 55, 38 and 25% of faecal samples, respectively (Table 1-1). Sixteen species were considered as important, and five as preferred food species. However, the majority of the species were sparse. For example, 53 species were found in <2% of all faecal samples, 12 of which were observed in only one faecal sample during the study period. Among 52 species for which the seed size was known, 5.8% (3) were small, 13.4% (7) were medium, and 80.8% (42) were large.

Table 1-1. Preferred (Pref.) and important (Imp.) species in the bonobo diet, with the seed frequency in faeces, light guild (P = Pioneer, NPLD = Non-Pioneer Light-Demanding, SB = Shade-Bearer, and T = Tolerant concerns species able to grow in habitats with various light regimes), and the main effect of gut transit on germination (+ = positive, - = negative, n.s. = non-significant).

Species	Family	Category	Seed frequency in feces (%)	Regeneration guild	Main effect of transit on germination
Musanga cecropioides	Urticaceae	Imp.	55	P	+
Aframomum sp.	Zingiberaceae	Imp.	38	T	+
Marantochloa leucantha	Marantaceae	Imp.	25	T	n.s.
Uapaca sp.	Euphorbiaceae	Imp.	17	NPLD	-
Dialium sp. [a]	Fabaceae	Pref., Imp.	16	SB	+
Landolphia sp.1	Apocynaceae	Imp.	15	n.a	+
Cissus dinklagei	Vitaceae	Imp.	15	SB	n.a.
Landolphia sp.3	Apocynaceae	Imp.	10	n.a	+
Piptostigma fasciculatum	Annonaceae	Pref., Imp.	10	SB	n.a.
Landolphia sp.2	Apocynaceae	Imp.	10	n.a.	+
Polyalthia Suaveolens	Annonaceae	Pref., Imp.	8	SB	n.a.
Inc. Local name: Lenkala	NA	Imp.	8	n.a.	n.a.
Cordia platythyrsa	Boraginaceae	Pref., Imp.	6	NPLD	n.a.
Pancovia laurentii	Sapindaceae	Pref., Imp.	6	SB	n.s.
Pycnanthus angolensis	Myristicaceae	Imp.	5	NPLD	n.a.
Annona senegalensis	Annonaceae	Imp.	3	P	n.a.

[a] Species for which germination tests have been conducted in Beaune et al. (2013b)

Germination capacity

Overall, considering the seeds from all 16 species tested (Fig. 1-2), seeds that were dispersed showed a significantly different temporal pattern of germination from control seeds ($P < 0.0001$). The mean germination rate increased from 0.15 to 0.24% germination/day, the final germination percentage increased from 42.8 to 67.3%, and the initial delay decreased by four days. Gut transit had a statistically significant effect on the temporal pattern of germination for 10 species (Fig. 1-S1). The initial delay before germination was decreased for 10 species (Table 1-2) and was particularly short for *Oncoba welwitschii*, *M. leucantha* and *Pancovia laurentii*, the first seeds of which germinated 26, 19 and 8 days faster, respectively, after gut passage.

Eight species had a higher mean germination speed after gut passage, but the effect was particularly striking for *Landolphia* sp.1 (an increase of 2.07% germination/day), and ten species showed an increased final germination percentage. Overall, the three germination properties of five species (*S. africana*, *Landolphia* sp.1, *O. welwitschii*, *M. cecropioides*, and *Aframomum* sp.) were enhanced after gut transit. Notably, the control seeds of *S. africana* did not germinate at all, whereas 45% of the dispersed seeds did germinate.

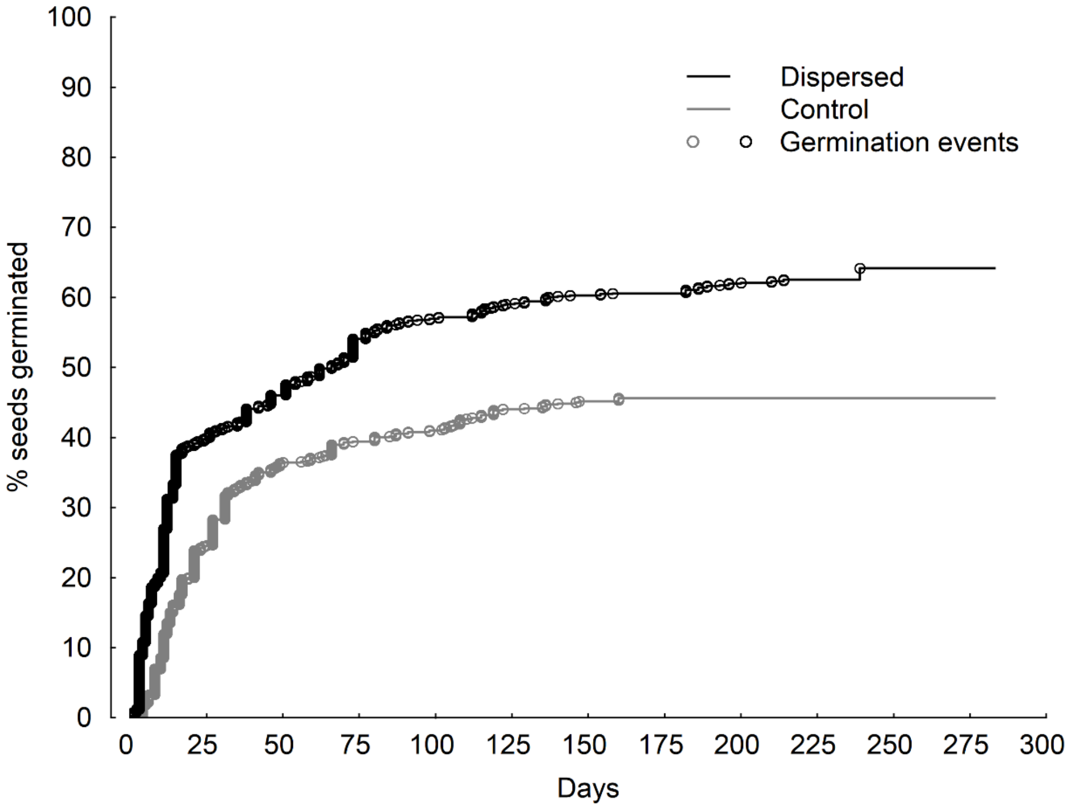


Fig. 1-2. Kaplan–Meier curves illustrating the temporal pattern of germination of all plant species for dispersed (N = 1 023) and control (N = 963) seeds.

Table 1-2. Comparison of the germination of control and dispersed seeds for the 16 species tested. Sample sizes (N), test durations (Length), initial delay in germination (Delay), mean speed of germination (Speed), total percentage germination when the test ended (Total), and logrank test *P*-value (*P*) are shown. Larger values for the three germination characteristics appear in bold.

Family	Species	Control					Dispersed					P
		N	length (days)	Germination characteristics			N	length (days)	Germination characteristics			
				Delay	Speed (%/ day)	Total (%)			Delay	Speed (%/ day)	Total (%)	
Anacardiaceae	*Sorindeia africana*	32	227	Na	Na	0	42	225	**4**	**0.20**	**45.2**	<0.000
Annonaceae	*Piptostigma fasciculatum* $^{I, P}$	40	263	Na	Na	0	47	261	Na	Na	0	Na
	Uvaria myschogyne	125	185	21	0.21	39.2	19	89	21	**0.47**	**42.1**	0.69
Apocynaceae	*Landolphia sp.1* ^{I}	44	106	5	0.77	81.8	48	33	**0**	**2.84**	**93.7**	<0.000
	Landolphia sp.2 ^{I}	46	306	4	**0.31**	**95.6**	69	340	**0**	0.26	88.4	<0.000
	Landolphia sp.3 ^{I}	56	112	8	**0.88**	98.2	60	283	**3**	0.35	**100**	<0.000
Euphorbiaceae	*Uapaca* sp.^{I}	40	188	6	**0.37**	**70.0**	60	238	**5**	0.11	26.7	0.012
Flacourtiaceae	*Oncoba mannii*	40	241	**11**	0.18	42.5	32	237	12	**0.41**	**96.9**	<0.000
	Oncoba welwitschii	48	237	27	0.06	12.5	44	244	**1**	**0.41**	**100**	<0.000
Malvaceae	*Grewia oligoneura*	36	227	Na	Na	0	70	230	Na	Na	0	Na
Marantaceae	*Megaphrynium macrostachyum*	24	275	Na	Na	0	6	238	Na	Na	0	Na
	Marantochloa leucantha ^{I}	84	209	21	**0.43**	89.2	216	283	**2**	0.32	**90.7**	0.28
	Sarcophrynium prionogonium	29	101	**4**	0.03	3.5	14	136	59	**0.73**	**100**	<0.000
Sapindaceae	*Pancovia laurentii* $^{I, P}$	34	46	11	**2.18**	**100**	32	230	**3**	0.22	50	0.48
Urticaceae	*Musanga cecropioides* ^{I}	203	280	13	0.12	33	180	231	**11**	**0.40**	**91.7**	<0.000
Zingiberaceae	*Aframomum* sp. ^{I}	82	283	Na	Na	0	84	231	**28**	**0.07**	**17**	<0.000
All species		963	283	4	0.15	42.8	1023	283	**0**	**0.24**	**67.3**	<0.000

^{I} Important species, ^{P} Preferred species

Habitat use

Overall, habitats with an understory composed of *woody* and *Haumania* vegetation (32 and 34% of all locations, respectively, Fig. 1-3A), and with an intermediate (1 – intermediate foliage cover) or low (0 – dense foliage cover) amount of light (52 and 29% of all locations, respectively, Fig. 1-3B) were the most frequent in the forest.

Bonobos did not build nests at random, regarding either the type of understory vegetation (G-test: d.f. = 4, $P < 0.05$), or the amount of light (G-test: d.f. = 3, $P < 0.05$). Instead, they preferentially chose habitats with an understory composed of *Haumania* (66% of all nests) and a *woody* vegetation (25% of all nest) (Fig. 1-3a), and an intermediate amount of light (71% of all nests) (Fig. 1-3b). Despite these preferences, they also built nests in habitats containing the three other understory vegetation types, even if these were minimal, and with high and low amounts of light.

Similarly, bonobos were more active in habitats with a specific understory vegetation (G-test: d.f. = 4, $P < 0.05$) and a specific amount of light (G-test: d.f. = 3, $P < 0.05$). They showed a preference for forests with a *Haumania* understory vegetation (48% of all signs) (Fig. 1-3a), and an intermediate level of light (65% of all signs) (Fig. 1-3b). They also used all the four other understories, even though the use of the category *open* was marginal, and they were active in habitats with low and high levels of light (11 and 22% of all signs, respectively).

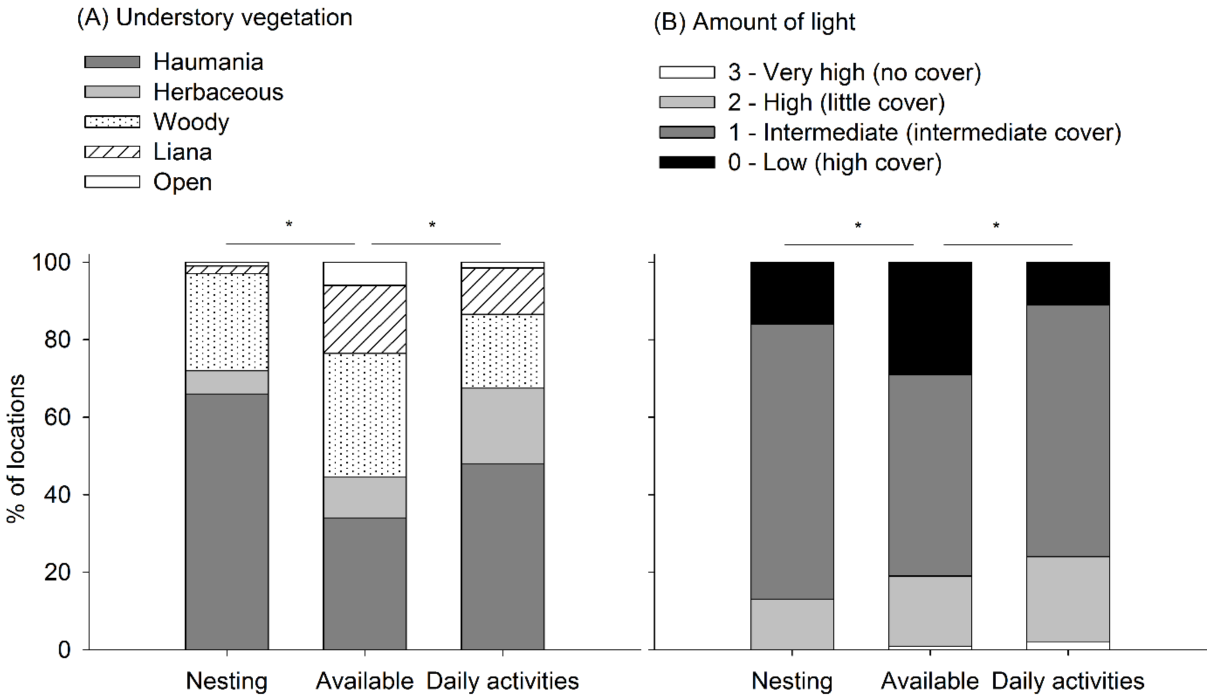


Fig. 1-3. Habitat type availability and frequency of use by bonobos for nesting and daily activities. Habitat types are described by (A) understory vegetation, and (B) amount of light at ground level.

Regeneration guild of the plant species

Among the 50 dispersed plant species for which the life form was known, bonobos dispersed 33 species (66%) of trees, nine (18%) of lianas and eight (16%) of herbs. Among the 37 tree species for which the regeneration guild was known, the SB was the best-represented guild with 18 species (49%) (Table 1-S1). Six species (16%) were pioneer, and five others (13.5%) were classified as NPLD.

Discussion

We found that bonobos dispersed 77 species in the forest–savanna mosaic, which falls within the range of what has been reported for bonobos living in primary evergreen lowland rainforest in the heart of the Congo Basin (Beaune et al. 2013). Almost all the faecal samples (99.4%) contained seeds, which suggests an overall high frequency of seed dispersal events by bonobos. However, the provided service was quantitatively and qualitatively not uniform for different plant species: bonobos dispersed important and preferred species in disproportionally high quantities, and the effect of gut transit on seed germination varied depending on the species considered, although it had an overall positive effect. More importantly, they dispersed a majority of species that thrive in limited light conditions in the forest understory (SB) (49%), and, interestingly, they also favoured habitats with an intermediate level of light, where they deposited particularly large quantities of seeds, among which SB species. This ecological match between shade-bearers and their deposition sites should enhance seedling recruitment, and thus represent a case of directed seed dispersal. Bonobos are therefore likely to maintain the successional process from secondary to primary forests by (i) moving large SB seeds away from high density-dependent mortality close to parent plants, and (ii) depositing them in particularly appropriate sites. Moreover, more than 80% of all species dispersed were large-seeded, and all SB species were large-seeded. In fact, up to 94.2% of species dispersed by bonobos are not ingested by the main sympatric primate, *Cercopithecus ascanius*, since less than 1% of their dungs contained seeds longer than 5 mm in Uganda (Lambert 1999). Likewise, only four (22%) SB species are also dispersed by hornbills (Table 1-S1). This great ape therefore plays a paramount functional role for the regeneration of late successional forests.

These results are of particular concern given the increasing pressure hunting exerts on the community of large frugivores in the region (Fa et al. 2002). In the mosaic, frugivorous primates (*Lophocebus atterimus*, *Cercopithecus wolfi*, and *C. neglectus*) are locally extinct or very rare (*C. ascanius* can be occasionally observed), and hornbills, (*Bycanistes albotibialis*, *B. fistulator*, *Ceratogymna atrata*) even though they are relatively abundant, are increasingly hunted as other vertebrates most favored by hunters are extirpated. A relic population of forest elephants (*Loxodonta* cyclotis) persists in some forest blocs further north, but it is very fragile, unprotected, and its range does not overlap with our study site. Also, rodents and ruminants occasionally disperse seeds, but they are mostly seed-predators and not likely playing a significant role in seed dispersal (Gautier-Hion et al. 1985, Effiom et al. 2014). We therefore suspect that there is very low functional redundancy among the large frugivore community, which strengthens the unique and crucial character of bonobo-mediated seed dispersal service for large seeds and SB species. This finding is of paramount importance for the conservation of the landscape, because the long-term maintenance of rich communities associated with old mature forests might falls to that threatened ape.

Bonobos marginal use of open habitats undoubtedly limits their ability to facilitate the establishment of pioneer species, and in the recolonization of such habitats. Nevertheless, their dispersal services might not be limited to the regeneration of mature forests, but could contribute to the maintenance of a soil seed bank, which is highly important for early gap regeneration. Those are indeed predominantly composed of seeds of pioneer species (Castillo and Stevenson 2010, Daïnou et al. 2011), which are able to subsist long periods of time (Dalling and Brown 2009). Bonobos could thus indirectly favour early successional vegetation growth in the event of local disturbance. For instance, the four most frequently dispersed species establish and grow well in high light conditions, and herbs, including some species that require much light (*M. leucantha, M. macrostachyum,* some *Aframomum* spp.) (Alexandra Ley pers. comm.), were also frequently dispersed. Moreover, a pilot study using direct observations allowed us to record 8 and 20% of bonobo occurrences within 50 and 100 m, respectively, of the forest edge, which are areas of transitional forest composed of P and NPLD species. Bonobos are also regularly observed to use the savanna where they feed on stalks of *Hyparrhenia diplandra* and fruits of the small fire-resistant tree *Annona senegalensis* (local population, pers. comm.). That species is relatively abundant in savannas and could function as a ‘stepping stone’ for seed dispersers’ movements between forest interior and savanna, and facilitate vegetative succession in the colonisation front. This natural expansion which is currently taking place is however restricted by anthropogenic fires (Favier et al. 2004), so this process is complex and the actual role of frugivores remains unclear. Our data did not allow us to detect a significant use of open habitats by bonobos. Regarding their defecation pattern, we assumed that seeds could be deposited in all habitat types visited based on the simplistic assumption of a frequent (95 min interval) and homogeneous defecation pattern in the habitat. However most animals’ behaviour varies heterogeneously across space and time and could largely influence defecation patterns (Russo et al. 2006). Our method was thus not optimal to obtain a thorough estimation of bonobo-generated seed rain patterns.

Finally, we showed that gut transit positively influenced the seed germination of the majority of the species tested by enhancing the mean speed and final germination percentage, and shortening the initial delay. Notably, among these species, two were the top most frequently dispersed and six were also frequently dispersed. This combination of increased germination potential and high amounts of dispersed seeds provides cumulative advantages. A higher final germination percentage may be beneficial by increasing the number of potential seedlings that can establish and survive to subsequent life stages, hence increasing plant fitness (Harper 1977). A shorter initial delay, and mean speed of germination of the whole seed cohort, may be particularly beneficial to escape seed predation and pathogens, and to confer the seeds/seedlings with a competitive advantage over conspecifics (Traveset and Verdú 2002). Even an increase of only a few days may impact seedling growth (Cook 1980). However, this improved germination trait might translate into a higher plant fitness only for non-dormant species, because seed dormancy might be selected to spread mortality over time (Traveset and Verdú 2002) and be a better strategy than germinating rapidly in some environmental conditions. It is also worth mentioning that among nine important species, six were positively influenced by gut transit, whereas among seven non-important species, only three were positively influenced.

These results could indicate particularly strong mutualism and the potential influence of dispersers' behaviour on plant's trait evolutionary change (e.g. seed coat thickness, Traveset and Verdú, (2002)). Finally, only one species showed significant and much lower values for two germination properties, and no one showed an alteration in all three properties after gut transit, suggesting that it does not damage seeds, even when it negatively affects some germination properties. Furthermore, a lower germination potential could be counterbalanced by an increased quantity of dispersed seeds, as long as some seeds are still viable after gut transit. Species might indeed derive more overall benefits by having many seeds dispersed away from parent plants (i.e., avoiding density-dependent mortality) and deposited at safe sites, even if their germination potential is reduced compared to that of non-dispersed seeds.

Overall, those results confirm the crucial role of large frugivores across tropical regions (Bueno et al. 2013, Vidal et al. 2013, Arroyo-Rodríguez et al. 2015, Petre et al. 2015), and particularly in degraded habitats (Agmen et al. 2010, Lenz et al. 2011, Albert et al. 2014, Arroyo-Rodríguez et al. 2015, Lindsell et al. 2015). However, our findings are especially interesting because the bonobo is an endangered species, and despite their rarity in forest–savanna mosaics, they play a very important function. Particular attention should be paid to large frugivores in human-altered landscapes across tropical and temperate regions (Matías et al. 2010, Grünewald et al. 2010, Lenz et al. 2011, Bueno et al. 2013, Albert et al. 2014, Arroyo-Rodríguez et al. 2015, Lindsell et al. 2015, Pellerin et al. 2016), and especially if they are threatened, because they likely play key but fragile ecological function, and failure to maintain their populations could disrupt plant-animal interactions, and lead to a shift in the composition of the whole plant community (Vanthomme et al. 2010, Kurten 2013, Effiom et al. 2014).

Conclusion

We showed that the bonobo dispersed a majority of large-seeded species that few or no other sympatric frugivore can disperse. More importantly, they also dispersed a majority of shade-bearers species, which all had large seeds, and were deposited more often in locations with intermediate light availability. This dispersal pattern should enhance shade-bearers establishment, and we thus hypothesized that bonobos performed directed seed dispersal for those plants. We concluded that they play a unique and paramount functional role since the long-term maintenance of forest succession to a climax state and the conservation of a rich community in this landscape might falls to that threatened frugivore. That finding is of particular concern given the growing rates of bushmeat extraction (Fa et al. 2002), and forest degradation (Mayaux et al. 2013, Haddad et al. 2015) in the region.

Management plans that aim to implement effective conservation in human-modified and impoverished landscapes should pay particular attention to animals that have unique and keystone function, and invest in long-term conservation programmes because the disruption of animal-mediated forest regeneration process can be subtle and need decades to be seen. It can nevertheless have harmful and long-lasting consequences on forest dynamics and ultimately on human well-being. In that regard, the traditional taboo concerning bonobos and the community-based conservation programme in the mosaic offer a remarkable opportunity to involve the local community into conservation efforts and ensure both their development and the resilience of the forest system.

Supplementary material

Table 1-S1. Dispersed species with seed size, light guild (P = Pioneer, NPLD = Non-Pioneer Light-Demanding, SB = Shade-Bearer, and T = Tolerant concerns species able to grow in habitats with various light regimes), general habitat description (MM = mixed mature, YS = young secondary, OS = old secondary) and whether they are dispersed by hornbills.

Scientific name	Nb feces with seeds (%)	Life form	Guild	General habitat description	Seed size length	width	Hornbill dispersed[a]
Anacardiaceae							
Sorindeia africana	18 (1)	Tree	SB	MM	15	11.5	
Annonaceae							
Annickia chlorantha	7 (0)	Tree	SB	MM	19.5	10	Yes
Annona senegalensis	57 (3)	Tree	P	Savanna/ fallow	9.5	4.5	
Isolona hexaloba	49 (2)	Tree	SB	MM	12.5	10	
Piptostigma fasciculatum	236 (10)	Tree	SB	MM	22.5	10	
Polyalthia suaveolens	193 (8)	Tree	SB	MM	10	8.5	Yes
Xylopia hypolampra	6 (0)	Tree	P	YS/OS	10	6.5	Yes
Uvaria sp.	76 (3)	Tree	SB	MM	10[b]	6[b]	
Apocynaceae							
Landolphia sp2.	225 (10)	Liana	-	-	25	14	
Landolphia sp3.	238 (10)	Liana	-	-	21	12	
Landolphia sp1.	336 (15)	Liana	-	-	21.5	13	
Boraginaceae							
Cordia platythyrsa	136 (6)	Tree	NPLD	MM/YS/OS	15	15	
Burseraceae							
Santiria trimera	49 (2)	Tree	SB	MM	14	22	Yes
Clusiaceae							
Garcinia kola	1 (0)	Tree	SB	MM	30	20	
Symphonia globulifera	1 (0)	Tree	SB	MM	21.5	12.5	

Euphorbiaceae							
Plagiostyles africana	7 (0)	Tree	NPLD	OS/MM	10	18	Yes
Uapaca spp.	386 (17)	Tree	NPLD	YS/OS	24	13	Yes
Fabaceae (caesalpinoideae)							
Dialium spp.	372 (16)	Tree	SB	OS/MM	11	9.5	
Flacourtiaceae							
Oncoba mannii	12 (1)	Tree	P	YS	8	4	
Hypericaceae							
Harungana madagascariensis	53 (2)	Tree	P	YS	2	0.5	
Malvaceae							
Grewia oligoneura	3 (0)	Tree	SB	Swamp	10	9	
Cola diversifolia	18 (1)	Tree	SB	MM	14	9.5	
Marantaceae							
Marantochloa leucantha	560 (25)	Herb	T	Open/ disturbed	9	5.5	
Megaphrynium macrostachyum	7 (0)	Herb	T	Open	14	11	
Megaphrynium trichogynum	4 (0)	Herb	T	Forest understory/ gaps	13.5	7	
Hypselodelphys violacea	3 (0)	Herb	T	Open/forest edges	-	-	
Sarcophrynium brachystachyum/ schweinfurthianum	6 (0)	Herb	T	Forest understory/ open	12	7	
Sarcophrynium prionogonium	17 (1)	Herb	T	Forest understory/ open	14.5	4.5	
Thaumatococcus daniellii	2 (0)	Herb	T	Forest understory/ open	20	13	
Moraceae							
Myrianthus arboreus	47 (2)	Tree	P	YS/OS	17	8	
Myristicaceae							
Pycnanthus angolensis	108 (5)	Tree	NPLD	OS	17.5	11.5	Yes
Olacaceae							
Heisteria	3 (0)	Tree	SB	MM	10	6.5	

parvifolia							
Strombosia sp.	1 (0)	Tree	SB	MM	23	-	Yes
Sapindaceae							
Pancovia laurentii	141 (6)	Tree	SB	MM	13	9	
Sapotaceae							
Chrysophyllum lacourtianum	7 (0)	Tree	SB	MM	28.5	16	
Omphalocarpum elatum	1 (0)	Tree	SB	MM	40	25	
Thymelaceae							
Dicranolepis baertsiana	4 (0)	Tree	T	S/fallow/MM	-	-	
Tiliaceae							
Desplatsia dewevrei	5 (0)	Tree	NPLD	MM	18.5	8	
Urticaceae							
Musanga cecropioides	1251 (55)	Tree	P	YS	<2	<2	Yes
Vitaceae							
Cissus dinklagei	342 (15)	Liana	SB	MM	14.5	9	
Zingiberaceae							
Aframomum spp.	855 (38)	Herb	T	YS/OS/MM	5	2	
Non identified species							
NID_local.name: Bempura	11 (0)	Liana	-	-	-	-	n.a
NID_local.name: Enkwanzala	24 (1)	Liana	-	-	-	-	n.a.
NID_local.name: Ketshu	6 (0)	Liana	-	-	4	2.5	n.a.
NID_local.name: Maniankima	3 (0)	Liana	-	-	-	-	n.a.
NID_local.name: Mbombal-ngaa	3 (0)	Tree	-	-	-	-	n.a.
NID_local.name: Mosima	27 (1)	Tree	-	-	28.5	13.5	n.a.
NID_local.name: Motsio	42 (2)	Tree	-	-	-	-	n.a.
NID_local.name: Omonobari	8 (0)	Tree	-	-	-	-	n.a.
NID_local.name: Lenkala	182 (8)	Liana	-	-	-	-	n.a.

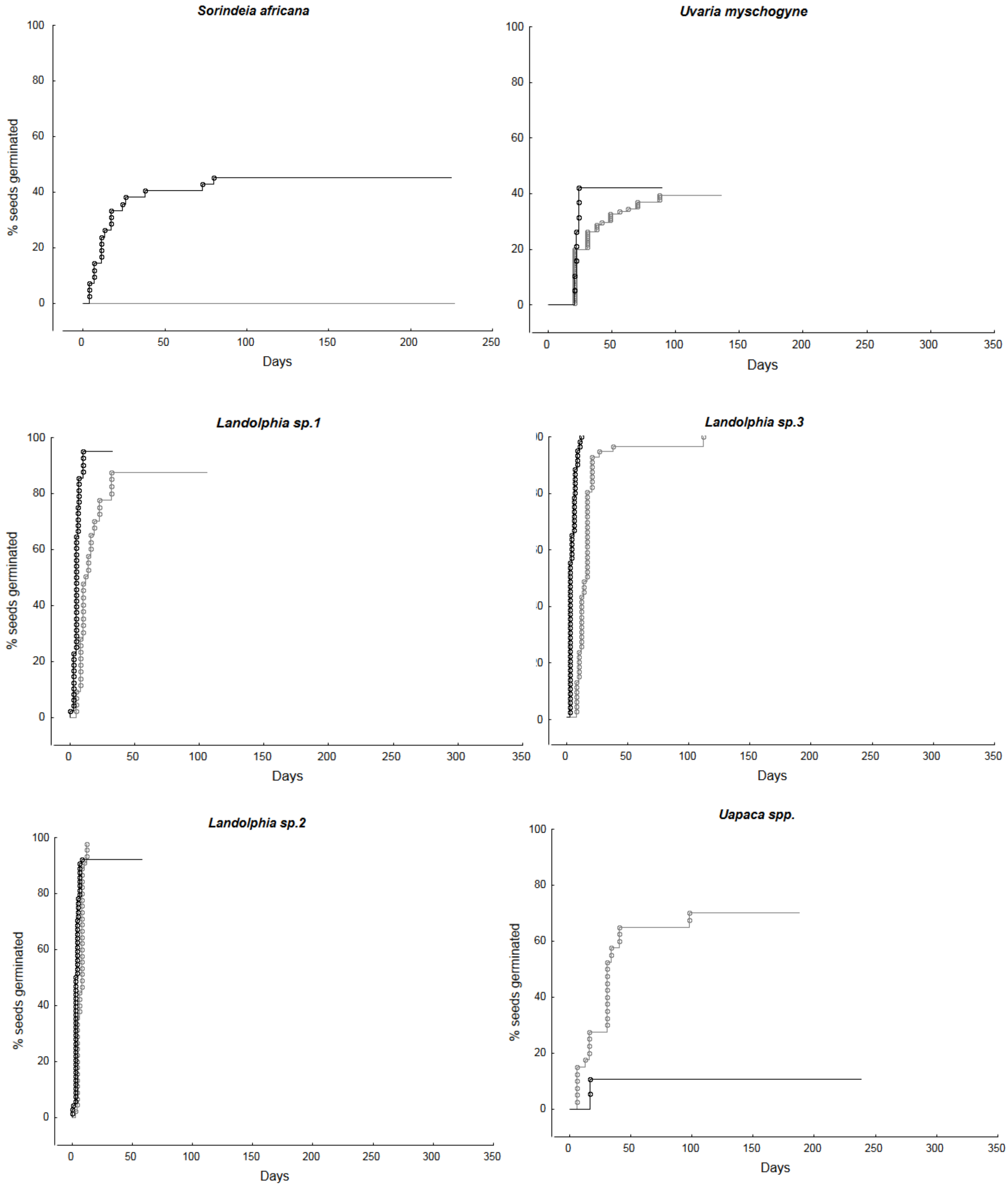
NID_local.name : Unknown	2 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	46 (2)	-	-	-	12.5	7	n.a.
NID_local.name : Unknown	10 (0)	-	-	-	15.5	11.5	n.a.
NID_local.name : Unknown	8 (0)	-	-	-	20.5	12.5	n.a.
NID_local.name : Unknown	3 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	2 (0)	-	-	-	11	7	n.a.
NID_local.name : Unknown	78 (3)	-	-	-	11	10.5	n.a.
NID_local.name : Unknown	1 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	7 (0)	-	-	-	14.5	9	n.a.
NID_local.name : Unknown	3 (0)	-	-	-	9	6	n.a.
NID_local.name : Unknown	1 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	3 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	2 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	1 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	2 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	3 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	20 (1)	-	-	-	-	-	n.a.
NID_local.name : Unknown	1 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	1 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	6 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	1 (0)	-	-	-	15	8.5	n.a.
NID_local.name : Unknown	1 (0)	-	-	-	-	-	n.a.

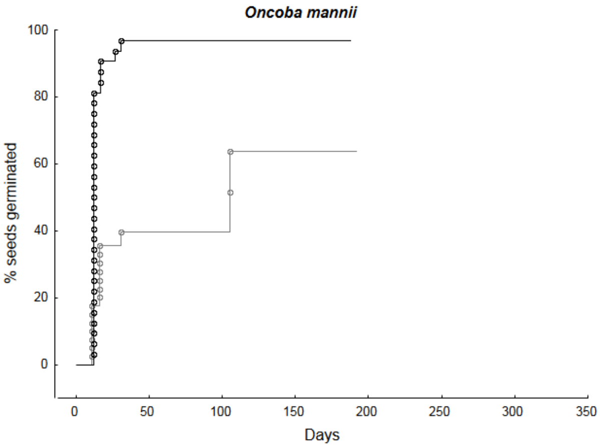
NID_local.name : Unknown	5 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	18 (1)	-	-	-	8	6	n.a.
NID_local.name : Unknown	8 (0)	-	-	-	10	8.5	n.a.
NID_local.name : Unknown	1 (0)	-	-	-	-	-	n.a.
NID_local.name : Unknown	5 (0)	-	-	-	-	-	n.a.

[a] Clark et al., 2001; Poulsen et al., 2002; Whitney et al., 1998

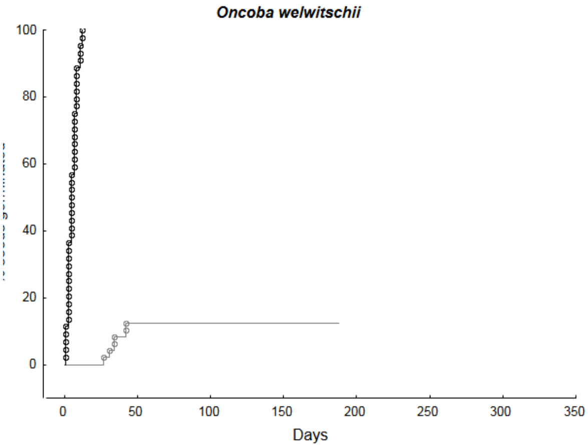
[b] Mean seed size calculated with other species from the same genus (8 species for *Uvaria* spp)

Fig. 1-S1. Kaplan–Meier curves illustrating the temporal pattern of germination of each plant species tested.

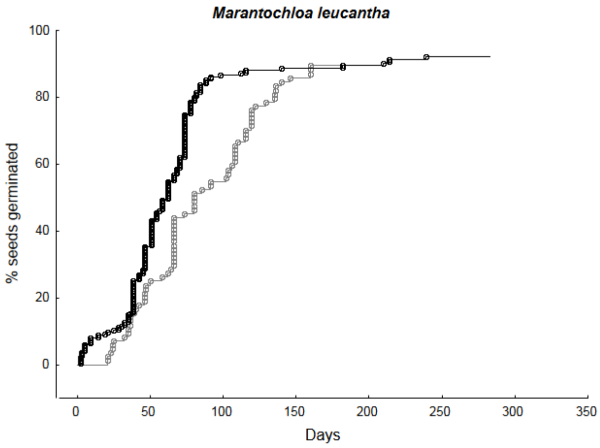




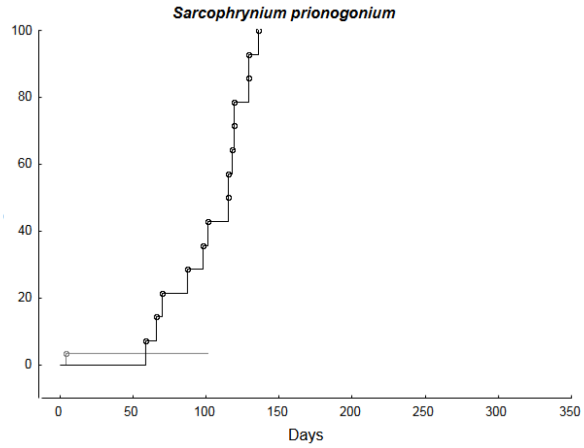
Oncoba mannii



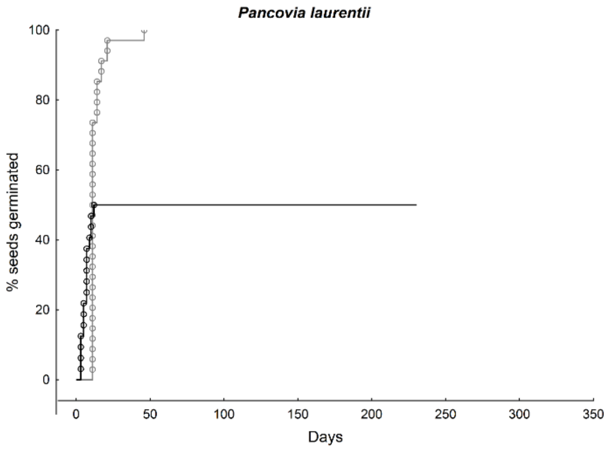
Oncoba welwitschii



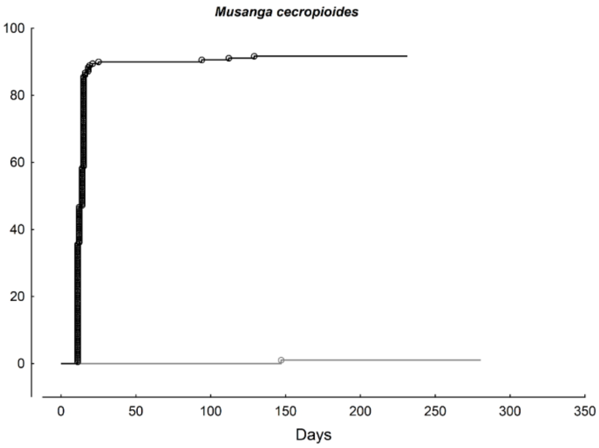
Marantochloa leucantha



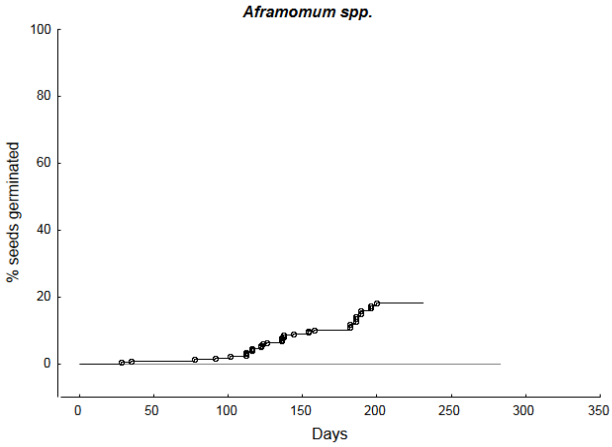
Sarcophrynium prionogonium



Pancovia laurentii



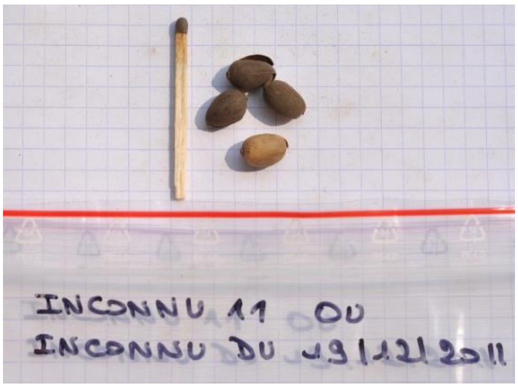
Musanga cecropioides



Aframomum spp.

Fig. 1-S2. Photographs of fourteen unknown species dispersed by bonobos


MOSIMA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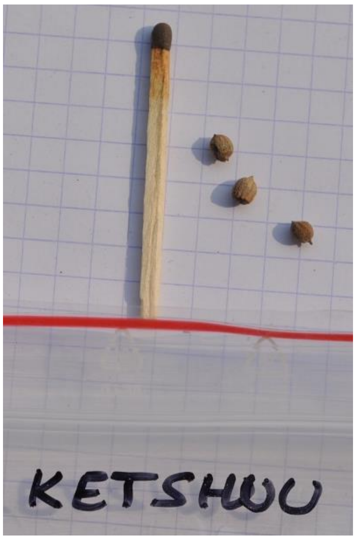
du 19/04/2012


KETSHUU


INCONNU DU 21/08/2011


INCONNU 1 DU 18/04/2012.

Chapitre 2.

Forest cover, hunting pressure, and fruit availability influence seed dispersal in a forest-savanna mosaic of the Congo Basin

Trolliet, F., P.-M. Forget, M.-C. Huynen, and A. Hambuckers. *In press*. Forest cover, hunting pressure, and fruit availability influence seed dispersal in forest-savanna mosaic of the Congo Basin. *Biotropica*.

Dans le chapitre précédent, nous avons vu que les bonobos assurent une dispersion des graines efficace pour de nombreuses espèces de plantes dans la mosaïque de forêts-savanes. Plus particulièrement, ils apparaissent comme une composante essentielle de la communauté de frugivores de par leur rôle dans la dispersion de plantes ayant des grandes graines que peu ou pas d'autres frugivores ne peuvent ingérer et disséminer.

Néanmoins, de nombreuses espèces de plantes ont leurs graines qui sont aussi dispersées par d'autres taxons de frugivores que les primates, et y compris des espèces ayant des grosses graines.

Par exemple, les grands oiseaux frugivores tels que les calaos sont des disperseurs de graines importants dans les forêts de l'ancien monde, et peuvent aussi disperser des graines de taille conséquente par endozoochorie. Leur rôle en tant que disperseur de graines pourrait devenir de plus en plus important à mesure que les populations de gros mammifères s'affaiblissent, et les services qu'ils assurent sont possiblement plus résilients que ceux de mammifères terrestres dans les habitats fragmentés de par leur haute mobilité. Il est donc primordial d'explorer les réponses d'autres systèmes plantes-frugivores, et en particulier ceux qui impliquent des calaos, aux perturbations anthropiques afin d'obtenir une compréhension plus générale du fonctionnement des processus de régénération forestière. Ainsi, nous allons dans ce chapitre examiner les capacités de dispersion des graines d'une espèce d'arbre dépendante des grands frugivores, dont les calaos, en fonction de variables environnementales.

In the previous chapter, we saw that bonobos provide effective seed dispersal for numerous plant species in this forest-savanna mosaic. Notably, they appeared as a crucial component of the frugivore community because of their role in the dispersal of large-seeded plants.

However, many large-seeded plant species depend and other frugivore taxa than primates for their dispersal. For instance, large birds such as hornbills are important seed dispersers in the Paleotropics and can disperse large seeds by endozoochory. Also, their role as seed disperser could be increasingly important as large mammal populations diminish, and the services they ensure are possibly more resilient than those provided by terrestrial mammals in fragmented habitats thanks to their high mobility. It is therefore crucial to explore the response of other plant-frugivore systems, and particularly those that involve hornbills, to anthropogenic disturbances in order to get a more general understanding of functioning of the processes of forest regeneration. In this chapter, we will explore the seed dispersal capacity of a tree species that depend on large frugivores for its dispersal, including hornbills, according to environmental variables.

Résumé

La fragmentation des forêts, la diminution du couvert forestier, et la chasse, sont reconnues comme les principales menaces qui affectent la dispersion des graines par les animaux. Cependant, leurs effets combinés sur les taux de dispersion des graines n'ont été que rarement explorés, et jamais en Afrique. Notre objectif était d'examiner les effets de la couverture forestière, de la pression de chasse, de l'abondance de frugivores, et de la disponibilité en fruits à l'échelle locale et du paysage sur les taux de dispersion des graines de *Staudtia kamerunensis* (Myristicaceae). Afin d'estimer les pourcentages d'échec de dispersion (graines non-dispersées), nous avons quantifié les restes de fruit dans des collecteurs sous 34 arbres adultes distribués dans cinq sites contrastés dans une mosaïque de forêts-savanes semi-naturelle en République Démocratique du Congo. Nous avons utilisé des analyses statistiques prenant en compte l'autocorrélation spatiale, et nos résultats indiquent que la couverture forestière dans le paysage autour des arbres, la pression de chasse, laquelle est associée à l'abondance du principal disperseur, ainsi que la disponibilité en fruits dans les sites, ont un effet significatif sur le pourcentage d'échec de dispersion des graines. La combinaison d'une forte disponibilité en fruits et d'une diminution de l'abondance de disperseurs de graines ont probablement fait augmenter le niveau de satiation des disperseurs et conduit à la saturation du système de dispersion des graines. Notre étude met en évidence les effets de deux facteurs majeurs associés aux activités anthropiques : la couverture forestière et la chasse, sur la dispersion des graines zoochores. Ces résultats pourraient avoir des conséquences importantes sur notre compréhension des interactions arbres-frugivores et la conservation des communautés tropicales.

Abstract

Forest fragmentation, reduced forest cover, and hunting pressure are the main threats affecting animal-mediated seed dispersal. However, their combined effects on seed dispersal rates have been simultaneously investigated only rarely, and never in Africa. We aimed to disentangle the effects of forest cover, hunting pressure, frugivore abundance, and fruit availability at the local and landscape scales on the seed dispersal rates of *Staudtia kamerunensis* (Myristicaceae). To estimate the percentages of seed dispersal failure (undispersed seeds), we quantified fruit remains below fruiting trees distributed across five contrasting sites in a semi-natural forest-savanna mosaic in the Democratic Republic of Congo. We used statistical analyses accounting for spatial autocorrelation and found that forest cover in the surrounding landscape, hunting level, the associated abundance of dispersers, and fruit availability all had significant effects on the percentage of seed dispersal failure. The combination of high fruit availability and reduced abundance of seed dispersers could accelerate seed disperser satiation, causing the seed dispersal system to be saturated. Our study highlights how two major factors associated with anthropogenic activities, forest cover and hunting, affect seed dispersal by animals. These findings could have far-reaching implications for our understanding of tree-frugivore interactions and the conservation of tropical communities.

Introduction

Anthropogenic pressures exert harmful effects on ecological functions such as animal-mediated seed dispersal (Markl *et al.* 2012). Bushmeat hunting (Wang *et al.* 2007, Holbrook & Loiselle 2009, Markl *et al.* 2012, Boissier *et al.* 2014, Naniwadekar *et al.* 2015) and forest loss and fragmentation (Galetti *et al.* 2006, Kirika *et al.* 2008, Cordeiro & Howe 2003, Uriarte *et al.* 2011, Mendes *et al.* 2015, Jesus *et al.* 2012) alter the interactions of animal communities with plants and disrupt various components of seed dispersal. For instance, a decrease in the abundance and diversity of frugivores has been associated with reduced visitation rates, fewer seeds removed, and shorter seed dispersal distances (Markl *et al.* 2012). Few studies, however, have evaluated the dual effect of hunting and forest loss or fragmentation on seed dispersal (Peres 2001, Galetti *et al.* 2006, Wright & Duber 2001).

Moreover, while a significant amount of research on the impact of anthropogenic activities has been conducted in tropical America (see Markl *et al.* 2012), relatively few studies have investigated dispersal by fruit-eating animals in tropical Africa in relation to either defaunation (Wang *et al.* 2007, Kirika *et al.* 2008b, Babweteera & Brown 2009) or forest cover loss or fragmentation (Farwig *et al.* 2006, Kirika *et al.* 2008, Cordeiro & Howe 2003). The intensive rate of bushmeat extraction in the Afrotropics threatens the mammalian (Fa *et al.* 2002) and avian (Whytock *et al.* 2016, Trail 2007) frugivore communities. It is therefore of paramount importance to investigate how forest cover and hunting influence seed dispersal in zoochorous plants in Afrotropical systems.

The family Myristicaceae is a pantropical plant model used to study animal-mediated seed dispersal. Its various species produce dehiscent fruits composed of two valves and a large seed surrounded by a bright red fleshy aril, which depends on large frugivores for its dispersal (Queenborough *et al.* 2013). This structure allows seed production and removal rates to be estimated efficiently and the impact of defaunation to be reliably assessed (Cf. Boissier *et al.* 2014). With its consistent fruit morphology across tropical regions, the family Myristicaceae permits easy comparisons between continents. Yet, although seed dispersal of Myristicaceae species has been widely studied across the Neotropics (Howe & Estabrook 1977, Howe & Vande Kerckhove 1980, 1981, Holbrook & Loiselle 2009, Ratiarison & Forget 2013, Boissier *et al.* 2014), this process has received much less attention in the Paleotropics. *Staudtia kamerunensis,* is one of the few studied species of this family in Africa, and variations in its seed dispersal rates in response to human and environmental factors have not yet been investigated (Clark *et al.* 2004, 2005). This species is reported to be primarily dispersed by hornbills, which are being increasingly hunted as other vertebrates favored by hunters disappear (Fa *et al.* 2000, Whytock *et al.* 2016). In the Neotropics, toucans and primates remove a large proportion of seeds from Myristicaceae trees species (*Virola kwatae*, *V. michelii*, Boissier *et al.* 2014, *V. flexuosa*, Holbrook & Loiselle 2009). However, hunting and forest loss primarily affect the abundance and movements of large vertebrates (Fa *et al.* 2002, Jerozolimski & Peres 2003, Bregman *et al.* 2014, Cramer *et al.* 2007), in turn reducing seed removal rates for Myristicaceae and other large-seeded plants (Boissier *et al.* 2014, Holbrook & Loiselle 2009, Cramer *et al.* 2007). Thus, it is necessary to understand how hunting pressure and forest cover affect frugivore seed dispersal services to assess the long-term resilience of many plant species.

In the present study, we explored how the amount of forest cover, hunting pressure, and the abundance of large frugivores influence the percentage of seed dispersal failure in *S. kamerunensis* in a semi-natural, fragmented forest-savanna mosaic. The causes of the landscape's fragmented structure are complex and difficult to unravel, making it risky to explore the effect of forest fragmentation *per se*. Cattle ranching and savanna fires maintain the savanna and alter forest edges; fragmentation facilitates access to the forest interior for hunting and slash-and-burn agriculture, which in turn contribute to forest degradation in terms of animal community and canopy cover. Moreover, these types of threats are increasing due to human population growth (Geist & Lambin 2002). We therefore considered forest cover as a proxy for suitable frugivore habitat estimates. In addition to forest cover, hunting, and frugivore abundance, the amount of fruits available at varying spatial scales can also influence the abundance and diversity of frugivores visiting fruiting trees, and consequently the frequency of fruit-frugivore interactions and seed dispersal events. Indeed, seed removal is positively related to crop size (Blendinger & Villegas 2011, Vergara *et al.* 2010) and fruit availability (Martínez & García 2014, Hampe 2008). We also took into account fruit availability at the local (crop size) and landscape (site) scales to explore the causal mechanisms determining seed dispersal. We predicted that as hunting pressure increases and forest cover and frugivore abundance decrease, the percentage of seed dispersal failure should increase. We also predicted that as fruit availability at the local and landscape scales decrease, seed dispersal failure should increase. However, a decrease in disperser abundance could alternately accelerate frugivore satiation, thereby decreasing the percentage of seed dispersal (Hampe 2008, Forget & Jansen 2007).

Material & methods

Study area and forest sites

The study took place in western Democratic Republic of Congo (D.R. Congo) in the area surrounding the WWF (World Wide Fund for Nature) Malebo Research Station in Bandundu province (2°29'3.87" S, 16°30'4.16" E). Annual rainfall averages 1500 mm. The main dry season occurs from June to August, followed by the main rainy season from September to January and consecutive short rainy and dry seasons from January to May. The study area is characterized by a mix of tropical semi-evergreen lowland rain forest and savanna matrix. The landscape is highly fragmented, with a system of forest patches and corridors mainly associated with the hydrographic network. As a transitional ecosystem, or ecotone, its fragmented spatial structure is natural, yet also influenced by anthropogenic activities. Shifting slash-and-burn agriculture encroaches on forest patches, while cattle ranching, with its associated yearly fire regimes, restricts the colonization of forests.

We conducted fieldwork in an area of approximately 30 x 20 km in the mosaic landscape (Fig. 2-S1 in Supplementary material), in five forested sites that we delineated according to the positions of the *S. kamerunensis* trees studied. The Mbanzi and Nkombo sites were located in an extensive forest bloc (>500 km²), while the three other sites were located in a more fragmented area. The Minkalu site was a 4.6 km² forest patch, and the Nkala-North and Nkala-

South sites (hereafter, Nkala-N. and Nkala-S., respectively) were both located in a 17.6 km^2 forest patch. The five sites thus had contrasting levels of surrounding forest cover, and they also endured different levels of human disturbance and hunting pressure. The Mbanzi village, originally founded as a hunting camp, is home to around 600 people, including many hunters. The forest around Mbanzi was thus assumed to be under relatively high hunting pressure. The Nkombo forest was further away from human settlements, and anthropogenic pressure was probably more limited. The other forest sites belonged to nearby village communities practicing subsistence hunting and slash-and-burn agriculture. Indeed, the Nkala-N., Nkala-S., and Minkalu sites were located in a more densely populated area where hunting pressure was high, yet home to an ethnic group that does not hunt bonobos (*Pan paniscus*), following a traditional taboo and conservation programs of the WWF and Mbou-Mon-Tour NGOs. Therefore, these three sites hosted relatively high densities of primates (mainly bonobos) compared to the two sites in the extensive forest. Apart from these specificities, all medium to large animals (primates, duikers, bush pigs, giant rats, porcupines, and hornbills) were hunted.

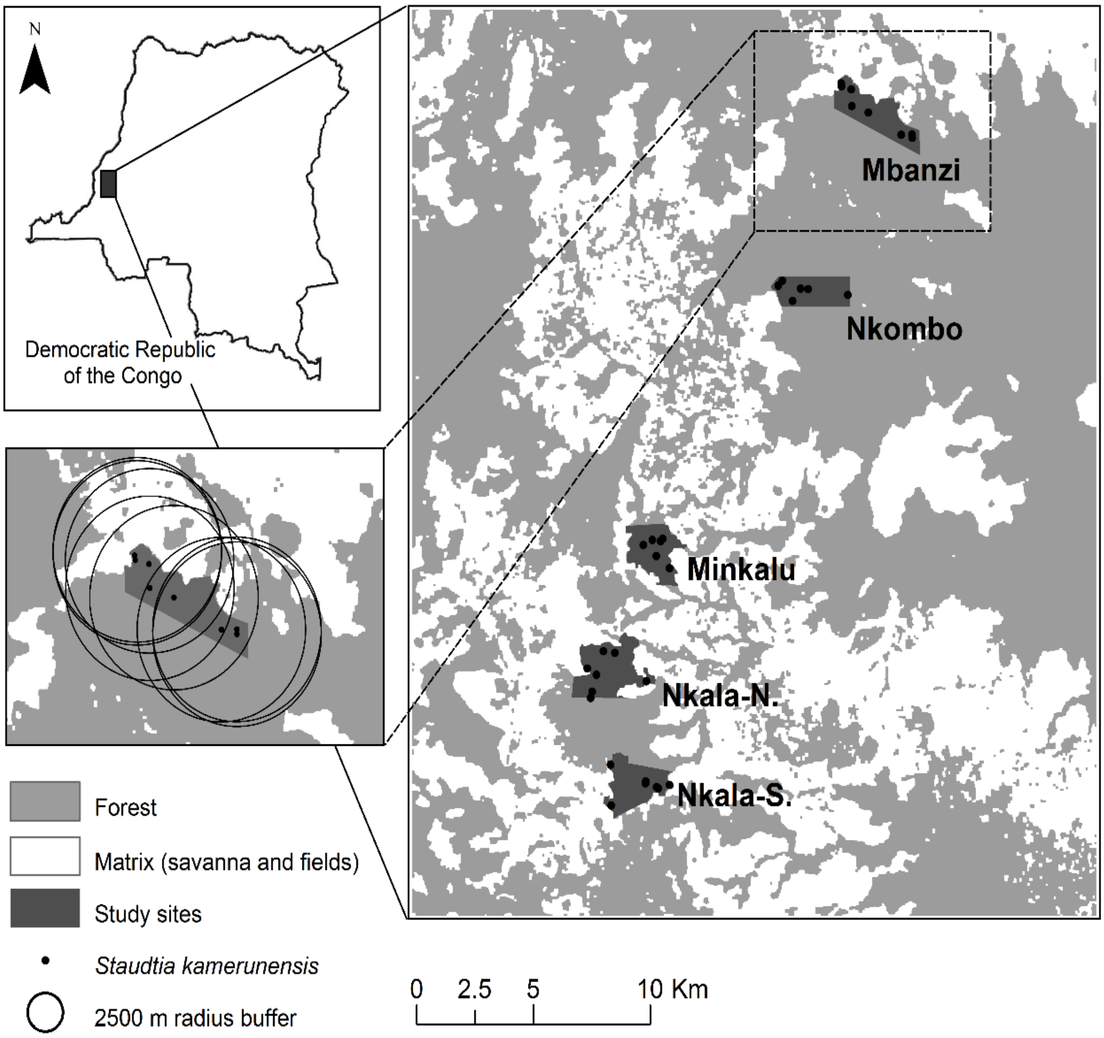


Figure 2-1. Map of the study area in the forest-savanna mosaic in western D.R. Congo, with the five sites (Mbanzi, Nkombo, Minkalu, Nkala-N., and Nkala-S.), 34 *Staudtia kamerunensis* trees and an example of the 2,500 m radius ring buffer around trees used to calculate forest cover.

Study species

Staudtia kamerunensis produces dehiscent fruits composed of two valves and a large seed (28.2 x 17.7 mm) that matures during the dry season (June-August) and attracts hornbills (Clark *et al*. 2005), as well as great apes (Idani *et al*. 1994, Head *et al*. 2011) and other primates (Gautier-Hion *et al.* 1985). This common emergent tree is considered to be a “biomass hyperdominant” species (Bastin *et al.* 2015) and is frequently logged in Central Africa (de Wasseige *et al.* 2012).

Staudtia kamerunensis fruit availability

To quantify fruit availability at the local (tree) scale, we followed the method in Howe & Kerckhove (1981). We set up one to four fruit traps (2.25 m² each) made of plastic mesh below fruiting trees to cover at least 5 percent of the canopy projection area on the floor. We hung them up on the surrounding vegetation 1.5 m above the ground to prevent predation from terrestrial animals. We installed fruit traps in 2013, below the canopy of 34 trees distributed across the five sites. From the beginning to the end of the 2013 fruiting season, we gathered all collected fruits weekly and classified them into four categories following Boissier *et al*. (2014): (1) intact open fruit (naturally dehisced fruit with two valves and a seed), (2) empty fruit (two valves without a seed), (3) single fruit valve, and (4) seed. We calculated the crop size as the sum of the number of whole fruits, empty fruits, and single fruit valves divided by two during the entire fruiting season. To obtain the annual tree crop size, we extrapolated this estimate to the whole crown area (*Ca*), which we calculated as follows:

$$Ca = \pi * ((r_n * r_s * r_e * r_w)^{0.25})^2$$

, where r_i are the projections of the radius from the trunk to the terminal branch in the four cardinal directions.

To quantify fruit availability at the site scale, we recorded and measured the diameter at breast height (DBH) of all *S. kamerunensis* fruiting trees encountered on a system of line-transects (see below). We calculated an index of fruit availability for each site by summing up the basal area of all fruiting trees and dividing by transect length (cm^2/km). The index is therefore a function of both *S. kamerunensis* fruiting tree density and trunk size (DBH), which is considered the most accurate way to estimate the fruit abundance of tropical trees (Chapman *et al*. 1992). This species fruits during the dry season, a period of relatively low overall fruit availability (Serckx *et al.* 2014), and is among the most common trees in the study area (6.63 stem/ha, Bastin 2014). We therefore considered *S. kamerunensis* a good predictor of overall fruit availability during the study period.

Hunting pressure and abundance of frugivores

We quantified hunting activity and the richness and abundance of the main diurnal frugivores that can disperse *S. kamerunensis* seeds (i.e., hornbills and frugivorous primates) by conducting a survey on the same system of line-transects, as well as on REConnaissanCE (RECCE) transects (Vanthomme et al. 2010), totaling 131 km across the five sites. We recorded all direct and indirect traces of the presence of frugivores (feces, footprints, calls, nests) and hunting activity (rifle cartridges, gunshots, traps, fires). For quantification, we summed up all observations for each category (hornbills, primates, and hunting activity) and calculated Kilometric Abundance Indexes (KAI, observations/km), allowing for efficient inter-site comparisons (Mathot & Doucet 2006, Vanthomme et al. 2010).

Forest cover

We used a simplified representation of the study area with two vegetation categories, forest and savanna, based on a Landsat 7 satellite image using ArcGIS (version 9.3) software. With GPS, we delineated the main areas of slash-and-burn agriculture in the study sites (one in Nkala-N. and Nkala-S., the other near Mbanzi) that could not be detected on the satellite image. We excluded these agricultural areas from the category “forest” and included them in the category “matrix”. To quantify the amount of forest cover, we defined 2500-m ring buffers around each tree. The area covered in these buffers (1963 ha) is within range of the estimated home range size of *B. albotibialis* (Holbrook & Smith 2000). Within each ring buffer, we calculated the percentage of forest pixels. Because the mosaic has a complex spatial structure, with forest patches connected by a system of forest corridors surrounded by isolated forest islands, including some savanna areas, this method provided more information and was thus more relevant for characterizing forest habitats in the landscape than simply measuring the distance to forest edge or fragment size (Moran & Catterall 2014).

Tableau 2-1. Explanatory variables tested to explain seed dispersal failure of *Staudtia kamerunensis* in a forest-savanna mosaic in western D.R. Congo.

Scale	Variable	Description
Local	Tree crop size	Number of fruits collected below each tree during the entire fruiting season
Landscape	Forest cover	Percent of forest cover within 2500 m buffer rings around each tree
Landscape	Hunting pressure	Signs of hunting activity encountered per km of transect (nb of obs./km)
Landscape	Frugivore abundance	Signs of frugivore presence encountered per km of transect (nb of obs./km). Calculated for primates and *Bycanistes albotibialis*
Landscape	Fruit availability	Index derived from the mean sum of the basal area of *Staudtia kamerunensis* fruiting trees encountered per km of transect (cm²/km)

Fruit-frugivore interactions

To define the diurnal frugivore assemblage feeding on *S. kamerunensis* fruits, we conducted 121.5 h of focal observations on fruiting trees across the five sites in 2012 (Mbanzi and Nkomob) and 2013 (Nkala-N., Nkala-S., and Minkalu) (Table 2-S3). Dense foliage reduced visibility, so we were unable to systematically observe each feeding event to estimate seed removal rates. We could nonetheless observe each species actually ingesting seeds, and local hunters also confirmed the consumption of *S. kamerunensis* fruits by these species. To determine the contribution of each frugivore species to the seed removal rate, we recorded the time spent in the focal tree by each individual and hypothesized that it was proportional to its quantitative contribution to seed removal, although that method is flawed in that it ignores actual seed removal events. We used 10 x 42 binoculars for observation during early morning (0600-1000 h) and late afternoon (1500-1800 h) sessions and regularly changed the focal tree to sample the maximum number of fruiting trees during each session. Due to logistical constraints, we only performed afternoon sessions in Mbanzi and Nkombo.

Seed dispersal failure

To estimate the percentage of seed dispersal failure (SDF) (i.e., the proportion of seeds that failed to be dispersed away from the parent tree), we counted the fruits and seeds from the fruit-seed traps of the 34 fruiting trees sampled. Percentage of SDF was calculated as:

$$SDF = \left(\frac{S_T}{F_T}\right) \times 100 = \left(\frac{S_g + F_i}{F_i + F_e + F_b}\right) \times 100$$

, where S_T is the number of undispersed seeds (S_g being the number of loose seeds found in the traps and F_i the number of intact open fruits) and F_T the number of fruits produced (F_e being the number of empty fruits and F_b the number of broken fruits [half the number of single valves]), given that each fruit contained a single seed.

Statistical analysis

We performed all statistical analyses with R software. We verified that SDF (dependent variable) could be considered normally distributed (Kolmogorov-Smirnov, d = 0.122, P > 0.688). To determine which variables influenced SDF (Table 2-1), we first conducted multivariate analyses with the glmulti function of the glmulti R package (Calcagno & Mazancourt 2010) to select the "best model" (based on AIC) among all possible candidate models. We used the lme function of the nmle R package (Pinheiro et al. 2012), including a spatial autocorrelation term of the dependent variable having an exponential spatial correlation structure, according to Dormann et al. (2007). This procedure allowed us to take into account the spatial autocorrelation, i.e., the fact that observations that are closer to each other in space could have more related values than observations further from each other. If spatial autocorrelation is not considered, the assumption that residuals are independent and identically distributed, one of the key assumptions of standard statistical analysis, is violated. We considered linear, exponential, and pairwise interaction effects. However, the results were very sensitive to the distribution selection of the dependent variable, most likely due to the high level of multi-collinearity between explanatory variables (Table 2-S2). We therefore considered it more reliable to investigate the effect of each explanatory variable using univariate analysis.

Results

Study site characteristics

The five selected sites differed in terms of the percentage of forest cover (49–99.6%), hunting pressure (0.9–1.66 obs. /km), and abundance of frugivores (*Bycanistes albotibialis*, the main hornbill species: 1.76–4.36 obs./km, primates: 0.47–4.96 obs./km; see Table 2-S1 for further details). The fruit availability index varied among sites from 0 to 5266 cm²/km. In Nkombo, we obtained a value of 0 cm²/km, indicating the absence of fruiting *S. kamerunensis* trees on the transect system (Table 2-2).

Fruit-frugivore interactions

During observation sessions at focal fruiting trees, the white-thighed hornbill, *Bycanistes albotibialis* (Bucerotideae), visited fruiting trees at a rate of 1 visit/h, which represents more than 95.5 percent of the presence of frugivores (considering observations from all sites together, and from each site separately). We observed another species, the black-casqued hornbill, *Ceratogymna atrata* (Bucerotideae), entering fruiting trees on five occasions, and a red-tailed monkey, *Cercopithecus ascanius* (Cercopithecidae), entering a tree only once.

Seed-dispersal failure

The mean percentage of seed dispersal failure was 72.4 ± 38.9 but showed great variation across the mosaic, with values as low as 17.6 percent in Mbanzi and reaching up to and beyond 100 percent (177.9 percent in Nkala-N). In total, there were five trees with values exceeding 100 percent, including four in Nkala-N. (107.2, 159.6, 168.5, and 177.9%) and one in Nkala-S. (110.1%). These particularly high percentages indicate a higher number of seeds (S_T) relative to fruits (F_T, i.e., number of seeds produced). The two sites were characterized by the lowest percentages of forest cover (58.9 ± 4.4% and 54.5 ± 3.6%, respectively) and the highest *S. kamerunensis* fruit availability (5266 and 2456 cm²/km). Conversely, the two lowest mean percentages of seed dispersal failure were found in Mbanzi (48.7 ± 22.5%) and Nkombo (51.1 ± 10.1%), the two sites in the continuous forest block, thus having the highest mean value of forest cover (Mbanzi: 73 ± 14.5%, Nkombo: 89.6 ± 6.2%). They were also characterized by the two lowest values of *S. kamerunensis* fruit availability (683 and 0 cm²/km, respectively).

Table 2-2. Main characteristics of the study sites and the selected *Staudtia kamerunensis* trees in the forest-savanna mosaic in western D.R. Congo.

Site	No. trees	Forest cover[a] (%)		Tree crop size (nb of fruits)		Site fruit availability (cm^2/km)[b]	Kilometric Abundance Index (KAI, observations/km)			Seed dispersal failure (%)	
		Mean ± SD	Min-Max	Mean ± SD	Min-Max		Hunting pressure	*Bycanistes albotibialis*	Primates	Mean ± SD	Min- Max
Mbanzi	8	73.0 ± 14.5	56.6-90.3	4747 ± 5264	483-13,567	683	1.19	3.13	0.94	48.7 ± 22.5	17.6- 89.1
Nkombo	6	89.6 ± 6.2	82.5-99.6	6219 ± 7299	20,687-37,317	0	0.46	4.36	0.47	51.1 ± 10.1	44.3- 70.7
Minkalu	6	60.5 ± 4.5	55.3-67.3	3629 ± 3156	465-8704	239	1.28	2.24	1.35	64.1 ± 31	20.5- 96.3
Nkala-N.	7	58.9 ± 4.4	54.5-66.8	2965 ± 3607	518-10,746	5266	1.66	1.76	4.56	123.6 ± 43.6	74.8- 177.9
Nkala-S.	7	54.5 ± 3.6	49.0-60.2	1286 ± 1109	184-2837	2456	0.9	2.23	4.96	73.6 ± 24.7	35.9- 110.1

[a] Percentage of forest cover calculated in a 2500 m radius ring buffer around each tree

[b] Index calculated on the basis of fruiting *S. kamerunensis* trees encountered on the transects

Statistical analysis

Through univariate analysis, we found that only tree crop size (t = -1.122, P = 0.270) was not statistically significant. The effects of forest cover (t = -2.638, P = 0.013, R^2= 25%), hunting pressure (t = 2.846, P = 0.008, R^2= 25%), abundance of *B. albotibialis* (t = -3.089, P = 0.041, R^2= 28%), primates (t = 3.615, P = 0.001, R^2= 30%), and fruit availability (t = 5.375, P < 0.000, R^2= 48%) were all statistically significant. The amount of forest cover and *B. albotibialis* abundance had a positive effect on seed dispersal (Fig. 2-1A and 2-2A, respectively), while hunting pressure, primate abundance, and fruit availability had the reverse effect (Fig. 2-1B, 2-2B, and 2-3, respectively).

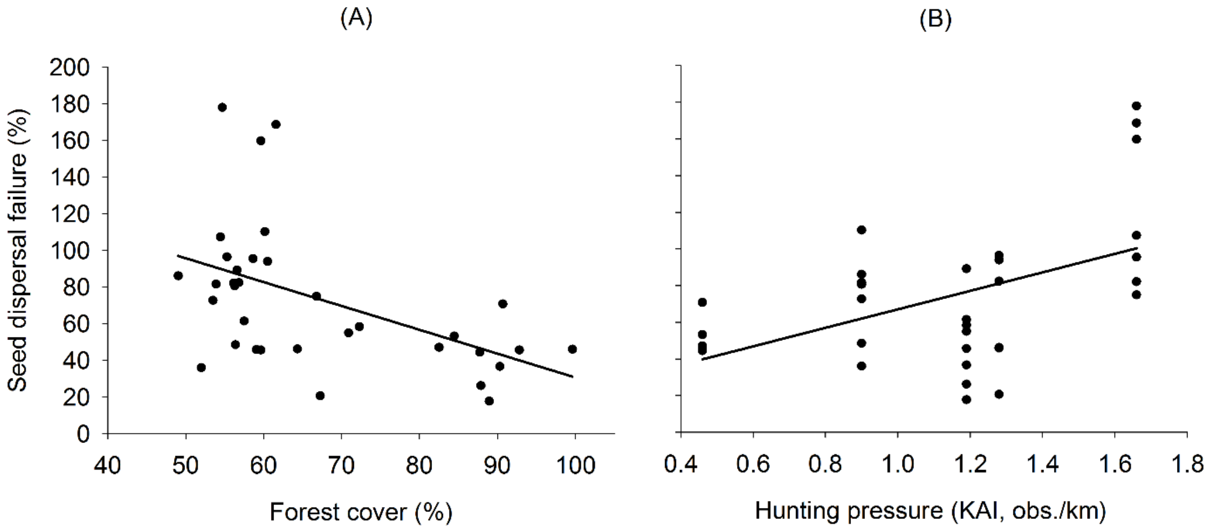


Figure 2-1. Scatter plot of (A) percentage of forest cover and (B) hunting pressure against the percentage of seed dispersal failure, with the model simulation accounting for spatial autocorrelation of the response variable.

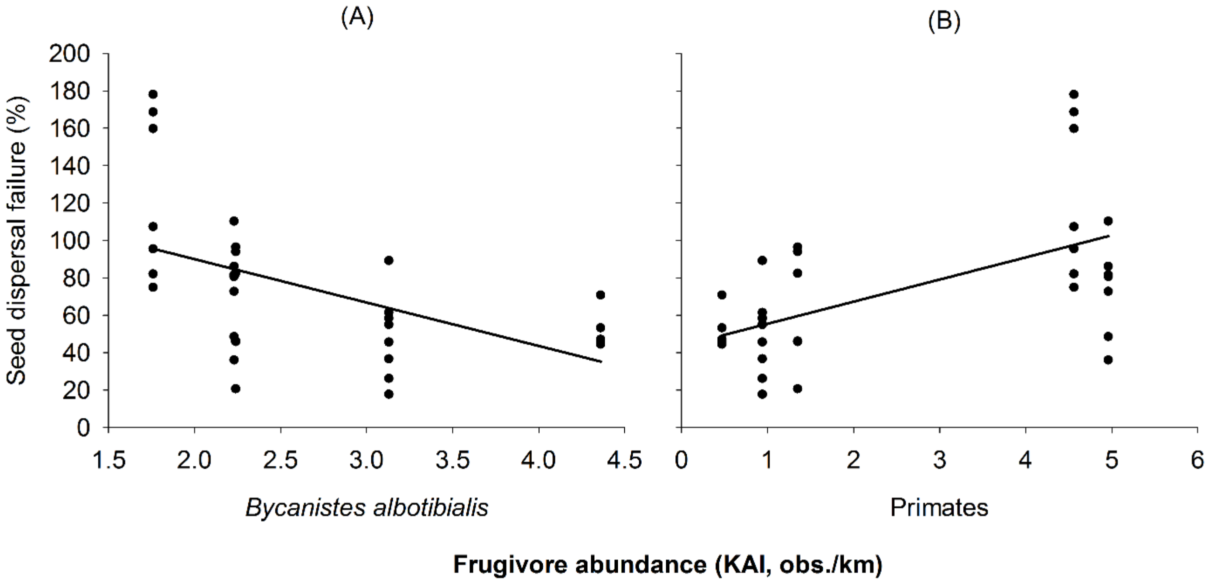


Figure 2-2. Scatter plot of (A) *Bycanistes albotibialis* (the main seed disperser) and (B) primate abundance against the percentage of seed dispersal failure, with the model simulation accounting for spatial autocorrelation of the response variable.

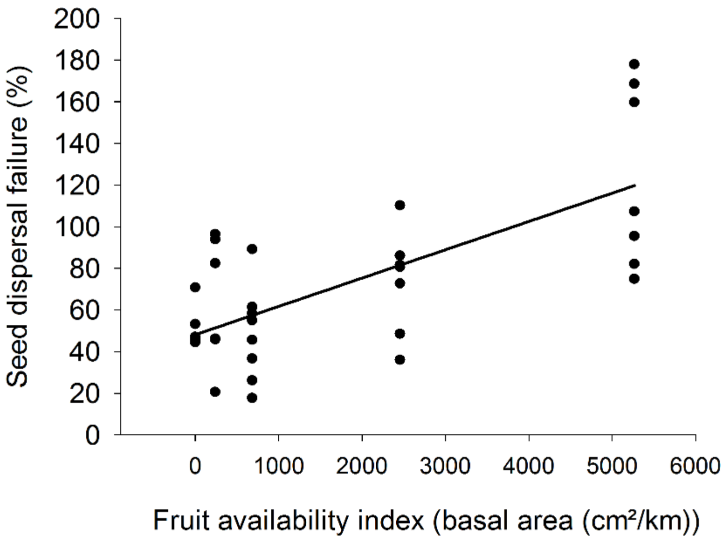


Figure 2-3. Scatter plot of fruit availability against the percentage of seed dispersal failure, with the model simulation accounting for spatial autocorrelation of the response variable.

Discussion

Here, we showed that forest cover in the surrounding landscape, hunting pressure (which was negatively associated with the abundance of the most frequently observed disperser, *B. albotibialis*), and fruit availability explained variations in seed dispersal failure for *Staudtia kamerunensis*. This study is the first to evaluate the combined effects of these major environmental characteristics on seed dispersal by animals in Africa.

Seed dispersal system

According to the focal observations conducted across the forest-savanna mosaic, the greater occurrence of *B. albotibialis* confirms observations made by Clark *et al.* (2005) in Cameroon, where hornbills accounted for more than 93 percent of the visits and *B. albotibialis* was the main seed disperser visiting *S. kamerunensis* fruiting trees. Since hornbills appear to be consistent seed dispersers rather than seed predators (Whitney *et al.* 1998, Holbrook & Smith 2000), we assume that our focal observations correctly reflect seed dispersal rates, rather than predation by hornbills. In Clark *et al.* (2005), *B. albotibialis* accounted for no more than 43.2% of the visits, while the piping hornbill (*B. fistulator*) and the black-casqued hornbill (*C. atrata)* accounted for 25.1% and 25.5% of the visits, respectively. These species were also present in our study area and could potentially appear as important seed dispersers with the aid of a greater and more systematic sampling effort than conducted here. Observations were of low duration and were unevenly distributed across sites, trees, years, and time periods and could thus have had a significant influence on the frugivores that were recorded. Additionally, our observations did not include periods of bat activity. Bats have been observed to disperse Myristicaceae seeds in Africa (Seltzer *et al.* 2013), though they are not common consumers of these plants. We may have underestimated the relative role of other frugivores in some sites, such as primates, hornbills, or bats, and our results on seed removal might thus be confounded by their activity. Generally speaking, the lack of direct observations and data on actual seed removal events leaves uncertain the respective role of frugivore species, limiting the robustness of our conclusions. Despite these shortcomings, the studied large-seeded tree species appears to have a highly specialized dispersal strategy, as confirmed by other studies on Myristicaceae species in Asia (Kitamura & Poonswad 2013), Central America (Howe & Vande Kerckhove 1981, 1980), and South America (Holbrook & Loiselle 2009, Boissier *et al.* 2014, Ratiarison & Forget 2013, Queenborough *et al.* 2013). Plants with a restricted seed disperser assemblage are known to be particularly sensitive to human disturbances (Howe *et al.* 1985, Cordeiro & Howe 2003, Holbrook & Loiselle 2009, Uriarte *et al.* 2011, Ratiarison & Forget 2013), especially when they have large seeds that only larger vertebrates can ingest and disseminate (Vanthomme *et al.* 2010, Markl *et al*. 2012).

Extreme values of SDF

Five trees had an SDF exceeding 100 percent, indicating a higher number of seeds relative to fruits below the tree crowns. The most likely explanation is that some proportion of seeds could drop from dehiscent fruits whose empty valves remained attached to the tree (F. Trolliet and P.-M. Forget, pers. obs. in D.R. Congo and Gabon, respectively), causing us to count undispersed fallen seeds in the fruit-seed traps but omitting the valves remaining in the crown. From this perspective, we would overestimate the proportion of undispersed seeds relative to fruits. This hypothesis is supported by the fact that frugivore foraging activity in crowns can cause empty valves to drop. The high percentage of dispersal failure at the sites with relatively low hornbill abundance could be caused by relatively low levels of forager activity, and hence, more valves remained attached to the crowns of the sampled trees. Consequently, had we monitored the trees at some time point after fruiting had finished, we could have collected more empty fruits and obtained lower values of dispersal failure. Additionally, these values could be due to spatially contagious seed dispersal between conspecifics. In tropical forests, frugivores travel between feeding trees that fruit simultaneously and tend to disperse seeds in a contagious manner (Schupp *et al.* 2002). This process has already been reported for bird-dispersed tree species (Alcántara *et al*. 2000, Kwit et al. 2004), including *S. kamerunensis* (Clark *et al*. 2004) and, as shown by Wang *et al*. (2007), it can be fairly pronounced, as up to 42 percent of the seeds found below *Antrocaryon klaineanum* trees belonged to conspecifics. Notably, we only found trees with particularly high values at sites with the lowest landscape forest covers and the highest *S. kamerunensis* site fruit availability indexes (*i.e.*, fruiting tree densities). These conditions could respectively constrain hornbill movements and facilitate repeated travels between neighboring fruiting trees and could additively increase the probability of contagious inter-conspecific seed dispersal events. However, this process, which does not exclude the first hypothesis, remains weakly supported by our data and deserves further investigation.

Effect of hunting, forest cover and fruit availability

While several studies have investigated the effects of forest area and hunting on a range of tree species separately (e.g. Holbrook & Loiselle 2009, Uriarte et al. 2011), the present investigation considers the effects of both variables. This is highly relevant given their association with human activities, which increasingly threaten wildlife and ecosystem functioning (Brooks et al. 2002, Dirzo et al. 2014), and may have additive effects (Peres 2001). However, our study design has a relatively limited number of replications for factors considered at the site scale (hunting and fruit availability). Studies that consider more replicates of each factor tested would allow more robust conclusions to be drawn and are greatly desirable.

The observed variation in mean seed dispersal failure is reflected by the contrasting abundances of *B. albotibialis* at the different sites (Table 2-2). Those subject to the highest hunting pressures housed the lowest abundances of *B. albotibialis* and trees with the highest percentages of seed dispersal failure. We believe that the significant effect of the abundance of primates could be an artifact due to the strong correlation with hunting pressure and *B. albotibialis* abundance (Table 2-S2). Indeed, during the focal observations at fruiting trees, we only observed a primate once. More importantly, a study on seed dispersal by bonobos in the area during the same period did not show any sign of *S. kamerunensis* fruit consumption (Trolliet et al. 2016). It is unlikely that bonobos are among key dispersers of this species.

Because the processes that shape the fragmented spatial structure of the mosaic are complex (natural and human-aided), it is risky to attribute our results to a specific cause of forest fragmentation or forest loss. Rather, it is more appropriate to underline the detrimental effect of a decrease in the amount of remaining habitat for frugivores (i.e., forest) on seed dispersal. In addition, it is important to note that the two main agricultural areas were in proximity to Nkala and Mbanzi, which had the highest and lowest percentages of seed dispersal failure, respectively. This suggests that the agricultural matrix does not have a strong effect on the results. We believe that because *B. albotibialis* is able to exploit disturbed habitats (Chasar et al. 2014), matrix quality has a weaker effect than the strong contrast between forested and non-forested habitats.

Bycanistes albotibialis has been reported to move across anthropogenic barriers (roads, villages) and heterogeneous habitats and to use disturbed secondary and fragmented forests (Stauffer & Smith 2004 [*B. cylindricus* refers to *B. albotibialis*], Chasar *et al*. 2014). In our study site, we also regularly observed this species travelling between forest patches and flying above savannas over several hundred meters. Thus, this species cannot be considered a strict forest specialist and is therefore likely to provide excellent seed dispersal services across human-dominated landscapes. This bird species might play a relatively important role in such ecosystems, because it ensures long-distance seed dispersal and moves seeds from primary to early successional forests in the vicinity of human activities where other hornbills (*Ceratogymna atrata*) and large frugivorous mammals, such as primates and elephants, are less likely to visit (Laurance *et al*. 2006, Buij *et al*. 2007, Chasar *et al*. 2014). However, our results provide evidence that the extent of forest cover has a strong effect on the foraging activity of *B. albotibialis*. As a generalization, hornbill dispersed trees surrounded by more forest within a few kilometers might have higher proportions of seeds removed than trees close to a matrix habitat.

The role of hornbills, especially *B. albotibialis*, as seed dispersers is believed to be increasing compared to that of large frugivorous mammals whose populations are rapidly declining (Whitney *et al*. 1998, Holbrook & Smith 2000, Chasar *et al*. 2014). Primates and elephants are indeed particularly sensitive to forest fragmentation (Blake *et al.* 2008, Marsh & Colin 2013) and are primarily targeted by bushmeat hunters (Fa et al. 2002). The ecological services provided by these animals might thus become increasingly impoverished in anthropogenic ecosystems. Yet we showed that hunting activity negatively affects the seed dispersal capacity of a hornbill-dependent tree species. This result, as well as our observations in the field, confirms the growing threats of habitat loss and hunting to African hornbills (Trail 2007, Whytock *et al.* 2016, Atuo *et al.* 2015). When larger vertebrates have been extirpated, the remaining smaller mammals and birds become increasingly hunted (Fa *et al.* 2000). Consequently, the ecological role of hornbills as seed dispersers in such anthropogenic systems is imperiled, and the long-term persistence of those services should not be taken for granted.

Finally, we showed that fruit availability at the site increases the percentage of seed dispersal failure. This result has to be interpreted along with the effect of hunting and the lower abundance of hornbills associated with an increase in seed dispersal failure. The sites characterized by high fruit availability also hosted relatively low abundances of hornbills. These two factors have probably caused the seed dispersal system to reach a saturation point, where frugivores were satiated and many fruits remained untouched. Interestingly, Forget & Jansen (2007) drew the same conclusion regarding the seed dispersal of *Carapa surinamensis* (ex *procera*) in South-America: the effect of hunting (and reduced disperser activity) was stronger when large amounts of seeds were available, which possibly resulted from disperser satiation.

The main drawback of this interpretation is that dispersers were likely feeding on fruit species other than *S. kamerunensis,* which could reduce the influence of that tree species on the satiation level of dispersers, in turn weakening our conclusion. Nevertheless, *S. kamerunensis* is among the most common tree species in the area (Bastin 2014), and it fruits during the dry season, a period of relatively low fleshy fruit availability (Serckx *et al.* 2014). We therefore believe that *S. kamerunensis* fruits account for a relatively large share of community-wide fruit availability, and hence the satiation level of dispersers, during this period.

Supplementary material

Table 2-S1. Kilometric Abundance Indexes (KAI, observations/km) of large vertebrate animal species in the five sites across a forest-savanna mosaic in western D.R. Congo.

	Mbanzi	Nkombo	Minkalu	Nkala N.	Nkala S.
Bycanistes albotibialis	3.13	4.36	2.24	1.76	2.23
Ceratogymna atrata	0.22	1.31	0.25	0.09	0.27
Bycanistes fistulator	0.47	0.18	0.13	0	0.58
Pan paniscus	absent	absent	1.10	4.11	4.28
Cercopithecus spp[a].	0.94	0.47	1.35	0.45	0.68
Potamocherus porcus	4.81	6.56	2.21	1.56	4.31
Cephalophus spp.[b]	4.69	4.79	2.61	1.95	3.17
Loxodonta cyclotis	3.88	10.56	absent	absent	absent

[a] *Cercopithecus spp.* includes mainly *C. ascanius*, and potentially *C. mona wolfi* and *C. neglectus*, even though those two species are rare and difficult to observe.

[b] *Cephalophus spp*. includes *C. dorsalis* and *C. monticola.*

Table 2-S2. Correlations values between the significant explanatory variables.

	Forest cover	Hunting	*B. albotibialis* abundance	Primate abundance
Hunting	0.078	-	-	-
B. albotibialis’ abundance	-0.125	0.957	-	-
Primates’ abundance	0.177	0.962	0.922	-
Fruit availability	-0.201	-0.944	-0.864	-0.972

Table 2-S3. Effort sampling for focal observations and time with frugivores at each *Staudtia kamerunensis* tree in the five sites across a forest-savanna mosaic in western D.R. Congo.

Site/Focal trees	Observation time	Time with frugivores			
		Bycanistes albotibialis	*Ceratogymna atrata*	*Cercopithecus ascanius*	Total
Mbanzi	30h 02’	2h 11’		0h 06’	2h 17’’
1	2h 30’				
2	5h 19’	0h 25’			
3	1h 35’				
4	0h 43’				

5	1h 39’				
6	0h 40’	0h 03’			
7	1h 25’				
8	1h 53’	0h 03’			
9	1h 00’				
10	0h 22’				
11	0h 32’				
12	0h 16’				
13	2h 23’	0h 27’			
14	3h 25’	1h 11’		0h 06’	
15	2h 04’				
16	0h 25’				
17	2h 06’				
18	1h 41’	0h 02’			
Nkombo	33h 38’	0h 57’	0h 02’	0h 00’	0h 59’
1	5h 14’				
2	3h 55’		< 0h 01’		
3	2h 18’				
4	13h 25’	0h 53’	< 0h 01’		
5	4h 29’	0h 03’	0h 01’		
6	1h 09’				
7	0h 51’				
8	2h 17’	< 0h 01’			
Minkalu	18h 14’	0h 25’	0h 00’	0h 00’	0h 25’
1	1h 49’	0h 05’			
2	2h 51’	0h 02’			
3	1h 45’				
4	3h 07’	0h 16’			
5	1h 26’				
6	2h 59’	0h 02’			
7	2h 14’				
8	1h 50’				
Nkala N.	16h 05’	0h 04’	0h 00’	0h 00’	0h 04’
1	3h 16’	0h 01’			
2	2h 00’				
3	1h 05’	0h 01’			
4	1h 48’				
5	1h 39’				
6	1h 05’				
7	5h 12’	0h 02’	< 0h 01’		
Nkala S.	23h 31’	0h 24’	0h 00’	0h 00’	0h 24’
1	2h 06’	0h 01’			
2	3h 41’	0h 01’			
3	0h 16’				
4	3h 33’	0h 02’			
5	3h 19’	0h 11’			
6	0h 31’				
7	0h 41’				
8	8h 00’	0h 09’			

Chapitre 3.

On the influence of frugivores on the spatial organization of Afrotropical forests: evidence that hornbills generate recruitment foci under a Myristicaceae tree

Trolliet, F., P.-M. Forget, J.-L. Doucet, J.-F. Gillet and A. Hambuckers. *To be submitted to Oecologia*.

Les résultats du chapitre 1 ainsi que d’autres travaux récemment menés sur les bonobos vivant dans la mosaïque montrent que ceux-ci utilisent préférentiellement des zones de forêts à un stade de succession relativement avancé et où ils peuvent facilement trouver des fruits charnus. En utilisant l’habitat de manière non-aléatoire, les bonobos sont susceptibles de générer une pluie de graines biaisée en faveur de ces zones plus fréquemment visitées et de créer ainsi des foyers de recrutement, influant par conséquent l’organisation spatiale de la végétation.

Dans le chapitre 2, nous avons observé que le nombre de graines conspécifiques sous certains arbres de *Staudtia kamerunensis* était anormalement haut. Bien que ce résultat ne concerne que quelques arbres, nous avons émis l’hypothèse que les visites répétées des calaos aux arbres conspécifiques pourraient avoir entrainé une dispersion des graines contagieuse, c’est-à-dire que les arbres en question pourraient agir comme des foyers de dispersion. Dans le cas où ce processus surviendrait pour d’autres plantes zoochores, les frugivores génèreraient une pluie de graines spatialement structurée, et donc une organisation particulière des plantules.

Dans ce chapitre, nous allons ainsi examiner la communauté de plantules sous des arbres zoochores afin de vérifier si les primates et les calaos créent un tel patron spatial de régénération, puis tester l’influence de variables environnementales sur ce processus.

The results from chapter 1 along with other works recently conducted on bonobos living in the mosaic show that they preferentially use forest areas at a relatively advanced successional stage and where they can easily find fleshy fruits. By using their habitat in a non-random manner, bonobos are likely to generate a seed rain biased in favor of these areas that are more frequently visited and so to create recruitment foci, thereby influencing the spatial organization of vegetation

In chapter 2, we observed that the number of conspecific seeds under some *Staudtia kamerunensis* trees was abnormally high. Although this result only concerned few trees, we raised the hypothesis that repeated visits of hornbills at conspecific trees could have generated a contagious dispersal of seeds, and so that these trees could act a dispersal foci. In the case that this process would occur for other zoochoric plants, frugivores would generate a spatially structured seed rain and so a particular organization of seedlings.

In this chapter, we will thus examine the seedling community under zoochoric trees in order to verify if primates and hornbills can generate such a spatial pattern of regeneration, and test the influence of environmental variables on this process.

Résumé

La dispersion des graines zoochores est reconnue pour influencer l'organisation spatiale des communautés de plantes, mais les mécanismes par lesquels les frugivores génèrent de tels patterns demeurent confus. Ici, nous avons exploré l'influence des calaos et des primates dans la création de foyer de recrutement dans une mosaïque de forêts-savanes en R.D. Congo. Premièrement, nous avons examiné l'occurrence d'agrégats de plantules sous deux arbres zoochores, à savoir, *Staudtia kamerunensis* (Myristicaceae) et *Dialium* spp. (Fabaceae – Caesalpinioidea) en comparaison avec des emplacements contrôles. Deuxièmement, nous avons examiné si la disponibilité en fruits dans le voisinage et la quantité de forêt dans le paysage influençaient de tels patterns d'agrégation de plantules. Nous avons observé que la densité et la richesse spécifique des plantules dispersées par les calaos ainsi que la densité de plantules dispersées par les primates étaient significativement plus élevés sous les arbres de *S. kamerunensis* que dans les plots contrôles, alors que de tels patterns ne furent pas détectés sous les arbres de *Dialium* spp. en comparaison avec les plots contrôles. Aussi, nous avons montré qu'une quantité croissante de forêt dans le paysage tendait à faire augmenter la densité de plantules dispersées par les calaos, bien que la tendance était faible (R= 0.065). Nous avons conclus que *S. kamerunensis* agit comme un foyer de recrutement et joue un rôle structurant dans les forêts afrotropicales. Nous avons suspecté que les calaos étaient le principal taxon responsable de l'agrégation sous cet arbre, et soulignons leur importance écologique dans les paysages fragmentés et où les abondances de grands frugivores tels que les primates sont réduites. Nos résultats ont des conséquences importantes pour notre compréhension des mécanismes causaux responsables des patterns spatiaux dans les communautés de plantes tropicales.

Abstract

Animal-mediated seed dispersal is recognized to influence the spatial organization of plant communities but little is known about how frugivores cause such patterns. Here, we explored the influence of hornbills and primates in generating recruitment foci in a forest-savanna mosaic landscape in D.R. Congo. Firstly, we examined the occurrence of seedling clumpings under two zoochoric trees, namely *Staudtia kamerunensis* (Myristicaceae) and *Dialium* spp. (Fabaceae - Caesalpiniodea) in comparison to control locations. Secondly, we examined if the availability of fruits in the neighborhood and the amount of forest cover in the landscape influenced such seedling clumping patterns. We found that the density and species richness of hornbill-dispersed, and the density of primate-dispersed seedlings were significantly higher under *Staudtia kamerunensis* trees than at control locations, while such patterns were not detected under *Dialium* spp. trees compared to control locations. Also, we found that an increasing amount of forest cover in the landscape tended to increase the density of hornbill-dispersed seedlings, although the tendency was weak ($R^2 = 0.065$). We concluded that *S. kamerunensis* acts as a recruitment foci and plays a structuring role in Afrotropical forests. We suspected that hornbills were the main taxa responsible for the clumping under that tree, and highlight their ecological importance in fragmented landscapes where abundances of large frugivores such as primates are reduced. Our findings have important consequences for our understanding of the causal mechanisms responsible for spatial patterns in tropical plant communities.

Introduction

The influence of dispersal-limitation processes on species coexistence and biodiversity patterns is now widely established (Nathan and Muller-landau 2000, Hubbell 2001, Hubbell et al. 2007, Terborgh 2012). However, empirical evidence attesting the role of seed-dispersing animals in shaping the spatial organization of plant communities via non-random seed dispersal patterns has been overlooked (but see Forget and Sabatier, 1997; Levine and Murrell, 2003). Frugivores are the main dispersal vectors for the majority of tropical plant species (Howe and Smallwood 1982) and their movements determine the location of seed deposition and the subsequent probability of seedling establishment (Russo et al. 2006, Santamaría et al. 2007, Côrtes and Uriarte 2012, Poulsen et al. 2012, Razafindratsima and Dunham 2015). Seed-dispersing animals are therefore believed to have a major impact on the spatial arrangements of plant populations. More particularly, evidences show that various species of birds and primates, by moving between particularly attractive locations (sleeping sites, fruiting trees, display sites, latrines etc.), tend to deposit disproportionately more seeds at these locations than at random or relatively less attractive ones (McConkey 2000, Wenny 2001, Schupp et al. 2002, Clark et al. 2004, Kwit et al. 2004, Russo and Augspurger 2004, García et al. 2007, Wang et al. 2007, Herrera and García 2009, González-Zamora et al. 2014). By dispersing seeds in such a spatially contagious manner, they generate the so-called seed dispersal foci (Clark et al. 2004). In Africa, some evidence suggest that volant frugivores create spatially contagious patterns of seed deposition at fruiting trees (Carrière et al. 2002a, Clark et al. 2004), while there does not seem to be a consensus on the role of primates (Wang et al., 2007 but see Clark et al., 2004).

Once seeds are deposited, various biotic (e.g. secondary dispersal, seed predation, pathogen, fungi) and abiotic processes (e.g. amount of light, water, exchangeable nutrient contents) influence post-dispersal seed fate, the seed-to-seedling transition stage, and eventually determine patterns of seedling establishment (Forget and Milleron 1991, Nicotra et al. 1999, Hilhorst and Karssen 2000, Wang and Smith 2002, Clark et al. 2012). These filters can be so powerful that the compositional patterns of the surviving seedling cohort become discordant with that of the initial seed rain (Herrera et al. 1994, Carrière et al. 2002b, Alcomb 2003). The spatio-temporal variation of post-dispersal processes reduce therefore the predictability of seed deposition patterns on recruitment patterns. Nonetheless, studies have found that a continuous seed input originating from the activity of seed-dispersing animals at a given location can persist to the seedling stage and translate into a particular pattern of seedling recruitment, or recruitment foci (sensu McDonnell and Stiles, 1983; Wenny, 2001). However, while such patterns have been widely studied under remnant trees in anthropogenic habitats such as pastures (Hooper and Bullington 1973, McDonnell and Stiles 1983, Guevara et al. 1992, Slocum and Horvitz 2000, Carrière et al. 2002b, Berens et al. 2008, Slocum 2012, Cottee-jones et al. 2016), relatively few studies have explicitly examined the influence of frugivores on the spatial organization of the vegetation in forests through the generation of recruitment foci (Julliot 1997, Russo and Augspurger 2004, Terborgh and Nuñez-Iturri 2006, Wiegand et al. 2016). Some findings support the hypothesis that Neotropical primates create recruitment foci (Julliot 1997, Russo and Augspurger 2004, Terborgh and Nuñez-Iturri 2006), whereas data from Afrotropical forests are scant (but see Carrière et al., 2002b; Haurez et al., 2015;

Vanthomme et al., 2010). Notably, Carrière et al. (2002b) reported that the presence of a Myristicaceae species enhanced animal-mediated seed rain and influenced forest regrowth in the context of fallows in Cameroon.

Additionally, it remains unclear what are the environmental variables and at what scale they influence the behavior of seed-dispersing animals (Wiegand et al. 2016). For instance, increasing evidence shows a positive influence of fruiting trees within the neighborhood (i.e., at a local scale) on frugivore activity (Manasse and Howe 1983, Carlo 2005, Saracco et al. 2005, Pizo and Almeida-Neto 2009, Albrecht et al. 2012, Serckx et al. 2014). It is hypothesized that the presence of several fleshy-fruited trees within close vicinity could additively attract frugivores, thereby enhancing the seed rain, and in turn leave a particular signal in the seedling carpet.

Furthermore, habitat attributes at larger scales such as the amount of forest cover in the landscape, which is associated with higher food resources and shelter, can enhance level of frugivore activity, facilitate their visitation to fruit patches and consequently impact the regenerating plant community (Trolliet et al. *In press*, Urquiza-Haas et al. 2009, Ahumada et al. 2011, Jesus et al. 2012, Moran and Catterall 2014, Serckx et al. 2016).

In this study, we aimed to explore the influence of frugivores on the spatial structure of the vegetation in tropical forest through the generation of recruitment foci in a mosaic landscape. Our objective was twofold. Firstly, we tested the hypothesis that fruiting trees act as recruitment foci. For this purpose, we examined the occurrence of seedling clumping under two zoochoric trees, namely *Staudtia kamerunensis* (Myristicaceae) and *Dialium* spp. (Fabaceae-Caesalpiniodea) in comparison to control locations located further away. Fruits of both tree taxa are dispersed by primates (Gautier-Hion et al. 1985, Poulsen et al. 2001, Beaune et al. 2013b, Trolliet et al. 2016), while those of *S. kamerunensis* are frequently consumed by hornbills too (Trolliet et al. *In press*, Clark et al. 2005). We predicted that the seedling community under those trees should be composed of more individuals and species dispersed by hornbills and primates compared to control locations, and that the effect should be especially pronounced for *S. kamerunensis* (Carrière et al. 2002b). Secondly, we tested the hypothesis that the fruit neighborhood and the amount of forest cover in the landscape influence frugivore activity and modify seedling clumping patterns. We predicted that as the amount of fruits known to be consumed by hornbills and primates in the neighborhood and the amount of forest cover increase (Trolliet et al. *In press*, Serckx et al. 2016), the density and richness of seedlings dispersed by these taxa should increase. Because hornbills are particularly resilient in disturbed landscapes (Lenz et al. 2011, Chasar et al. 2014), we further predicted that the effect of forest cover should be relatively more pronounced for primate-dispersed species.

Material & methods

Study area

The study took place in western Democratic Republic of Congo in an area of about 30 × 20 km surrounding the WWF-Malebo research station, in the Bandundu province (2°29’3.87” S, 16°30’4.16” E). Annual rainfall averages 1500 mm, and the main dry season occurs from June to August. The study area is situated in a forest-savanna mosaic, a landscape that is highly fragmented with a system of forest patches and corridors mainly associated with the hydrographic network. This fragmented spatial structure is natural, yet maintained by anthropogenic activities. Shifting slash-and-burn agriculture encroaches on forest patches, while cattle ranching, with its associated yearly fire regimes, restricts the colonization of forests. The forest system includes diverse forests types such as riverine gallery forests, recolonizing Uapaca guineensis transition forests, old secondary forests, Marantaceae forests, mature forests dominated by species of the families Annonaceae, Caesalpinioideae and Olacaceae, and old growth monodominant Gilbertiodendron dewevrei forests. In the study area, the density of *Staudtia kamerunensis* trees (DBH > 10 cm) is 6.63 stem/ha while that of *Dialium* spp. is 5.53 stem/ha.

The community of frugivores in the landscape is affected by subsistence hunting from local population, although a traditional taboo proscribes killing or eating bonobo (*Pan paniscus*). Moreover, a community-based conservation program allows the maintenance of a relatively healthy population of this great ape in some parts of the mosaic (Serckx et al. 2014, Trolliet et al. 2016). The community of large frugivorous birds is especially dominated by three species of hornbill (*Bycanistes albotibialis*, *Bycanistes fistulator* and *Ceratogymna atrata*), which are well represented across the forest-savanna mosaic studied (Trolliet et al. *In press*), as well as the Great Blue Turaco (*Corythaeola cristata*) and the African grey parrot (*Psittacus erithacus*).

Study taxa

Staudtia kamerunensis (Myristicaceae) is a common evergreen, monoicous tree species considered as a “biomass hyperdominant” species (Bastin et al. 2015), and it is a logged timber in Central Africa under the name of Niové (de Wasseige et al. 2012). Its trees produce dehiscent fruits composed of two valves and a large seed (28 × 18 mm) which matures during the dry season (June-August) and attracts primarily hornbills, as shown by visual observations conducted in Cameroon (Clark et al. 2005) and in the study area (Trolliet et al. *In press*), but its fruits are consumed by primates too (Gautier-Hion et al. 1985, Idani et al. 1994, Head et al. 2011).

Dialium spp. (Fabaceae, Caesalpinioidea) is an evergreen, hermaphrodite genus including several species that are morphologically close (*D. pachyphyllum, D. guineense, D. bipindense*, and *D. dinklagei*). All its species produce black-brown indehiscent pods that contain a single seed (11 × 9.5 mm) surrounded by a sugary pulp consumed by primates and actively sought by bonobos (*Pan paniscus*) for which it is even a preferred food (Poulsen et al. 2001, Beaune et al. 2013b, Trolliet et al. 2016). *Dialium* spp. fruiting season last approximately six months.

Sampling design

We surveyed the seedling community following the sampling design of Julliot (1997), which consist of batches composed of plots under reproductive trees of the studied taxa and random plots as controls. Depending on crown size, we randomly established one or two 25m² (5 × 5 m) plots under reproductive trees, and established one or two neighboring control plots. Control plots were located 50 m away and in random direction from the tree plots, and were not established under trees of the two taxa of interest. Each plot or pair of plots is referred to as a location. We established a total of 32 locations under *S. kamerunensis* trees (corresponding to 1,300 m²) and 26 locations under *Dialium* spp. trees (1,150 m²), and sampled a total of 4,900 m² (including all locations). For the analysis, we excluded all seedlings belonging to conspecific species as the adult trees present in the neighborhood.

Seedling communities

In each plot, we identified all seedlings measuring 0.5-2 m in height (N= 6,304) (Vanthomme et al. 2010) to genus, species or morphospecies level using vegetative characteristics. Plant identification was performed in the field by two local experienced parataxonomists who previously aided in the identification of 474 samples of 178 tree species in the same study area. Samples are registered in the herbarium and botanical library of the Université Libre de Bruxelles (‘‘BRLU’’), with reference IDs Bastin-Serckx#1-474. We also completed a reference herbarium of each morphospecies. Then, experienced botanists (JLD, JFG, and Olivier Lachenaud at the Herbarium of the National Botanic Garden, Meise) double-checked these samples and identified further unidentified species. For each species, we indicated whether it was consumed and possibly dispersed by primates and hornbills with the aid of literature (see Table 3-S1 for further details).

Fruit availability indexes

To quantify the availability of fleshy fruits in the neighborhood of each location, we recorded, identified, and measured the diameter at breast height (DBH) of all trees with a DBH ≥ 30 cm and whose crown was included, even partially, within a 15-m radius from the survey plots. Therefore, the area covered (706 m²) also included the crown projection of large neighboring trees whose trunk was situated further away from it. So, the assemblage of trees that have been recorded were located within the range used in Saracco et al. (2005) to characterize fruit neighborhoods. We assumed that most trees with a DBH > 30 cm were reproductive adults, although that method is flawed for some very large species which have a minimum fruiting diameter (MFD) > 30 cm. For those species for which the MFD was known, we excluded trees that had a DBH < MFD (see Table 3-S2). We distinguished tree species whose seeds are dispersed by abiotic means from those dispersed by animals, and for the latter, we further specified if they were dispersed by primates and hornbills with the aid of the literature (Table 3-S1). Then, for each location, we summed-up the basal area of all trees known to be consumed by (i) primates and (ii) hornbills to obtain two indexes characterizing the fruit neighborhood (FN) relevant for primates (hereafter, $FN^{primate}$) and hornbills (hereafter, $FN^{hornbills}$), respectively. Those indexes are therefore a function of both tree density and trunk size

(DBH), which is considered to be the most accurate way to estimate fruit abundance of tropical trees (Chapman et al. 1992).

Percentage of forest cover

We used a simplified map of the study area with two vegetation categories, ‘forest’ and ‘matrix’, that we created using a non-supervised classification of a Landsat7 satellite image with the ArcGIS software (version 9.3). In addition, we delineated on the field using a GPS the main areas of slash-and-burn agriculture not detected in the forest on the satellite image. We excluded these agricultural areas from the category ‘forest’ and included them in the category ‘matrix’. To quantify the amount of forest cover, we defined a ring buffer around each location in which we calculated the percentage of forest pixels (each pixel = 30 × 30m). This method was more relevant to characterize forest habitat than measuring the distance to forest edge or fragment size only (Moran and Catterall 2014) because the mosaic had a complex spatial structure with forest patches not clearly delimited but connected by a system of forest corridors and surrounded by isolated forest islands. Each ring buffer had a 2500m radius owing to the fact that Trolliet et al. (2016) showed that this variable had a significant influence on the seed dispersal of *S. kamerunensis* in the study area.

Statistical analysis

All statistical analysis were performed with R software (R Core Team, 2015) using the nmle R package (Pinheiro et al. 2012). We systematically included a spatial autocorrelation term of the dependent variable having an exponential spatial correlation structure, according to Dormann et al. (2007), to take into account the fact that observations that are closer to each other are more related than more distant observations. We proceeded to the statistical analysis in two steps. Firstly, we aimed to test the specific effect of each of the two tree taxa on recruitment foci. We therefore ran the analysis on two distinct datasets, each containing the data on the respective taxa. We compared the density and richness of hornbill-dispersed and primate-dispersed species (i) between plots under *S. kamerunensis* trees and control plots, and (ii) between plots under *Dialium* spp. trees and control plots. We also considered each batch (tree and control plots) as a random term (so the test is equivalent to a paired t-test).

Secondly, rather than testing the effect of specific trees, we aimed to test the influence of ecological process at larger spatial scales, namely, the percentage of forest cover and the fruit neighborhood ($FN^{primate}$ and $FN^{hornbill}$) on the seedling community. Therefore, we ran the analysis on a dataset including tree and control locations. We considered the density and species richness of hornbill- and primate-dispersed seedlings as response variables. We squared-root transformed the density and richness of hornbill-dispersed seedlings to meet assumption of normality. For each of these, we proceeded to an exhaustive analysis of the explanatory variables considering linear and interaction terms. We selected the best model based on AIC but with p-values of the retained terms in the model < 0.05. Finally we tested if the models were significantly better than null models using the likelihood ratio test.

Results

Comparison of the seedling community between tree and control locations

The density of hornbill-dispersed and primate-dispersed seedlings were both significantly higher under *S. kamerunensis* trees than in control locations (Fig. 3-S1a and 3-S1c, respectively; Table 3-1), but only the density of hornbill-dispersed seedling was significantly different between locations under *Dialium* spp. trees and control locations, the latter having a greater density (Fig. 3-S1b).

Regarding species richness (Fig. 3-S2, Table 3-1), the richness of hornbill-dispersed seedlings was significantly different between locations under *S. kamerunensis* and control locations, those under *S. kamerunensis* having more species (Fig. 3-S2a).

Table 3-1. Mean density and richness of the seedling community dispersed by primates or hornbills, surveyed under *Staudtia kamerunensis* trees, *Dialium* spp. trees and in control locations. Significant p-values are shown in bold.

Tree species	Characteristic of the seedling community	Location type		t	DF	p-value
		Under tree	Control			
Staudtia kamerunensis	Density ^{hornbill}	4. 9 ± 3.4	3.7 ± 2.6	2.18	62	**0.044**
	Richness ^{hornbill}	2.9 ± 1.4	2.3 ± 1.2	2.17	62	**0.044**
	Density ^{primate}	19.7 ± 8	16.2 ± 7.2	2.55	62	**0.013**
	Richness ^{primate}	9.0 ± 2.8	8.0 ± 2.5	1.99	62	0.051
Dialium spp.	Density ^{hornbill}	3.2 ± 2.0	4.6 ± 2.2	-2.70	27	**0.012**
	Richness ^{hornbill}	2.5 ± 1.2	2.9 ± 1.4	-1.71	27	0.100
	Density ^{primate}	17.8 ± 10.0	20.9 ± 7.8	-0.95	27	0.349
	Richness ^{primate}	7.6 ± 2.5	8.6 ± 2.7	-0.95	27	0.349

Forest cover and fruit neighborhood

The percentage of forest cover in the landscape varied from 32.0 to 99.4%. To quantify the fruit neighborhoods, we used a total of 765 zoochoric trees (mean DBH = 54.4 ± 28.2 cm) over a total of 801 recorded around the plots (the difference being due to species for which we lacked clear information on whether its fruits were consumed by hornbills or primates). Their density varied from 1 to 16 trees per location. More particularly, FN ^{hornbill} varied from 0 to 32,834 cm^2, while FN ^{primate} varied from 830 to 44,847 cm^2.

The mean density of hornbill-dispersed seedlings varied from 0 to 16 seedlings/25 m^2 (mean= 4.48 ± 3.2), while the mean species richness varied from 0 to 6 species/25 m^2 (mean= 2.7 ± 1.4). Among all the models tested to explain variations of the density of hornbill-dispersed seedlings, forest cover was the best one, and had a positive influence on the density of hornbill-dispersed seedlings ($p= 0.012$) (Table 3-S3, Fig. 3-1). Yet, this variable explained only a little of the observed variation ($R^2= 0.065$). No model was found to explain the variation in richness of hornbill-dispersed seedlings.

Concerning the primate-dispersed seedlings, their density varied from 3 to 43.5 seedlings/25 m² (mean= 18.0 ± 8), while their species richness varied from 2.5 to 16.5 species/25 m² (mean= 8.1 ± 2.5). No model was found to explain variations of the community of primate-dispersed seedlings (Table 3-S4).

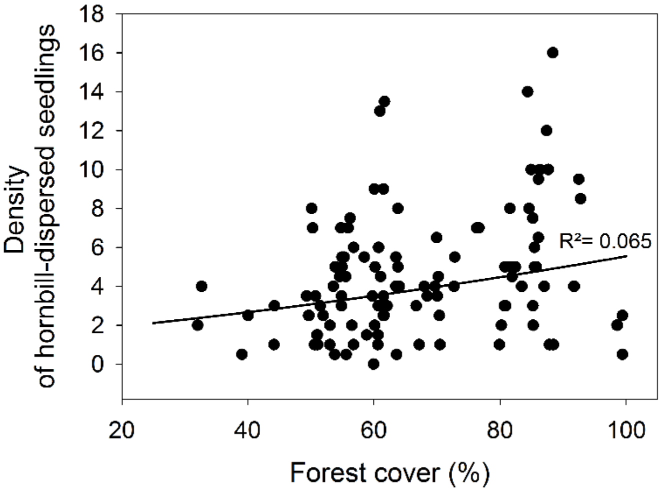


Figure 3-1. Density of hornbill-dispersed seedlings as a function of the percentage of forest cover in the landscape of the survey plots in a forest-savanna mosaic in D.R. Congo.

Discussion

We showed that the density and richness of hornbill and primate-dispersed seedlings were greater under the crown of *S. kamerunensis* trees than in random locations in the forest. On the contrary, we found that the density of hornbill dispersed species was lower under the crown of *Dialium* sp. than in random locations. Also, we found that the amount of forest cover in the landscape increased the density of hornbill-dispersed seedlings, although the trend was weak.

Staudtia kamerunensis as a structuring tree in Afrotropical forests

The investigation of the communities of seedlings known to be dispersed by hornbills and primates revealed a significant difference between plots under *S. kamerunensis* trees and control plots, with higher abundances in the former. This finding is in line with Carrière et al. (2002b) who detected that a Myristicaceae tree species (*Pycnanthus angolensis*) acted as a foci of regeneration, probably due to the visits of frugivores. The fruits of Myristicaceae trees are indeed consumed by both hornbills and primates (Gautier-Hion et al. 1985, Idani et al. 1994, Clark et al. 2004, Head et al. 2011), so it is here difficult to assess which of those taxa had a greater impact on the observed pattern. Moreover, it is important to note that almost all the species recorded to be dispersed by hornbills have also been recorded to be dispersed by primates, according to our literature survey. Primates could generate similar recruitment patterns in terms of species composition as those generated by hornbills. Therefore, the apparent strong redundancy in seed dispersal services provided by both frugivore taxa may weaken any detectable signal owing to the specific activity of one of them at *S. kamerunensis* trees relative to control locations. The attribution of seed dispersers to each plant species have been done according to various references that cover a wide range of tropical regions and frugivore species and is thus quite general (Table 3-S1). It would therefore be relevant to derive a more conservative and realistic seed disperser assemblage by considering not all potential seed disperser species but rather the most important ones, and to exclude those seed disperser species that are absent from the study site under investigation.

Notably, *S. kamerunensis* has been reported to act as seed dispersal foci because the abundance and species richness of bird-generated seed rain were greater under its crown than that of primate- or wind-dispersed species (Clark et al., 2004). Yet, the composition of the seedling carpet is not necessarily an exact representation of the composition of the seed rain and large inconsistencies between the seed and seedling bank of animal-dispersed plants have already been reported (Herrera et al. 1994, Carrière et al. 2002b, Alcomb 2003). Indeed, the seed-to-seedling transition stage and seedling survival are influenced by numerous biotic (e.g. consumption of large seeds by rodents, greater mortality of highly abundant species (Mangan et al. 2010)) and abiotic processes (e.g. amount of light filter out species with specific regeneration guild (Nicotra et al. 1999), soil exchangeable cation contents) that can potentially change the composition pattern of the ultimate seedling bank in a non-random manner, as observed by Carrière et al. (2002b) in Cameroon. In this perspective, predicting patterns of seedling recruitment according to those of the seed rain becomes risky. Therefore, our finding is essential because we were able to detect a signal owing to frugivore activity and the seed rain they generated despite those post-dispersal environmental and ecological filters. We conclude that this plant-frugivore system has a structuring role and might thus represent one of the multiple mechanisms that influence the spatial organization of Afrotropical plant communities.

On the importance of hornbills in disturbed landscapes

Although our data did not allow us to detect a greater influence of hornbills or primates on the accumulation of seedlings under *S. kamerunensis* trees, we suspect that hornbills had a greater influence on the observed patterns. According to visual observations conducted in Cameroon (Clark et al. 2005) and in the study area (Trolliet et al. *In press*), hornbills were by far the most frequent frugivore taxa visiting *S. kamerunensis* fruiting trees. More particularly, the accumulation of heterospecific seeds under *S. kamerunensis* in Cameroon has been attributed to repeated visits by large birds (hornbills and turacos) rather than by primates (Clark et al. 2004). Indeed, a study on seed dispersal by bonobos in the study area, where it is the most abundant primate species, did not show any sign of *S. kamerunensis* seeds in bonobo's faeces (Trolliet et al. 2016), even though they could only eat the aril. The importance of hornbills is further supported by the fact that only the species richness of hornbill-dispersed, but not of primate-dispersed (although it was close to the significance threshold), seedlings was significantly higher under *S. kamerunensis* trees than in control plots.

The comparison of the seedling community between plots under *Dialium* spp. trees and control plots did not support our prediction. More particularly, our results on the community of primate-dispersed seedlings did not show any evidence that primates generated recruitment foci under *Dialium* spp. trees. Fruits of *Dialium* are mainly consumed by primates across African tropical forests, and particularly sought by bonobos, which is the main representative of the primate community in the sites investigated here (Idani 1986, Clark et al. 2001, Poulsen et al. 2001, Kunz and Linsenmair 2008, Tsuji et al. 2010, Beaune et al. 2013b, Haurez et al. 2015a, Trolliet et al. 2016). Yet, primates are usually preferentially targeted by hunters and their abundance in the mosaic might be too low to generate a seed input that is great enough to cause a persistent clumping of seedlings at fruiting trees. Additionally, primate movements are more affected in fragmented landscape such as in this heterogeneous mosaic as compared to hornbills. For instance, some species of the genus *Bycanistes* can be regularly observed to fly above the savanna (especially *B. albotibialis*, the main frugivore visiting *S. kamerunensis* trees in our area (Trolliet et al. *In press*), and are resilient in fragmented, human-dominated landscapes (Lenz et al. 2011, Chasar et al. 2014). In contrast to *Dialium* spp., Myristicaceae fruits are largely consumed by hornbills, as previously exposed. Therefore, we suggest that this taxa act as a mobile link and play a critical role for the resilience of the ecosystem by linking the process of regeneration among environmental features such as fruiting trees, and probably among forest patches too (Lundberg and Moberg 2003).

Our study provides some evidence that primates did not generate the clumping of seedlings, which is in line with study led in Cameroon that found no evidence that monkeys generated contagious seed rain under feeding trees (Clark et al. 2004). Nevertheless, it is difficult to conclude on the role of primates in general as we only investigated two tree taxa. It would thus be relevant to explore the seed rain and seedling community under trees that are used repeatedly such as known favoured large fruiting trees, or sleeping sites (Julliot 1997, Russo and Augspurger 2004, Terborgh and Nuñez-Iturri 2006, Haurez et al. 2015a, Petre et al. 2015). Additionally, the result obtained under *Dialium* spp. for seedling density which is in opposite direction in regard to our prediction needs to be further examined. It seems unlikely that frugivores would prefer to visit random trees (possibly abiotically dispersed or not reproductive) than the selected reproductive *Dialium* spp. where they can feed. For this reason, we hypothesize that the lower seedling densities under the *Dialium* spp. was the result of allelopathic suppression of germination or seedling growth as demonstrated with extracts of bark, leaf or branch from members of the Leguminosae family (e.g.. Arruda et al., 2005; Joshi, 1991; Kato-Noguchi, 2003; Souza Filho et al., 2010).

Forest cover and fruit neighborhood

We detected that the amount of forest cover around the survey plots was associated with an increase in the density of hornbill-dispersed recruits. Our finding supports the hypothesis that the amount of forest cover enhances the abundance and/or activity of forest frugivorous birds, hence their visitation rates at fruiting trees, which in turn enhance the seed rain to eventually lead to a specific signal in the seedling cohort. This result is supported by the observed increase in dispersal of *S. kamerunensis* seeds with increasing forest cover at the same scale (Trolliet et al., 2016). However, contrary to our prediction, the amount of forest cover around all survey plots did not seem to influence recruitment patterns of primate-dispersed seedlings. This last finding is somewhat surprising because the bonobos living in the areas have been reported to be influenced by forest structure at a scale up to 2700 m (Serckx et al. 2016).

Finally, we did not find evidence that the fruit neighborhood influenced regeneration patterns. Interestingly, Blendinger and Villegas (2011) concluded that tree trait was more influential than the local fruit neighborhood on bird visitation rate, which corroborate our result. Inter-specific competition for dispersers is a process that probably dilute frugivore activity and seed rain at any specific location (Blendinger and Villegas 2011).

It is worth noting that our plots were relatively small and we may have missed a proportion of seedlings resulting from frugivore activity at neighboring trees. It would thus be relevant to use larger survey plots than ours to be able to sample the seedling bank under all neighboring fleshy-fruiting trees and detect the signal induced by frugivores more easily. Additionally, the radius used to quantify the fruiting trees neighboring the survey plots (15 m) might be too small to properly characterize the fruit neighborhood as other studies have found an influence of neighboring fruiting trees at greater scales (Manasse and Howe 1983, Carlo and Morales 2008). It would therefore be interesting to test the effect of fruit neighborhoods quantified with increasing radiuses around the survey plots to detect threshold and peak values at which different organisms respond.

Conclusion

Our study provides evidence that *Staudtia kamerunensis* acts as a recruitment foci due to its attractiveness to frugivores, and probably more to hornbills. Similarly, Carrière et al. (2002b) found that *Pycnanthus angolensis* facilitated forest regeneration in fallows by attracting frugivores, which reinforce the value of interactions between Myristicaceae species and frugivorous birds for forest regrowth and dynamic in fragmented area lacking large frugivores such as primates. Also Myristicaceae trees generally fruit during the dry season, which is a period of fleshy-fruit scarcity and play therefore a key role in the ecosystem by providing food to important seed dispersers. Additionally, we found that the amount of forest cover in the landscape had a positive influence on the density of hornbill-dispersed seedlings, though the tendency was relatively weak and suggests that other variables influenced the assemblage of recruits.

Surveying the seedling community under the crown of large fleshy-fruited trees has proved to be very useful to investigate the cascading consequences of defaunation on forest regeneration (Nuñez-Iturri and Howe 2007, Vanthomme et al. 2010). This method maximizes the amount of information on seed-dispersers activity and represent a more efficient sampling strategy than sampling the seedling community at random. In this context, our findings permit us to refine this protocol which was used so far to investigate the impact frugivore extirpation on the recruitment of primate-dispersed (Nuñez-Iturri and Howe 2007) or animal-dispersed plants in general (Vanthomme et al. 2010). Surveying the heterospecific regeneration under *S. kamerunensis* crowns could serve as an efficient tool for monitoring the consequences of hornbill extirpation on plant recruitment, and help developing comparative studies across tropical forests in Central Africa. Hornbills are increasingly persecuted for body parts trade (Atuo et al. 2015), or consumption by local population when other species have already disappeared (Fa et al. 2000, Whytock et al. 2016). Consequently, their depletion, could reduce the density of some plant species, as observed in Asian tropical forests (Naniwadekar et al. 2015), and have long term impact on the spatial arrangement of Afrotropical forests.

Our investigation of the role of primates was less conclusive. We hence suggest that more efforts should be allocated to understand the specific influence of important seed disperser taxa such as large frugivorous birds and primates in creating clumping of seedlings via non-random seed dispersal patterns (i.e. related to environmental attributes that influence seed-disperser's behavior). We believe that integrating such biotic interactions with post-dispersal biotic and abiotic processes will allow a significant improve in our understanding of the mechanisms responsible for the spatial patterns observed in tropical plant communities, a key challenge in ecology (Wiegand et al. 2016).

Supplementary material

Table 3-S1. Seedling species, dispersal mode, and whether they are dispersed by primates and hornbills (hornbills: Gautier-Hion et al. 1985, Whitney et al. 1998, Clark et al. 2001, Poulsen et al. 2002; primates: Badrian and Malenky 1984, Gautier-Hion et al. 1985, Tutin et al. 1997, Clark et al. 2001, Poulsen et al. 2001, Tsuji et al. 2010, Beaune et al. 2013a, Effiom et al. 2013, 2014, Serckx et al. 2015).

Family	*Species*	Dispersal mode	primate dispersed	hornbill dispersed
?	*Cf Vitex congolensis / cf Oldfieldia africana*	Zoochorous		
?	*inc 124 Motiambuli*	?		
?	*inc 149*	?		
?	*inc 150*	?		
?	*inc 150 bis*	?		
?	*inc 169*	?		
?	*inc 179*	?		
?	*inc 215*	?		
?	*inc 215*	?		
?	*inc 231*	?		
?	*inc 251*	?		
?	*inc 260*	?		
?	*inc 263*	?		
?	*inc 264*	?		
?	*inc 42*	?		
?	*inc 42*	?		
?	*inc 42*	?		
?	*inc 42*	?		
?	*inc 75*	?		
?	*inc 79*	?		
?	*inc 86*	?		
?	*inc alt 57C1*	?		
?	*inc Bolu 2*	?		
?	*inc compo 49A*	?		
?	*inc Esau 2*	?		

?	inc idem 56	?		
?	*inc Monkuma 2*	?		
?	*inc Mosimi*	?		
Acanthaceae	*Acanthaceae sp.2*	Abiotic		
	Thomandersia hensii	Abiotic		
	Whitfieldia elongata	Abiotic		
Anacardiaceae	*Sorindeia africana*	Zoochorous	x	
	Sorindeia spp.	Zoochorous	x	
Annonaceae	*Annickia chlorantha*	Zoochorous	x	x
	inc 125 Annonaceae sp.	Zoochorous		
	inc 247 Annonaceae sp.	Zoochorous		
	inc Mokoli	Zoochorous		
	Isolona hexaloba	Zoochorous	x	
	Monodora angolensis	Zoochorous	x	
	Neostenanthera myristifolia	Zoochorous		
	Piptostigma fasciculatum	Zoochorous	x	
	Polyalthia suaveolens	Zoochorous	x	x
	Xylopia aethiopica	Zoochorous	x	x
	Xylopia hypolampra	Zoochorous	x	x
	Uvariodendron sp.	Zoochorous	x	
	Isolona sp.	Zoochorous	x	
	Xylopia staudtii - rubescens	Zoochorous	x	x
Apocynaceae	*Funtumia africana*	Abiotic		
	Picralima nitida	Zoochorous		
	Rauvolfia macrophylla	Zoochorous	x	x
	Rauvolfia vomitoria	Zoochorous	x	
Boraginaceae	*Cordia platythyrsa*	Zoochorous	x	
Burseraceae	*Dacryodes edulis*	Zoochorous	x	x
	Santiria trimera	Zoochorous	x	x
Canabaceae	*Celtis tessmannii*	Zoochorous	x	x
Cardiopteridaceae	*Leptaulus zenkeri*	Zoochorous		
Chrysobalanaceae	*Dactyladenia sp.1*	Zoochorous		
	Licania elaeosperma	Zoochorous		
	Maranthes glabra	Zoochorous		
	Parinari excelsa	Zoochorous	x	
Clusiaceae	*Garcinia cf ovalifolia*	Zoochorous	x	
	Garcinia kola	Zoochorous	x	
	Garcinia punctata	Zoochorous	x	
	Garcinia smeathmannii	Zoochorous	x	
Ebenaceae	*Diospyros conocarpa*	Zoochorous	x	
	Diospyros ferrea	Zoochorous	x	
	Diospyros iturensis	Zoochorous	x	
	Diospyros sp1	Zoochorous	x	
Euphorbiaceae	*Crotonogyne sp.*	Abiotic		
	Dichostemma glaucescens	Abiotic		
	Duvigneaudia inopinata	Zoochorous	x	

	Euphorbiaceae sp.	?		
	inc 106 Euphorbiaceae	?		
	inc 11	?		
	inc 22 Euphorbiaceae	?		
	inc 221	?		
	inc 89 Euphorbiaceae sp.	?		
	Macaranga sp.	Zoochorous	x	x
	Plagiostyles africana	Zoochorous	x	x
	Uapaca spp.	Zoochorous	x	x
Fabaceae	*Afzelia bipindensis*	Zoochorous		
	Angylocalyx pynaertii	Zoochorous		x
	Aphanocalyx microphyllus	Abiotic		
	Baphia sp.	Abiotic		
	cf schefflerodendron gilbertianum	Abiotic		
	Daniellia pynaertii	Abiotic		
	Dialium pachyphyllum	Zoochorous	x	
	Dialium tessmannii	Zoochorous	x	
	Dialium tessmannii or zenkeri	Zoochorous	x	
	Dialium zenkeri	Zoochorous	x	
	Fillaeopsis discophora	Abiotic		
	inc Molieme	?		
	Lebruniodendron leptanthum	Abiotic		
	Loesenera walkeri	?		
	Millettia laurentii	Abiotic		
	Pentaclethra eetveldeana	Abiotic		
	Pentaclethra macrophylla	Abiotic		
	Phyllocosmus africanus	Zoochorous		
	Piptadeniastrum africanum	Abiotic		
	Prioria oxyphylla	Abiotic	x	
	Scorodophloeus zenkeri	Abiotic		
	Tesmania africana	Abiotic		
Flacourtiaceae	*Casearia barteri*	Zoochorous	x	
	Maranthes cf gabunensis	Zoochorous		
	Oncoba mannii	Zoochorous	x	
	Scottellia klaineana	Zoochorous	x	
Gentianaceae	*Beilschmiedia congolana*	Zoochorous	x	x
Guttiferae	*Symphonia globulifera*	Zoochorous	x	
Huaceae	*Afrostyrax kamerunensis*	Zoochorous		
	Afrostyrax lepidophyllus	Zoochorous		
Hypericaceae	*Endodesmia calophyloides*	Zoochorous		
Hypocrataceae	*Salacia sp.*	Zoochorous	x	
Irvigiaceae	*Irvingia gabonensis*	Zoochorous	x	
	Irvingia grandifolia	Zoochorous	x	
Ixonanthaceae	*Phyllocosmus africanus*	Zoochorous		
Lauraceae	*Beilschmiedia congolana*	Zoochorous	x	x
	Beilschmiedia sp.1 08/01	Zoochorous	x	x

Malvaceae	*Cola acuminata*	Zoochorous	x	
	Cola cf. ballayi	Zoochorous	x	
	Cola griseiflora	Zoochorous	x	
	Cola lateritia	Zoochorous	x	
	Grewia oligoneura	Zoochorous	x	
	Octolobus spectabilis	Zoochorous		
	Pterygota bequaertii	Abiotic		
	Cola cf diversifolia	Zoochorous	x	
Melastomataceae	*Memecylon cf laurentii*	Zoochorous		
	Warneckea sp.2	Zoochorous		
	Warneckea sp1	Zoochorous		
Meliaceae	*Entandrophragma angolense*	Abiotic		
	Guarea cedrata	Zoochorous	x	x
	Lovoa trichilioides	Abiotic		
	Trichilia martineaui	Zoochorous	x	x
	Trichilia sp.	Zoochorous	x	x
	Trichilia sp.2	Zoochorous	x	x
	Trichilia sp.4	Zoochorous	x	x
	Trichilia sp.5	Zoochorous	x	x
Moraceae	*Ficus sp.*	Zoochorous	x	x
Myristicaceae	*Coelocaryon preussii*	Zoochorous	x	x
	Myristicaceae spp.	Zoochorous	x	x
	Staudtia kamerunensis var. gabonensis	Zoochorous		x
Ochnaceae	*Campylospermum elongatum*	Zoochorous		
	Campylospermum sp.1	Zoochorous		
	Campylospermum sp.2 cf bukobense	Zoochorous		
	Campylospermum sp.3	Zoochorous		
	Ochna calodendron	Zoochorous		
	Ochna cf afzelii	Zoochorous		
	Rhabdophyllum sp.	Zoochorous		
	Rhabdophyllum sp.1 08/01	Zoochorous		
Olacaceae	*Heisteria parvifolia*	Zoochorous	x	x
	Olax spp.	Zoochorous		
	Olax subscorpioidea	Zoochorous	x	
	Ongokea gore	Zoochorous	x	
	Strombosia pustulata	Zoochorous	x	x
	Strombosiopsis tetrandra	Zoochorous	x	x
Pandaceae	*Microdesmis cf. puberula*	Zoochorous	x	
	Microdesmis sp.	Zoochorous	x	
Passifloraceae	*Barteria fistulosa*	Zoochorous	x	
	Barteria letouzey	Zoochorous	x	
	Barteria sp.1	Zoochorous	x	
	cf Barteria sp.2	?		
	Paropsia guineensis	Abiotic		
Polygalaceae	*Carpolobia alba*	Zoochorous		

Putranjivaceae	*Beilschmiedia sp.1 08/01*	Zoochorous	x	x
	Drypetes capillipes	Zoochorous	x	
	Drypetes cf ituriensis	Zoochorous	x	
	Drypetes cf principum	Zoochorous	x	
	Drypetes paxii	Zoochorous	x	
	Drypetes sp.2 08/01	Zoochorous	x	
	Drypetes sp.4 08/01	Zoochorous	x	
	Drypetes sp.5 08/01	Zoochorous	x	
	Drypetes sp.6 08/01	Zoochorous	x	
	Drypetes sp.7 08/01	Zoochorous	x	
	Drypetes sp1.	Zoochorous	x	
	Drypetes sp1. 08/01	Zoochorous	x	
	Drypetes sp3. 08/01	Zoochorous	x	
Rhizophoraceae	*cf Cassipourea sp.*	Zoochorous		
Rubiaceae	*Aidia micrantha*	Zoochorous	x	
	Aulacocalyx jasminiflora	Zoochorous		
	cf Pauridiantha rubens	Zoochorous		
	cf Psycotria sp.2	Zoochorous		
	cf Rubiaceae sp.28	Zoochorous		
	cf Tricalysia sp.2	Zoochorous		
	Colletoecema dewevrei	Zoochorous		
	inc 35	Zoochorous		
	inc 96	Zoochorous		
	inc cf Rubiaceae sp.29	?		
	inc RUB spp.	Zoochorous		
	Massularia acuminata	Zoochorous	x	
	Oxyanthus sp.	Zoochorous		
	Psychotria sp.1	Zoochorous	x	
	Psychotria sp.3	Zoochorous	x	
	Rothmannia sp.1	Zoochorous		
	Rubiaceae sp.1 08/01	Zoochorous		
	Rubiaceae sp.1 14/01	Zoochorous		
	Rubiaceae sp.10	Zoochorous		
	Rubiaceae sp.11	Zoochorous		
	Rubiaceae sp.12	Zoochorous		
	Rubiaceae sp.12	Zoochorous		
	Rubiaceae sp.13	Zoochorous		
	Rubiaceae sp.14	Zoochorous		
	Rubiaceae sp.15	Zoochorous		
	Rubiaceae sp.16	Zoochorous		
	Rubiaceae sp.17	Zoochorous		
	Rubiaceae sp.18	Zoochorous		
	Rubiaceae sp.19	Zoochorous		
	Rubiaceae sp.2	Zoochorous		
	Rubiaceae sp.20	Zoochorous		
	Rubiaceae sp.22	Zoochorous		

	Rubiaceae sp.23	Zoochorous		
	Rubiaceae sp.24	Zoochorous		
	Rubiaceae sp.25	Zoochorous		
	Rubiaceae sp.26	Zoochorous		
	Rubiaceae sp.27	Zoochorous		
	Rubiaceae sp.3	Zoochorous		
	Rubiaceae sp.4	Zoochorous		
	Rubiaceae sp.5	Zoochorous		
	Rubiaceae sp.6	Zoochorous		
	Rubiaceae sp.7	Zoochorous		
	Rubiaceae sp.8	Zoochorous		
	Rubiaceae sp.9	Zoochorous		
	Tricalysia sp.1	Zoochorous	x	
Rutaceae	*Citropsis articulata*	Zoochorous		
	Zanthoxylum sp.	Zoochorous	x	
Sapindaceae	*Blighia welwitschii*	Zoochorous	x	x
	Chytranthus sp.1	Zoochorous	x	
	Chytranthus sp.2	Zoochorous	x	
	inc 208	?		
	Laccodiscus pseudostipularis	Zoochorous		
	Pancovia sp. (cf laurentii)	Zoochorous	x	
	Radlkofera calodendron	Zoochorous		
	Zanha golungensis	Zoochorous	x	
	Ganophyllum giganteum	Zoochorous	x	
Sapotaceae	*Chrysophyllum africanum*	Zoochorous	x	
	Chrysophyllum boukokoënse	Zoochorous	x	
	Chrysophyllum pruniforme	Zoochorous	x	
	inc 112 Sapotaceae	Zoochorous		
	Pouteria altissima	Zoochorous	x	
	Synsepalum cerasiferum	Zoochorous	x	
	Quassia africana	Zoochorous	x	
Simaroubaceae				
	Quassia silvestris	Zoochorous	x	
Sterculiaceae	*Chlamydocola chlamydantha*	Zoochorous	x	
	Leptonychia sp.	Zoochorous		
Thymelaceae	*Dicranolepis baertsiana*	Zoochorous	x	
Tiliaceae	*Desplatsia subericarpa*	Zoochorous	x	
	Duboscia macrocarpa	Zoochorous	x	
	Grewia sp.	Zoochorous	x	
Violaceae	*Rinorea illicifolia*	Abiotic		
	Rinorea sp.1 08/01	Abiotic		

Table 3-S2. Tree species for which the minimum fruiting diameter was known and used to calculate the fruit neighborhood.

Species	Familly	Minimum fruiting diameter (cm)	Reference
Canarium schweinfurthii	Burseraceae	41	Doucet, 2003
Coelocaryon preussii	Myristicaceae	39	Doucet, 2003
Pycnanthus angolensis	Myristicaceae	36	Doucet, 2003
Ricinodendron heudelotii	Euphorbiaceae	40	Madron and Daumerie, 2004

Table 3-S3. Results of the models tested to explain variation of density and richness of hornbill-dispersed seedlings. Significant p-values are shown in bold.

Models	Response variables					
	Density $^{\text{hornbill}}$			Richness $^{\text{hornbill}}$		
	Coefficient	p-value	AIC	Coefficient	p-value	AIC
Forest	0.012	**0.012**	259.0	0.003	0.054	111.9
FN $^{\text{hornbill}}$	0.000	0.238	265.3	0.000	0.816	115.6
FN $^{\text{hornbill}}$	0.000	0.916	261.0	0.000	0.783	113.9
Forest	0.012	**0.011**		0.005	0.054	
FN $^{\text{hornbill}}$	0.000	0.172	261.6	0.000	0.417	155.0
Forest	0.019	**0.012**		0.007	0.056	
FN $^{\text{hornbill}}$ x Forest	0.000	0.236		0.000	0.372	

Table 3-S4. Results of the models tested to explain variation of density and richness of primate-dispersed seedlings.

Models	Response variables					
	Density $^{\text{primate}}$			Richness $^{\text{primate}}$		
	Coefficient	p-value	AIC	Coefficient	p-value	AIC
Forest	-0.006	0.285	323.2	-0.005	0.054	146.2
FN $^{\text{primate}}$	0.000	0.927	324.4	0.000	0.220	145.2
FN $^{\text{primate}}$	0.000	0.758	325.1	0.000	0.520	147.0
Forest	-0.007	0.270		-0.005	0.103	
FN $^{\text{primate}}$	0.000	0.429	326.3	0.000	0.531	147.0
Forest	0.002	0.855		-0.002	0.654	
FN $^{\text{primate}}$ x Forest	0.000	0.378		0.000	0.615	

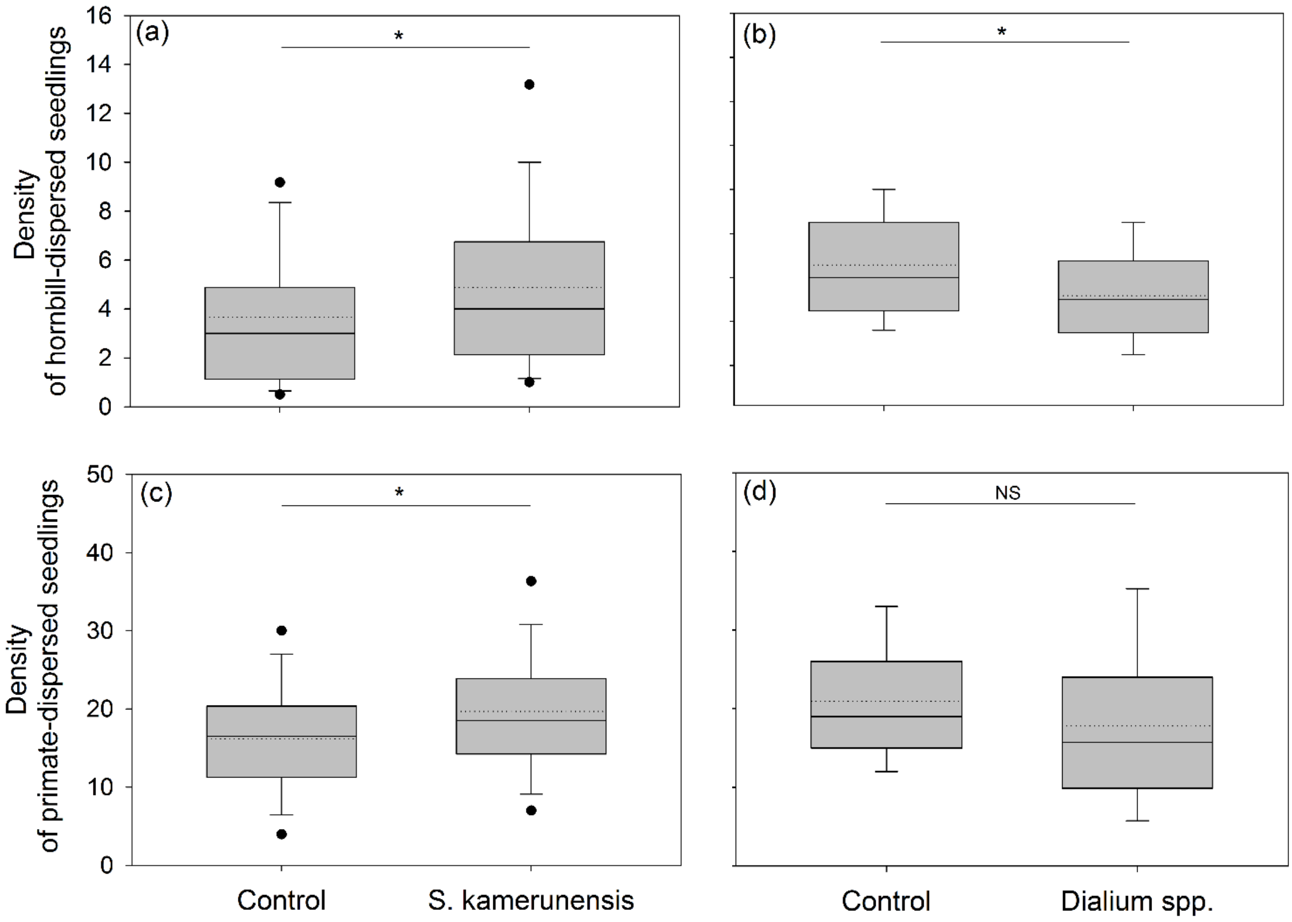


Figure 3-S1. Comparison of the density of hornbill-dispersed seedlings between (a) locations under *Staudtia kamerunensis* adult trees and control locations and (b) locations under *Dialium* spp. adult trees and control locations, and of the density of primate-dispersed seedlings between (c) locations under *Staudtia kamerunensis* adult trees and control locations and (d) locations under *Dialium* spp. adult trees and control locations in a forest-savanna mosaic in D.R. Congo. Black circles indicate 5th and 95th percentiles, solid lines indicate the median, and dotted lines indicate the mean. *= $p < 0.05$ and NS= non-significant.

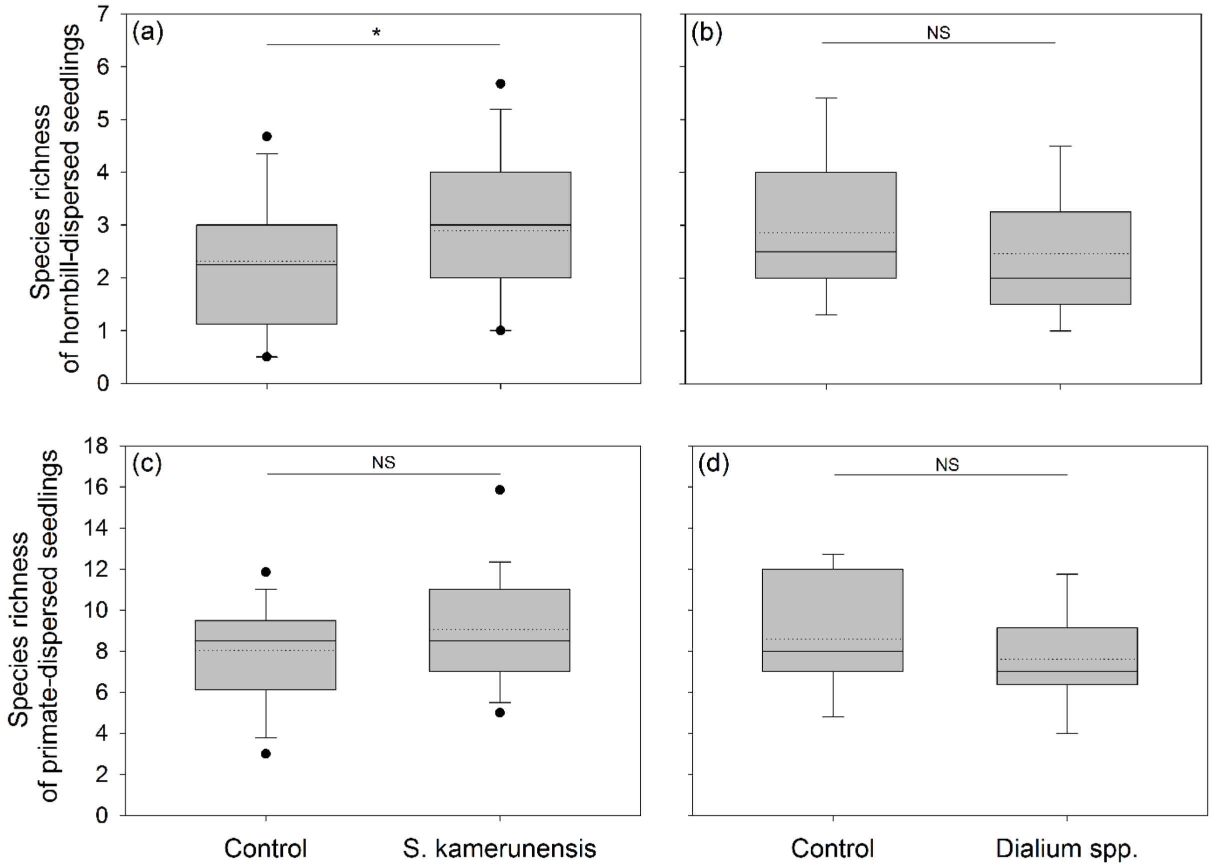


Figure 3-S2. Comparison of the species richness of hornbill-dispersed seedlings between (a) locations under *Staudtia kamerunensis* adult trees and control locations and (b) locations under *Dialium* spp. adult trees and control locations, and of the species richness of primate-dispersed seedlings between (c) locations under *Staudtia kamerunensis* adult trees and control locations and (d) locations under *Dialium* spp. adult trees and control locations in a forest-savanna mosaic in D.R. Congo. Black circles indicate 5th and 95th percentiles, solid lines indicate the median, and dotted lines indicate the mean. *= $p < 0.05$ and NS= non-significant.

Chapitre 4.

A complete assemblage of large frugivores is necessary for the maintenance of a diverse Afrotropical seedling community

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A shorter version of this manuscript (excluding the analysis of soil variables) is in preparation for submission.

Les groupes de bonobos et d'éléphants dans la mosaïque persistent grâce à des programmes de conservation de la faune sauvage menés par des ONG locales. Néanmoins, de tels programmes sont géographiquement très restreints, que ce soit dans la mosaïque ou dans l'ensemble de l'aire de distribution de ces animaux. Or, ces deux espèces de grands mammifères sont affectées par la destruction de l'habitat et la chasse. Aussi, bien que les calaos soient hautement mobiles et voyagent fréquemment entre les fragments de forêt, leurs activités semblent affectées par la quantité de couverture forestière dans le paysage. De plus, les grands oiseaux tels que les calaos sont de plus en plus ciblés par les chasseurs alors que les populations de grands mammifères s'épuisent.

Dans ce contexte, les fonctions écologiques de ces trois taxons de frugivores sont sérieusement menacées. La question se pose donc de savoir comment l'extirpation de ces disperseurs de graines importants peut influencer la régénération de la forêt, et plus précisément si leur extirpation sélective peut être fonctionnellement remplacée par les taxons subsistants. C'est cette problématique que nous avons explorée dans ce quatrième chapitre.

The groups of bonobos and elephants living in the mosaic persist thanks to wildlife conservation programs led by local NGOs. However, such programs are geographically very limited, either in the mosaic or in the range of distribution of these animals. Yet, these two species of large mammals are affected by habitat destruction and hunting. Also, despite hornbills are highly mobile and travel frequently between forests patches, their activities seem to be affected by the amount of forest cover in the landscape. Additionally, large birds such as hornbills are increasingly targeted by hunters as populations of large mammals are being depleted.

In this context, the ecological functions of these three frugivore taxa are thus severely threatened. The question arises of knowing how the extirpation of these seed dispersers can impact forest regeneration, and more precisely, whether their selective extirpation can be functionally compensated for by the remaining frugivores species. We explore this problematic in Chapter 4.

Résumé

La défaunation est associée à des changements de la composition des communautés de plantes en régénération, mais le niveau de redondance fonctionnel des différents grands disperseurs de graines reste mal connu parce qu'ils sont souvent extirpés simultanément. De plus, alors que les processus de dispersion des graines et de filtrage de l'habitat sont tous deux reconnus comme influant la communauté de plantes, les tentatives empiriques d'éclaircir la contribution relative de ces deux processus sont rares. Ici, nous avons premièrement exploré le niveau de complémentarité fonctionnel des calaos, des primates et des éléphants pour le recrutement de plantules zoochores. Nous avons de plus examiné l'influence de paramètres pédologiques. Nous avons échantillonné la communauté de plantules zoochores (4900 m^2) dans cinq sites abritant des abondances contrastées de frugivores dans un paysage de mosaïque en R. D. Congo. Une sélection ascendante des variables explicatives et une analyse de partition de variation prenant en compte des variables spatiales ont montré que (i) les contenus échangeables en azote, potassium et phosphore expliquaient 17 % de la variation de la densité de plantules, (ii) l'abondance des primates, la proportion d'argile, le contenu échangeable en potassium du sol et les variables spatiales expliquaient 32 % de la variation de la richesse spécifique et (iii) l'abondance de calaos, la présence d'éléphants de forêts, la proportion d'argile du sol et les variables spatiales expliquaient 24 % de la variation de la moyenne pondérée de la longueur des graines dont sont issues les plantules. De manière générale, nous concluons que la redondance fonctionnelle entre les calaos, les primates et les éléphants dépend de la variable réponse considérée. Ces trois espèces ont une influence redondante sur la densité de plantules, les primates ont une influence plus forte sur la richesse spécifique et enfin les éléphants et les calaos ont des influences plus fortes sur la longueur moyenne des graines de la communauté de plantules zoochores, bien que leur influence spécifique soit relativement faible. Nous avons aussi montré l'importance du processus de filtrage du sol dans l'organisation de la communauté de plantules. Nous discutons finalement du rôle probable d'évènements stochastiques à échelle fine pour expliquer la grande part de variation inexpliquée des variables réponses (entre 68 et 83 %).

Abstract

Defaunation has been associated to compositional changes in the regenerating plant community, but the level of functional redundancy of different large seed dispersers are poorly known because they are often simultaneously extirpated. Moreover, while both seed dispersal and habitat filtering processes are recognized to influence plant community, empirical attempts to unravel their relative contribution are scant. Here, we firstly explored the level of functional complementarity among hornbills, primates and elephants for the recruitment of animal-dispersed seedlings. We also examined the influence of soil parameters. We surveyed the community of animal-dispersed seedlings (4 900 m^2) among five sites housing contrasted abundance of frugivores in a mosaic landscape in D.R. Congo. A forward selection of explanatory variables and a variation partitioning analysis accounting for spatial variables showed that (i) total soil nitrogen, exchangeable potassium and phosphorus contents explained 17% of the variation in the density of seedlings, (ii) the abundance of primates, soil clay content, exchangeable potassium content and spatial variables explained 32% of the variation in seedling richness and (iii) the abundance of hornbills, the presence of forest elephants, soil clay content, and spatial variables explained 24% of the variation in mean weighted seed length of the seeds from which the seedlings arised. Overall, we conclude that whether hornbills, primates and elephants have functionally redundant role depends on the response variable considered. The three species had a redundant influence on the seedling density, while primates had a stronger influence on species richness and elephants and hornbills had stronger influences on the mean seed length of the community of animal-dispersed seedlings, although their specific influence was relatively weak. We also highlighted the importance of soil filtering processes in shaping patterns of seedling recruitment and discuss of the probable role of stochastic events at fine scale in accounting for the large part of unexplained variation of the response variables (68 - 83%).

Introduction

The so-called Anthropocene defaunation, caused by excessive hunting, habitat loss and degradation, is among the most pervasive threat to wildlife. Besides affecting animal populations, defaunation has cascading effects on community-level trophic interactions such as animal-mediated seed-dispersal, especially since frugivores serve as the main dispersal vector for the majority of tropical plant species (Howe and Smallwood 1982, Peres and Palacios 2007, Markl et al. 2012, Neuschulz et al. 2016). For instance, defaunation can indirectly reduce the quantity of seeds being disseminated away from parent trees where high rates of density-dependent mortality are observed, and in turn reduce the recruitment capacity of plants. Because Large frugivores provide unique ecosystem services by ensuring the dissemination of very large amounts of seeds from numerous species, including the largest-seeded ones that smaller frugivores cannot disperse (Vidal et al. 2013, McConkey et al. 2015, Neuschulz et al. 2016, Trolliet et al. 2016), their extirpation has particularly severe consequences on forest regeneration: it shifts the composition of the whole plant community by decreasing the abundance and diversity of animal-dispersed plants (Nuñez-Iturri and Howe 2007, Wright et al. 2007, Nuñez-Iturri et al. 2008, Terborgh et al. 2008, Vanthomme et al. 2010, Harrison et al. 2013, Camargo-Sanabria et al. 2014, Effiom et al. 2014). Yet, large animals are disproportionally affected by habitat loss and degradation, and preferentially targeted by hunters (Fa et al. 2005, Peres and Palacios 2007, Ripple et al. 2016).

The unsustainable rate of bushmeat extraction and habitat degradation in Central Africa, a region that holds the greatest number of large frugivores on Earth (Forget *et al*. 2007), including four great ape species (*Gorilla beringei* and *G. gorilla, Pan paniscus* and *P. troglodytes*), the forest elephant (*Loxodonta cyclotis*) and several hornbills species, is a particularly sever threat to all these large seed dispersers (Fa et al. 2002, 2005, Trail 2007, Junker et al. 2012, Maisels et al. 2013, Breuer et al. 2016, Whytock et al. 2016). As a consequence ecosystem functioning and the provision of services become imperiled too (Fa et al. 2002, Abernethy et al. 2013, Malhi et al. 2016, Osuri et al. 2016). It is therefore critically important to gain a precise understanding of the causes and consequences of the observed trophic downgrading to predict the long term capacity of tropical forests to maintain their biodiversity and ecosystem services and implement relevant conservation plans (Abernethy et al. 2013).

However, although the patterns resulting from defaunation are relatively consistent across the tropics, we still only have a rough understanding of the causal link between defaunation and its cascading consequences. For instance, it remains unclear whether the selective removal of important large frugivore taxa has a comparable impact, i.e. whether these taxa have redundant or complementary functional roles. Unraveling the level of functional redundancy among species playing critical ecological functions such as frugivores in the context of environmental changes remains a major challenge in biology and conservation (Brodie et al. 2009b, Schleuning et al. 2012, Bueno et al. 2013, Sutherland et al. 2013, Plein et al. 2016, Rother et al. 2016). Recent work suggests that large frugivores have non-redundant role as seed disperser (Clark et al. 2001, Bueno et al. 2013, McConkey and Brockelman 2016, Rother et al. 2016), but we are still lacking empirical evidence regarding their level of functional complementarity in terms of plant recruitment (but see Brodie et al. 2009a). Most studies that have explored the effect of defaunation on forest regeneration have considered the extirpation of the whole community of large frugivores (Wright et al. 2007, Terborgh et al. 2008, Harrison et al. 2013) or of single taxa (primates: Nuñez-Iturri and Howe 2007, Nuñez-Iturri et al. 2008, Effiom et al. 2013, Chaves et al. 2015), whereas very few have attempted to understand whether the extirpation of different large seed dispersers had a similar impact on the plant community. In Africa, Effiom et al. (2014) and Vanthomme et al. (2010) suggested that the loss of large mammals was not compensated for by birds in terms of forest regeneration, which supports the hypothesis of complementary roles of those two guilds as seed disperser (Clark et al. 2001, Poulsen et al. 2002).

Interestingly, the western congolian forest-savanna mosaic is a landscape made of forest sites characterized by variable regimes of subsistence hunting and conservation programs, and results in contrasted abundances of the three main representatives large frugivores in Afrotropical forests, which are moreover seriously hit by anthropogenic activities, namely: primates, hornbills, and forest elephants (Fa et al. 2002, Trail 2007, Junker et al. 2012, Maisels et al. 2013, Whytock et al. 2016). These taxa are all recognized to be critically important seed dispersers in tropical forests, but they show however wide differences in size, foraging and ranging behavior which should influence the effectiveness of their seed dispersal services, i.e. their impact on forest regeneration (Trolliet et al. *In press*, 2016, Clark et al. 2001, Blake et al. 2009, Campos-Arceiz and Blake 2011). This ecological setting provides an opportunity to explore the impact of the selective extirpation of these frugivores on forest regeneration, thereby enabling us to tackle the question of functional redundancy among taxa. Here, our first and main goal was to investigate how variation in abundance of those large frugivores influenced the composition of the seedling community, i.e. whether their respective depletion could be functionally compensated for by the presence of the other taxa. We hypothesized that due to wide differences in size, foraging, and ranging behavior, these taxa should not have redundant functions, and variation in their abundance among sites should cause significant differences in the community of animal-dispersed seedlings. More particularly, because forest elephants have among the most diverse frugivorous diet in tropical forests, provide long distance seed dispersal, and are capable of dispersing very large seeds (Chapman et al. 1992b, Blake et al. 2009, Campos-Arceiz and Blake 2011), we predicted that the density, species richness, and mean seed lengths of the community of animal-dispersed seedlings should be reduced in sites where they are absent. Also, we predicted that these effect should be particularly marked where the abundance of large primates is reduced, as they are known to provide unique and critical seed dispersal services (Trolliet et al. 2016). Additionally, as an ecotone, the forest-savanna mosaic is probably characterized by heterogeneous soil conditions and fertility across sites (Favier et al. 2004). Yet, plant community composition in tropical forest is also largely recognized to be influenced by soil parameters (Chase 2014, Réjou-Méchain et al. 2014, Vleminckx et al. 2014, Ilunga Muledi et al. 2016). Therefore, attempting to explain variation in the seedling community with the sole role of frugivore activity would undoubtedly skew our understanding of the actual consequences of defaunation. Conversely, considering the complementary influence of abiotic processes should allow us to gain a better grasp of the mechanisms explaining vegetation patterns. Therefore, our second objective was to explore the influence of various edaphic variables in order to disentangle the relative importance of seed dispersal limitation and environmental filtering (deterministic) processes in explaining variation in the above-mentioned parameters of the seedling community, a fundamental but still pending question in ecology (Sutherland et al. 2013, Chase 2014) for which empirical support is scant (but see Clark et al., 2012; Norden et al., 2009).

Material & methods

Study area and forest sites

The study took place in Western Democratic Republic of Congo (D.R. Congo), in the area surrounding the WWF (World Wide Fund for Nature) Malebo research station, in the Bandundu province (2°29’3.87” S, 16°30’4.16” E). Annual rainfall averages 1500 mm. The main dry season occurs from June to August, followed by the main rainy season from September to January, and consecutive short rainy and dry seasons from January to May. The study area is situated in a forest-savanna mosaic, a landscape characterized by a mix of tropical semi-evergreen lowland rain forest and savanna matrix. The landscape is highly fragmented with a system of forest patches and corridors mainly associated with the hydrographic network. As a transitional ecosystem, or ecotone, its fragmented character is natural. Yet anthropogenic activities also influence its spatial structure. Shifting slash-and-burn agriculture encroaches on forest patches, while cattle ranching, with its associated yearly fire regimes, restricts the colonization of forests.

We conducted fieldwork in an area of about 30 × 20 km in the mosaic landscape, within five forested sites that bore different levels of hunting pressure, and characteristics. The Mbanzi, Nkombo and Mbominzoli sites were located in an extensive forest bloc (> 500 km^2) that forest elephants (*Loxodonta cyclotis*) are known to seasonally visit (Fig. 4-S1). The Mbanzi village, originally founded as a hunting camp, is home to around 600 people including a large group of hunters, so the forest around was assumed to be under relatively high hunting pressure. Thanks to the presence of the WWF-DRC Malebo research station and conservation program in the area, forest elephants are not hunted. The Nkombo and Mbominzoli forests were located further away from human settlements, and anthropogenic pressure was probably more limited. The later site hosts a large mammal monitoring program supported by the Mbou-Mon-Tour NGO. It is moreover located within the geographical limits of an ethnic group which do not hunt bonobos (*Pan paniscus*) following a traditional taboo. The other two forest sites, Nkala and Minkalu, belonged to nearby village’s communities practicing subsistence hunting. Hunting pressure was high, yet home to the same ethnic group who does not hunt bonobos, and under the conservation programs of the WWF-DRC and Mbou-Mon-Tour NGOs. Nkala, Minkalu and Mbominzoli hosted therefore relatively higher densities of primates (mainly bonobos) compared to Mbanzi and Nkombo. Hornbills, even though they are not the main target of hunters, are increasingly hunted as other species disappear (Trail 2007, Whytock et al. 2016).

Seedling community

We sampled the seedling community in plots under the crown of adult zoochoric trees of *Staudtia kamerunensis* (N= 32) and *Dialium* spp. (N= 26). These species primarily attract hornbills and primates, respectively (Trolliet et al. *In press*, 2016, Clark et al. 2004, Beaune et al. 2013b). Surveying the heterospecific regeneration under zoochoric trees is known to maximize the amount of information regarding seed dispersers' activity, standardize conditions, and enable efficient inter-sites comparisons (Nuñez-Iturri and Howe 2007, Vanthomme et al. 2010). We randomly established one or two 25-m² (5 × 5 m) plots (depending on crown size) under those trees. In order to account for the activity of frugivores not visiting them (e.g. forest elephants) and to perform a more comprehensive survey of the seedling community, we completed the sampling with plots located 50 m away and in random direction. We established one or two control plots in order to match the area of the plots under the two tree species cited above. Each plot or pair of plots is referred to as a location. Sampling efforts are presented in Table S1.

In each plot, we identified all seedlings measuring 0.5-2 m in height (Vanthomme et al. 2010) to genus, species or morphospecies level on the basis of leaf characteristics. Plant identification was performed in the field by two local experienced guides who previously aided in the identification of 474 samples of 178 tree species in the same study area, which are registered in the herbarium and botanical library of the Université Libre de Bruxelles (‘‘BRLU’’), with reference IDs Bastin-Serckx#1-474. We also completed a reference herbarium in the field in which we gathered a twig and leaf sample of each species and regularly checked the consistency of plant identification for known and unidentified morphospecies throughout the sampling period. Then, experienced botanists (JLD, JFG, and Olivier Lachenaud at the Herbarium of the National Botanic Garden Meise) double-checked these samples and identified further unidentified species. For each species, we indicated whether it was dispersed by animals or by abiotic means, and also determined the seed length with the aid of the literature (see Table S2).

We included the location type (under *S. kamerunensis* tree, under *Dialium* spp. tree, or random) in the statistical analysis (see further) to control for its potential attractiveness to specific seed disperser taxa and the subsequent signal in the seedling community (Clark et al. 2004, Kwit et al. 2004, Slocum 2012). Additionally, to control for the potential effect of forest amount in the landscape on the level of frugivore activity (Trolliet et al. *In press*, Serckx et al. 2016), we calculated the percentage of forest cover in 2500 m-radius ring buffers around each location following the method in Trolliet et al. (2016). Those areas of forest did not include fallows or active agricultural fields.

Soil variables

Soil samples (the 0-15cm layer below the litter) were collected at 2 random positions in each plot and bulked to make a unique sample for each plot or pair of plots. The following soil properties were determined following standard methods described in Pansu and Gautheyrou (2006): texture (% clay, sand and silt), pH-H_2O, pH-Cohex, effective cation exchange capacity (ECEC), content in exchangeable nutrients (Ca, K, Mg, Al, Fe, Mn, Mo, Zn and P), and total nitrogen content (Nt). Samples were air-dried and sieved through a 2-mm screen. Texture (% clay, silt and sand) was determined on composite samples (two for each site) by wet sieving and pipetting methods after organic matter destruction with H_2O_2 and clay dispersion with Na citrate. pH was measured using glass electrodes (Mettler-Toledo) on soil suspension 1:5 (v/v) in deionized water (pH-H_2O) or in the 0.0166 M hexamminecobalt trichloride exchange solution (pH-Cohex). Exchangeable nutrients were measured in the exchange solution by atomic emission spectroscopy (ICP-OES, Vista MPX, Varian). Effective cation exchange capacity (ECEC) was determined on the same extract by spectrophotometry. Total nitrogen content was determined by flash combustion at 1350 °C in a C-N elemental analyzer (Dumas method). Results are presented in Table S3.

Frugivore community

We characterized the large frugivore community and hunting levels by conducting a survey on a system of line-transects as well as on REConnaissanCE (RECCE) transects (Vanthomme et al. 2010) for a total of 170 km across the five sites. We recorded all direct and indirect traces of primates, hornbills, elephants (faeces, footprints, calls, nests…), and hunting activity (rifle cartridges, gunshots, traps, fires). As a mean of quantification, we summed up all observations found for each of the four categories, and calculated Kilometric Abundance Indexes (KAI, observations/km), (Table 4-S4, Fig. 4-1), allowing efficient inter-sites comparisons (Mathot & Doucet 2006, Vanthomme *et al.* 2010). Due to the difficulty to assess whether two consecutives elephant tracks should be considered independent or not, and due to their large home ranges, we suspected high level of pseudo-replication and were not confident that the tracks encountered were a reliable indication of their relative abundance in each site. We therefore simply reported for the presence or absence of forest elephants in each site.

Statistical analysis

All the analysis were conducted in the R software (R Development Core Team, 2015). For each location, we used the mean density, mean species richness, and the mean weighted seed length of animal-dispersed seedlings as response variables. We classified the explanatory variables previously described in a biotic and an abiotic component. In the biotic component, we included the abundance/presence of frugivores, the location type, and the percentage of forest cover in the landscape. Those two last variables were included in the biotic component as they are hypothesized to directly affect seed disperser activity. In the abiotic component, we included the soil variables. Furthermore, we considered a spatial component in which spatial variables were reporting for the spatial autocorrelation of the response variables resulting from spatially structured environmental and ecological processes considered or not in our datasets. This component was generated through Moran's eigenvector maps (MEM; Dray et al., 2006), a spatially explicit method allowing the detection of multiscale spatial patterns in uni- or multivariate response datasets. The MEM eigenfunctions (i.e., the spatial explanatory variables) were generated using (1) a connectivity matrix based on the largest edge of the minimum spanning tree (t), and (2) a weighting function $f_{ij} = 1 - (d_{ij}/4t)^2$, where d_{ij} is the Euclidean distance between two locations. The combination of these connectivity and weighting matrices corresponded to a principal coordinate of neighbor matrices (PCNM; Borcard and Legendre, 2002) adapted to the MEM framework (Dray et al. 2006). Only positively correlated spatial variables were used in this study. These biotic, abiotic, and spatial explanatory datasets were included in a variation partitioning analysis (Borcard et al. 1992, Peres-Neto and Legendre 2010). The variation partitioning analysis allows to define the shared and pure fractions of explanation for each response variable. A shared fraction is jointly explained by two or more components, while a pure fraction is solely explained by the component itself. The explanatory power of all fractions was considered through the adjusted coefficient of determination (R^2_{adj}; Ezekiel, 1930). In order to reduce the number of explanatory variables within the abiotic, biotic and spatial components while maintaining the explanatory power as high as possible, a forward selection with double stopping criterion was performed on each dataset, following Blanchet et al. (2008). Within the biotic and abiotic components, only the variables displaying less than 70% of correlation among each other were kept in order to reduce levels of collinearity (but all variables are considered in the discussion). Tests of significance were computed by permutation (9999 iterations) of the residuals of the general and partial multiple linear regressions of the variation partitioning (Anderson and Legendre 1999).

Results

The five sites differed in terms of hunting pressure (0.56–1.28 obs./km), and abundance of primates (0.47-5.7 obs./km), hornbills (2.54-5.85 obs./km), and presence of forest elephants (Fig. 4-1, Table 4-S4). Primates were mainly represented by the bonobo, but also by several monkey species (*Cercopithecus ascanius*, and potentially *C. mona wolfi* and *C. neglectus*, even though these two species are rare and difficult to observe). Hornbills were mainly represented by *Bycanistes albotibialis*, but also by *Ceratogymna atrata* and *Bycanistes fistulator*. According to collinearity analysis, 7 variables from the abiotic component (% sand, % silt, Mg, Al, pH-Cohex, Ca, and Fe) induced collinearity problems and were excluded from the statistical analysis (Table 4-S5). Since only presence of elephants and not their abundance was used, this variable was not considered in the collinearity analysis. Yet, the sites where elephants were

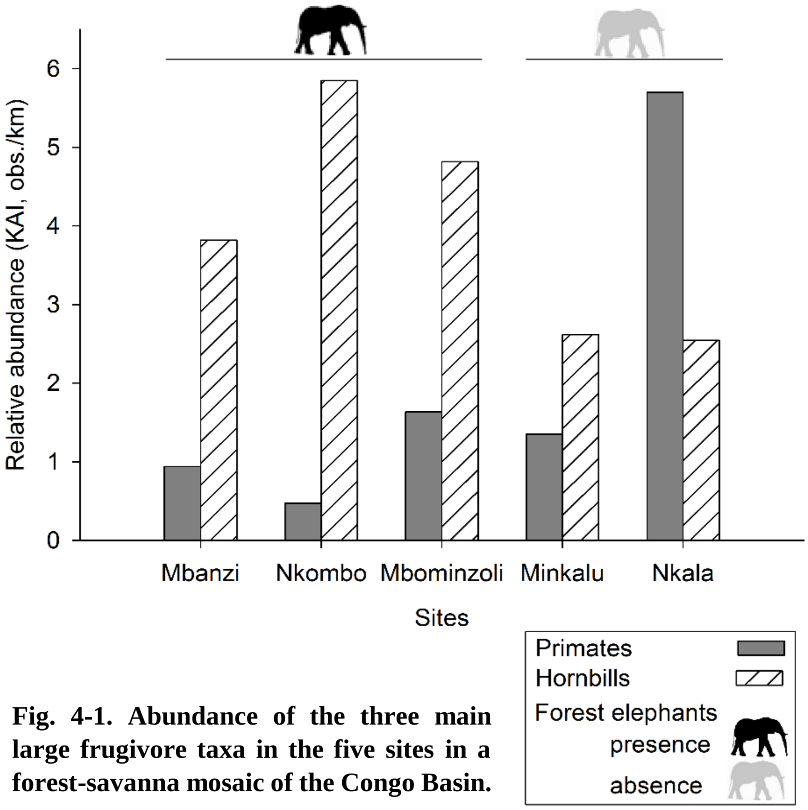

Fig. 4-1. Abundance of the three main large frugivore taxa in the five sites in a forest-savanna mosaic of the Congo Basin.

present housed higher abundances of hornbills than those without elephants (Fig. 4-1). We therefore cannot statistically fully distinguish the effect of the abundance of hornbill from that of the presence of elephants.

Finally, the minimum spatial resolution allowing to detect spatial correlation was 7.4 km (i.e., the minimum distance allowing all plots to be connected in the spanning tree), which broadly corresponds to the distance between two neighboring sites.

Seedling community

Among the 248 morphospecies found during the survey (N= 6 300 individual seedlings), 34 (14%) had an unknown dispersal mode and 185 (86%) were dispersed by animals. Among those, the seed length was unknown for 71 species, representing 1 306 individuals (21%). The descriptive statistics (density, species richness and mean weighted seed length) of each site are presented in Table 1.

Table 4-1. Site means and standard deviations of the response variables (density, species richness, and mean weighted seed length of the animal-dispersed seedlings).

Sites	Density	Species richness	Seed length
	Mean ± SD	Mean ± SD	Mean ± SD
Mbanzi	26.7 ± 12.4	11.1 ± 3.0	15.1 ± 3.1
Nkombo	22.3 ± 7.6	9.3 ± 2.4	16.7 ± 3.4
Mbominzoli	20.0 ± 8.3	9.4 ± 2.3	18.9 ± 3.6
Minkalu	25.8 ± 10.4	12.7 ± 3.3	18.0 ± 2.0
Nkala	25.1 ± 10.3	12.5 ± 3.6	14.9 ± 2.8

The model selection procedure only retained a significant abiotic component which included soil exchangeable potassium (K), phosphorus (P), and total nitrogen (Nt) contents to explain variation in the density of animal-dispersed seedlings ($R^2_{adj} = 0.17, P= 0.005$), (Fig. 4-2a, Table 4-S6). While exchangeable K and Nt contents had a positive effect (Fig. 4-3a and 4-3b, respectively), exchangeable P content had a negative effect on the density of seedlings (Fig. 4-3c).

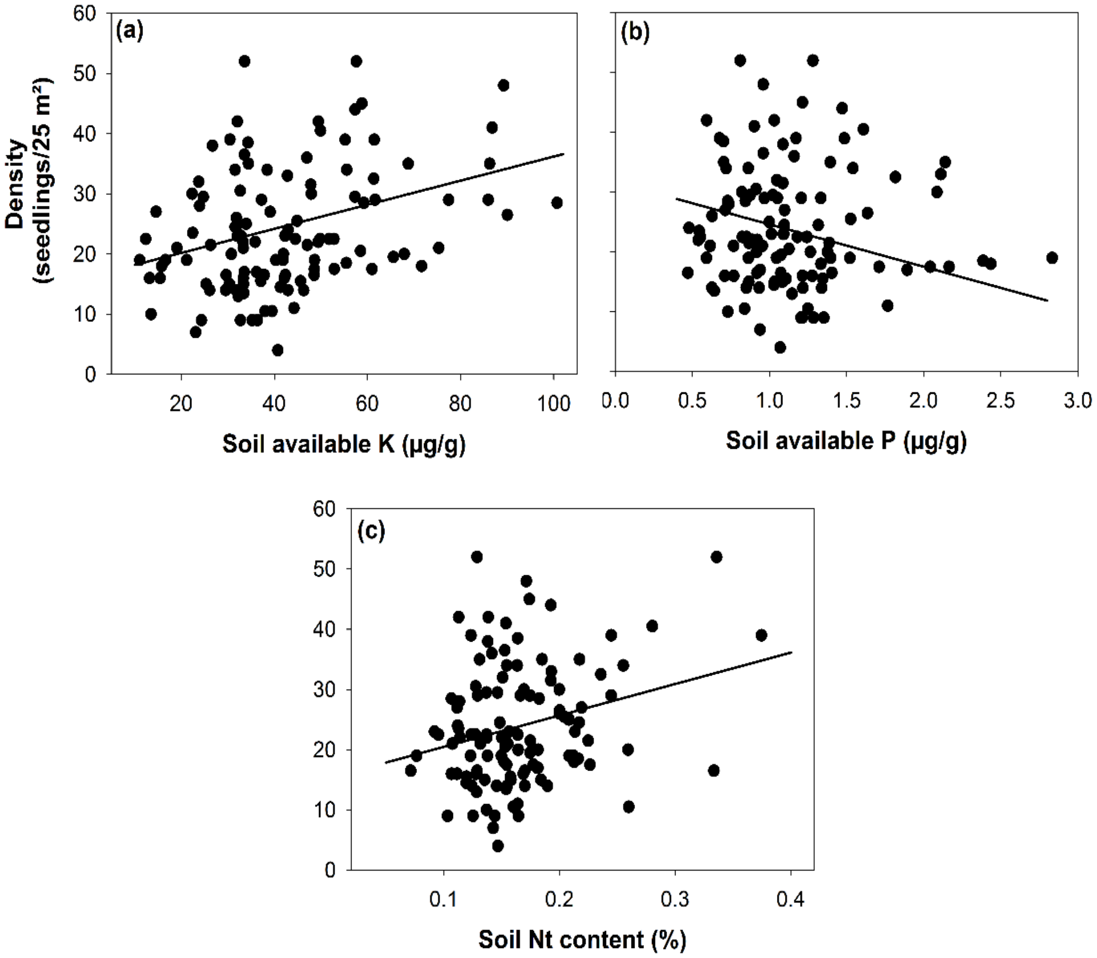

Fig. 4-3. Mean density of animal-dispersed seedlings in 25 m² plots as a function of (a) soil exchangeable K, (b) soil exchangeable P, and (c) total nitrogen contents.

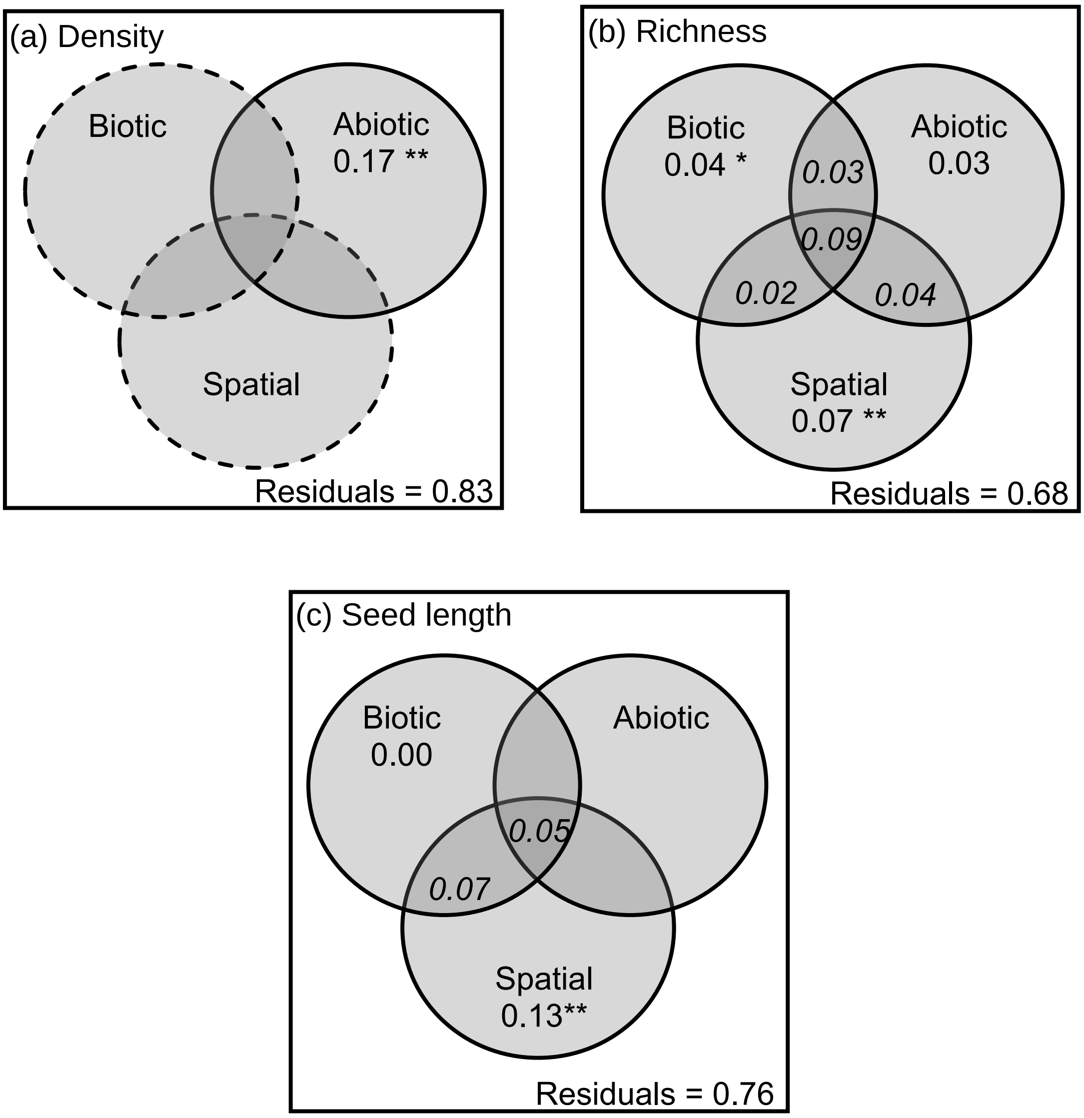

Fig. 4-2. Variation partitioning of the three response variables ((a) density, (b) richness and (c) mean weighted seed length of animal-dispersed seedlings) among a biotic, an abiotic, and a spatial component.

In (a) the abiotic component = exchangeable K and P, and total Nt contents;

In (b) the biotic component = location type and the abundance of primates and the abiotic component = the soil clay, exchangeable K and P contents;

In (c) the biotic component = abundance of hornbills and the abiotic component = soil clay content.

Plain-line and dotted-line circles of the Venn diagrams show significant ($P < 0.05$) and non-significant ($P > 0.05$) components, respectively. The values give the R^2_{adj} of the associated partial regressions for the pure fractions (except for the italic values which give R^2_{adj} computed by subtraction of other R^2, which are therefore non-testable), and the asterisks and the double asterisks indicate significant ($P < 0.05$) and highly significant signals ($P < 0.01$), respectively. Values < 0 are not shown.

Among the models explaining the variation in species richness of animal-dispersed seedlings, the selection procedure retained a model with a significant biotic component containing the location type and the abundance of primates (R^2_{adj} = 0.18, P= 0.005), and a significant abiotic component containing soil clay, exchangeable K and P contents (R^2_{adj} = 0.20, P= 0.005), (Fig. 4-2b). The abundance of primates, the percentage of clay, and K content had a positive effect (Fig. 4-4a, 4-4b, and 4-4d, respectively), while exchangeable P content presented a negative effect on the species richness (Fig. 4-4c). Random locations had a mean of 10.6 ± 2.99 animal-dispersed species while locations under *Staudtia* and *Dialium* trees had a mean of 12.3 ± 3.59 and 10.6 ± 2.59 species, respectively. The selection procedure also detected a significant spatial structure of the response variable (R^2_{adj} = 0.22, P= 0.005). Together, the three explanatory datasets explained 32% of the total variability of the species richness of animal-dispersed seedlings. The variation partitioning analysis revealed that the pure effect of the location type and the abundance of primates were significant (R^2_{adj} = 0.04, P = 0.04), and that the pure spatial component was highly significant (P= 0.01, R^2_{adj} = 0.07), (Fig. 4-2b). This pure spatial effect posits that there is a signal of the response variable that is structured in space which remain significant after having accounted for the effect of the other significant variables.

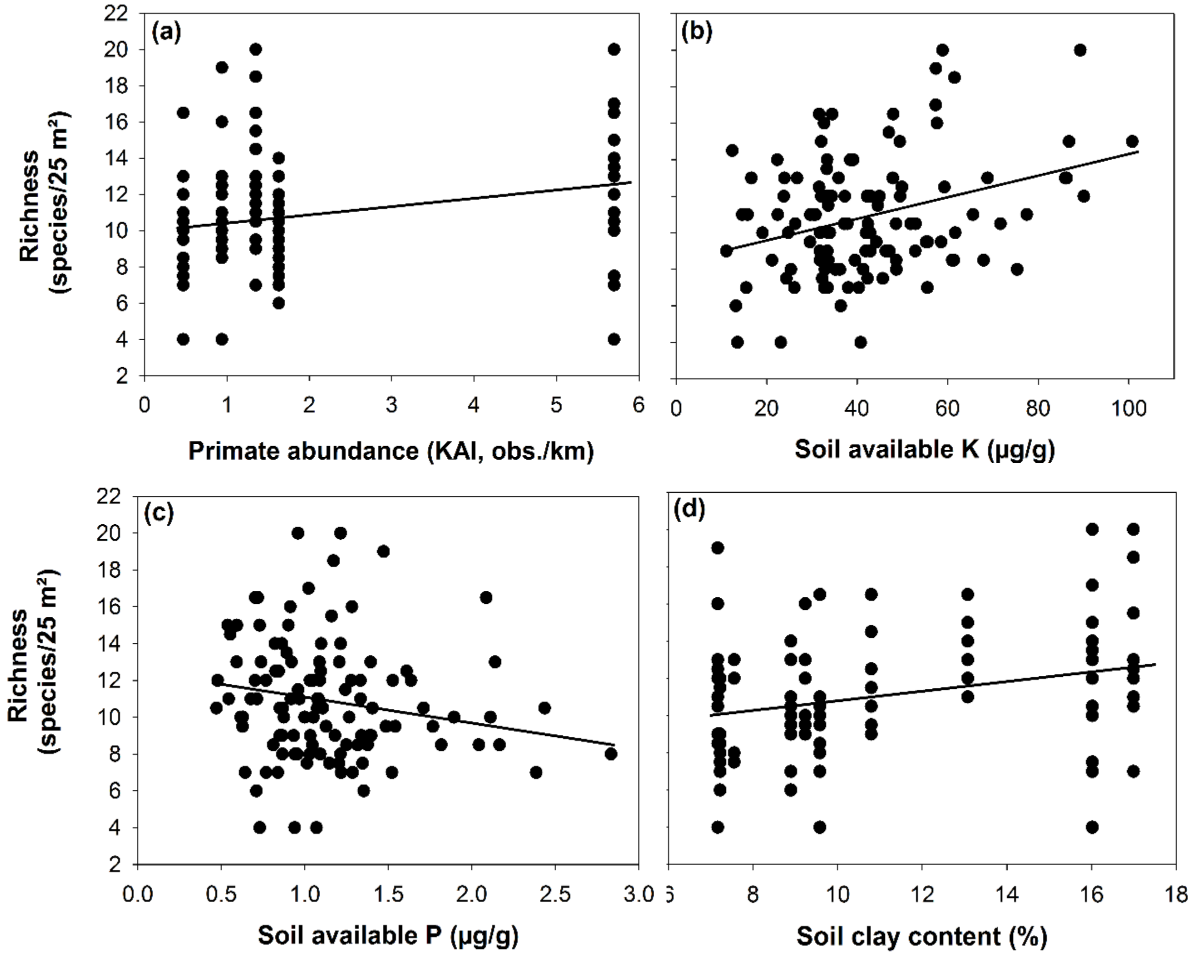

Fig. 4-4. Mean species richness of animal-dispersed seedlings in 25 m² plots as a function of (a) primate abundance, (b) soil exchangeable K, (c) soil exchangeable P, and (d) soil clay contents

The model selection procedure retained a significant biotic component represented by the abundance of hornbills, which had a positive effect on the mean seed length of animal-dispersed seedlings (R^2_{adj} = 0.12, P= 0.005), a significant abiotic component represented by the soil clay content, which had a negative effect (R^2_{adj} = 0.04, P= 0.04), and a significant spatial structure (R^2_{adj} = 0.25, P= 0.005), (Fig 4-2c, Fig. 4-5). Together, the three components explained 24% of the total variability of the mean seed length in the animal-dispersed seedling community among the plots. The variation partitioning revealed that the spatial component had a significant pure signal remaining after controlling for the effect of the two other variables (R^2_{adj} = 0.13, P= 0.005), (Fig. 4-2c). Levels of collinearity between the explanatory variables are presented in Table S5.

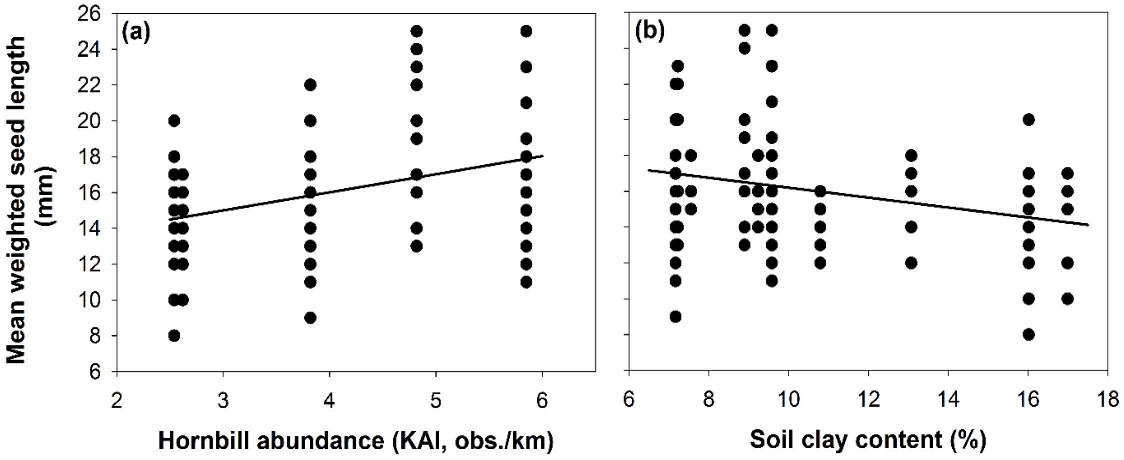

Fig. 4-5. Mean weighted seed length of animal-dispersed seedlings in 25 m² as a function of (a) hornbill abundance, and (b) soil clay content.

Discussion

Here, we showed that both seed dispersal and habitat filtering processes influenced compositional patterns of the community of animal-dispersed seedlings. While several studies have investigated each processes separately (e.g., Condit et al., 2013; Fayolle et al., 2012; Hubbell et al., 2007; Réjou-Méchain et al., 2008; Schupp et al., 2002; Vleminckx et al., 2016; Wiegand et al., 2016) or used modeling technics to address theoretical questions related to the relative importance of neutral versus deterministic processes (Chave and Leigh 2002, Réjou-Méchain and Hardy 2011), our study provides rare and strong empirical evidence of the complementary roles of these ecological mechanisms together (Norden et al. 2007, 2009).

The density of animal-dispersed seedlings was only explained by soil variables (Nt, K, and P contents), while variation in the richness and mean seed length of animal-dispersed species were explained by both the assemblage of frugivores and soil variables. Particularly, the abundance of primates, the K and N contents, and the percentage of clay explained variation in species richness, and the abundance of hornbills and the percentage of clay explained that of the mean seed length of the seedling community.

Functional complementarity between frugivores depends on the variable considered

We did not find any evidence that the reduction in abundance of any of the frugivore taxa influenced the density of animal-dispersed seedlings. This result does not support our prediction, but is however in line with the previous finding of Vanthomme et al. (2010) in Central Africa where the density of seedlings in hunted and non-hunted sites did not differ significantly. Since the seeds are nevertheless dispersed by animals, our results suggest that the three frugivore taxa have redundant roles regarding the abundance of seedlings that eventually establish. More precisely, and given the assemblage of large frugivores in each site, we firstly conclude that the absence of forest elephants is functionally compensated for by the presence of primates and hornbills. However, it remains unclear whether one of these taxa played a more important role than the other, or whether the cumulative activity of both hornbills and primates allowed to maintain the seedling density in sites where elephants are absent. In addition, if we focus on the sites where elephants are absent, we conclude that the reduction in primate abundance was compensated for by the presence of hornbills, and inversely. However, it is important to note that none of these two taxa was completely absent from our sites, and that the remaining population, though small, could continue to provide valuable seed dispersal services that maintain their functional role in terms of plant recruitment. Also, the forest elephants are part of a relic fragile population (Inogwabini et al. 2011), so their function might already be partially lost (McConkey and O’Farrill 2015, 2016), which would prevent us from detecting their signature in the regenerating cohort. Therefore, we cannot exclude that a more marked contrast in abundance of the frugivores studied here could allow one drawing more robust conclusions. Indeed, it has been observed in both Afrotropical and Neotropical forests that the extirpation of primates reduced the representation of primate-dispersed species in the seedling community (Nuñez-Iturri and Howe 2007, Vanthomme et al. 2010, Effiom et al. 2014). More particularly, Effiom et al. (2014) concluded that the presence of large frugivorous birds did not functionally compensated for the reduction in primate abundance in Nigeria. Further research to understand the link between frugivore population size, seed dispersal effectiveness, and its consequences on forest regeneration is critically important to be able to understand correctly the cascading effects of selective defaunation on ecosystem functioning (McConkey and O’Farrill 2015).

The analysis of the richness of animal-dispersed species revealed different associations. Here, we found that the reduction in primate abundance caused a decrease in species richness, a finding that has already been documented in the Neotropics (Nuñez-Iturri and Howe 2007, Nuñez-Iturri et al. 2008, Terborgh et al. 2008) and the Paleotropics (Vanthomme et al. 2010, Harrison et al. 2013). We therefore conclude that hornbills did not replace the ecological services lost with the reduction in primate numbers. This finding supports the conclusion of Clark et al. (2001) and Poulsen et al. (2002) in that these two taxa play not redundant roles as seed dispersers.

It is worth mentioning that we detected a significant pure signal of the spatial structure of the richness. Given that the inferior detection threshold for this spatial structure was 7.4 km, which broadly correspond to the distance between two neighboring sites, that signal aroused from a source of environmental variation among sites, or at a larger scale. In our study, we did not account for the presence of frugivorous bats, which are important seed dispersers in Afrotropical forests (Seltzer et al. 2013) and affected by forest fragmentation (Rocha et al. 2016). Their abundance could therefore vary among sites surrounded by contrasted amount of forest cover which could influence the seed dispersal services they provide and the subsequent patterns of seedling recruitment. Additionally, variation in the species richness of adult zoochoric trees among sites could have influenced the observed patterns and merit further investigation (Effiom et al. 2014).

Finally, we showed that a decreasing abundance of hornbills significantly reduced the mean weighted seed length of the seedling community. Notably, the abundances of hornbills was positively correlated with the presence of elephants: the sites housing the lowest abundances of hornbills did not house any elephant (Nkala and Minkalu), and inversely (Fig. 4-1). Therefore, the variable presence/absence of elephants could hardly add any significant gain in addition to the variable hornbill during the variable selection procedure. So, our result should be interpreted cautiously because we cannot exclude that the extirpation of elephants could have significantly disrupted the recruitment of large seeded species and caused a reduction in the mean seed length in the seedling community. We suggest that it is more careful to associate the observed reduction in mean seed length to the extirpation of both hornbills and elephants. Especially, this categorical variable, unlike hornbill abundance, is a rough characterization of the actual elephant population in that is does not provide information on differences in their abundance among the three sites where they are present, which probably limits its explanatory power and under-estimate the true influence of this species on the seedling community. Interestingly, we detected a significant pure spatial signal of the mean seed length, which explains an equal part of variation as the abundance of hornbills (R^2_{adj}= 0.13 vs 0.12, respectively). As previously explained, this signal posits that the explanatory variables tested explained only a fraction of the variation of the response variable. Moreover, it is important to remind that the minimal detection threshold for the spatial structure (7.4 km) precludes the possibility that local processes (within sites) are responsible for the signal detected. We suspect that some differences in the activity level of elephants between Mbanzi, Nkombo, and Mbominzoli that could not be reported with the categorical variable used here could account for the remaining spatial structure that has been detected. Also, post-dispersal processes that differentially impact species with different seed size could be important. For instance, larger seeds tend to be more prone to predation by rodents and insects than smaller seeds (Foster 1986). We therefore have to conclude that the presence of primates did not functionally compensated for a lack of recruitment of large-seeded trees in the sites where hornbill abundance was low and the forest elephants extirpated. This result is somewhat surprising because the bonobo, which is the main representative of the primate community in Nkala and Minkalu, provides excellent seed dispersal services for large-seeded plants in those sites (Trolliet et al. 2016). Beside the influence of post-dispersal processes that can lead to inconsistencies between the composition of the seed bank and that of the seedling community, bonobo could generate non-random spatial patterns of seed deposition and seedling recruitment, such as the clumping of seedling at nesting sites and leave a very spatially structured signature within their home range (Julliot 1997, Russo and Augspurger 2004, Haurez et al. 2015a). This aspect would require further investigation.

On the importance of considering habitat filtering processes

The variation partitioning analysis allowed us to detect the relative contribution of biotic and abiotic processes in the observed pattern of the seedling community. Notably, we found that Nt, exchangeable K, and P contents in soil explained 17% of the variation in the density of seedlings, which highlight the strong influence of abiotic processes relative to the role of frugivores. Conversely, the (shared) fraction of variation of the mean seed length explained by seed dispersal process was three fold greater than that explained by soil filtering (12 vs 4%, respectively). However, those two processes were more balanced when it came to explain variation in species richness (18 vs 20%, respectively).

Nitrogen, potassium and phosphorus are known to be important limiting elements for regenerating plants in the tropics (Wright et al. 2011), which comforts our finding regarding their importance to explain variation in the density and richness of seedlings. Especially, phosphorus is believed to be the most limiting element in tropical forests, and is known to largely influence productivity, plant growth and distribution (Sollins 1998, Vitousek et al. 2010, Cleveland et al. 2011, Holste et al. 2015). However, we showed that it had a negative impact on species richness, a finding in line with a study in Congo in which phosphorus had a negative effect on timber tree seedling survival (Medjibe et al. 2014). Also, Condit et al. (2013) showed that some tree species in Panama showed a preference for soils with low phosphorus content. Here, our result would suggest that a large proportion of such species with a preference for low soil exchangeable phosphorus, at least at the life stage studied, occur in our area so that as phosphorus content increases, the mean density and richness of the seedling community decrease. Another result that needs to be highlighted is the positive influence of exchangeable potassium content on both the density and richness of seedlings, which also confirm the result of Medjibe et al. (2014). We suggest that a limited availability of potassium could induce a selection pressure, excluding species more vulnerable to nutrient deficiency and favoring those most able to establish and survive as early as the seed-to-seedling transition stage. For instance species that have seeds with more reserve i.e. large seeds, are likely to have a competitive advantage (Foster, 1986; see below). Consequently, the number of species able to persist under such conditions is constrained.

Also, the percentage of clay in the soil positively explained some proportion of the variation of the number of species observed. This response could be related to soil water conductivity. Indeed, sandy soils are better drained than clay soils and are consequently drier and more nutrient poor (Vitousek and Sanford 1986). Therefore, a likely explanation would be that soil texture differentially influence the survival of species according to their seed size at the seed or seed-to-seedling transition stage by controlling rate of water imbibition and germination. Such a filtering process has been reported in arid conditions (Leishman and Westoby 1994, Leishman et al. 2000), particularly during extreme water stress situation (Khurana and Singh 2004) (note that the main dry season in our study area is rather marked with very few rainfall during ~ 3 months). Given that larger seeds have more reserves (Foster 1986), sandy soils could lower germination and increase mortality of smaller, weaker seeds more than that of large ones. Notably, we showed that an increase in the percentage of clay was responsible for a decrease in the mean weighted seed length in the seedling carpet. While the influence of soil texture on the distribution of plant species in tropical forests is recognized (Fayolle et al. 2012, Réjou-

Méchain et al. 2014, Vleminckx et al. 2014), its direct influence on the establishment of plants species with varying seed size have, to our knowledge, not yet been reported. Moreover, knowing that seeds of shade-bearer species tend be larger than those of fast-growing pioneer species (Cf Foster, 1986; Foster and Janson, 1985), our finding is congruent with previous work in Central Africa that showed that slow-growing shade tolerant species were favored in resource-poor sandy soils (Fayolle et al. 2012). Also, this is in line with Réjou-Méchain et al. (2014) who found that soil filtering was stronger in the earlier stages of forest succession; whose corollary is that the species composing early successional forest, which tend to be small-seeded, are particularly sensitive to soil conditions. Hence, as smaller-seeded species are disfavored in sandy soils relative to larger-seeded ones, a decreasing percentage of sand (which is strongly negatively correlated with the percentage of clay, Table S5) would tend to reduce the filtering process, enabling greater establishment of small-seeded plants and thereby reducing the mean weighted seed length of the seedling community. This process could thus explain why species richness increased along with the percentage of clay. As only plants with higher ability to persist in environments with reduced water and nutrient availability are found in sandy soils, a decreasing proportion of sand in the soil reduces filtering pressure and allows the establishment of more species with contrasting strategies (r or K). This finding is supported by the general idea that richer soils support more productive ecosystems, which enhance diversity (Chase 2010).

Conclusion

Generally speaking, our results stress out the importance to consider abiotic confounding variables when one attempts to explore the consequences of defaunation on forest regeneration, and particularly when assessing level of functional redundancy. Our study gave a more complete understanding of the dataset than by considering each component separately, although the main limitation of our method is that there remains a shared fraction for which it is unclear which component had a greater weight, which limit the robustness of our conclusion (Fig 4-2). Overall, we also conclude that despite the number of explanatory variables considered, we explained a relatively limited proportion of the variability of the response variables. This suggests a limited influence of spatial processes at the landscape scale such as variation in animal abundance, hence of their extirpation. The large amounts of unexplained variation (68 - 83%) may find their source in stochastic processes which have a greater influence at fine spatial scales (Chase 2014), and/or in past events that are known to disturb the local environment such as logging and slash-and-burn activity. Given the difficulty to find replicates sites in tropical regions, many studies are doomed to compare few sites to explore the consequences of defaunation on ecosystem functioning, thereby risking pseudo-replication and drawing biased conclusions as the effect of abiotic parameters are not quantified. We therefore call for studies explicitly testing the influence of complementary abiotic and biotic ecological processes to better understand the causal mechanisms shaping biodiverse tropical forests, and considering spatial effects to detect the influence of factors not taken into account.

Finally, we should also keep in mind that explanatory variables in those complex degraded tropical ecosystems are often inter-correlated (Table S5) which limit our capacity to evaluate the respective contribution of these collinear variables and draw robust conclusion. The replication of such studies in various environmental conditions will eventually permit an assessment of the true effect of the numerous biotic and abiotic processes involved in tropical forest regeneration.

Supplementary material

Table 4-S1. Sampling efforts and distribution across and in the five sites for the seedling survey.

Survey plots location	Sampling efforts (m²)					
	Sites					Total
	Mbanzi	Nkombo	Mbominzoli	Minkalu	Nkala	
Under *Staudtia kamerunensis*	250	250	250	300	250	1 300
Under *Dialium* spp.	275	225	250	150	250	1 150
Random	525	475	500	450	500	2 450
Total	1 050	950	1 000	900	1 000	4 900

Table 4-S2. Dispersal mode and seed length of all the species encountered during the survey.

Family	***Species***	**Dispersal mode**	**seed length**
?	*Cf Vitex congolensis / cf Oldfieldia africana*	Zoochorous	?
?	*inc 124 Motiambuli*	?	?
?	*inc 149*	?	?
?	*inc 150*	?	?
?	*inc 150 bis*	?	?
?	*inc 169*	?	?
?	*inc 179*	?	?
?	*inc 215*	?	?
?	*inc 215*	?	?
?	*inc 231*	?	?
?	*inc 251*	?	?
?	*inc 260*	?	?
?	*inc 263*	?	?
?	*inc 264*	?	?
?	*inc 42*	?	?
?	*inc 42*	?	?
?	*inc 42*	?	?
?	*inc 42*	?	?
?	*inc 75*	?	?
?	*inc 79*	?	?
?	*inc 86*	?	?
?	*inc alt 57C1*	?	?
?	*inc Bolu 2*	?	?

?	*inc compo 49A*	?	?
?	*inc Esau 2*	?	?
?	inc idem 56	?	?
?	*inc Monkuma 2*	?	?
?	*inc Mosimi*	?	?
Acanthaceae	*Acanthaceae sp.2*	Abiotic	?
	Thomandersia hensii	Abiotic	?
	Whitfieldia elongata	Abiotic	?
Anacardiaceae	*Sorindeia africana*	Zoochorous	15.0
	Sorindeia spp.	Zoochorous	?
Annonaceae	*Annickia chlorantha*	Zoochorous	19.5
	inc 125 Annonaceae sp.	Zoochorous	?
	inc 247 Annonaceae sp.	Zoochorous	?
	inc Mokoli	Zoochorous	?
	Isolona hexaloba	Zoochorous	12.5
	Monodora angolensis	Zoochorous	13.0
	Neostenanthera myristifolia	Zoochorous	?
	Piptostigma fasciculatum	Zoochorous	23.0
	Polyalthia suaveolens	Zoochorous	10.0
	Xylopia aethiopica	Zoochorous	6.0
	Xylopia hypolampra	Zoochorous	14.0
	Uvariodendron sp.	Zoochorous	15.0
	Isolona sp.	Zoochorous	11.0
	Xylopia staudtii - rubescens	Zoochorous	20.0
Apocynaceae	*Funtumia africana*	Abiotic	11.5
	Picralima nitida	Zoochorous	26.5
	Rauvolfia macrophylla	Zoochorous	8.0
	Rauvolfia vomitoria	Zoochorous	6.0
Boraginaceae	*Cordia platythyrsa*	Zoochorous	15.0
Burseraceae	*Dacryodes edulis*	Zoochorous	55.0
	Santiria trimera	Zoochorous	14.0
Canabaceae	*Celtis tessmannii*	Zoochorous	9.0
Cardiopteridaceae	*Leptaulus zenkeri*	Zoochorous	11.5
Chrysobalanaceae	*Dactyladenia sp.1*	Zoochorous	?
	Licania elaeosperma	Zoochorous	?
	Maranthes glabra	Zoochorous	?
	Parinari excelsa	Zoochorous	26.0
Clusiaceae	*Garcinia cf ovalifolia*	Zoochorous	8.0
	Garcinia kola	Zoochorous	30.0
	Garcinia punctata	Zoochorous	17.5
	Garcinia smeathmannii	Zoochorous	15.0
Ebenaceae	*Diospyros conocarpa*	Zoochorous	13.5
	Diospyros ferrea	Zoochorous	1.0
	Diospyros iturensis	Zoochorous	20.0
	Diospyros sp1	Zoochorous	20.0

Euphorbiaceae	*Crotonogyne sp.*	Abiotic	8.0
	Dichostemma glaucescens	Abiotic	11.0
	Duvigneaudia inopinata	Zoochorous	21.5
	Euphorbiaceae sp.	?	?
	inc 106 Euphorbiaceae	?	?
	inc 11	?	?
	inc 22 Euphorbiaceae	?	?
	inc 221	?	?
	inc 89 Euphorbiaceae sp.	?	?
	Macaranga sp.	Zoochorous	4.7
	Plagiostyles africana	Zoochorous	10.0
	Uapaca spp.	Zoochorous	21.0
Fabaceae	*Afzelia bipindensis*	Zoochorous	35.0
	Angylocalyx pynaertii	Zoochorous	25.0
	Aphanocalyx microphyllus	Abiotic	18.0
	Baphia sp.	Abiotic	17.5
	cf schefflerodendron gilbertianum	Abiotic	?
	Daniellia pynaertii	Abiotic	27.5
	Dialium pachyphyllum	Zoochorous	11.0
	Dialium tessmannii	Zoochorous	12.0
	Dialium tessmannii or zenkeri	Zoochorous	11.0
	Dialium zenkeri	Zoochorous	8.0
	Fillaeopsis discophora	Abiotic	117.5
	inc Molieme	?	?
	Lebruniodendron leptanthum	Abiotic	?
	Loesenera walkeri	?	?
	Millettia laurentii	Abiotic	23.5
	Pentaclethra eetveldeana	Abiotic	25.0
	Pentaclethra macrophylla	Abiotic	65.0
	Phyllocosmus africanus	Zoochorous	3.0
	Piptadeniastrum africanum	Abiotic	62.0
	Prioria oxyphylla	Abiotic	25.0
	Scorodophloeus zenkeri	Abiotic	22.5
	Tesmania africana	Abiotic	16.5
Flacourtiaceae	*Casearia barteri*	Zoochorous	?
	Maranthes cf gabunensis	Zoochorous	?
	Oncoba mannii	Zoochorous	8.0
	Scottellia klaineana	Zoochorous	5.0
Gentianaceae	*Beilschmiedia congolana*	Zoochorous	?
Guttiferae	*Symphonia globulifera*	Zoochorous	17.5
Huaceae	*Afrostyrax kamerunensis*	Zoochorous	18.0
	Afrostyrax lepidophyllus	Zoochorous	20.0
Hypericaceae	*Endodesmia calophyloides*	Zoochorous	15.0
Hypocrataceae	*Salacia sp.*	Zoochorous	?
Irvigiaceae	*Irvingia gabonensis*	Zoochorous	33.5

	Irvingia grandifolia	Zoochorous	32.5
Ixonanthaceae	*Phyllocosmus africanus*	Zoochorous	3.0
Lauraceae	*Beilschmiedia congolana*	Zoochorous	?
	Beilschmiedia sp.1 08/01	Zoochorous	?
Malvaceae	*Cola acuminata*	Zoochorous	30.0
	Cola cf. ballayi	Zoochorous	30.0
	Cola griseiflora	Zoochorous	20.0
	Cola lateritia	Zoochorous	27.5
	Grewia oligoneura	Zoochorous	10.0
	Octolobus spectabilis	Zoochorous	6.0
	Pterygota bequaertii	Abiotic	3.5
	Cola cf diversifolia	Zoochorous	14.0
Melastomataceae	*Memecylon cf laurentii*	Zoochorous	?
	Warneckea sp.2	Zoochorous	?
	Warneckea sp1	Zoochorous	?
Meliaceae	*Entandrophragma angolense*	Abiotic	15.0
	Guarea cedrata	Zoochorous	6.0
	Lovoa trichilioides	Abiotic	?
	Trichilia martineaui	Zoochorous	14.5
	Trichilia sp.	Zoochorous	14.5
	Trichilia sp.2	Zoochorous	14.5
	Trichilia sp.4	Zoochorous	14.5
	Trichilia sp.5	Zoochorous	14.5
Moraceae	*Ficus sp.*	Zoochorous	?
Myristicaceae	*Coelocaryon preussii*	Zoochorous	26.0
	Myristicaceae spp.	Zoochorous	25.0
	Staudtia kamerunensis var. gabonensis	Zoochorous	16.0
Ochnaceae	*Campylospermum elongatum*	Zoochorous	?
	Campylospermum sp.1	Zoochorous	?
	Campylospermum sp.2 cf bukobense	Zoochorous	?
	Campylospermum sp.3	Zoochorous	?
	Ochna calodendron	Zoochorous	?
	Ochna cf afzelii	Zoochorous	6.0
	Rhabdophyllum sp.	Zoochorous	5.5
	Rhabdophyllum sp.1 08/01	Zoochorous	5.5
Olacaceae	*Heisteria parvifolia*	Zoochorous	12.0
	Olax spp.	Zoochorous	11.0
	Olax subscorpioidea	Zoochorous	15.5
	Ongokea gore	Zoochorous	15.0
	Strombosia pustulata	Zoochorous	22.0
	Strombosiopsis tetrandra	Zoochorous	13.0
Pandaceae	*Microdesmis cf. puberula*	Zoochorous	7.0
	Microdesmis sp.	Zoochorous	7.5
Passifloraceae	*Barteria fistulosa*	Zoochorous	5.5
	Barteria letouzey	Zoochorous	?

	Barteria sp.1	Zoochorous	?
	cf Barteria sp.2	?	?
	Paropsia guineensis	Abiotic	6.0
Polygalaceae	*Carpolobia alba*	Zoochorous	7.5
Putranjivaceae	*Beilschmiedia sp.1 08/01*	Zoochorous	?
	Drypetes capillipes	Zoochorous	9.5
	Drypetes cf ituriensis	Zoochorous	9.5
	Drypetes cf principum	Zoochorous	15.5
	Drypetes paxii	Zoochorous	9.5
	Drypetes sp.2 08/01	Zoochorous	9.5
	Drypetes sp.4 08/01	Zoochorous	9.5
	Drypetes sp.5 08/01	Zoochorous	9.5
	Drypetes sp.6 08/01	Zoochorous	9.5
	Drypetes sp.7 08/01	Zoochorous	9.5
	Drypetes sp1.	Zoochorous	9.5
	Drypetes sp1. 08/01	Zoochorous	9.5
	Drypetes sp3. 08/01	Zoochorous	9.5
Rhizophoraceae	*cf Cassipourea sp.*	Zoochorous	?
Rubiaceae	*Aidia micrantha*	Zoochorous	?
	Aulacocalyx jasminiflora	Zoochorous	8.5
	cf Pauridiantha rubens	Zoochorous	1.0
	cf Psycotria sp.2	Zoochorous	?
	cf Rubiaceae sp.28	Zoochorous	?
	cf Tricalysia sp.2	Zoochorous	?
	Colletoecema dewevrei	Zoochorous	?
	inc 35	Zoochorous	?
	inc 96	Zoochorous	?
	inc cf Rubiaceae sp.29	?	?
	inc RUB spp.	Zoochorous	?
	Massularia acuminata	Zoochorous	5.0
	Oxyanthus sp.	Zoochorous	6.0
	Psychotria sp.1	Zoochorous	?
	Psychotria sp.3	Zoochorous	?
	Rothmannia sp.1	Zoochorous	8.0
	Rubiaceae sp.1 08/01	Zoochorous	?
	Rubiaceae sp.1 14/01	Zoochorous	?
	Rubiaceae sp.10	Zoochorous	?
	Rubiaceae sp.11	Zoochorous	?
	Rubiaceae sp.12	Zoochorous	?
	Rubiaceae sp.12	Zoochorous	?
	Rubiaceae sp.13	Zoochorous	?
	Rubiaceae sp.14	Zoochorous	?
	Rubiaceae sp.15	Zoochorous	?
	Rubiaceae sp.16	Zoochorous	?
	Rubiaceae sp.17	Zoochorous	?

	Rubiaceae sp.18	Zoochorous	?
	Rubiaceae sp.19	Zoochorous	?
	Rubiaceae sp.2	Zoochorous	?
	Rubiaceae sp.20	Zoochorous	?
	Rubiaceae sp.22	Zoochorous	?
	Rubiaceae sp.23	Zoochorous	?
	Rubiaceae sp.24	Zoochorous	?
	Rubiaceae sp.25	Zoochorous	?
	Rubiaceae sp.26	Zoochorous	?
	Rubiaceae sp.27	Zoochorous	?
	Rubiaceae sp.3	Zoochorous	?
	Rubiaceae sp.4	Zoochorous	?
	Rubiaceae sp.5	Zoochorous	?
	Rubiaceae sp.6	Zoochorous	?
	Rubiaceae sp.7	Zoochorous	?
	Rubiaceae sp.8	Zoochorous	?
	Rubiaceae sp.9	Zoochorous	?
	Tricalysia sp.1	Zoochorous	?
Rutaceae	*Citropsis articulata*	Zoochorous	10.0
	Zanthoxylum sp.	Zoochorous	3.5
Sapindaceae	*Blighia welwitschii*	Zoochorous	26.0
	Chytranthus sp.1	Zoochorous	32.0
	Chytranthus sp.2	Zoochorous	32.0
	inc 208	?	?
	Laccodiscus pseudostipularis	Zoochorous	14.0
	Pancovia sp. (cf laurentii)	Zoochorous	15.0
	Radlkofera calodendron	Zoochorous	35.0
	Zanha golungensis	Zoochorous	18.0
	Ganophyllum giganteum	Zoochorous	18.5
Sapotaceae	*Chrysophyllum africanum*	Zoochorous	30.0
	Chrysophyllum boukokoënse	Zoochorous	28.5
	Chrysophyllum pruniforme	Zoochorous	24.0
	inc 112 Sapotaceae	Zoochorous	?
	Pouteria altissima	Zoochorous	15.0
	Synsepalum cerasiferum	Zoochorous	17.5
Simaroubaceae	*Quassia africana*	Zoochorous	20.0
	Quassia silvestris	Zoochorous	?
Sterculiaceae	*Chlamydocola chlamydantha*	Zoochorous	25.0
	Leptonychia sp.	Zoochorous	12.0
Thymelaceae	*Dicranolepis baertsiana*	Zoochorous	?
Tiliaceae	*Desplatsia subericarpa*	Zoochorous	15.0
	Duboscia macrocarpa	Zoochorous	10.0
	Grewia sp.	Zoochorous	?
Violaceae	*Rinorea illicifolia*	Abiotic	9.0
	Rinorea sp.1 08/01	Abiotic	15.5

Table 4-S3. Values obtained for the soil variables at each location.

site	location	pH-H2O	pH-Cohex	ECEC (cmolc/kg)	Al	Ca	Fe	K	Mg	Mn	Mo	P	Zn	N_{tot}	Sand	Slit	Clay
					(μg/g)									(%)			
Nkala	1	4.41	3.54	1.80	140.96	96.59	12.48	58.81	21.60	9.95	0.09	1.21	67.57	0.17	63.7	23.2	13.1
Nkala	2	4.60	3.66	3.20	140.23	205.92	6.16	57.32	27.23	13.12	0.07	1.02	30.74	0.15	63.7	23.2	13.1
Nkala	3	4.24	3.14	2.37	102.18	20.64	23.71	52.87	17.38	2.49	0.06	1.71	28.76	0.23	61.8	22.2	16.0
Nkala	4	4.54	3.31	2.85	78.68	20.39	15.02	32.02	11.33	2.48	0.06	1.09	42.42	0.16	61.8	22.2	16.0
Nkala	5	4.31	3.58	8.48	387.52	159.40	11.22	85.96	103.37	20.58	0.29	1.21	45.41	0.24	61.8	22.2	16.0
Nkala	6	4.50	3.56	4.54	363.07	77.08	12.77	100.75	51.05	22.93	0.25	0.73	39.46	0.18	61.8	22.2	16.0
Nkala	43	4.05	3.18	0.33	95.20	11.64	20.78	22.32	7.81	1.08	0.07	0.82	7.93	0.17	61.8	22.2	16.0
Nkala	44	4.17	3.10	1.81	95.11	28.16	24.88	32.24	10.36	2.35	0.07	1.15	16.75	0.13	61.8	22.2	16.0
Nkala	45	4.08	3.58	4.00	265.44	29.47	16.05	34.43	16.80	4.38	0.17	0.70	14.11	0.13	63.7	23.2	13.1
Nkala	46	4.27	3.59	2.16	259.80	76.22	14.57	47.84	29.53	7.45	0.16	1.09	13.80	0.19	63.7	23.2	13.1
Nkala	59	4.35	3.66	1.71	303.88	30.23	10.13	42.35	22.17	4.75	0.20	0.47	4.38	0.07	61.8	22.2	16.0
Nkala	60	4.34	3.66	4.07	300.74	24.92	12.72	33.27	20.81	3.07	0.21	0.89	7.64	0.14	61.8	22.2	16.0
Nkala	61	4.14	3.23	1.80	93.27	13.43	19.49	23.10	7.95	2.64	0.06	0.94	11.68	0.14	61.8	22.2	16.0
Nkala	62	4.11	3.09	3.42	97.58	34.24	19.24	24.73	13.04	2.62	0.07	0.87	10.07	0.14	61.8	22.2	16.0
Nkala	91	4.29	3.34	0.52	124.68	56.37	16.44	65.57	17.41	5.17	0.08	1.07	11.33	0.17	63.7	23.2	13.1
Nkala	92	4.47	3.62	3.32	188.49	36.59	8.34	86.79	46.95	8.35	0.11	0.90	6.18	0.15	63.7	23.2	13.1
Nkala	93	4.27	3.55	0.49	100.98	13.72	7.07	32.03	7.38	2.42	0.11	0.59	5.92	0.11	63.7	23.2	13.1
Nkala	94	4.39	3.68	2.88	187.18	27.43	4.35	49.38	15.69	14.37	0.13	0.54	8.75	0.11	63.7	23.2	13.1
Nkala	113	3.98	3.11	1.71	75.93	30.90	21.89	42.14	13.59	4.97	0.06	1.28	7.91	0.13	63.7	23.2	13.1
Nkala	114	4.13	3.23	0.79	77.64	17.98	16.82	33.34	10.59	2.57	0.07	1.21	2.64	0.17	63.7	23.2	13.1
Mbanzi	7	4.19	3.27	2.32	41.32	94.24	17.81	48.58	18.56	13.51	0.05	2.04	21.07	0.15	84.2	8.6	7.2
Mbanzi	8	4.36	3.31	1.25	28.93	25.67	17.18	52.80	10.01	4.27	0.05	1.18	71.80	0.16	84.2	8.6	7.2
Mbanzi	9	4.09	3.14	2.03	54.30	30.46	22.15	47.07	12.47	3.34	0.05	1.39	47.91	0.22	81.0	9.8	9.2
Mbanzi	10	4.21	3.12	3.41	54.05	42.29	29.12	55.55	13.07	4.49	0.06	1.54	37.37	0.26	81.0	9.8	9.2
Mbanzi	11	4.16	3.15	3.37	66.17	26.37	26.82	44.89	11.21	3.02	0.05	1.53	43.67	0.20	84.2	8.6	7.2
Mbanzi	12	4.12	3.01	2.37	44.06	35.11	29.77	49.91	16.87	6.15	0.06	1.61	45.08	0.28	84.2	8.6	7.2

Mbanzi	53	4.17	3.22	1.96	80.27	16.70	28.28	37.80	9.46	2.81	0.06	1.07	25.85	0.17	84.2	8.6	7.2
Mbanzi	54	4.03	3.08	2.90	92.43	21.88	32.94	33.38	11.32	2.17	0.06	1.03	10.61	0.18	84.2	8.6	7.2
Mbanzi	55	4.20	3.32	2.99	63.10	49.78	22.80	37.25	15.69	3.99	0.06	1.33	11.72	0.17	81.0	9.8	9.2
Mbanzi	56	4.18	3.29	0.96	56.64	23.81	21.18	32.67	11.10	2.60	0.06	0.91	10.74	0.13	81.0	9.8	9.2
Mbanzi	95	4.13	3.13	0.83	45.62	27.00	26.83	57.62	10.64	2.20	0.06	1.28	25.68	0.34	84.2	8.6	7.2
Mbanzi	96	4.25	3.44	1.95	40.61	25.76	15.96	35.87	9.57	2.09	0.07	0.92	8.05	0.15	84.2	8.6	7.2
Mbanzi	97	4.05	3.27	1.70	47.55	65.89	24.24	57.34	17.38	13.40	0.06	1.47	8.24	0.19	84.2	8.6	7.2
Mbanzi	98	4.63	3.63	0.98	33.36	123.54	8.56	30.45	25.21	10.12	0.06	0.68	10.09	0.12	84.2	8.6	7.2
Mbanzi	99	4.06	3.20	1.62	69.34	35.63	33.32	41.93	14.79	5.00	0.06	1.27	10.36	0.26	81.0	9.8	9.2
Mbanzi	100	4.37	3.45	0.63	41.32	35.89	14.29	16.61	13.40	3.35	0.06	0.59	7.29	0.08	81.0	9.8	9.2
Mbanzi	101	4.17	3.29	0.91	103.82	37.33	53.47	67.90	26.41	8.54	0.07	1.38	11.99	0.16	84.2	8.6	7.2
Mbanzi	102	4.22	3.22	0.27	64.54	30.23	25.19	33.61	9.04	5.95	0.06	0.81	6.23	0.13	84.2	8.6	7.2
Mbanzi	103	4.00	3.19	1.60	42.34	33.36	30.93	49.45	18.97	3.83	0.06	1.03	7.19	0.14	84.2	8.6	7.2
Mbanzi	104	4.08	3.23	0.63	59.15	18.63	25.04	26.69	6.63	2.19	0.06	1.09	9.09	0.14	84.2	8.6	7.2
Mbanzi	105	4.15	3.24	0.67	58.69	14.69	22.23	33.31	5.96	2.66	0.06	0.77	5.82	0.16	84.2	8.6	7.2
Mbanzi	106	3.94	3.06	0.72	62.76	14.53	30.79	40.74	7.36	2.69	0.07	1.07	6.50	0.15	84.2	8.6	7.2
Mbanzi	109	4.05	2.96	3.66	110.29	39.08	35.82	60.97	22.78	5.54	0.07	2.17	16.91	0.18	84.2	8.6	7.2
Mbanzi	110	4.09	3.13	1.45	83.77	12.88	24.42	31.73	10.42	1.19	0.07	0.93	10.44	0.12	84.2	8.6	7.2
Mbanzi	111	4.19	3.14	1.21	70.52	10.30	25.38	29.64	5.05	1.41	0.06	0.92	7.68	0.13	84.2	8.6	7.2
Mbanzi	112	4.17	3.24	2.53	101.45	12.35	19.74	30.75	6.07	0.88	0.08	0.92	5.65	0.18	84.2	8.6	7.2
Minkalu	13	4.42	3.65	3.28	225.03	63.99	8.88	89.26	59.33	13.09	0.14	0.96	22.87	0.17	45.9	37.1	17.0
Minkalu	14	4.33	3.55	6.04	330.89	76.97	14.24	61.47	58.94	18.29	0.23	1.17	24.29	0.24	45.9	37.1	17.0
Minkalu	15	4.63	3.60	1.40	62.10	62.66	7.15	31.56	18.16	5.41	0.05	1.10	7.45	0.15	66.8	22.4	10.8
Minkalu	16	4.35	3.32	2.58	89.82	182.64	12.47	71.64	47.12	22.65	0.05	2.44	8.49	0.21	66.8	22.4	10.8
Minkalu	17	4.32	3.24	1.92	53.73	73.39	10.64	47.94	18.48	9.78	0.05	2.09	12.45	0.20	66.8	22.4	10.8
Minkalu	18	4.44	3.43	1.41	49.14	64.92	10.34	44.54	12.73	5.55	0.05	1.24	16.23	0.13	66.8	22.4	10.8
Minkalu	19	4.41	3.61	2.47	243.82	11.60	10.66	34.31	17.82	5.69	0.15	0.70	8.28	0.16	45.9	37.1	17.0
Minkalu	20	4.18	3.37	4.97	199.85	177.08	18.97	68.77	44.10	14.39	0.14	1.39	13.95	0.22	45.9	37.1	17.0
Minkalu	21	4.40	3.73	4.45	210.20	48.58	5.65	37.99	21.02	9.16	0.13	0.84	52.19	0.16	45.9	37.1	17.0

Minkalu	22	4.58	3.68	2.24	152.32	90.00	6.37	37.09	32.63	21.74	0.08	1.11	21.64	0.12	45.9	37.1	17.0
Minkalu	47	4.88	3.72	1.72	96.43	238.58	2.13	59.25	67.43	35.97	0.06	0.84	7.83	0.11	45.9	37.1	17.0
Minkalu	48	4.91	3.68	3.03	180.75	268.71	1.98	42.95	99.43	40.68	0.11	0.48	15.61	0.11	45.9	37.1	17.0
Minkalu	49	4.18	3.42	1.84	158.45	103.89	12.73	44.21	18.39	6.30	0.11	1.77	23.46	0.16	66.8	22.4	10.8
Minkalu	50	4.37	3.55	1.03	124.17	43.79	9.61	46.29	26.55	4.27	0.09	0.85	17.30	0.15	66.8	22.4	10.8
Minkalu	51	4.26	3.70	2.22	246.31	23.20	4.60	12.37	11.63	6.14	0.17	0.55	12.40	0.10	66.8	22.4	10.8
Minkalu	52	4.28	3.59	1.53	312.68	74.37	10.62	49.83	27.28	13.92	0.22	0.82	12.36	0.12	66.8	22.4	10.8
Minkalu	107	4.54	3.61	1.96	263.18	48.94	1.54	22.44	25.83	80.21	0.18	0.54	1.31	0.11	45.9	37.1	17.0
Minkalu	108	4.33	3.48	1.63	347.97	26.86	16.57	46.98	37.12	5.88	0.25	1.16	4.23	0.14	45.9	37.1	17.0
Mbominzoli	23	4.23	3.32	2.05	95.47	28.83	18.66	23.75	8.59	2.71	0.06	1.05	14.25	0.15	87.1	5.6	7.2
Mbominzoli	24	4.40	3.38	2.36	84.99	17.51	20.48	33.56	7.13	2.01	0.09	0.96	14.37	0.15	87.1	5.6	7.2
Mbominzoli	25	4.21	3.20	4.01	108.04	65.86	21.33	45.63	13.13	4.72	0.06	1.34	14.52	0.16	87.1	5.6	7.2
Mbominzoli	26	4.14	3.39	4.21	125.57	47.19	28.88	61.34	23.00	8.66	0.06	1.82	14.20	0.24	87.1	5.6	7.2
Mbominzoli	27	4.33	3.34	0.55	77.05	41.39	21.82	41.30	15.39	4.73	0.06	1.03	9.31	0.12	87.1	5.6	7.2
Mbominzoli	28	4.23	3.34	2.14	61.34	24.28	13.85	24.33	8.54	2.78	0.06	1.20	10.64	0.14	87.1	5.6	7.2
Mbominzoli	29	4.23	3.26	2.57	99.80	36.09	18.11	29.55	10.05	3.38	0.06	0.63	19.92	0.17	86.6	4.5	8.9
Mbominzoli	30	5.20	3.75	1.46	45.41	36.16	6.09	77.44	13.68	4.43	0.06	0.97	6.57	0.13	86.6	4.5	8.9
Mbominzoli	31	4.45	3.37	2.58	51.19	25.87	19.60	39.09	10.81	4.45	0.06	1.10	72.04	0.22	86.6	4.5	8.9
Mbominzoli	32	4.38	3.41	1.29	59.68	35.83	17.43	48.54	14.93	5.51	0.06	1.40	10.72	0.33	86.6	4.5	8.9
Mbominzoli	63	4.17	3.17	4.06	80.29	57.49	23.24	36.35	13.39	5.10	0.06	1.35	7.30	0.10	86.6	4.5	8.9
Mbominzoli	64	4.13	3.21	4.21	82.23	72.66	22.93	55.47	21.47	7.17	0.06	2.38	8.22	0.22	86.6	4.5	8.9
Mbominzoli	65	4.23	3.31	2.16	45.79	31.19	23.46	42.91	11.96	4.14	0.06	1.34	5.43	0.15	86.6	4.5	8.9
Mbominzoli	66	4.15	3.12	3.34	53.14	32.33	25.19	33.53	13.39	4.13	0.07	1.89	9.11	0.18	86.6	4.5	8.9
Mbominzoli	67	4.17	3.30	0.28	64.60	11.20	19.74	13.17	5.49	1.78	0.06	0.71	5.78	0.11	87.1	5.6	7.2
Mbominzoli	68	4.19	3.26	3.15	60.35	15.66	22.17	26.09	7.47	1.54	0.07	1.22	6.50	0.19	87.1	5.6	7.2
Mbominzoli	69	4.23	3.31	1.40	51.95	35.68	17.86	35.22	14.12	3.99	0.05	1.21	7.74	0.13	87.1	5.6	7.2
Mbominzoli	70	4.46	3.37	1.17	74.20	37.98	19.02	32.71	18.47	5.37	0.06	1.29	4.70	0.16	87.1	5.6	7.2
Mbominzoli	71	4.25	3.34	3.02	93.89	17.28	17.40	11.08	6.22	1.68	0.07	0.86	2.03	0.14	87.1	5.6	7.2
Mbominzoli	72	4.11	3.15	2.43	96.91	30.99	21.77	40.32	12.84	9.91	0.07	1.52	3.97	0.15	87.1	5.6	7.2
Mbominzoli	73	4.33	3.43	1.87	43.58	16.95	14.63	23.94	6.20	3.25	0.06	0.74	3.55	0.11	86.6	4.5	8.9

Mbominzoli	74	4.49	3.50	2.03	42.69	15.34	12.35	14.58	10.95	2.83	0.06	0.71	3.45	0.11	86.6	4.5	8.9
Mbominzoli	75	4.21	3.44	1.66	60.24	11.70	14.58	38.46	7.92	1.88	0.06	0.86	3.97	0.16	86.6	4.5	8.9
Mbominzoli	76	4.24	3.27	2.63	47.88	41.17	20.13	33.95	11.32	5.29	0.06	1.00	4.42	0.21	86.6	4.5	8.9
Mbominzoli	77	4.00	3.09	2.32	93.39	58.56	31.54	41.86	13.25	6.17	0.06	1.40	3.81	0.21	86.6	4.5	8.9
Mbominzoli	78	4.29	3.36	1.45	44.30	16.66	17.86	15.75	7.52	2.08	0.06	1.33	5.17	0.15	86.6	4.5	8.9
Nkombo	33	4.26	3.12	2.55	96.88	36.67	26.00	55.21	15.22	6.47	0.07	1.49	19.08	0.37	81.6	8.8	9.6
Nkombo	34	4.18	3.25	1.47	89.80	9.89	24.00	25.33	6.34	1.89	0.06	0.87	10.01	0.14	81.6	8.8	9.6
Nkombo	35	4.09	3.12	3.23	91.23	18.66	28.53	39.48	8.95	3.79	0.08	1.25	30.66	0.26	81.6	8.8	9.6
Nkombo	36	4.17	3.21	0.18	86.84	18.56	22.94	31.77	10.48	3.49	0.06	1.32	20.97	0.22	81.6	8.8	9.6
Nkombo	37	4.20	3.31	1.97	72.29	13.05	23.75	31.57	8.11	1.18	0.07	0.72	9.41	0.15	81.6	8.8	9.6
Nkombo	38	4.28	3.27	2.18	65.09	79.27	21.06	58.50	13.84	4.26	0.06	1.13	12.12	0.15	81.6	8.8	9.6
Nkombo	39	4.07	3.10	3.68	105.20	16.97	29.66	32.86	8.76	2.06	0.08	1.09	32.64	0.21	81.6	8.8	9.6
Nkombo	40	4.08	3.20	0.78	73.73	22.95	32.51	21.16	9.58	5.09	0.07	1.05	7.98	0.12	81.6	8.8	9.6
Nkombo	41	4.20	3.25	0.37	43.42	86.54	21.99	90.06	25.46	8.89	0.05	1.64	27.89	0.20	85.7	6.8	7.6
Nkombo	42	4.25	3.33	1.80	51.36	32.28	18.06	42.27	12.93	5.05	0.06	1.01	18.02	0.09	85.7	6.8	7.6
Nkombo	57	4.10	3.38	2.77	123.27	24.43	18.70	33.44	8.65	4.34	0.09	0.64	12.89	0.15	81.6	8.8	9.6
Nkombo	58	4.26	3.32	0.34	84.22	22.85	25.71	31.81	11.97	6.70	0.06	0.63	20.43	0.20	81.6	8.8	9.6
Nkombo	79	4.12	3.35	1.69	100.48	49.47	26.91	61.64	29.46	8.89	0.07	1.05	4.61	0.17	81.6	8.8	9.6
Nkombo	80	4.08	3.25	1.26	66.04	9.52	31.19	13.51	6.09	2.47	0.07	0.73	4.09	0.14	81.6	8.8	9.6
Nkombo	81	4.09	3.20	1.15	111.73	18.79	32.03	36.16	9.44	6.58	0.07	0.94	3.33	0.18	81.6	8.8	9.6
Nkombo	82	3.99	3.16	1.95	88.05	13.17	31.19	30.36	8.75	2.82	0.06	1.08	5.22	0.16	81.6	8.8	9.6
Nkombo	83	4.15	3.27	1.55	63.11	29.73	38.89	51.80	17.18	6.17	0.06	0.85	7.84	0.14	81.6	8.8	9.6
Nkombo	84	4.12	3.22	1.70	73.73	16.01	35.37	26.31	10.54	3.32	0.06	0.87	7.42	0.17	81.6	8.8	9.6
Nkombo	85	4.10	3.13	1.48	151.84	16.64	27.97	42.81	17.49	5.19	0.09	2.11	3.85	0.19	81.6	8.8	9.6
Nkombo	86	4.12	3.27	3.07	152.68	7.34	20.37	48.62	8.88	3.43	0.08	2.83	2.03	0.21	81.6	8.8	9.6
Nkombo	87	4.40	3.55	1.27	53.12	11.24	11.19	19.06	6.32	1.30	0.06	0.62	3.98	0.11	81.6	8.8	9.6
Nkombo	88	4.23	3.43	2.07	53.85	17.38	15.82	15.46	7.23	3.81	0.07	0.77	2.91	0.11	81.6	8.8	9.6
Nkombo	89	4.22	3.33	1.84	49.77	40.40	29.48	86.25	15.17	5.03	0.06	2.14	5.95	0.19	85.7	6.8	7.6
Nkombo	90	4.19	3.18	2.18	60.68	79.56	27.71	75.31	21.47	6.33	0.06	0.95	5.03	0.13	85.7	6.8	7.6

Table 4-S4. Main characteristics of the study sites in terms of conservation programs, hunting pressure, and large frugivore community in D.R. Congo.

Site	Conservation / monitoring programs (main NGOs involved)	Hunting pressure (obs./km)	Large frugivores		
			Abundance (obs./km)		Forest elephants
			Primates	Hornbills	
Mbanzi	Elephant monitoring [WWF]	1.19	0.94	3.82	Present
Nkombo	Elephant monitoring [WWF] until 2013	0.46	0.47	5.85	Present
Mbominzoli	Large mammal monitoring [MMT] hunting taboo for bonobos	0.56	1.63	4.82	Present
Minkalu	Bonobos habituation [MMT, WWF] hunting taboo for bonobos	1.28	1.35	2.62	Absent
Nkala		0.98	5.70	2.54	Absent

[MMT] = Mbou-Mon-Tour

[WWF] = WWF-DRC

Table 4-S5. Correlation among biotic and abiotic explanatory variables. Bold indicate a level of correlation > 0.70 and variables that were excluded from the statistical analysis.

	Biotic variables		Abiotic variables															
Biotic variables		hornbills	pH H2O	**pH Cohex**	ECEC	Al	Ca	**Fe**	K	Mg	Mn	Mo	P	Zn	Nt	% sand	**% silt**	% clay
	primates	-0.63																
Abiotic variables	pH.H2O		1.00	**0.75**	0.05	0.18	0.48	**-0.71**	0.19	0.44	0.44	0.18	-0.26	0.13	-0.23	-0.39	0.39	0.38
	pH.Cohex			1.00	0.15	0.54	0.38	**-0.80**	0.13	0.47	0.41	0.54	-0.43	0.02	-0.37	-0.56	0.56	0.51
	ECEC				1.00	0.51	0.32	-0.14	0.32	0.50	0.21	0.48	0.20	0.29	0.26	-0.28	0.25	0.33
	Al					1.00	0.25	-0.39	0.28	0.58	0.41	**0.96**	-0.18	0.10	-0.04	-0.68	0.67	0.67
	Ca						1.00	-0.40	0.46	**0.77**	0.58	0.19	0.12	0.16	0.01	-0.44	0.46	0.38
	Fe							1.00	0.00	-0.37	-0.41	-0.39	0.31	-0.06	0.34	0.58	-0.58	-0.53
	K								1.00	0.58	0.24	0.25	0.38	0.29	0.36	-0.21	0.21	0.18
	Mg									1.00	0.60	0.56	0.02	0.17	0.07	-0.59	0.59	0.54
	Mn										1.00	0.37	-0.07	0.03	-0.08	-0.51	0.53	0.44
	Mo											1.00	-0.24	0.09	-0.06	-0.61	0.60	0.60
	P												1.00	0.11	0.51	0.20	-0.19	-0.22
	Zn													1.00	0.35	-0.14	0.13	0.16
	Nt														1.00	0.13	-0.14	-0.10
	% sand															1.00	**-0.99**	**-0.94**
	% silt																1.00	**0.90**
	% clay																	1.00

Table 4-S6. Proportion of the variation (R^2_{adj}) of the three response variables (density, species richness, and mean seed length of animal-dispersed seedlings) explained by each explanatory selected by the forward selection according to Blanchet et al. (2008), and among the three components (biotic, abiotic, and spatial) considered in the variation partitioning analysis according to Borcard et al. (1992). The variable 'Location type' refers to whether survey plots were placed under *S. kamerunensis* tree, under *Dialium* spp. tree, or at random.

	Response variables						
	Density			**Species richness**			**Seed length**
Biotic component	None			Location type	Primate abundance		Hornbill abundance
Per variable[a]	0.00			0.09	0.09		0.12
Total[b]	0.00			0.18 **			0.12 **
Pure[b]	0.00			0.04 *			0.00
Abiotic component	K	P	Nt	% clay	K	P	% clay
Per variable[a]	0.1	0.03	0.04	0.12	0.05	0.03	0.04 *
Total[b]	0.17 **			0.20 **			0.04
Pure[b]	0.17 **			0.03			-0.01
Spatial component							
Total[b]	0.00			0.22 **			0.25 **
Pure[b]	0.00			0.07 **			0.13 **
Total	0.17			0.32			0.24

[a] R^2_{adj} obtained from the forward selection. Level of significance per variable is not illustrated.

[b] Fractions (R^2_{adj}) obtained from the variation partitioning analysis. * and ** indicate significant ($p < 0.05$) and highly significant ($p < 0.01$) levels, respectively.

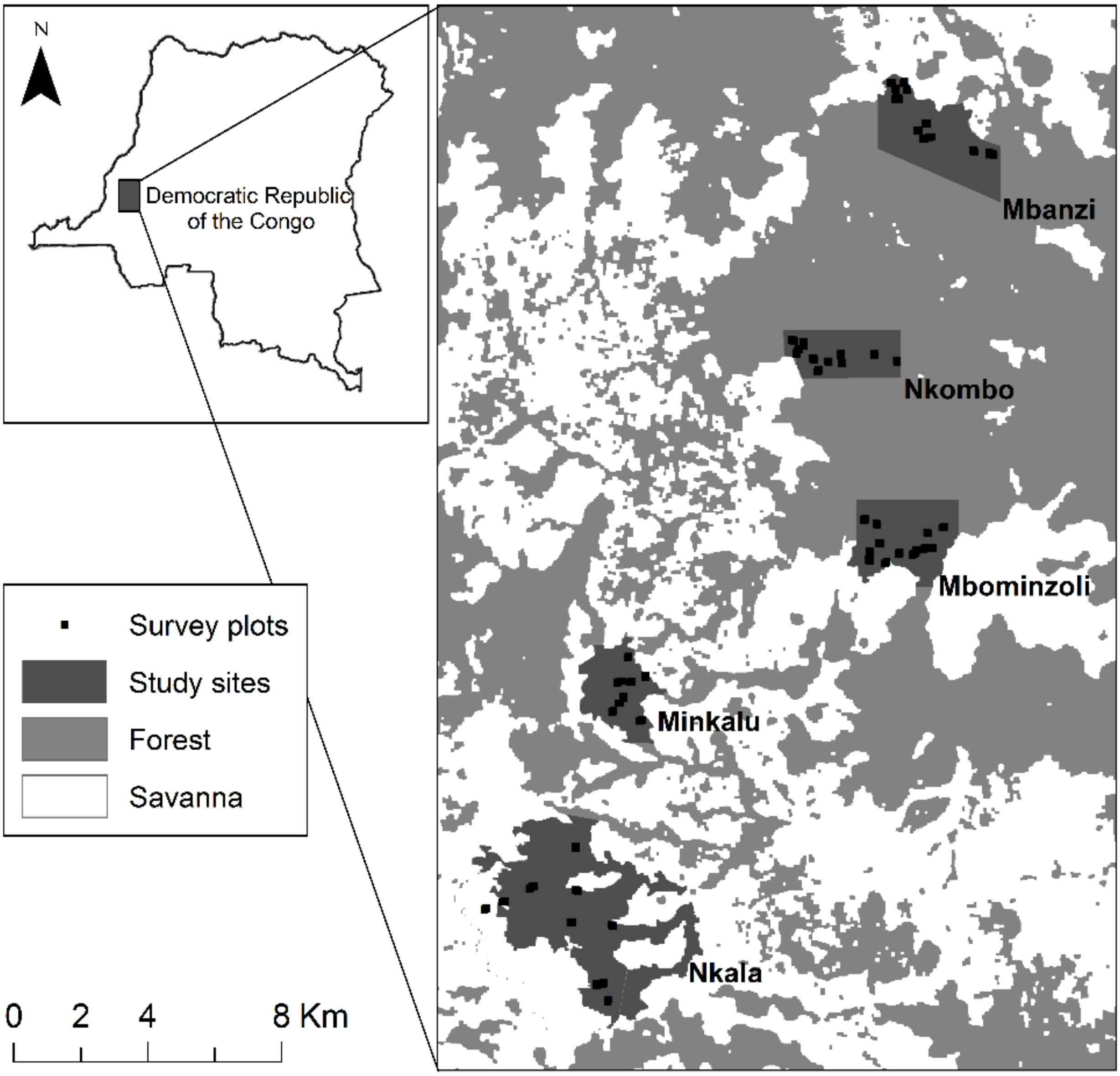

Fig. 4-S1. Map of the study area in the forest-savanna mosaic in D.R. Congo, with the five sites (Mbanzi, Nkombo, Mbominzoli, Minkalu, and Nkala) and the location of the survey plots.

Synthèse générale et perspectives

L’objectif principal de cette thèse était de mieux comprendre comment les services de dispersion des graines assurés par les frugivores ainsi que leur rôle dans la régénération des plantes sont affectés dans un paysage anthropisé. Ainsi, nous nous sommes focalisés d’une part sur les processus de dispersion des graines zoochores, puis d’autre part sur le processus de régénération des plantes.

Dans les deux premiers chapitres, nous avons examiné la dispersion des graines zoochores en adoptant d’abord la perspective d’un grand frugivore (Chapitre 1), puis celle d’une espèce d’arbre zoochore à grandes graines (Chapitre 2) :

Ch. 1. Quel rôle joue le bonobo, une espèce de grand frugivore rare et menacée, dans la dispersion des graines au sein d’un paysage affecté par les activités anthropiques ?

Dans cette étude, nous avons vu que :

- Plus de 80 % des espèces de plantes dispersées par les bonobos ont des graines de grande taille (> 1cm) que peu ou pas d’autres frugivores ne peuvent disperser.
- Près de 50 % des plantes dispersées sont sciaphiles, lesquelles ont toutes des graines de grande taille.
- Les bonobos ont montré une préférence pour les habitats avec une quantité intermédiaire de lumière au sol, lesquels facilitent probablement l’établissement d’espèces sciaphiles.
- Nous avons déduit qu’en dépit de sa rareté, cette espèce de primate menacée joue certainement un rôle crucial dans la régénération des forêts matures.
- Les plans de gestion devraient prêter attention aux frugivores de grandes tailles dans les paysages altérés par les activités anthropiques car ceux-ci peuvent fournir des services écosystémiques uniques et primordiaux.

Ch. 2. Comment la couverture forestière, la chasse et la disponibilité en fruits affectent-ils les capacités de dispersion d’une espèce d’arbre à grande graines, Staudtia kamerunensis *(Myristicaceae) ?*

Dans cette étude, nous avons vu que :

- *S. kamerunensis* semble avoir un système de dispersion des graines très spécialisé : une seule espèce de calaos, *Bycanistes albotibialis* (Bucerotideae), représente le principal frugivore observé dans ses arbres en fruits, avec plus de 95 % du temps total d’observation.
- La pression de chasse, la diminution du couvert forestier et la disponibilité en fruits à l’échelle du site font augmenter l’échec de dispersion des graines.
- Une forte disponibilité en fruits et une faible abondance de disperseurs tendraient à accélérer la satiation de ces derniers et suggèreraient que le système plante-frugivore peut atteindre un point de saturation lorsque la densité des disperseurs devient trop faible.
- Les plans de gestion devraient accorder plus d’importance à la conservation des calaos car ils assurent une fonction unique, particulièrement dans les paysages perturbés.

Dans les deux chapitres suivants, nous nous sommes concentrés sur la régénération forestière à proprement parler, tout en nous plaçant à l'échelle de la communauté végétale afin d'avoir une compréhension plus globale de ce processus dans le paysage. Nous avons tout d'abord étudié le rôle des frugivores dans la création de foyers de recrutement (Chapitre 3), puis exploré l'influence spécifique de différents taxons de frugivores sur la composition de la communauté de plantules (Chapitre 4). Dans ce dernier chapitre, nous avons aussi cherché à définir la part relative du sol sur la régénération végétale.

Ch. 3. Est-ce que les arbres zoochores agissent comme des foyers de recrutement via l'attraction de calaos et de primates ? Est-ce que la disponibilité en fruits dans le voisinage et la quantité de surface forestière dans le paysage influencent ce patron spatial de régénération?

Dans cette étude, nous avons vu que :

- Les arbres de *S. kamerunensis* agissent comme foyers de recrutement. Sous leur couronne, on observe une densité et une richesse spécifique particulièrement hautes, au contraire de ce qui est observé sous les couronnes de *Dialium* spp.
- Les calaos pourraient être les vecteurs les plus importants de cette organisation spatiale des plantules.
- La quantité de couverture forestière dans le paysage a un effet positif, mais faible, sur la densité de plantules dispersées par les calaos.
- *S. kamerunensis* joue un rôle structurant dans les forêts afrotropicales et les calaos forment un taxon clé dans les paysages anthropisés.

Ch. 4. Est-ce que différents taxons de frugivores (calaos, primates et éléphants) ont un rôle fonctionnel redondant sur la composition des communautés de plantules zoochores ? Et, quelle est l'importance relative de la dispersion des graines et des paramètres du sol sur la régénération des plantes ?

Dans cette étude, nous avons vu que :

- Les paramètres du sol expliquent une faible part (17 %) de la variation de la densité de plantules zoochores.
- Ensemble, les paramètres de sol et la composition de la communauté de frugivores expliquent 32 et 24 % de la variation de la richesse spécifique et de la taille moyenne des graines des plantules zoochores, respectivement.
- La redondance fonctionnelle des trois taxons de frugivores dépend de la variable réponse considérée.
- Il ne semble y avoir un rôle redondant que pour la densité de plantules zoochores.
- Les primates jouent un rôle particulièrement important en ce qui concerne la richesse spécifique, alors que les calaos et les éléphants semblent particulièrement importants pour assurer la régénération de plantes à grandes graines.

Fragilité du processus de régénération des plantes

Au travers des deux premiers chapitres, nous avons pu montrer l'importance écologique des frugivores dans le processus de dispersion des graines. Plus particulièrement, nous avons montré que les fruits des espèces à grandes graines représentent une part considérable du régime alimentaire des bonobos, lesquels sont susceptibles d'être les uniques disperseurs de nombreuses de ses plantes. Ensuite, nous avons montré que la dispersion des graines d'un arbre zoochore semblait dépendre étroitement de l'action d'une seule espèce de calaos. Ainsi, chacun de ses deux taxons de frugivores semblent jouer un rôle unique pour la dispersion et donc la régénération d'un ensemble d'espèces de plantes. Bien que ces travaux soient des études de cas, donc focalisées sur des systèmes bien spécifiques, ceux-ci adoptent des perspectives complémentaires et illustrent clairement la fragilité des interactions entre les frugivores et les plantes à grandes graines à l'échelle de la communauté. Ainsi, les activités anthropiques qui menacent ces frugivores pourraient directement affecter les capacités de reproduction et donc la survie de ces espèces d'arbres car ils ont peu de chances d'être disséminés par d'autres frugivores, d'une part car l'assemblage de grands frugivores capables d'ingérer des grandes grandes graines est naturellement restreint, mais surtout car les populations de disperseurs diminuent à cause des pressions humaines. Ainsi, notre étude sur les bonobos a montré qu'ils avaient une préférence pour les forêts à un stade de succession relativement avancé et on sait qu'ils apprecient les lieux situés au-delà de 750 m des lisières (Serckx et al., 2016), or on peut constater que les milieux offrant ces caractéristiques se rarifient.

Par ailleurs, le chapitre 2 illustre à quel point la diminution des ressources forestières (populations animales, couverture forestière) peut faire diminuer le nombre de graines qui sont disséminées à distance des arbres parents. Ainsi, il est important de souligner les risques d'une anthropisation croissante sur la dynamique des interactions mutualistes entre les frugivores et les plantes zoochores à grandes graines. Un aspect qui mériterait d'être étudié est l'impact des activités anthropiques sur les taux de dispersion des graines d'essences étroitement dépendantes des bonobos (comme par exemple les espèces reprises dans le tableau 1-2) de la même manière que nous l'avons fait pour *S. kamerunensis*. Il serait aussi pertinent d'étudier les capacités d'établissements des plantules des mêmes essences dans leurs lieux de dépôts. Cela permettrait de confronter les résultats sur les taux de germination avec ceux obtenus en condition contrôlées dans le cadre de ce projet. De plus, cela nous permettrait de préciser les assemblages de frugivores qui visitent les différentes espèces d'arbres, de déterminer leur contribution relative à l'enlèvement des graines (Haurez et al. 2015b), et d'évaluer de manière générale le niveau de résilience des interactions plantes-frugivores (Wang et al. 2007).

Par ailleurs, le chapitre 4 nous a permis de montrer que la régénération d'essences ayant des grandes graines peut être perturbée lorsque l'abondance des grands frugivores diminue, ce qui confirme leur rôle unique dans la régénération de ces plantes, comme se fût déjà montré ailleurs en Afrique Central (Vanthomme et al. 2010). Cependant, il est important de rappeler que le rôle présumé capital des bonobos dans la régénération d'espèces à grandes graines n'a pas pu être détecté au travers de l'étude de la communauté de plantules. Cette discordance peut être expliquée par le fait que les éléphants, qui sembleraient eux avoir une influence importante sur les plantules, sont capables de disperser des graines plus grandes que les autres frugivores

(Chapman et al. 1992b, Campos-Arceiz and Blake 2011, Beaune et al. 2013d). Il est aussi possible que l'ombre de dispersion générée par chaque frugivore (c-à-d, la distribution spatiale des graines déposées par les disperseurs) soit si déterminante sur le succès d'établissement des plantules que le rôle présumé d'un frugivore dans l'enlèvement, l'ingestion et la dispersion des graines ne concorde pas avec son influence ultime sur l'établissement des plantules. Plusieurs études ont en effet montré l'importance de considérer le niveau d'agrégation des graines dispersées à une échelle fine et de la proximité aux arbres parents afin de prédire le succès d'établissement (Forget et al. 2000, Andresen 2002, Santos-Heredia et al. 2010, Poulsen et al. 2012). Ainsi, l'ombre de dispersion générée par les calaos pourrait favoriser d'avantage l'établissement des plantules que celle générée par les bonobos. Ces derniers sont connus pour déféquer fréquemment aux sites de nids et pourraient alors générer un patron de dispersion relativement aggloméré. Sachant que les fèces de bonobos attirent les granivores (Beaune et al. 2012), un tel patron de dépôt pourrait être associé à un taux de prédation post-dispersion élevé et donc un faible potentiel de survie des graines. Pour tester une telle hypothèse, il serait pertinent de comparer l'influence de l'ombre de dispersion générée par les calaos et par les bonobos sur le destin des graines et les capacités d'établissement des plantules, et en particulier pour les graines de grandes tailles. Ceci pourrait mettre en valeur les mécanismes biotiques qui affectent le rôle écologique des disperseurs de graines et nous permettre de mieux comprendre leur influence ultime sur la régénération des forêts. Enfin, un phénomène qui a été peu discuté jusqu'à présent dans la littérature concernant les forêts tropicales est celui des interactions allélopathiques. Des substances issues du métabolisme secondaire des plantes sont susceptibles de se répandre dans le sol via la formation de la litière et d'inhiber plus ou moins la germination des différentes espèces. L'existence de telles interactions devrait être aussi explorée de la même manière que nous l'avons fait avec des caractéristiques physico-chimiques du sol, afin de comprendre d'une manière plus complète les mécanismes affectant l'établissement des jeunes plantes.

Entre fragilité et résilience des frugivores dans un paysage anthropisé

Comme nous l'avons vu, les frugivores sont largement tributaires des habitats forestiers qui leur fournissent la vaste majorité de leurs ressources. Néanmoins, les deux premiers chapitres font ressortir un point commun très intéressant dans le contexte actuel de déforestation et d'altération des forêts au travers des régions tropicales. Les bonobos et les calaos semblent en effet présenter une certaine résilience au caractère hétérogène du paysage. Les bonobos utilisent régulièrement les forêts secondaires et même les zones ouvertes telles que la savane, que ce soit pour se nourrir, se reposer, ou simplement pour se déplacer et pouvoir accéder à des zones de forêt plus rapidement (Fig. 5-1). Il est très intéressant de voir qu'une espèce de primate hautement frugivore n'évite pas totalement les zones de matrice et ne se limite pas à l'habitat forestier. Ceci confirme des observations faites sur d'autres primates utilisant la matrice, souvent à proximité d'activités anthropiques (chimpanzés : McLennan 2013, babouins : Kunz & Linsenmair 2008, colobes noirs et blanc : Anderson *et al.* 2006, chlorocèbes : Grassham *et* *al.* 2015). De même, des groupes de calaos (en particulier du genre *Bycanistes*) peuvent être facilement observés en train de survoler la savane sur des distances de plusieurs centaines de mètres. Malgré le manque de données concrètes sur les mouvements de ces oiseaux au travers de la mosaïque, nos observations confirment qu'ils se déplacent activement au travers de paysage perturbées, comme observé ailleurs en Afrique ((Lenz et al. 2011, Chasar et al. 2014), Fig. 5-2.) Aussi, nous avons pu mettre en avant l'implication des calaos dans le maintien d'agrégats de régénération au travers de la mosaïque malgré une faible influence de la couverture forestière. Ce résultat confirme donc que leur mobilité leur confère un avantage fonctionnel important par rapport aux autres vertebrés arboticoles dont les mouvements sont plus affectés par les zones discontinues, en liant le processus de dispersion des graines entre différents lieux du paysages (Bacles et al. 2006, Neuschulz et al. 2013).

En ce qui concerne plus précisément la matrice dans la mosaïque, elle est majoritairement composée de savanes que nous pouvons qualifier de semi-naturelles. Bien qu'elles soient entretenues par des activités anthropiques (pâturage du bétail, implantations humaines, feux), au même titre que certaines zones de forêt dégradée (zones d'agriculture actives et jachères à proximité des implantations humaines), leur majorité n'est pas sujette à une gestion active et continue tout au long de l'année (Fig. 5-1). Par ailleurs, il faut rappeler que la structure fragmentée de la mosaïque résulte aussi d'un gradient écologique naturel entre les vastes étendues forestières du bassin du fleuve Congo au Nord et les zones plus sèches au Sud (Fig. 0-9, p. 32). Le caractère morcelé de ce paysage existe donc probablement depuis très longtemps. Ainsi le niveau de perturbation n'est pas directement comparable à celui que l'on peut observer dans de nombreux paysages tropicaux où la fragmentation résulte d'une déforestation récente et de grande envergure et où les zones d'agriculture et de pâturage sont utilisées de manière permanentes et intensives (e.g. Anderson *et al.* 2006). Le comportement des animaux vivant dans la mosaïque n'est donc probablement pas représentatif de celui que l'on pourrait observer dans des agroécosystèmes plus récents. Ainsi, il serait important d'explorer le comportement d'utilisation de l'habitat par les frugivores dans la mosaïque et en particulier de tester l'influence de la qualité de la matrice (différents régimes d'utilisation et de fréquentation par l'homme, ressources disponibles etc.) sur la présence des frugivores dans et à proximité (effet de lisière affectant le comportement des animaux dans la forêt) de ces zones (Anderson et al. 2006, Kupfer et al. 2006, Hockings et al. 2015). Cette évaluation est une première étape primordiale afin de mieux comprendre les conséquences des activités anthropiques sur les interactions trophiques impliquées dans les processus écologiques nécessaires au maintien de la biodiversité à l'échelle du paysage. De manière plus appliquée, cela permettrait aussi de savoir quelles seraient les mesures optimales à mettre en place pour assurer une connectivité fonctionnelle entre les différentes zones du paysage. Alors que les mesures de conservations se focalisent souvent sur des zones de forêts prédéfinies, la survie de nombreux grands vertébrés dépend aussi de la capacité des individus à voyager à plus grande échelle (dispersion des juvéniles, migrations saisonnières en particulier.

Fig. 5-1. Bonobos se reposant dans une savane en bordure de forêt (gauche © Z. Clay) et vue sur une zone de savane typique de la mosaïque (droite © F. Trolliet).

Fig 5-2. Couple de calaos à cuisse blanche (*Bycanistes albotibialis*) perché sur un arbre à l'extérieur de la forêt (© R.-M. Lafontaine)

Quelle fonction écologique à l'échelle du paysage?

Dans la présente thèse, nous nous sommes principalement focalisés sur la fonction écologique des frugivores au sein même des forêts et à une échelle spatiale relativement réduite. Néanmoins, les changements globaux actuels se traduisent par une complexification de la structure spatiale (îlots forestiers plus ou moins grands et isolés) et de la nature (niveaux de perturbations et stades de succession végétative contrastés) des paysages forestiers. Ceci nous pousse à adapter notre manière d'évaluer les fonctions écologiques des frugivores. En effet, à mesure que les forêts sont fragmentées et dégradées, les frugivores dont le comportement est plus flexible, qui montrent une utilisation généraliste de l'habitat et une mobilité leur permettant de se déplacer efficacement entre des zones de forêts distantes, ou à des stades de succession variés, auront un rôle écologique particulièrement important pour le maintien de la biodiversité à l'échelle du paysage. Ainsi, l'adaptabilité comportementale des bonobos et des calaos à cuisse blanche (*Bycanistes albotibialis*) pourraient leur conférer une fonction tout à fait particulière dans le contexte socio-écologique de la mosaïque. Il serait très intéressant de voir si les calaos assurent un transport des graines inter-fragments (García et al. 2010, Lenz et al. 2011). En agissant comme un lien mobile en maintenant les connections entre différentes zones du paysage forestier (Lundberg and Moberg 2003), ils permettraient ainsi d'éviter les extinctions locales d'espèces de plantes et d'assurer un brassage génétique à travers la mosaïque (Bacles et al. 2006).

Par ailleurs, les frugivores qui utilisent des zones ouvertes et/ou dégradées peuvent dynamiser la succession végétative et permettre la (re)colonisation de la forêt dans des zones récemment déforestées tel que les jachères, ou dans de nouveaux habitats tel que la savane. Un tel rôle a déjà été suggéré pour *B. albotibialis* par Chasar et al. (2014) au Cameroun. Aussi, nous avons dans le chapitre 1 mis en avant l'utilisation de tels habitats par les bonobos, et de leur rôle dans la dispersion de graines d'espèces de plantes héliophiles, essentielles aux premiers stades de succession de la végétation. Le rôle fonctionnel de tels frugivores pourrait donc avoir une très haute valeur pour la conservation de paysages anthropisés (Lindsell et al. 2015). Précisons cependant que la dynamisation du processus de régénération forestière dans des zones dégradées peut être assurée à condition que les graines dispersées aient un profil de régénération qui corresponde aux conditions environnementales dans lesquelles elles sont déposées, en particulier en ce qui concerne la quantité de lumière disponible. Ainsi, un volet capital qui reste à étudier afin de mieux évaluer l'influence des frugivores dans la régénération forestière au sein de paysages anthropisés est à l'interface entre le comportement d'utilisation de l'habitat, le patron spatiale de dépôt des graines et la manière dont les différents lieux de dépôt influencent les capacités d'établissement des plantes (Haurez et al. 2015a). Il faudrait aussi déterminer quels frugivores ont un rôle important dans (i) la dynamique des premiers stades de succession forestière dans les zones ouvertes et dégradées via la dispersion d'espèces typiques de ces zones (espèces héliophiles et pionnières) et (ii) le remplacement des peuplements des forêts matures et du maintien d'une diversité génétique au sein de ces derniers.

Conclusion

De manière générale, la mosaïque de forêts-savanes à l'ouest de la République Démocratique du Congo est un paysage aux caractères, en même temps, unique et modèle. Unique, de par son équilibre particulier entre le niveau d'anthropisation et de fragmentation de l'habitat, et la présence de grands vertébrés emblématiques tels que les bonobos et les éléphants de forêt. Modèle, car il illustre néanmoins un système socio-écologique de plus en plus commun au travers des régions tropicales : un paysage forestier hétérogène, constitué d'une matrice abritant des activités anthropiques qui s'étalent et d'une zone forestière où se côtoient les populations humaines locales dépendantes des ressources naturelles et les acteurs de la conservation de la biodiversité souvent restreints à protéger des espèces menacées d'extinction dans des fragments de forêts. C'est dans cette dernière perspective qu'il est important de valoriser nos différents résultats dans le but de protéger le plus intelligemment possible les organismes qui assurent les processus écologiques nécessaires au maintien de forêts riches et vivantes. Nous avons mis en avant la complexité et la fragilité de la régénération naturelle des forêts tropicales humides. Il est aujourd'hui capital de mettre en avant les aspects primordiaux de ce processus de régénération afin d'optimiser les efforts de conservation :

- Le rôle fonctionnel des grands frugivores est unique de par leur capacité à disperser des graines de grandes tailles. Ils assurent ainsi le maintien de forêts matures et de la diversité biologique qui y est associée.
- Les calaos jouent un rôle fonctionnel unique de par leur mobilité à l'échelle du paysage, qui permet fort probablement de lier les processus de régénération entre des zones distantes et/ou déconnectées.
- La chasse et la déforestation menacent ces taxons clés, et par voie de conséquences, la résilience des écosystèmes forestiers tropicaux dans leur ensemble ainsi que les services écosystémiques qu'ils fournissent aux populations humaines, que ce soit à échelle locale que globale.

Dans un souci de gestion, il apparaît donc nécessaire d'agir à la fois sur ces trois constats, en poursuivant ou entreprenant les actions de conservations des différents frugivores clés et en aidant, par des programmes de développement, les habitants tributaires de ces milieux pour leur vie quotidienne, à mettre en place des pratiques agricoles mieux adaptées à la conservation de ces habitats.

Annexes

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Focus on:

Use of camera traps for wildlife studies. A review

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As human threats continue to impact natural habitats, there is an increasing need to regularly monitor the trends in large vertebrate populations. Conservation efforts must be directed appropriately, but field work necessary for data collection is often limited by time and availability of people. Camera traps are used as an efficient method to insure continuous sampling and to work in difficult to access areas. In the present study, we illustrate how this instrument is serving a diverse field of studies, such as animal behavior, population monitoring and fauna-flora interaction. By looking at the material and technical aspects of various models of camera trap for implementation in different field studies in animal ecology, we highlight the need to choose appropriate camera trap models for the target species and to set up solid sampling protocols to successfully achieve study objectives.

Keywords. Wildlife management, population census, animal behaviour, photography, traps, surveillance systems.

Utilisation des pièges photographiques pour l'étude de la faune sauvage (synthèse bibliographique). Alors que les pressions anthropiques continuent de dégrader les habitats naturels, le besoin de suivre régulièrement les tendances des populations de grands vertébrés augmente. Les efforts de conservation doivent être de plus en plus ciblés mais les travaux de terrains nécessaires à la récolte de données sont souvent limités par le temps et le nombre de personnes disponibles. Les pièges photographiques apparaissent ainsi comme une méthode efficace pour assurer un échantillonnage continu et dans des zones difficilement accessibles. Nous illustrons ici la manière dont cet outil est utilisé pour une diversité de thèmes d'études de terrain tels que le comportement animal, le suivi de populations et les interactions faune-flore. En analysant les aspects techniques et matériels permettant d'assurer différents types de travaux d'écologie animale, nous mettons en évidence la nécessité de sélectionner du matériel et de mettre en place un protocole d'échantillonnage adapté à l'espèce et aux objectifs fixés de l'étude.

Mots-clés. Gestion de la faune et de la flore sauvages, recensement de la population, comportement animal, photographie, piège, système de surveillance.

1. INTRODUCTION

The observed rapid decline in biodiversity, particularly among large vertebrates, throughout the world and the degradation of natural habitats hosting their populations are nowadays widely accepted as fact. It has therefore never been so important to understand how animal populations respond to modern threats and to document the functioning of ecosystems and intra-community interactions (Barrows et al., 2005) as to be able to implement appropriate management and conservation strategies. Regular updating of data on animal population density and on the degree of inter-species interactions is thus crucial to assess the spatio-temporal variations in populations and communities (Bouché et al., 2012). Camera traps are increasingly being used to study wildlife behavior and to conduct population estimations (Cutler et al., 1999; Long et al., 2008; O'Connell et al., 2011; Rovero et al., 2013). In the present study, we undertook a literature review on camera trapping studies, to present some technical aspects of commercially available camera models and provide an overview of sampling procedures and uses of camera trapping data.

2. MATERIALS AND METHODS

We conducted a general literature review on camera trapping using the SciVerse Scopus® database and Google Scholar®. The list of scientific papers consulted is not exhaustive and we do not claim to document all

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