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How complementary are large frugivores for tree seedling recruitment? A case study in the Congo Basin

Research Article

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Abstract

Large frugivores provide critical seed dispersal services for many plant species and their extirpation from forested ecosystems can cause compositional shifts in regenerating plant cohorts. Yet, we still poorly understand whether large seed-dispersers have complementary or redundant roles for forest regeneration. Here, to assess the functional complementarity of large-bodied frugivores in forest regeneration, we quantified the effects of varying abundance of hornbills, primates and the forest elephant on the density, species richness and the mean weighted seed length of animal-dispersed tree species among seedlings in five sites in a forest–savanna mosaic in D. R. Congo, while accounting for percentage forest cover and the local presence of fruiting trees. We found that the abundance of primates was positively associated with species richness of seedlings, while percentage forest cover was negatively associated ($R^2 = 0.19$). The abundance of hornbills, the presence of elephants and percentage forest cover were positively associated with mean seed length of the regenerating cohort ($R^2 = 0.13$). Spatially explicit analysis indicated that some additional processes have an important influence on these response indices. Primates would seem to have a preponderant role for maintaining relatively high species richness, while hornbills and elephant would seem to be predominantly responsible for the recruitment of large-seeded trees. Our results could indicate that these taxa of frugivores play complementary functional roles for forest regeneration. This suggests that the extirpation of one or more of these dispersers would likely not be functionally compensated for by the remaining taxa, hence possibly cascading into compositional shifts.

Introduction

The Anthropocene defaunation, which is caused by excessive hunting, habitat loss and degradation, is one of the most pervasive threats to biodiversity. Besides affecting animal populations, defaunation also has cascading effects on community-level trophic interactions such as animal-mediated seed-dispersal (Markl *et al.* 2012, Peres & Palacios 2007). A decrease in frugivore diversity may reduce the flux of seeds being disseminated away from parent trees, thus exposing animal-dispersed tree species to high rates of density-dependent mortality (Terborgh 2013). Large frugivores provide unique services by disseminating many seeds from numerous species, including the largest seeds that smaller-bodied vertebrates cannot disperse (McConkey *et al.* 2015, Sekar *et al.* 2017). Therefore, the removal of large-bodied species may have particularly severe consequences for forest regeneration such as a shift from a community predominantly composed of large-seeded species to a community predominantly composed of species dispersed by small-bodied frugivores and abiotic means (Effiom *et al.* 2014, Harrison *et al.* 2013, Markl *et al.* 2012). Yet, large animals are disproportionately affected by habitat loss and degradation, and hunting (Fa *et al.* 2005, Poulsen *et al.* 2017, Ripple *et al.* 2016).

We only have a vague understanding of the causal link between defaunation and the regeneration of plant cohorts. In particular, even though it is a question of central importance in ecology and conservation (Rother *et al.* 2016, Schleuning *et al.* 2012), it remains unclear to what extent large seed-dispersers play complementary (or additive) or redundant functional roles in forest regeneration. The answer to this question will advance our understanding of the consequences of trophic downgrading and our ability to predict the long-term capacity of tropical forests to maintain their biodiversity and ecosystem services (Abernethy *et al.* 2013).

Pioneer work from Gautier-Hion *et al.* (1985) suggested that animal-mediated seed-dispersal was partitioned along fruit syndromes, and recent studies confirm that large vertebrates play complementary roles as seed dispersers (Clark *et al.* 2001, McConkey & Brockelman 2016, Rother *et al.* 2016). However, most evidence to date on net effect of large frugivores on seedling recruitment relates to the extirpation of the whole community of frugivores (Harrison *et al.* 2013, Terborgh *et al.* 2008, Wright *et al.* 2007) or of particular taxa (e.g. primates: Chaves *et al.* 2015, Effiom *et al.* 2013; elephants: Beaune *et al.* 2013). In Africa, Effiom *et al.* (2014) and Vanthomme *et al.* (2010) demonstrated that large birds did not compensate for the loss of large primates for the recruitment of large-seeded species, confirming that these guilds are essential complementary seed dispersers (Clark *et al.* 2001, Poulsen *et al.* 2002).

Whether the contributions of large frugivores to plant recruitment are equivalent is a particularly relevant question in Central Africa, a region that holds the largest frugivores on Earth (Forget *et al.* 2007) and which experiences an unsustainable rate of bushmeat extraction (Abernethy *et al.* 2013, Bennett *et al.* 2007). Here, we build on previous studies that assessed the cascading effects of defaunation on forest regeneration (Effiom *et al.* 2014, Harrison *et al.* 2013, Vanthomme *et al.* 2010) by evaluating how variation in abundance of the three main groups of large-bodied dispersers (primates, hornbills and forest elephant) influences seedling recruitment in D.R. Congo. Additionally, we tested the indirect effect of the nearby presence of fleshy-fruited trees and percentage forest cover in the landscape on seedling recruitment. These vegetation traits affect seed-disperser activity which subsequently leaves a signal in the seedling community (Clark *et al.* 2004, Slocum 2012, Trolliet *et al.* 2017). We hypothesized that due to large differences in size, foraging and ranging behaviour (Campos-Arceiz & Blake 2011, Clark *et al.* 2001, Trolliet *et al.* 2016, 2017), the three taxa should perform complementary functions, and variation in their abundance among sites should cause significant differences in the community of seedlings of animal-dispersed species.

Methods

Study area and forest sites

Field data collection took place between June 2013 and May 2015 in the Bandundu province (2°29′3.87′′S, 16°30′4.16′′E) of the D.R. Congo in an area of approximately 30 × 20 km surrounding the WWF (World Wide Fund for Nature) Malebo station. The study area is situated in a forest–savanna mosaic. The forest system includes several forests types such as riverine gallery forest, *Uapaca guineensis* ecotones, old secondary forest, Marantaceae forest, mature forest dominated by Annonaceae, Fabaceae and Olacaceae, and old-growth monodominant *Gilbertiodendron dewevrei* forest. Further information on the study area, which has already been used for other studies on animal-mediated seed dispersal, can be found in Trolliet *et al.* (2016, 2017).

We conducted fieldwork within five forested sites that bore different levels of hunting pressure and characteristics. The first three sites, namely Mbanzi, Nkombo and Mbominzoli, were located in an extensive forest block (> 500 km^2) visited seasonally by the forest elephant (*Loxodonta africana cyclotis*) (Appendix 1). Mbanzi village, originally founded as a hunting camp, is home to around 600 people, including a large group of hunters, so the forest was assumed to be under relatively high hunting pressure. To our knowledge, the local human population does not hunt the forest elephant and its poaching in the area is reduced. The Nkombo and Mbominzoli forests were located farther away from human settlements where anthropogenic pressure was probably more limited. The latter site hosts a large-mammal monitoring programme supported by the Mbou-Mon-Tour NGO. The site is also located within the geographic limits of an ethnic group which, because of a traditional taboo, does not hunt the bonobo (*Pan paniscus*) (Inogwabini *et al.* 2007). The other two forest sites, Nkala and Minkalu, belong to nearby village communities that practice subsistence hunting. Hunting pressure was high, yet home to the same ethnic group which does not hunt bonobo and which is under the bonobo conservation programmes of the WWF-DRC and Mbou-Mon-Tour NGOs. Thus, Nkala, Minkalu and Mbominzoli hosted relatively higher densities of bonobo compared with Mbanzi and Nkombo. Hornbills, even though they are not the main target of hunters, are increasingly hunted across African forests as other species disappear (Trail 2007, Whytock *et al.* 2016).

Frugivore community

We characterized the large-frugivore community and hunting levels at each site by conducting surveys on a system of line-transects and forest reconnaissance trails (Hall *et al.* 1998, Walsh & White 1999) for a total of 170 km. During the main dry season (June to August) of 2013 and 2014, the first author and two local field assistants recorded all direct (encounters, calls) and indirect signs of primates (faeces, footprints, nests), hornbills, elephants (faeces, footprints) and hunting activity (rifle cartridges, gunshots, traps, fires). We calculated encounter rates (kilometric abundance index (KAI), observations km^{-1}) by summing all observations collected for each of the categories of hunting, primates and hornbills for each site (Appendix 2, Figure 1) (Mathot & Doucet 2006, Vanthomme *et al.* 2010). Because elephant tracks that were close to one another could not be considered independent, and due to their large home ranges, the number of tracks encountered was not a reliable indication of elephant relative abundance. We therefore reported its presence or absence at each site.

Environmental variables

We included the plot type (under a *Staudtia kamerunensis* tree, under a *Dialium* spp. tree, or random) and percentage forest cover in the landscape in our analysis. We calculated the percentage forest cover in circular buffers around each location following the method in Trolliet *et al.* (2017). Each buffer had a 2500-m radius owing to the fact that the amount of forest cover included in such areas around *S. kamerunensis* trees is known to influence the seed dispersal of this species (Trolliet *et al.* 2017). Forest cover did not include recently deforested areas such as shifting agriculture mosaics made of cultivated fields and fallows with young secondary vegetation, as visually assessed in the field.

Seedling community

We sampled the seedling community in 25-m^2 (5 × 5 m) plots located under the crown of large (dbh > 30 cm) animal-dispersed trees of *S. kamerunensis* (52 plots under 32 trees) and *Dialium* spp. (46 plots under 26 trees) and distributed among the five sites (Appendix 1). As far as possible, we established two plots under each tree, but we only established one plot under trees whose crown was not large enough to cover two plots. *Staudtia* trees produce fruits that primarily attract hornbills, as shown by visual observations conducted in Cameroon (Clark *et al.* 2004) and in the study area (Trolliet *et al.* 2017; > 95% of visits by frugivores), although their fruits are consumed by primates too (Gautier-Hion

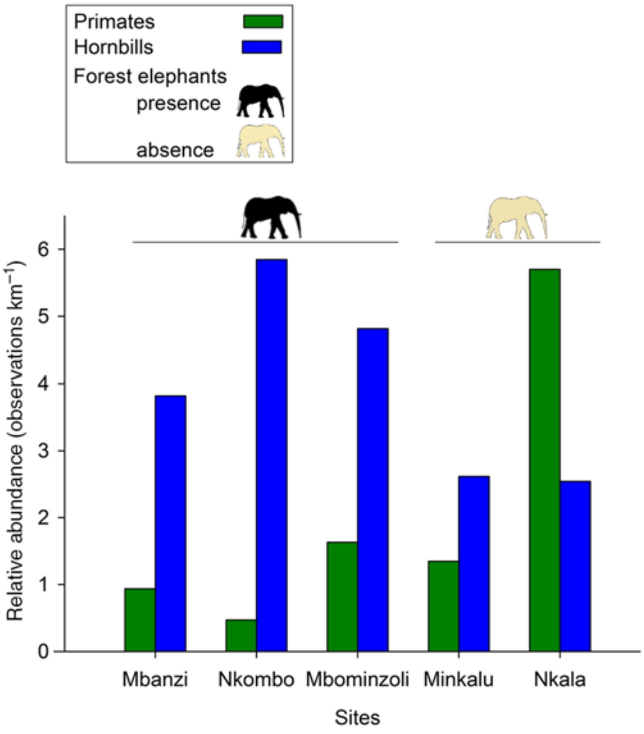

Figure 1. Abundance of the three main large frugivore taxa in five sites in the forest–savanna mosaic around the Malebo field station in the Bandundu province, Democratic Republic of the Congo.

et al. 1985). *Dialium* spp. trees produce pods that attract primates (Poulsen *et al.* 2001, Trolliet *et al.* 2016). Surveying heterospecific regeneration under animal-dispersed trees maximizes the amount of information on seed-disperser activity and enables inter-site comparisons (Nuñez-Iturri & Howe 2007, Vanthomme *et al.* 2010). To account for the activity of frugivores not visiting these areas and to perform a more comprehensive survey of the seedling community, we sampled one or two plots 50 m from the focal tree in a random direction. Each plot or pair of plots is referred to as a location (Appendix 3).

In each plot, we identified all seedlings 0.5–2 m in height (Vanthomme *et al.* 2010) to genus, species or morphospecies level. Plant identification was performed in the field by two locally experienced parataxonomists, who also previously helped in the identification of tree species in the study area. Samples were deposited in the herbarium and botanical library of the Université Libre de Bruxelles (BRLU), with reference IDs Bastin-Serckx#1-474. Botanists (two of us, JLD, JFG, and Olivier Lachenaud at the Herbarium of the National Botanic Garden Meise) double-checked seedling samples and identified unidentified species. For each species, we indicated whether it was dispersed by animals or by abiotic processes, and also determined the seed length with the aid of the literature. We only considered animal-dispersed species for the analyses (Appendix 4).

Statistical analysis

The analyses aimed to explain the variation of three response variables among the locations: seedling density, seedling species richness, and mean seed length of animal-dispersed seedling species (weighted by the abundance of seedlings). We classified the explanatory variables related to the presence or abundance of frugivores in an animal component, and the plot type and percentage forest cover in a vegetation component.

Furthermore, we considered a third – spatial – explanatory component to account for the spatial autocorrelation of both the response and the explanatory variables, both among and within the sites. Using a spatially explicit framework ensures a correct type I error rate by accounting for the non-independence of spatially distributed observations (Diniz-Filho & Bini 2005, Dray *et al.* 2012), and highlight multiscale spatial structures displayed by the response variables. These spatial patterns are signatures of underlying ecological processes and can therefore provide crucial ecological information (Dray *et al.* 2012, Fortin & Dale 2014, Legendre & Legendre 2012). The spatial component was generated through Moran's eigenvector maps (MEM, Dray *et al.* 2006), a spatial eigenvector-based method that breaks down the overall spatial autocorrelation into complementary multiscale spatial patterns. The spatial eigenvectors (hereafter referred to as spatial predictors or MEM variables) were generated following the method and recommendation in Bauman *et al.* (2018*a*, 2018*b*; details presented in Appendix 5). We only used positively correlated spatial variables, as we were interested in contagious ecological processes (i.e. displaying a positive spatial autocorrelation).

We included the animal, vegetation and spatial explanatory datasets in a variation partitioning analysis (Borcard & Legendre 1994, Peres-Neto & Legendre 2010). The latter allowed the assessment of the shared and pure contributions of the three explanatory components to the total variation of each response variable. A shared contribution was jointly explained by two or more components, while a pure contribution was solely explained by the component itself. The pure spatial component, in particular, allowed us to visualize the spatial patterns remaining in the response variables after removing the effect of the two other explanatory components. These pure spatial patterns can provide insights about possible underlying complementary processes (McIntire & Fajardo 2009, Peres-Neto & Legendre 2010). We estimated the explanatory power of the different effects using the adjusted coefficient of determination (R^2_{adj}; Peres-Neto *et al.* 2006).

To define the ecologically relevant parameters within the vegetation and the animal components while maintaining a low type-I error rate and controlling for overfitting, we performed a global test of significance separately on the animal and vegetation explanatory variables, and a forward model selection with two stopping criteria following Blanchet *et al.* (2008). The global tests for the spatial predictors as well as the test of the pure fractions of the variation partitioning were performed using a classical permutation of the model residuals (9999 iterations, Anderson & Legendre 1999). The shared fractions of the variation partitioning were tested using Moran spectral randomization (Wagner & Dray 2015), following the method of Bauman *et al.* (2019). All analyses were conducted using the R software.

Results

The five sites differed in terms of hunting pressure (0.56–1.28 obs. km^{-1}), abundance of primates (0.47–5.7 obs. km^{-1}), hornbills (2.54–5.85 obs. km^{-1}) and the presence of the forest elephant (Figure 1). The relative abundance of primates in Nkala was particularly high (5.7 obs. km^{-1}) compared with the other sites. Primates were mainly represented by the bonobo, but also by *Cercopithecus* spp. Hornbills were mainly represented by *Bycanistes albotibialis*, but also by *Ceratogymna atrata* and *Bycanistes fistulator* (Appendix 2). We confirmed the presence

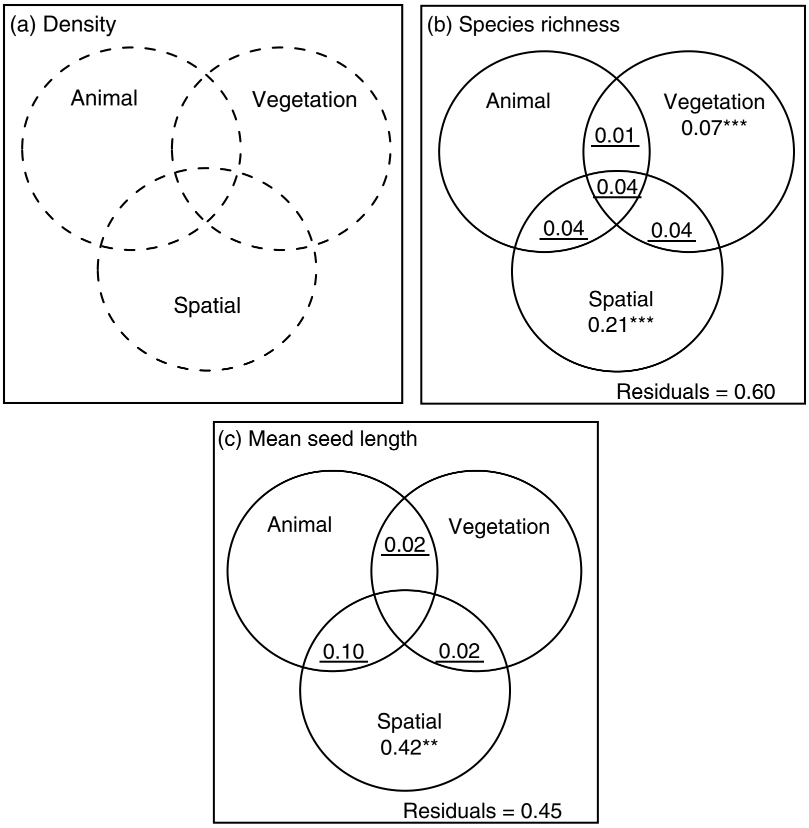

Figure 2. Values of the R^2_{adj} obtained from the partial regressions (variation partitioning analysis) among the animal, vegetation and spatial components. Values of R^2_{adj} are presented for the three response variables density (a), species richness (b) and mean weighted seed length of animal-dispersed species (c). Circles in the Venn diagrams with plain lines and dotted lines show significant ($P < 0.05$) and non-significant ($P > 0.05$) components, respectively. The values indicate pure contributions, except for the underlined values which give R^2_{adj} computed by subtraction of other R^2, which are therefore non-testable. The asterisks and the double asterisks indicate significant ($P < 0.05$) and highly significant signals ($P < 0.01$), respectively. Values < 0 are not shown. No component contained significant explanatory variables to explain variation in the density of seedlings. For species richness, the animal component contained the abundance of primates and the vegetation component contained the plot type and percentage forest cover. For mean seed length, the animal component contained abundance of hornbills and the vegetation component contained the percentage forest cover.

of the forest elephant in Mbanzi, Nkombo and Mbominzoli, and did not detect any sign of its presence in Nkala and Minkalu.

Among the 248 morphospecies found during the survey ($N = 6300$ 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 1306 individuals (21%). The descriptive statistics (density, species richness and mean weighted seed length) of each site are presented in Appendix 6.

The mean density of seedlings of animal-dispersed species presented no spatial structure at the scales encompassed by the study ($P > 0.178$ for all candidate spatial weighting matrices), and could not be explained by the animal or the vegetation components ($P = 0.206$ and $P = 0.062$, respectively) (Figure 2a, Appendix 7).

The selected model explaining the variation in the species richness of seedlings of animal-dispersed species displayed a significant animal component (abundance of primates; $R^2_{adj} = 0.08$, $P = 0.001$), and a significant vegetation component (percentage forest cover and plot type; $R^2_{adj} = 0.16$, $P = 0.001$) (Figure 2b, Appendix 7). The abundance of primates and the presence of *Staudtia* trees were associated with an increase in animal-dispersed species richness (Figure 3a-b). Also, the percentage forest cover was associated with a decrease in animal-dispersed species richness (Figure 3c). The variation in species richness displayed a broad-scale spatial pattern (Appendix 8; $R^2_{adj} = 0.327$, $P = 0.020$). Nearly half of this spatially structured variation of seedling species richness was related to spatial patterns observed in the vegetation and animal explanatory variables, while a residual spatial pattern remained unexplained by these ecological variables (Appendix 8) ($R^2_{adj} = 0.21$, $P = 0.001$; Figure 2b, Appendix 7). However, none of the shared fractions of variation was significant. Together, the three explanatory datasets explained over a third of the total variation of the species richness ($R^2_{adj} = 0.40$).

Finally, variables from the animal component significantly explained variation in mean seed length of animal-dispersed species. More specifically, the mean seed length increased when the abundance of hornbills increased ($R^2_{adj} = 0.12$, $P = 0.001$; Figure 4a-b, Appendix 7). The mean seed length of the animal-dispersed species displayed a fine- to medium-scale spatial structure ($R^2_{adj} = 0.53$, $P = 0.001$). The spatial pattern consisted of a significantly higher value of mean seed length in nearly all the plots of the Mbominzoli site, around half of the plots of the Nkombo site, and a few plots scattered in the Nkala site (Appendix 8). This spatial pattern of the mean seed length was partly related to a similar structure in the distribution of the hornbill abundances ($R^2_{adj} = 0.10$, $P = 0.17$; Figure 2c). In addition, a strong residual spatial pattern remained in the mean weighted seed length, after removing the effect of hornbill abundance and percentage forest cover ($R^2_{adj} = 0.42$, $P = 0.001$; Figure 2c, Appendix 8). Overall, the three components explained over half ($R^2_{adj} = 0.55$) of the total variation of the mean seed length of the animal-dispersed species among locations.

Discussion

Our results highlight the influence of the three explanatory components, i.e. animal, vegetation and spatial components, on species richness and on mean seed length of the animal-dispersed species. The use of spatial predictors in the analyses showed that the effect of the plot type, percentage forest cover and the primate abundance (for the species richness) as well as the effect of the hornbill abundance (for the mean seed length) were spatially structured at

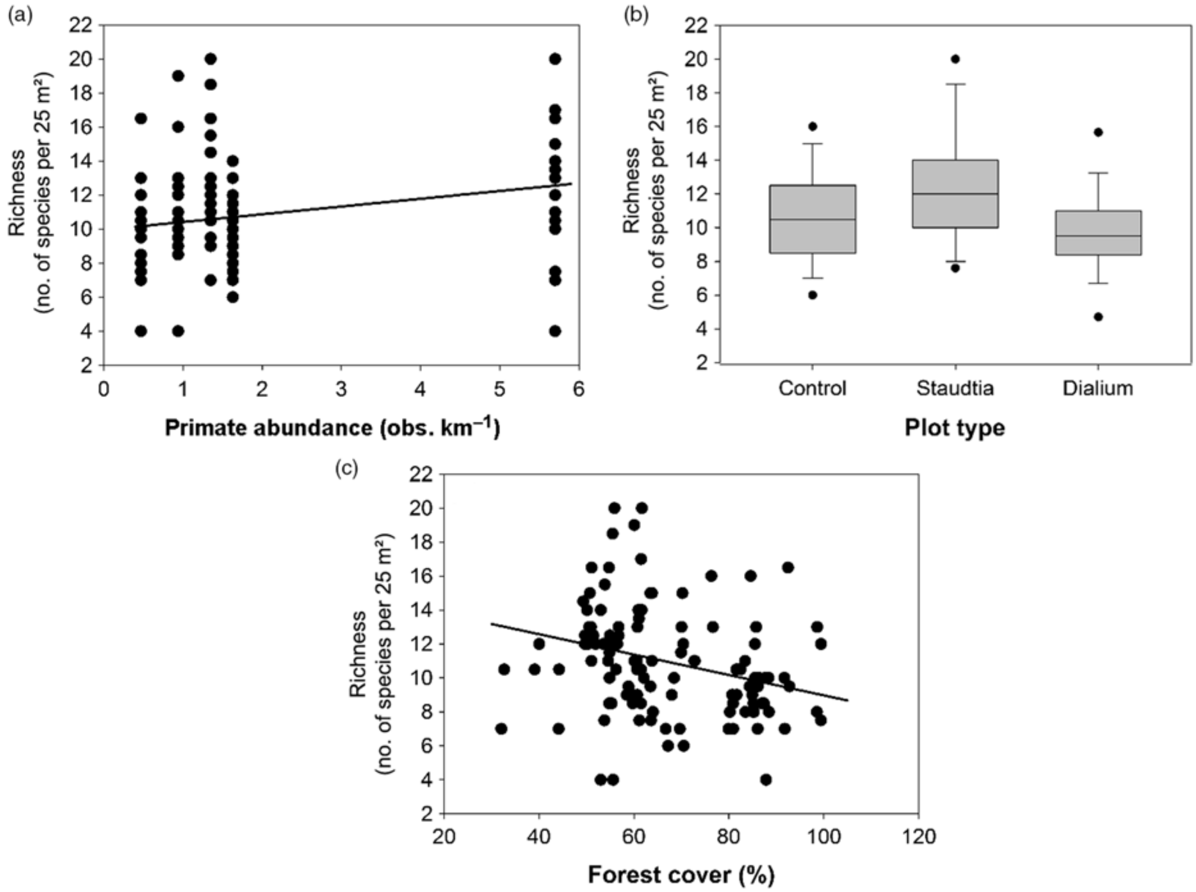

Figure 3. Mean species richness of seedlings of animal-dispersed species per 25 m^2 (represented by plain circles) in the forest–savanna mosaic around the Malebo field station in the Bandundu province, Democratic Republic of the Congo. Mean species richness is presented as a function of primate abundance (a), plot type (b) and percentage forest cover (c). In the plot type comparison, solid lines represent the median and black dots represent 5th/95th percentiles. In the two regressions against primate abundance and percentage forest cover, solid lines represent the linear regression.

different spatial scales. These spatial predictors also highlighted strong residual spatial patterns ($R^2_{adj} = 0.21$ and 0.42, for the species richness and mean seed length, respectively), hence indicating that some unmeasured ecological processes are still responsible for a strong spatial pattern in both the species richness and the mean seed length of the animal-dispersed species. This last result stresses the crucial role of spatially explicit statistical methods for the study of ecological processes involving dispersal and landscape properties (Dray *et al.* 2012).

Frugivores' influence on the species richness and mean seed length of animal-dispersed species

First, no significant effect of any of the three explanatory components could be detected on the density of seedlings of animal-dispersed species. Notably, this result is in line with the finding of Vanthomme *et al.* (2010), that the density of seedlings in Central African hunted and non-hunted sites do not differ significantly.

Secondly, the richness of animal-dispersed species was related to the abundance of primates, which supports the importance of primates as seed dispersers (Harrison *et al.* 2013, Nuñez-Iturri & Howe 2007, Poulsen *et al.* 2001, Terborgh *et al.* 2008, Vanthomme *et al.* 2010). We also found that species richness decreased with percentage forest cover. Areas surrounding plots with lower amounts of forest cover tend to include more transitional forests at edges (i.e. forests at early successional stages), which have more open understorey and more light reaching the forest floor compared with closed understorey in forest interiors. Such favourable light conditions promote greater survival of light-demanding species which die in low-light conditions. An increasing representation of forests at early successional stages could foster γ-diversity (Arroyo-Rodríguez *et al.* 2013) and allow a subsequent richer seed rain. Thus, we suggest that plots surrounded by less forest receive a richer seed rain that increases the richness of seedlings of animal-dispersed species. In addition to those landscape scale patterns, the richness of the seedling community was found to be influenced at the local scale by the presence of fleshy-fruited trees above survey plots. It has been reported that trees attract seed-dispersing animals and act as centres of regeneration, or seed-dispersal foci (*S. kamerunensis:* Clark *et al.* 2004; *Ficus*: Cottee-Jones *et al.* 2016). Here, we showed that *S. kamerunensis* was associated with higher species richness among seedlings. Possible underlying drivers of this pattern could be post-dispersal filtering processes (Fleury *et al.* 2014), soil heterogeneity (Muledi *et al.* 2016, Vleminckx *et al.* 2016), or varying influences of adult trees among sites (Effiom *et al.* 2014).

Thirdly, we showed that a decreasing abundance of hornbills significantly reduced the mean weighted seed length of the species in the seedling community. However, considering the strong positive correlation between the presence of hornbills and the forest elephant, we suggest that the observed reduction in seed length

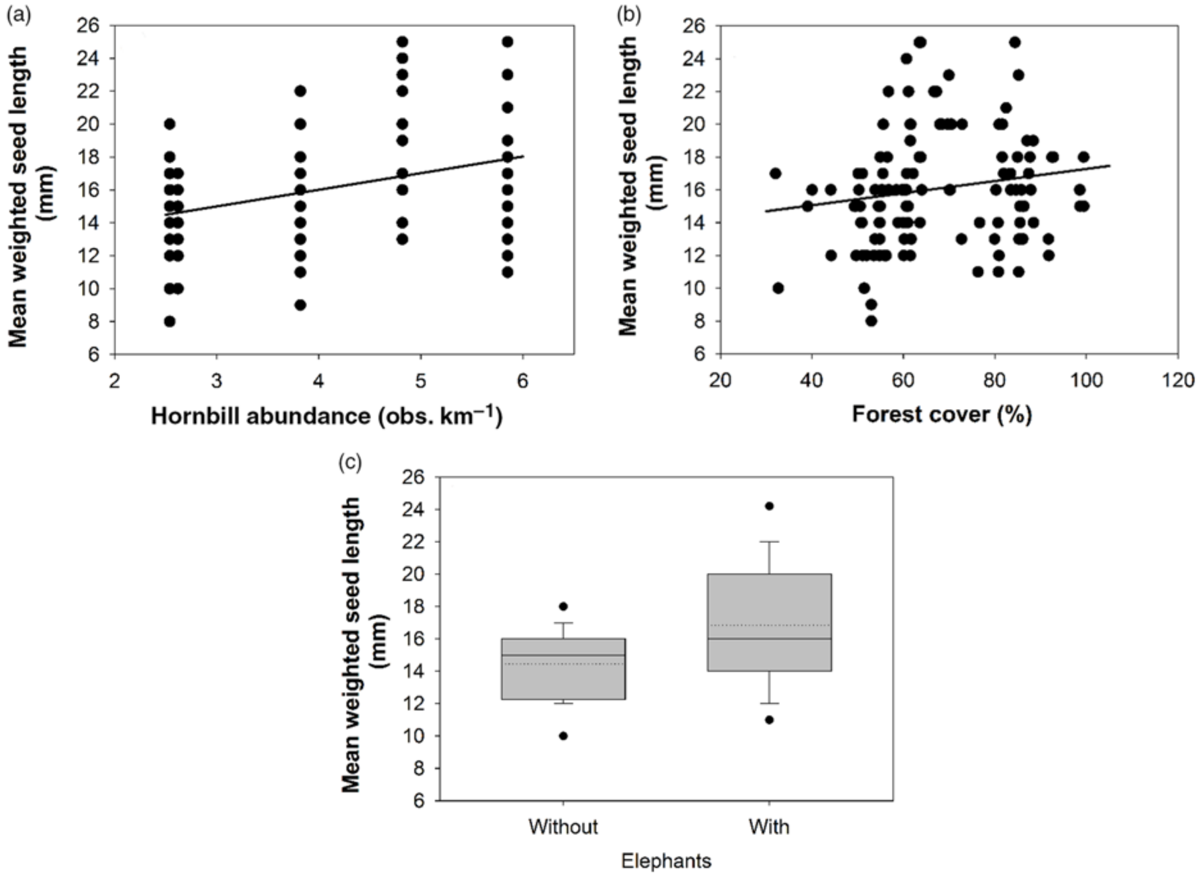

Figure 4. Mean weighted seed length of animal-dispersed species of seedlings per 25 m^2 in the forest–savanna mosaic around the Malebo field station in the Bandundu province, Democratic Republic of the Congo. Mean weighted seed length is presented as a function of hornbill abundance (a), percentage forest cover (b) and elephant presence (c).

is probably associated with the extirpation of both hornbills and elephant. Indeed, the absence of the elephant might have significantly disrupted the dispersal and recruitment of large-seeded species, thus reducing the mean seed length of species of the seedling community (Figure 4c). The remaining spatial pattern (i.e. unexplained by the plant and frugivore variables) detected for the mean seed length indicates that some additional unmeasured ecological processes influence the distribution of the mean seed-length values among seedling communities. Physico-chemical soil heterogeneity, known to typically display spatially autocorrelated patterns and to be crucial for seed germination as well as young life-stages of trees, could be responsible for a portion of the residual spatial patterns of both mean seed length and species richness. A future thorough consideration of soil variables will allow this hypothesis to be tested, therefore helping to better understand the mechanisms influencing species richness and mean seed length of animal-dispersed tree species.

In addition to the previously mentioned mechanisms, we suspect that some variation in the activity level of elephants between Mbanzi, Nkombo and Mbominzoli could account for a proportion of the remaining spatial structure. Also, larger seeds are more prone to predation by rodents and parasitism than smaller seeds (Foster 1986), so our results may partly be related to inter-site differences in post-deposition seed survival. The mean seed length increase in plots surrounded by more forest is consistent with our previous explanation related to the effect of understorey light on species richness. Light-demanding tree species, whose seedlings likely show greater survival in areas with relatively less forest cover, tend to have smaller seeds compared with shade-bearer tree species (Foster 1986).

Unexplained variation

The unexplained variation (i.e. the residuals of the variation partitioning analyses) could indicate both that some ecological processes other than those measured here influence our diversity indices, and that this variation is neutral (i.e. stochastic). Portions of the residual variability might be related to the activity of some frugivores and granivores (e.g. bats, duikers, rodents, bush pigs) that were not considered here. Particularly, biotic (seed predation, herbivory, pathogen, fungi etc.) and abiotic (amount of light, water etc.) post-dispersal processes (Clark *et al.* 2012, Mangan *et al.* 2010, Nicotra *et al.* 1999, Wang & Smith 2002) can affect seedling recruitment in a non-random fashion and change the composition pattern of the seedling cohort as regards to the initial seed rain (Alcomb 2003, Carrière *et al.* 2002, Herrera *et al.* 1994). Spatio-temporal variation in these processes within and among our sites might have eroded the signature of seed-dispersers on the seedling cohort. Additionally, the coarse resolution and limited sampling effort of the frugivore kilometric abundance index is likely to have limited statistical power, hence potentially causing underestimations of the actual frugivore effects. Notably, hornbill abundances were strongly positively correlated with the presence of the elephant (Figure 1), which made their respective influence not fully distinguishable. These collinearity issues, inherent to any ecological study (Dormann *et al.* 2013), make the task of accurately disentangling the degree of functional complementarity among seed dispersers delicate. Additionally, it is worth mentioning that since the forest elephant represents part of a relic fragile population (Inogwabini *et al.* 2011), its lack of significance in the analyses may have resulted from the partial loss of its ecological function (McConkey & O'Farrill 2016, Poulsen *et al.* 2018). Our sampling design contained only five replicates (sites) to explore the effect of frugivores, and plots, used as observations, were nested within sites. The replication of this kind of study with more observations of frugivore communities and the sampling of seed-disperser activity at finer spatial scales will allow further evaluation of the strength and the scale of the effects each taxon actually has on the regeneration of tropical forests. Finally, variation in demographic rates (e.g. birth, death), dispersion and recruitment can be neutral, hence yielding a varying – but common – intrinsic stochasticity in living communities (Bell *et al.* 2006, Hubbell 2001, 2006). The extent of this natural stochasticity, however, is impossible to evaluate at this point, as more potentially relevant ecological variables (soil heterogeneity) could still be measured and integrated to our models.

Functional complementarity, or redundancy?

The lack of variation in seedling density could suggest that hornbills, primates and elephant have a redundant functional role for forest regeneration in this forest–savanna mosaic. Given the assemblage of large frugivores at each site, the absence of the forest elephant would seem to be functionally compensated for by the presence of primates and hornbills as far as seedling density is concerned. Yet, we cannot exclude the possibility that other processes have had a more pronounced role in maintaining seedling densities at similar values among sites.

Secondly, this study suggests that the seed-dispersal services lost with the reduction in primate abundance was not compensated for by hornbills. This result supports the conclusion of Clark *et al.* (2001) and Poulsen *et al.* (2002) in that these two taxa play complementary roles as seed dispersers.

Finally, the presence of primates seemed not to functionally compensate for a lack of recruitment of large-seeded trees in the sites where hornbill abundance was low and the forest elephant was extirpated. Forest elephant species disperse the largest seeds among the tree community and play a unique function in tropical forests, and are thus complementary to other guilds (Blake *et al.* 2009, Campos-Arceiz & Blake 2011, Sekar *et al.* 2017). Yet, the result remains somewhat surprising since the bonobo, the main representative of the primate community in Nkala and Minkalu, also provides dispersal services for large-seeded plants: few plants dispersed by the bonobo are also dispersed by hornbills (Trolliet *et al.* 2016). We suggest that post-dispersal processes could have induced inconsistencies between the composition of the seed rain and that of the seedling community, and reduced the ultimate influence of the bonobo on the recruitment of large-seeded plants (Alcomb 2003, Carrière *et al.* 2002, Lugon *et al.* 2017).

Overall, our results would suggest that hornbills, primates and the forest elephant could play complementary functions in effectively dispersing a wide diversity of seed types and species and ensure their recruitment. In the context of increasing anthropogenic pressures on tropical ecosystems, we stress the importance of maintaining diverse large frugivore communities to ensure optimal ecosystem functioning.

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Literature cited

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

Alcomb SORB (2003) Bridging the gap: influence of seed deposition on seedling recruitment in a primate– tree interaction. *Ecological Monographs* **73**, 625–642.

Anderson MJ and Legendre P (1999) An empirical comparison of permutation methods for tests of partial regression coefficients in a linear model. *Journal of Statistical Computation and Simulation* **62**, 271–303.

Arroyo-Rodríguez V, Rös M, Escobar F, Melo FPL, Santos BA, Tabarelli M and Chazdon R (2013) Plant β-diversity in fragmented rain forests: testing floristic homogenization and differentiation hypotheses. *Journal of Ecology* **101**, 1449–1458.

Bauman D, Drouet T, Dray S and Vleminckx J (2018*a*) Disentangling good from bad practices in the selection of spatial or phylogenetic eigenvectors. *Ecography* **41**, 1638–1649.

Bauman D, Drouet T, Fortin M-J and Dray S (2018*b*) Optimizing the choice of a spatial weighting matrix in eigenvector-based methods. *Ecology* **99**, 2159–2166.

Bauman D, Vleminckx J, Hardy OJ and Drouet T (2019) Testing and interpreting the shared space-environment fraction in variation partitioning analyses of ecological data. *Oikos* **128**, 274–285.

Beaune D, Fruth B and Bollache L (2013) Doom of the elephant-dependent trees in a Congo tropical forest. *Forest Ecology and Management* **295**, 109–117.

Bell G, Lechowicz MJ and Waterway MJ (2006) The comparative evidence relating to functional and neutral interpretations of biological communities. *Ecology* **87**, 1378–1386.

Bennett EL, Blencowe E, Brandon K, Brown D, Burn RW, Cowlishaw G, Davies G, Dublin H, Fa JE, Milner-Gulland EJ, Robinson JG, Rowcliffe JM, Underwood FM and Wilkie DS (2007) Hunting for consensus: reconciling bushmeat harvest, conservation, and development policy in west and central Africa. *Conservation Biology* **21**, 884–887.

Blake S, Deem SL, Mossimbo E, Maisels F and Walsh P (2009) Forest elephants: tree planters of the Congo. *Biotropica* **41**, 459–468.

Blanchet FG, Legendre P and Borcard D (2008) Forward selection of explanatory variables. *Ecology* **89**, 2623–2632.

Borcard D and Legendre P (1994) Environmental control and spatial structure in ecological communities: an example using oribatid mites (Acari, Oribatei). *Environmental and Ecological Statistics* **1**, 37–61.

Campos-Arceiz A and Blake S (2011) Megagardeners of the forest – the role of elephants in seed dispersal. *Acta Oecologica* **37**, 542–553.

Carrière SM, Letourmy P and McKey DB (2002) Effects of remnant trees in fallows on diversity and structure of forest regrowth in a slash-and-burn agricultural system in southern Cameroon. *Journal of Tropical Ecology* **18**, 375–396.

Chaves OM, Arroyo-Rodríguez V, Martínez-Ramos M and Stoner KE (2015) Primate extirpation from rainforest fragments does not appear to influence seedling recruitment. *American Journal of Primatology* **77**, 468–478.

Clark CJ, Poulsen JR and Parker VT (2001) The role of arboreal seed dispersal groups on the seed rain of a lowland tropical forest. *Biotropica* **33**, 606–620.

Clark CJ, Poulsen JR, Connor EF and Parker VT (2004) Fruiting trees as dispersal foci in a semi-deciduous tropical forest. *Oecologia* **139**, 66–75.

Clark CJ, Poulsen JR and Levey DJ (2012) Vertebrate herbivory impacts seedling recruitment more than niche partitioning or density-dependent mortality. *Ecology* **93**, 554–564.

Cottee-Jones HEW, Bajpai O, Chaudhary LB and Whittaker RJ (2016) The importance of *Ficus* (Moraceae) trees for tropical forest restoration. *Biotropica* **48**, 413–419.

Diniz-Filho JAF and Bini LM (2005) Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Global Ecology and Biogeography* **14**, 177–185.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D and Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46.

Dray S, Legendre P and Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling* **196**, 483–493.

Dray S, Pélissier R, Couteron P, Fortin M-J, Legendre P, Peres-Neto PR, Bellier E, Bivand R, Blanchet FG, De Cáceres M, Dufour AB, Heegaard E, Jombart T, Munoz F, Oksanen J, Thioulouse J and Wagner HH (2012) Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs* **82**, 257–275.

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

Effiom EO, Birkhofer K, Smith HG and Olsson O (2014) Changes of community composition at multiple trophic levels due to hunting in Nigerian tropical forests. *Ecography* **37**, 367–377.

Fa JE, Ryan S and Bell D (2005) Hunting vulnerability, ecological characteristics and harvest rates of bushmeat species in afrotropical forests. *Biological Conservation* **121**, 167–176.

Fleury M, Silla F, Rodrigues RR, Hilton TZ and Galetti M (2014) Seedling fate across different habitats: the effects of herbivory and soil fertility. *Basic and Applied Ecology* **16**, 141–151.

Forget P-M, Dennis A, Mazer S, Jansen PA, Kitamura S, Lambert JE and Westcott DA (2007) Seed allometry and disperser assemblages in tropical rain forests: a comparison of four floras on different continents. In Dennis AJ, Schupp EW, Green RA and Westcott DA (eds), *Seed Dispersal: Theory and its Application in a Changing World*. Wallingford: CAB International, pp. 5–36.

Fortin M-J and Dale MRT (2014) *Spatial Analysis: A Guide for Ecologists*. Cambridge: Cambridge University Press.

Foster SA (1986) On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Botanical Review* **52**, 260–299.

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

Hall JS, White LJT, Inogwabini BI, Omari I, Morland HS, Williamson EA, Saltonstall K, Walsh P, Sikubwabo C, Bonny D, Kiswele KP, Vedder A and Freeman K (1998) Survey of Grauer's gorillas (*Gorilla gorilla graueri*) and eastern chimpanzees (*Pan troglodytes schweinfurthi*) in the Kahuzi-Biega National Park lowland sector and adjacent forest in eastern Democratic Republic of Congo. *International Journal of Primatology* **19**, 207–235.

Harrison R, Tan S, Plotkin J, Slik JWF, Detto M, Brenes T, Itoh A and Davies S (2013) Consequences of defaunation for a tropical tree community. *Ecology Letters* **16**, 687–694.

Herrera CM, Jordano P, Lopez-Soria L and Amat AJ (1994) Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecological Monographs* **64**, 315–344.

Hubbell SP (2001) *A Unified Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton University Press.

Hubbell SP (2006) Neutral theory and the evolution of ecological equivalence. *Ecology* **87**, 1387–1398.

Inogwabini B, Matungila B, Mbende L, Abokome M and Wa Tshimanga T (2007) Great apes in the Lake Tumba landscape, Democratic Republic of Congo: newly described populations. *Oryx* **41**, 1–7.

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

Legendre P and Legendre L (2012) *Numerical Ecology*, Third edition. Amsterdam: Elsevier.

Lugon AP, Boutefeu M, Bovy E, Vaz-De-Mello FZ, Huynen M-C, Galetti M and Culot L (2017) Persistence of the effect of frugivore identity on post-dispersal seed fate: consequences for the assessment of functional redundancy. *Biotropica* **49**, 293–302.

Mangan SA, Schnitzer SA, Herre EA, Mack KML, Valencia MC, Sanchez EI and Bever JD (2010) Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature* **466**, 752–755.

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

Mathot L and Doucet J-L (2006) Méthode d'inventaire faunique pour le zonage des concessions en forêt tropicale. *Bois et Forêt des Tropiques* **287**, 50–70.

McConkey KR and Brockelman W (2016) Nonredundancy in the dispersal network of a generalist tropical forest tree. *Ecology* **92**, 1492–1502.

McConkey KR and O'Farrill G (2016) Loss of seed dispersal before the loss of seed dispersers. *Biological Conservation* **201**, 38–49.

McConkey KR, Brockelman W, Saralamba C and Nathalang A (2015) Effectiveness of primate seed dispersers for an "oversized" fruit, *Garcinia benthamii*. *Ecology* **96**, 2737–2747.

McIntire EJB and Fajardo A (2009) Beyond description: the active and effective way to infer processes from spatial patterns. *Ecology* **90**, 46–56.

Muledi JI, Bauman D, Drouet T, Vleminckx J, Jacobs A, Lejoly J, Meerts P and Shutcha MN (2016) Fine-scale habitats influence tree species assemblage in a miombo forest. *Journal of Plant Ecology* **10**, 958–969.

Nicotra AB, Chazdon RL and Iriarte SVB (1999) Spatial heterogeneity of light and woodly seedling regeneration in tropical wet forests. *Ecology* **80**, 1908–1926.

Nuñez-Iturri G and Howe H (2007) Bushmeat and the fate of trees with seeds dispersed by large primates in a lowland rain forest in Western Amazonia. *Biotropica* **39**, 348–354.

Peres CA and Palacios E (2007) Basin wide effects of game harvest on vertebrate population densities in Amazonian forests: implications for animal mediated seed dispersal. *Biotropica* **39**, 304–315.

Peres-Neto PR and Legendre P (2010) Estimating and controlling for spatial structure in the study of ecological communities. *Global Ecology and Biogeography* **19**, 174–184.

Peres-Neto PR, Legendre P, Dray S and Borcard D (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* **87**, 2614–2625.

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

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

Poulsen JR, Koerner SE, Moore S, Medjibe VP, Blake S, Clark CJ, Akou ME, Fay M, Meier A, Okouyi J, Rosin C and White LJT (2017) Poaching empties critical Central African wilderness of forest elephants. *Current Biology* **27**, R134–R135.

Poulsen JR, Rosin C, Meier A, Mills E, Nuñez CL, Koerner SE, Blanchard E, Callejas J, Moore S and Sowers M (2018) Ecological consequences of forest elephant declines for Afrotropical forests. *Conservation Biology* **32**, 559–567.

Ripple WJ, Abernethy KA, Betts MG, Chapron G, Dirzo R, Galetti M, Levi T, Lindsey PA, Macdonald DW, Machovina B, Newsome TM, Peres CA, Wallach AD, Wolf C and Young H (2016) Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science* **3**, 160498.

Rother DC, Pizo MA and Jordano P (2016) Variation in seed dispersal effectiveness: the redundancy of consequences in diversified tropical frugivore assemblages. *Oikos* **125**, 336–342.

Schleuning M, Fru J, Klein A, Abrahamczyk S, Albrecht M, Andersson GKS, Bazarian S, Bo K, Dalsgaard B, Dehling DM and Gotlieb A (2012) Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology* **22**, 1925–1931.

Sekar N, Chia-Lo L and Sukumar R (2017) Functional nonredundancy of elephants in a disturbed tropical forest. *Conservation Biology* **31**, 1152–1162.

Slocum MG (2012) How tree species differ as recruitment foci in a tropical pasture. *Ecology* **82**, 2547–2559.

Terborgh JW (2013) Using Janzen–Connell to predict the consequences of defaunation and other disturbances of tropical forests. *Biological Conservation* **163**, 7–12.

Terborgh JW, Nuñez-Iturri G and Pitman N (2008) Tree recruitment in an empty forest. *Ecology* **89**, 1757–1768.

The Angiosperm Phylogeny Group (2009) An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APGIII. *Botanical Journal of the Linnean Society* **161**, 105–121.

Trail PW (2007) African hornbills: keystone species threatened by habitat loss, hunting and international trade. *Ostrich – Journal of African Ornithology* **78**, 609–613.

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

Trolliet F, Forget P-M, Huynen M-C and Hambuckers A (2017) Forest cover, hunting pressure, and fruit availability influence seed dispersal in a forest-savanna mosaic of the Congo Basin. *Biotropica* **49**, 337–345.

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

Vleminckx J, Doucet J-L, Morin-Rivat J, Biwolé AB, Bauman D, Hardy OJ, Fayolle A, Gillet J-F, Daïnou K, Gorel A and Drouet T (2016) The influence of spatially structured soil properties on tree community assemblages at a landscape scale in the tropical forests of southern Cameroon. *Journal of Ecology* **105**, 354–366.

Wagner HH and Dray S (2015) Generating spatially constrained null models for irregularly spaced data using Moran spectral randomization methods. *Methods in Ecology and Evolution* **6**, 1169–1178.

Walsh PD and White LJT (1999) What it will take to monitor forest elephant populations. *Conservation Biology* **13**, 1194–1202.

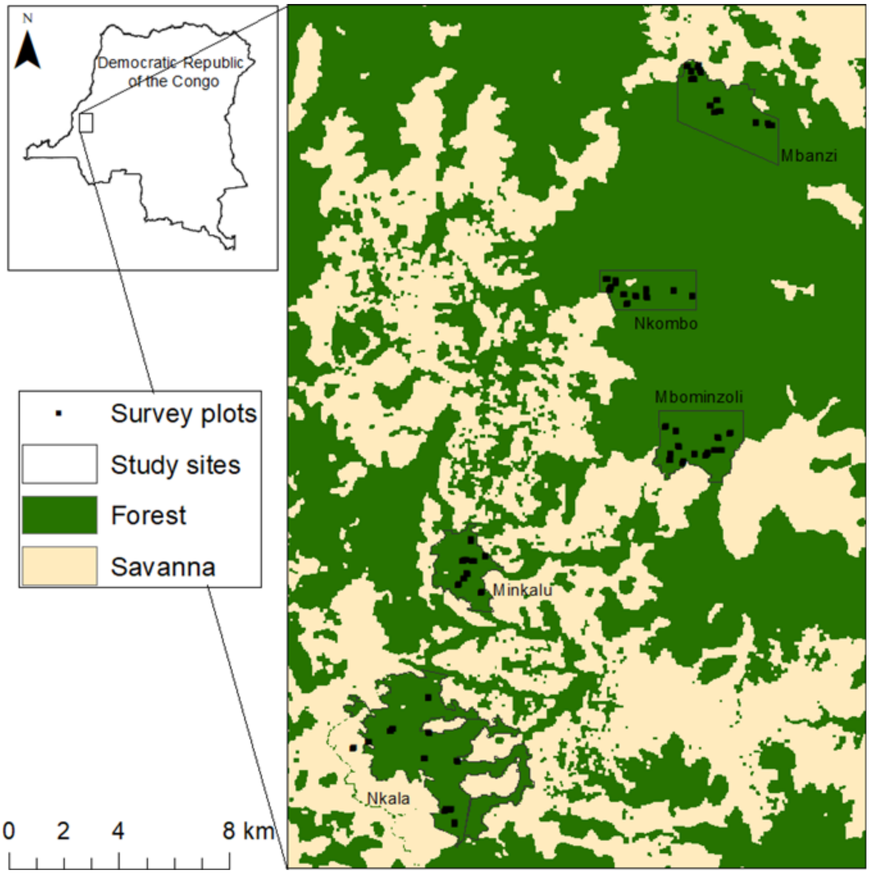
Wang BC andSmith TB (2002) Closing the seed dispersal loop. *Trends in Ecology and Evolution* **17**, 379–385.

Whytock R, Buij R, Virani M and Morgan B (2016) Do large birds experience previously undetected levels of hunting pressure in the forests of Central and West Africa? *Oryx* **50**, 76–83.

Wright SJ, Hernandéz A and Condit RR (2007) The bushmeat harvest alters seedling banks by favoring lianas, large seeds, and seeds dispersed by bats, birds, and wind. *Biotropica* **39**, 363–371.

Appendix 1

Map of the study area in the forest–savanna mosaic around the Malebo field station, Bandundu province, D.R. Congo, with the five sites (Mbanzi, Nkombo, Mbominzoli, Minkalu and Nkala) and the position of the survey plots.



Appendix 2

Main characteristics of the study sites in terms of conservation programmes, hunting pressure and large frugivore community in D.R. Congo. MMT = Mbou-Mon-Tour; WWF = WWF-DRC; [a]*Cercopithecus* spp. mainly include *C. ascanius* and potentially *C. mona wolfi* and *C. neglectus*, even though these two species are rare and difficult to observe.

			Large frugivores							
			Abundance (obs. km^{-1})							
Site	Conservation/ monitoring programmes (main NGOs involved)	Hunting pressure (obs. km^{-1})	*Pan paniscus*, Schwarz	*Cercopithecus* spp.[a]	Primates	*Bycanistes albotibialis*, Cabanis & Reichenow	*Ceratogymna atrata*, Temminck	*Bycanistes fistulator*, Cassin	Hornbills	Forest elephants, Blumenbach
Mbanzi	Elephant monitoring$^{\mathrm{WWF}}$	1.19	Absent	0.94	0.94	3.13	0.22	0.47	3.82	Present
Nkombo	Elephant monitoring$^{\mathrm{WWF}}$ until 2013	0.46	Absent	0.47	0.47	4.36	1.31	0.18	5.85	Present
Mbominzoli	Large mammals monitoring$^{\mathrm{MMT}}$ hunting taboo for bonobos	0.56	1.14	0.49	1.63	3.51	0.98	0.33	4.82	Present
Minkalu	Bonobos habituation$^{\mathrm{MMT,WWF}}$ hunting taboo for bonobos	1.28	1.10	0.25	1.35	2.24	0.25	0.13	2.62	Absent
Nkala		0.98	5.04	0.66	5.70	2.02	0.19	0.33	2.54	Absent

Appendix 3

Sampling efforts of seedling survey and distribution across the five sites in the forest–savanna mosaic in D.R. Congo.

	Effort sampling (m†)					
	Sites					
Plot types	Mbanzi	Nkombo	Mbominzoli	Minkalu	Nkala	Total
Under *Staudtia kamerunensis*	250	250	250	300	250	1300
Under *Dialium* spp.	275	225	250	150	250	1150
Random	525	475	500	450	500	2450
Total	1050	950	1000	900	1000	4900

Appendix 4

Seed length of each animal-dispersed plant species encountered during the seedling survey in the forest–savanna mosaic in D.R. Congo. Nomenclature follows APG III (The Angiosperm Phylogeny Group 2009). Name status is derived from the African Plants database of 'Conservatoire et Jardin Botaniques de la Ville de Genève' (http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php). If the genus is identified and the species determination is uncertain, 'cf.' is indicated before the species name. If the species or genus is not known, 'sp.' is used. In these cases, different morphospecies are further differentiated with numbers and sometimes date of sampling (day/month). In these cases, more complete samples (fertile) are needed in order to confirm the identifications.

Family	Species	Seed length (mm)
Anacardiaceae	*Sorindeia africana*	15.0
	Sorindeia spp.	?
Annonaceae	*Annickia chlorantha*	19.5
	Isolona hexaloba	12.5
	Isolona sp.	11.0
	Monodora angolensis	13.0
	Neostenanthera myristifolia	?
	Piptostigma fasciculatum	23.0
	Polyalthia suaveolens	10.0
	Uvariodendron sp.	15.0
	Xylopia aethiopica	6.0
	Xylopia hypolampra	14.0
	Xylopia staudtii – and/or *X. rubescens*	20.0
Apocynaceae	*Picralima nitida*	26.5
	Rauvolfia macrophylla	8.0
	Rauvolfia vomitoria	6.0
	unknown 125 Annonaceae sp.	?
	unknown 247 Annonaceae sp.	?
	unknown Mokoli	?
Aptandraceae	*Ongokea gore*	15.0
Boraginaceae	*Cordia platythyrsa*	15.0
Burseraceae	*Dacryodes edulis*	55.0
	Santiria trimera	14.0
Calophylaceae	*Endodesmia calophylloides*	15.0
Cannabaceae	*Celtis tessmannii*	9.0
Cardiopteridaceae	*Leptaulus zenkeri*	11.5
Celastraceae	*Salacia* sp.	?
Chrysobalanaceae	*Dactyladenia* sp. 1	?
	Licania elaeosperma	?
	Maranthes glabra	?
	Maranthes cf. *gabunensis*	?
	Parinari excelsa	26.0
Clusiaceae	*Garcinia* cf. *ovalifolia*	8.0
	Garcinia kola	30.0
	Garcinia punctata	17.5
	Garcinia smeathmannii	15.0
	Symphonia globulifera	17.5
Ebenaceae	*Diospyros conocarpa*	13.5
	Diospyros ferrea	1.0
	Diospyros iturensis	20.0
	Diospyros sp. 1	20.0
Erythropalaceae	*Heisteria parvifolia*	12.0
Euphorbiaceae	*Duvigneaudia inopinata*	21.5
	Macaranga sp.	4.7
	Plagiostyles africana	10.0
Fabaceae	*Afzelia bipindensis*	35.0
	Angylocalyx pynaertii	25.0
	Dialium pachyphyllum	11.0
	Dialium tessmannii	12.0
	Dialium tessmannii and/or *D. zenkeri*	11.0
	Dialium zenkeri	8.0
	unknown Molieme	?
Flacourtiaceae	*Casearia barteri*	?
	Oncoba mannii	8.0
	Scottellia klaineana	5.0
Huaceae	*Afrostyrax kamerunensis*	18.0
	Afrostyrax lepidophyllus	20.0
Ixonanthaceae	*Phyllocosmus africanus*	3.0
Irvingiaceae	*Irvingia gabonensis*	33.5
	Irvingia grandifolia	32.5
Lauraceae	*Beilschmiedia* sp. 1 08/01	?
	Beilschmiedia congolana	?
Malvaceae	*Chlamydocola chlamydantha*	25.0
	Cola acuminata	30.0
	Cola cf. *ballayi*	30.0
	Cola cf. *diversifolia*	14.0
	Cola griseiflora	20.0
	Cola lateritia	27.5
	Desplatsia subericarpa	15.0
	Duboscia macrocarpa	10.0
	Grewia oligoneura	10.0
	Grewia sp.	?
	Leptonychia sp.	12.0
	Octolobus spectabilis	6.0
Melastomataceae	*Memecylon cf laurentii*	?
	Warneckea sp. 2	?
	Warneckea sp. 1	?

(*Continued*)

Meliaceae	*Leplaea cedrata*	6.0
	Trichilia martineaui	14.5
	Trichilia sp.	14.5
	Trichilia sp. 2	14.5
	Trichilia sp. 4	14.5
	Trichilia sp. 5	14.5
Moraceae	*Ficus* sp.	?
Myristicaceae	*Coelocaryon preussii*	26.0
	Myristicaceae spp.	25.0
	Staudtia kamerunensis var. gabonensis	16.0
Ochnaceae	*Campylospermum elongatum*	?
	Campylospermum sp. 1	?
	Campylospermum cf. *bukobense*	?
	Campylospermum sp. 3	?
	Ochna calodendron	?
	Ochna cf. *afzelii*	6.0
	Rhabdophyllum sp.	5.5
	Rhabdophyllum sp. 1 08/01	5.5
Olacaceae	*Olax* spp.	11.0
	Olax subscorpioidea	15.5
Pandaceae	*Microdesmis* cf. *puberula*	7.0
	Microdesmis sp.	7.5
Passifloraceae	*Barteria fistulosa*	5.5
	Barteria letouzey	?
	Barteria sp. 1	?
	Cf. *Barteria* sp. 2	?
Phyllanthaceae	*Uapaca* spp.	21.0
Polygalaceae	*Carpolobia alba*	7.5
Putranjivaceae	*Drypetes capillipes*	9.5
	Drypetes cf. *ituriensis*	9.5
	Drypetes paxii	9.5
	Drypetes cf. *principum*	15.5
	Drypetes sp. 1	9.5
	Drypetes sp. 1 08/01	9.5
	Drypetes sp. 3 08/01	9.5
	Drypetes sp. 2 08/01	9.5
	Drypetes sp. 4 08/01	9.5
	Drypetes sp. 5 08/01	9.5
	Drypetes sp. 6 08/01	9.5
	Drypetes sp. 7 08/01	9.5
Rhizophoraceae	Cf. *Cassipourea* sp.	?
Rubiaceae	*Aidia micrantha*	?
	Aulacocalyx jasminiflora	8.5
	Colletoecema dewevrei	?
	Cf. *Pauridiantha rubens*	1.0
	Cf. *Psychotria* sp. 2	?
	Cf. *Rubiaceae* sp. 28	?
	Cf. *Tricalysia* sp. 2	?
	Massularia acuminata	5.0
	Oxyanthus sp.	6.0
	Psychotria sp. 1	?
	Psychotria sp. 3	?
	Rothmannia sp. 1	8.0
	Rubiaceae sp. 1 08/01	?
	Rubiaceae sp. 1 14/01	?
	Rubiaceae sp. 2	?
	Rubiaceae sp. 3	?
	Rubiaceae sp. 4	?
	Rubiaceae sp. 5	?
	Rubiaceae sp. 6	?
	Rubiaceae sp. 7	?
	Rubiaceae sp. 8	?
	Rubiaceae sp. 9	?
	Rubiaceae sp. 10	?
	Rubiaceae sp. 11	?
	Rubiaceae sp. 12	?
	Rubiaceae sp. 13	?
	Rubiaceae sp. 14	?
	Rubiaceae sp. 15	?
	Rubiaceae sp. 16	?
	Rubiaceae sp. 17	?
	Rubiaceae sp. 18	?
	Rubiaceae sp. 19	?
	Rubiaceae sp. 20	?
	Rubiaceae sp. 22	?
	Rubiaceae sp. 23	?
	Rubiaceae sp. 24	?
	Rubiaceae sp. 25	?
	Rubiaceae sp. 26	?
	Rubiaceae sp. 27	?
	Tricalysia sp. 1	?
	unknown 35	?
	unknown 96	?
	unknown cf. Rubiaceae sp. 29	?
	unknown Rubiaceae spp.	?
Rutaceae	*Citropsis articulata*	10.0
	Zanthoxylum sp.	3.5
Sapindaceae	*Blighia welwitschii*	26.0

(*Continued*)

	Chytranthus sp. 1	32.0
	Chytranthus sp. 2	32.0
	Ganophyllum giganteum	18.5
	Laccodiscus pseudostipularis	14.0
	Pancovia sp. (cf. *laurentii*)	15.0
	Radlkofera calodendron	35.0
	Zanha golungensis	18.0
	unknown 208	?
Sapotaceae	*Chrysophyllum africanum*	30.0
	Chrysophyllum boukokonse	28.5
	Chrysophyllum pruniforme	24.0
	Pouteria altissima	15.0
	Synsepalum cerasiferum	17.5
	unknown 112 *Sapotaceae*	?
Simaroubaceae	*Quassia africana*	20.0
	Quassia silvestris	?
Strombosiaceae	*Strombosia pustulata*	22.0
	Strombosiopsis tetrandra	13.0
Thymelaceae	*Dicranolepis baertsiana*	?

Appendix 5

Methodological details for the generation of the spatial predictors.

The spatial eigenvectors were generated following Bauman *et al.* (2018*a*, *b*). To do so, the spatial weighting matrix was optimized using the forward selection with double stopping criterion of Blanchet *et al.* (2008), from a set of four candidate matrices consisting of a Gabriel graph and a minimum spanning tree (connectivity matrices) either unweighted or weighted by a function decreasing linearly with the distance ($f_{ij} = 1 - d_{ij}/D_{max}$, where d_{ij} is the distance between sites i and j, and D_{max} is the maximum distance between two sites). The exclusive choice of graph-based connectivity matrices among the candidates was guided by the greater statistical power and detection accuracy of these matrices for irregular sampling designs, relative to distance-based matrices (Bauman *et al.* 2018*b*). This also allowed us to consider a much broader range of spatial scales than what distance-based MEM would have allowed.

The spatial weighting matrix consisting of the minimum spanning tree weighted by the linear function was selected for both the species richness and the mean weighted seed length of the animal-dispersed seedlings, with six and 12 spatial predictors forward-selected, respectively.

Appendix 6

Means and standard deviations of the response variables (density, species richness, and mean weighted seed length of animal-dispersed seedling species) for each study site in the forest–savanna mosaic in D.R. Congo.

	Density	Species richness	Seed length
Sites	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

Appendix 7

Proportion of the variation (R^2_{adj}) of the three response variables (density, species richness, and mean seed length of animal-dispersed seedlings species) explained by each explanatory variable selected by the forward selection according to Blanchet *et al.* (2008), and among the three components (animal, vegetation and spatial) considered in the variation partitioning analysis, in the forest–savanna mosaic in D.R. Congo. [a]R^2_{adj} obtained from the forward selection; [b]contributions (R^2_{adj}) obtained from the variation partitioning analysis. * and ** indicate significant ($P < 0.05$) and highly significant ($P < 0.01$) results, respectively.

	Response variables			
Contributions	Density	Species richness		Seed length
Animal component	None	Primate abundance		Hornbill abundance
Per variable[a]		0.08**		0.13**
Total[b]		0.08**		0.13**
Pure[b]		0.00		0.00
Vegetation component	None	Plot type	% forest cover	% forest cover
Per variable[a]		0.09**	0.07**	0.03
Total[b]		0.16**		0.03
Pure[b]		0.07**		0.00
Spatial component				
Total[b]		0.33**		0.53**
Pure[b]		0.21**		0.42**
Total	0.00	0.40		0.55

Appendix 8

Mapped general (a and b) and unexplained (residual) (c and d) spatial patterns of the species richness (a and c) and mean weighted seed length (b and d) of the animal-dispersed seedling species. The squares represent the sampled plots (see Appendix 1 for details). The size and colour of the squares are related to the corresponding response variable in such a way that the large black squares display a similar (high) value of the response variable, while the large white squares display a similar (low) value of the response variable. All four patterns are significantly positively autocorrelated.