

Drivers affecting mammal community structure and functional diversity under varied conservation efforts in a tropical rainforest in Cameroon

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Abstract

As well as leading to a loss of biodiversity (i.e. species richness and abundance), human activities also affect ecosystem functioning. Documenting how the suite of ecological roles changes following disturbance provides a complementary source of information for conservation management. To this end, we measured mammal diversity in terms of community structure (i.e. abundance, composition and species richness) and functional diversity in three sites differing in conservation effort in a tropical rainforest in Cameroon. Results show that sites without primary or secondary conservation efforts had lower mammal abundances and an altered mammal composition but similar species richness compared to better-protected areas. In terms of functional diversity, we found more variation of traits (i.e. FDis) in the site with primary conservation and higher abundances of functionally unique species (i.e. FOr) in sites with either primary or secondary conservation efforts. We found no overall difference in the abundance of specialist and generalist species between sites (i.e. FSpe). We identified several drivers affecting abundance, species richness and functional diversity of mammal communities, although there did not appear to be a common driver affecting all mammal diversity measures in a similar way. Our results suggest that, in addition to preserving mammal abundance and community composition, conservation efforts (both primary and secondary) are able to contribute to maintaining higher levels of functional diversity compared to areas devoid of conservation. We demonstrate that functional diversity metrics can provide valuable additional information about the status of mammal communities that can be used to better inform conservation management.

Introduction

The tropical rainforests of the Congo Basin show a high variability in their topographical range and are high in biodiversity levels (i.e. species richness and abundance) (Kamdem-Toham *et al.*, 2003; Gibson *et al.*, 2011). However, increasing human pressure for resources, such as bushmeat and timber, cause major losses in biodiversity which threaten the ecological functioning of tropical rainforests (Fa, Peres & Meeuwig, 2002; Cardinale *et al.*, 2006; Laurance *et al.*, 2006; Gibson *et al.*, 2011; Strindberg *et al.*, 2018). For example, many plants depend on animal agents for seed dispersal and a reduction in these animal species can cause a disrupted seed dispersal cycle, and thus altered ecosystem

functioning (Wang *et al.*, 2007; Campos-Arceiz & Blake, 2011; Petre *et al.*, 2015). Indeed, traditional measures of diversity are often unsuitable in detecting changes in ecological processes (Oliveira *et al.*, 2016). The functional diversity of an ecosystem informs about similarities or dissimilarities between species in a community, in terms of the value and range of their life history traits and functionality, related to their contribution to ecological processes (Tilman, 2001).

One way functional diversity can be explored is by assigning traits, associated with ecosystem functioning, to species and calculating the range and abundance of these traits, allowing the identification of species that are unique in their functional role, through analysing the dissimilarity of species' sets of traits (Mason *et al.*, 2005; Petchey &

Gaston, 2006; Mouchet *et al.*, 2010). Hence, measures of functional diversity offer insights into ecological processes and are arguably more useful in detecting changes in ecosystem functioning than more traditional measures of biodiversity, such as species richness, alone (Mazel *et al.*, 2018). As a result, functional diversity is increasingly studied in different taxonomical groups (e.g. birds; Hidas-Neto, Barlow & Cianciaruso, 2012; Monnet *et al.*, 2014; Sitters *et al.*, 2016; fish; Wu *et al.*, 2016; Colin *et al.*, 2018; Teichert *et al.*, 2018 and mammals; Flynn *et al.*, 2009; Ahumada *et al.*, 2011; Chillo & Ojeda, 2012) and on regional and global levels (Safi *et al.*, 2011; Magioli *et al.*, 2015; González-Maya *et al.*, 2017; Mazel *et al.*, 2018).

Because functional diversity measures may be associated with dynamics in ecosystems that may not be detected by traditional diversity measures, they can provide a valuable source of information for conservation management. The aim of this study was to determine how mammal community structure (i.e. abundance, richness and composition) and functional diversity co-vary over sites with different types of conservation in the tropical rainforest in Cameroon and to analyse the factors that affect mammal community structure and functional diversity. We selected three sites that differ in conservation effort and that were known to differ in habitat composition and human activity as a result of conservation history (Tagg *et al.*, 2015). As such, this study includes sites that differ in terms of official protected status and presence of active conservation efforts. This study had three specific objectives: (1) to describe the three sites in terms of mammal community structure; (2) to determine different indices of mammal functional diversity; and (3) to identify factors that affect the functional diversity, species richness and mammal abundance of the communities.

Although there is an overall decline in mammal abundance in the Congo Basin, even in protected areas (Craigie *et al.* 2010), active conservation management is expected to have a positive localised effect on mammal communities (Tranquilli *et al.*, 2012). Active conservation efforts have proven to be more successful in protecting great ape populations and deterring human activities (Tagg *et al.*, 2015). Hence, we expect to find higher mammal abundances and species richness levels with increasing active, on-the-ground conservation actions. Likewise, we expect that higher hunting pressures in the site with no conservation efforts will lead to an altered mammal community composition. We expect to find differences in mammal community structure (measured in terms of abundance, richness and composition) between sites that are reflected in functional diversity measures (Flynn *et al.*, 2009; Chillo & Ojeda, 2012; D'Agata *et al.*, 2014; Micheli *et al.*, 2014).

Materials and methods

Study sites

We selected three sites in the Dja Conservation Complex in southeast Cameroon: Ekom, La Belgique and Madjuh (Fig. 1). These sites vary in terms of conservation effort (i.e.

official protected status and level of active conservation management) and have previously been found to differ in habitat composition, resulting from historical logging activities, and illegal human activities (i.e. hunting, resource gathering). Ekom, the site with primary conservation efforts, is located within the Dja Biosphere Reserve (DBR) and has a protected status. It is situated 15 km southeast of the nearest village Ekom. Due to its protected status, logging has never occurred, and commercial hunting is illegal, although it still occurs despite the presence of eco-guards (Tagg *et al.*, 2015).

La Belgique is located in the northern periphery of the DBR and 11 km east of the villages Mimpala, Malen V and Doumo. It lies in the southern sector of Forest Management Unit (FMU) 10 047, which was unallocated at the time of this study. Research activities in La Belgique started in 2001 and are managed by Association de la Protection de Grands Singes (APGS). The site has no protected status and was inhabited by people until 30 years ago and selectively logged about 25 years ago. Today, forests in La Belgique have an altered habitat composition with relatively more young secondary forest. Active secondary conservation efforts (i.e. continuous research activities by APGS, environmental education and the provision of small-scale alternatives to bushmeat hunting) have had a positive effect on the protection of great ape populations in the area and have successfully deterred illegal human activities in recent years (Tagg *et al.*, 2015).

Madjuh is situated 10 km east from the nearest village Madjuh and in the northern sector of the FMU 10 047. Similar to La Belgique, Madjuh was selectively logged and has no official protected status. There are currently no conservation activities underway here. Local people rely heavily on the forest for resources and hunting for bushmeat occurs for sustenance and commercial reasons. Similar to the forest in La Belgique, the habitat composition of Madjuh is altered due to historic logging activities, showing higher levels of young secondary forest compared to Ekom (Tagg *et al.*, 2015).

All study sites are located in the same major eco-region: the transition zone of the Atlantic coastal rainforests of southern Nigeria and southwest Cameroon, and the evergreen forests of Equatorial Guinea and the Congo Basin (Letouzey, 1985). Surveys in the early 2000s showed high densities of indicator species (i.e. chimpanzees and gorillas) in the northern periphery of the DBR which were comparable to those within the reserve, suggesting that mammal communities were similar (Dupain *et al.*, 2004).

Sampling design

We opened 15 transects between January and April 2016 in each site (Fig. 1). Each transect was 6 km long and we placed transects parallel to each other and 600 m apart. Due to geographical barriers, not all transects obtained the intended length, resulting in a total of 86.9 km in Ekom, 89.2 km in La Belgique and 89.7 km in Madjuh, resulting in 265.8 km of transects in total. All transects were

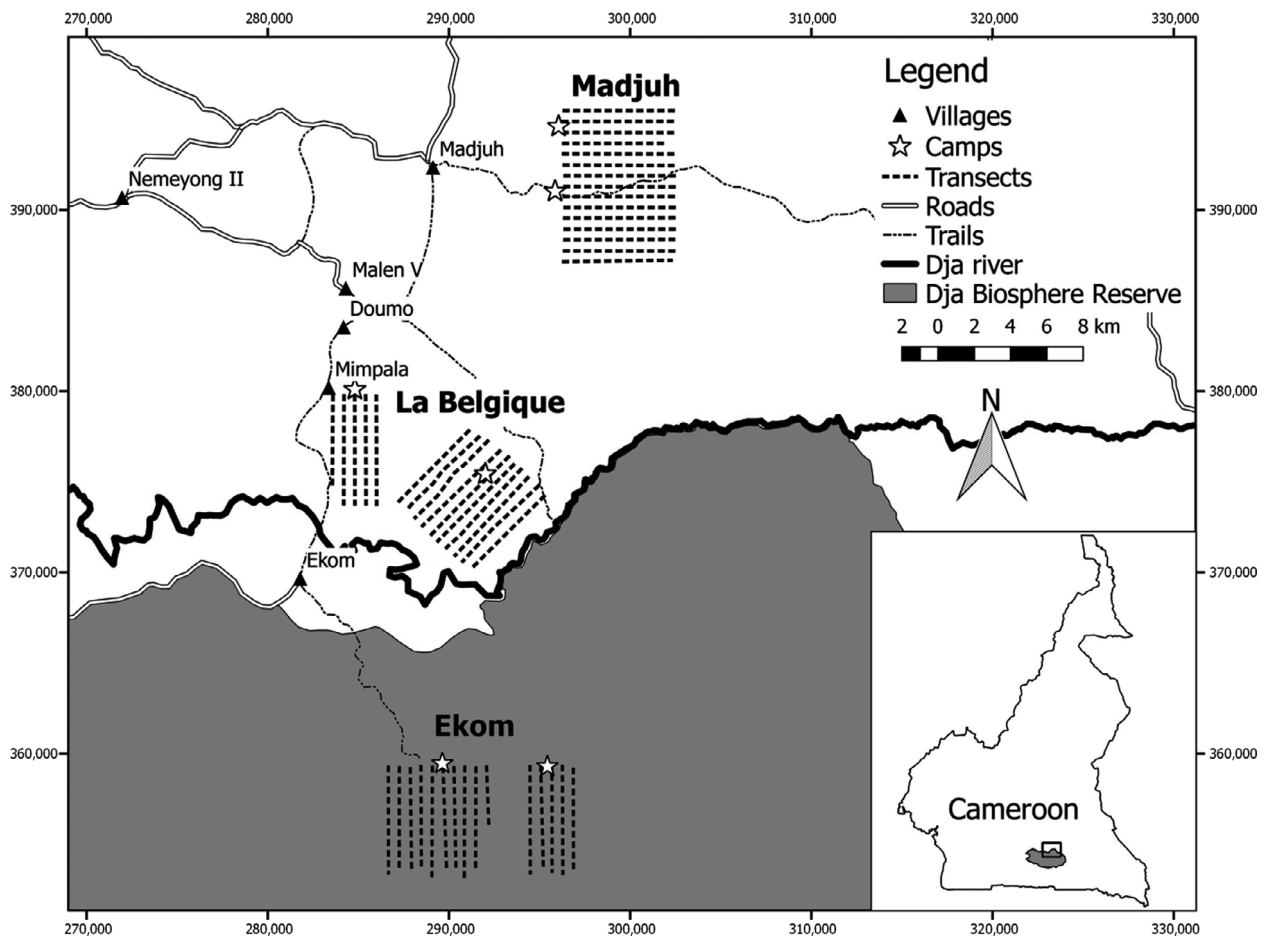


Figure 1 Locations of the three study sites Ekom, La Belgique and Madjuh in the Dja Conservation Complex, Cameroon.

perpendicular to major watercourses and crossed all habitat types. We used digital maps to set transect positioning.

Data collection

From April to July 2016, we conducted line transect surveys to record all mammal signs. Two teams, each comprising one researcher and three local assistants, walked at an average speed of 1.18 km h^{-1} along the transects. We sampled each site once. One assistant performed distance sampling for direct observations approximately 300 m in front of the rest of the team. We used strip transects (2 m wide) to measure all indirect signs of mammal activity including dung, footprints, signs of digging, feeding remains and sleeping sites. For chimpanzee *Pan troglodytes troglodytes* and gorilla *Gorilla gorilla gorilla* nests, we used a strip width of 20 and 10 m, respectively, which was appropriate for the undergrowth visibility in this area (pers. comm. J. Willie). We grouped signs for bay duiker *Cephalophus dorsalis*, black-fronted duiker *Cephalophus nigrifrons* and Peter's duiker *Cephalophus callipygus* together as red duikers (van Vliet *et al.*, 2007).

We also recorded all signs of human activity including snares, gun cartridges, rubbish, camps, fire remains, footprints,

direct encounters, machete cuts, bark stripping and signs of non-commercial logging activities. We grouped these signs together as 'human signs'. Furthermore, we recorded all old logging roads and human trails which were grouped separately as 'trails' since they do not necessarily indicate recent human activities, but do facilitate access to the forest. We determined habitat composition every 50 m on the transect according to six classifications from previous studies in the area (Dupain *et al.*, 2004; Willie *et al.*, 2012): young secondary forest (YSF), old secondary forest (OSF), near primary forest (NPF), light gaps (LG), riparian forest (RIP) and swamps (SW). We determined other site features concerning distance from transect stretches to nearest human villages, village trails, roads and Dja River using ArcGIS.

Species trait data

We selected five traits that relate to resource capture, use, release and energy flow within the ecosystem. As such, we selected traits that cover the species' effects on ecological processes and how they respond to disturbances (Flynn *et al.*, 2009; Cooke, Bates & Eigenbrod, 2019): feeding guild (relevant to the type of resource consumed and to functions such as

seed-dispersal, predation and herbivory (Ripple *et al.*, 2015)), body mass (covering the amount of resource consumed and processed and the contribution to ecological processes [e.g. food-web structure]), activity pattern (reflecting the temporal distribution of resource use and if species are able to react to disturbances [e.g. specific types of human hunting]), and habitat use and home range (reflecting on the spatial distribution and extent of resource intake and release (Flynn *et al.*, 2009; Safi *et al.*, 2011; Chillo & Ojeda, 2012)). Combinations of categories, except body mass and home range, were possible and were included as fuzzy coded data. We collected trait data from available literature (Supporting Information).

Statistical analyses

We divided each of the 45 6-km long transects into 600 m stretches and labelled them 1–10 within each transect. Only uneven numbered stretches were included for data analysis to ensure independent sample units, resulting in 73 stretches in Ekom and 75 in both La Belgique and Madjuh. We calculated the encounter rate as the sum of species-specific signs, human signs, trails and habitat types per 600 m stretch. To calculate overall mammal abundance, we pooled all mammal signs together. Data did not meet the assumptions of normality and were therefore analysed using nonparametric statistical approaches. For each species, we statistically compared the means across sites using Welch's ANOVA and Games-Howell post-hoc test (Cribbie & Keselman, 2003) using the “*oneway*” function in the “*userfriendlyscience*” package (Peters, 2018) in R 3.4.4 (R Development Core Team, 2008). We used rarefaction curves to assess if species richness was adequately observed and to test if the sampling effort was satisfactory for inter-site comparison. We extrapolated them beyond the reference sample size using the multinomial model (Chao *et al.*, 2009; Colwell *et al.*, 2012) in EstimateS (Colwell, 2013) to take into account differences in sample sizes and compared trends in mammal species richness between sites (Willie *et al.*, 2012). We compared mammal species composition between sites using a Multi-Response Permutation Procedure (MRPP), a multivariate testing method that assesses whether or not two sites differ significantly in composition (McCune & Grace, 2002) with absolute counts per transect entered as data. We performed analyses with the Bray-Curtis distance measure in PC-ORD 4.0 (McCune & Mefford, 1999).

To calculate and compare functional diversity between sites, we selected three abundance-weighted indices for functional diversity: functional dispersion (FDis), functional originality (FOri) and functional specialization (FSpe) (Villéger, Mason & Mouillot, 2008; Laliberte & Legendre, 2010; Villéger, Grenouillet & Brosse, 2013). We selected FDis to reflect on the diversity of functional traits present in the community through calculating the mean distance of individual species to the abundance-weighted centroid of all species in the total community and an indicator of trait diversity (Laliberte & Legendre, 2010). A greater spread of species in the trait space suggests a greater diversity of traits. FOri indicates how common species with unique traits are within the community and is calculated as the abundance-weighted mean distance to the nearest species within the functional space

(Mouillot *et al.*, 2013). Lastly, we quantified how specialist species (i.e. species with relatively specialised trait combinations) and generalist species (i.e. species with general trait combinations) change in abundance by calculating FSpe as the abundance-weighted mean distance in the functional space to the average value of all species present at the regional scale. Together, these three indices are able to detect if the diversity of functional traits is altered and if abundances of species with functionally ‘interesting’ traits (i.e. unique traits or specialist or generalist species) are changed, an important aspect for conservation management when conserving the ecological integrity of ecosystems. We calculated these abundance-weighted indices for each stretch using the ‘*qual_funct_space_fromdist*’ and ‘*multidimFD*’ functions (written by S. Villéger, for more details see Villéger *et al.*, 2008, 2013) in R 3.4.4 (R Development Core Team, R, 2008). We excluded stretches with no animal signs from the functional diversity analyses and compared the means of the indices between sites using the Welch's ANOVA with the Games-Howell post-hoc test.

We assessed variation in mammal abundance, species richness and abundance-weighted functional diversity between sites according to site characteristics using Generalised Linear Mixed Models (GLMMs). Models for mammal abundance and species richness used a Poisson distribution and log link function and models for FDis, FSpe and FOri used binomial errors and a logit link. The predictors that were entered in the models included: (1) Site (i) Ekom [primary conservation efforts], (ii) La Belgique [secondary conservation efforts] and (iii) Madjuh [no conservation efforts]; (2) Number of human signs; (3) Number of trails; (4) Distance to (i) villages, (ii) village trails, (iii) roads, and (iv) the Dja River and (5) Proportion of habitat type (i) YSF, (ii) OSF and (iii) NPF.

We corrected for multicollinearity between all predictors by calculating the variance inflation factor (VIF) and predictors with VIF > 5 were excluded from subsequent analyses (O'Brien, 2007). Distance to village trails and Distance to roads showed a high correlation with each other and we excluded both as predictors. We treated Site and site characteristics (Distance to villages, Distance to Dja River, Number of human signs and trails and Proportion of habitat type) in each sampling unit as fixed factors. We nested stretches in transects, and transects in Site, which we included as a random effect in our models, thus correcting for potential spatial autocorrelation (Tavares *et al.*, 2015; Tavares, De Moura & Siciliano, 2016). In the models analysing FDis, FSpe and FOri, we used mammal abundance as weight as this can influence these dependent variables. We generated a series of models and compared them based on a AICc value of <2 (Burnham & Anderson, 2002). Finally, we calculated the model-averaged parameter estimates of the variables that remained in the final model, together with their relative variable importance (RVI) (Burnham & Anderson, 2002).

Results

Habitat composition and human activity

Habitat composition and human activity showed significant differences between sites (Table 1). La Belgique and Madjuh

Table 1. Observed mean values (counts per 600 m stretch, except for distances which are expressed in kilometres) \pm standard error of analysed variables in Ekom (primary conservation), La Belgique (secondary conservation) and Madjuh (no conservation) in the Dja Conservation Complex, Cameroon

	Ekom (E)	La Belgique (LB)	Madjuh (M)	Significant differences
Habitat composition				
Young secondary forest	3.27 \pm 0.26	4.51 \pm 0.24	4.68 \pm 0.31	E-LB**; E-M**
Old secondary forest	4.71 \pm 0.25	3.81 \pm 0.26	3.96 \pm 0.27	E-LB*
Near primary forest	0.86 \pm 0.17	0.12 \pm 0.05	0.23 \pm 0.09	E-LB***; E-M**
Light gap	0.92 \pm 0.10	0.48 \pm 0.07	0.97 \pm 0.12	E-LB**; LB-M**
Riparian forest	0.96 \pm 0.16	1.31 \pm 0.17	0.93 \pm 0.16	
Swamp	1.27 \pm 0.17	1.57 \pm 0.18	1.23 \pm 0.20	
Human activity				
Human signs ^a	0.25 \pm 0.08	0.52 \pm 0.08	0.77 \pm 0.12	E-LB*; E-M**
Trails ^c	0.0 \pm 0.0	0.03 \pm 0.02	0.56 \pm 0.09	E-M***; LB-M***
Distance to				
Villages (km)	15.89 \pm 0.30	7.45 \pm 0.39	10.17 \pm 0.20	E-LB***; E-M***; LB-M***
Village trails (km)	15.86 \pm 0.30	5.66 \pm 0.36	2.12 \pm 0.15	E-LB***; E-M***; LB-M***
Dja river (km)	11.75 \pm 0.20	3.61 \pm 0.19	13.66 \pm 0.29	E-LB***; E-M***; LB-M***
Roads (km)	15.97 \pm 0.30	9.17 \pm 0.24	9.85 \pm 0.22	E-LB***; E-M***

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

^aInclude snares, gun cartridges, rubbish, camps, fire remains, footprints, direct encounters, machete cuts, bark stripping, and signs of non-commercial logging activities.

^bInclude old logging roads and human trails.

had higher levels of YSF and less NPF, indicating an altered habitat composition. The number of human signs was higher in La Belgique and Madjuh, while the number of trails was only higher in Madjuh.

Mammal community structure: abundance, species richness and composition

We found a significant difference for overall mammal abundance, measured as the number of signs per 600 m stretch, between all study sites ($F(2, 136.20) = 62.149$, $P < 0.001$; Fig. 2), with Ekom showing the highest mammal abundance, La Belgique intermediate levels and Madjuh the lowest abundance (all $P < 0.001$). Additional information on

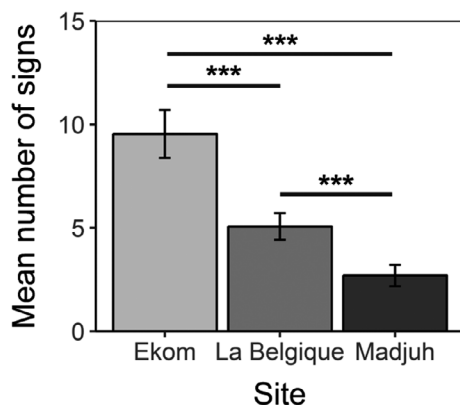


Figure 2 Mean encounter rate, measured as the number of signs per 600 m stretch \pm 95% CI for all mammals pooled together. *** $P < 0.001$.

species-specific abundances can be found in the Supporting Information.

Mammal surveys recorded 21 species in Ekom, 19 species in La Belgique and 19 species in Madjuh, comprising a species assemblage of 23 species across all sites (Supporting Information). Extrapolations of the rarefaction curves did not result in significant differences in species richness between study sites (Fig. 3).

MRPP analyses indicate that Ekom, La Belgique and Madjuh show compositional differences in their mammal assemblages based on absolute differences. The largest difference in mammal species composition is observed between Ekom and Madjuh ($T = -24.720$, $P < 0.001$) and La Belgique and Madjuh ($T = -13.810$, $P < 0.001$). The difference in mammal species composition between Ekom and La Belgique is significant, yet considerably smaller ($T = -3.219$, $P = 0.006$).

Functional diversity

We calculated FDis, FOr and FSpe on a stretch level and compared the means of these indices between sites (Fig. 4). FDis showed significant differences between sites ($F(2, 121.08) = 7.833$, $P < 0.001$) with Ekom showing higher FDis levels than Madjuh ($P < 0.001$). There was no significant difference between Ekom and La Belgique ($P = 0.117$) or between La Belgique and Madjuh ($P = 0.083$). FOr did significantly differ between sites ($F(2, 124.69) = 29.651$, $P < 0.001$) with Madjuh showing the lowest FOr levels compared to Ekom and La Belgique (both $P < 0.001$). FOr levels did not differ between Ekom and La Belgique ($P = 0.802$). The global test did not reveal any differences for FSpe levels between sites ($F(2, 131.34) = 1.309$, $P = 0.273$).

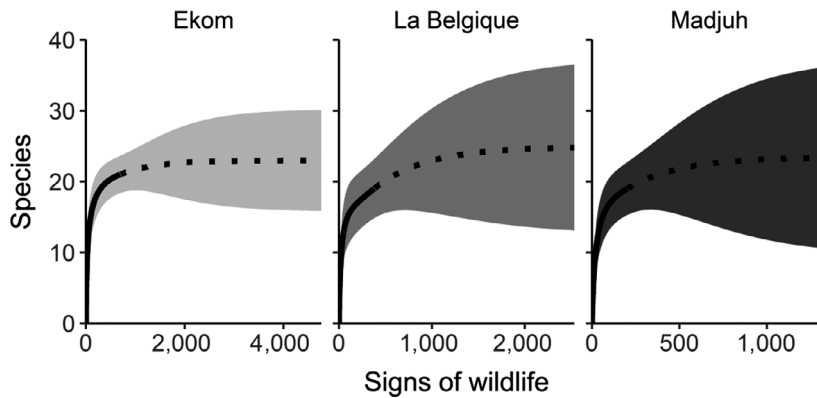


Figure 3 Rarefaction and corresponding extrapolation (dotted lines) for mammalian species richness. Solid lines indicate the observed number of species.

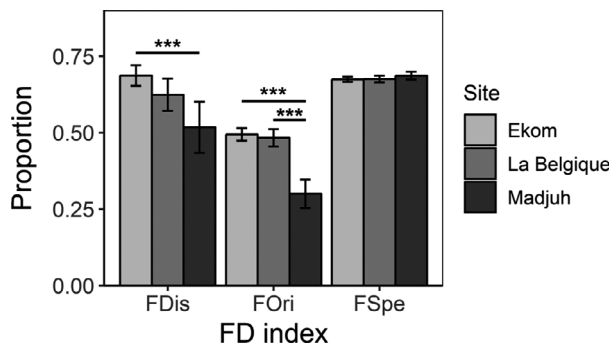


Figure 4 Average functional diversity levels per site for functional dispersion (FDis), functional originality (FOr) and functional specialisation (FSpe) ± 95% CI. *** $P < 0.001$.

Factors affecting mammal community structure and functional diversity metrics

We ran GLMMs to examine potential drivers that explain differences in mammal abundance, species richness and FDis, FOr and FSpe levels. Based on delta AICc < 2 model selection, we identified different drivers for the five targets (Table 2). Following the RVI approach for identifying drivers, we found that Site was most important in explaining differences in mammal abundances and that sites with secondary (La Belgique) and primary (Ekom) conservation efforts have a positive effect on mammal abundances. For species richness, we identified Site and Distance to the Dja River as major drivers. The site Ekom showed a positive significant effect on species richness. Distance to the Dja River has a negative effect on species richness. Furthermore, we found that Number of trails and Proportion of habitat type YSF were major drivers in explaining variation of FDis levels, both having a negative effect. FOr was likewise negatively affected by Number of trails, but positively affected by the site Ekom. We identified no important drivers for explaining differences in FSpe levels.

Discussion

The main objective of this study was to determine how mammal community structure and functional diversity in a tropical rainforest co-vary over sites with different conservation efforts. Overall, we found that primary and secondary conservation efforts benefit mammal abundance, composition and some, but not all, measures of functional diversity while species richness levels did not differ between sites. Furthermore, we identified drivers that explain differences in mammal abundance, species richness and functional diversity measures at a stretch level.

Our findings support earlier studies that confirm the efficacy of conservation efforts (both primary in Ekom, and secondary in La Belgique) (Tagg, Petre & Willie, 2011; N’Goran *et al.*, 2012; Tranquilli *et al.*, 2012; Tagg *et al.*, 2015). The lower mammal abundances and altered mammal species composition in La Belgique and Madjuh suggest that abundances decline disproportionately across species. One explanation for this uneven decline in abundance is that hunters selectively target species. For example, large-bodied species are often favoured by hunters as they provide more meat, meaning that these species experience higher hunting pressures (Abernethy *et al.*, 2013; Ripple *et al.*, 2016). Indeed, several large-bodied species experience significant losses in abundance in this study (e.g. chimpanzee, forest elephant *Loxodonta africana cyclotis*, red river hog *Potamochoerus porcus*, western lowland gorilla and the yellow-backed duiker *Cephalophus sylvicultor*). This effect may become more pronounced through time as large-bodied species are often less resilient to hunting due to their slower reproductive rates (Stokes *et al.*, 2010; Linder & Oates, 2011).

Although the differences in mammal abundances did not result in changes in species richness, as suggested by the rarefaction curves, we did record more species in total during our surveys in the primary conservation site (Ekom). The GLMMs also identified that primary conservation in Ekom has a positive effect on species richness levels. We additionally found more species closer to the Dja River, suggesting

Table 2. Statistics from the GLMM for mammal diversity measures (mammal abundance, species richness, FDis, FOr and FSpe, see Fig. 4) as a function of site characteristics

	Estimate	SE	z	P	RVI
Mammal abundance					
(Intercept)	1.137	0.109	10.395	<0.001	
Ekoum	1.031	0.133	7.769	<0.001	1.00
La Belgique	0.393	0.190	2.068	0.039	
Trails	-0.107	0.064	1.675	0.094	0.70
% Old secondary forest	-0.071	0.047	1.514	0.130	0.43
% Young secondary forest	-0.073	0.050	1.479	0.139	0.41
Distance to Dja River	-0.121	0.097	1.256	0.209	0.27
Distance to villages	0.048	0.069	0.694	0.488	0.07
Human signs	-0.019	0.043	0.446	0.655	0.06
Species richness					
(Intercept)	1.170	0.107	10.912	<0.001	
Ekoum	0.470	0.135	3.477	0.001	1.00
La Belgique	-0.066	0.224	0.295	0.768	
Distance to Dja River	-0.199	0.094	2.114	0.034	0.94
% Young secondary forest	-0.078	0.046	1.713	0.087	0.62
Trails	-0.100	0.063	1.595	0.111	0.61
Distance to villages	0.089	0.059	1.512	0.131	0.51
% Old secondary forest	-0.059	0.041	1.419	0.156	0.37
% Near primary forest	-0.038	0.037	1.017	0.309	0.23
Human signs	0.025	0.039	0.651	0.515	0.06
FDis					
(Intercept)	0.705	0.066	10.754	<0.001	
Trails	-0.252	0.106	2.375	0.018	1.00
% Young secondary forest	-0.156	0.079	1.978	0.048	0.83
% Old secondary forest	-0.107	0.070	1.536	0.124	0.46
Human signs	0.101	0.075	1.350	0.177	0.46
% Near primary forest	0.100	0.068	1.463	0.144	0.42
Distance to villages	0.074	0.065	1.140	0.254	0.26
Distance to Dja River	0.039	0.072	0.545	0.586	0.04
FOr					
(Intercept)	-0.576	0.179	3.213	0.001	
Trails	-0.310	0.137	2.269	0.023	1.00
Ekoum	0.537	0.223	2.410	0.016	0.94
La Belgique	0.414	0.220	1.886	0.059	
% Old secondary forest	-0.084	0.063	1.333	0.183	0.40
Distance to villages	-0.130	0.098	1.330	0.183	0.27
Human signs	0.077	0.071	1.085	0.278	0.22
% Young secondary forest	-0.061	0.071	0.855	0.392	0.13
% Near primary forest	0.042	0.055	0.757	0.449	0.07
Distance to Dja River	0.074	0.153	0.485	0.628	0.06
FSpe					
(Intercept)	0.752	0.061	12.395	<0.001	
Distance to Dja river	0.036	0.067	0.535	0.593	0.18
% Young secondary forest	-0.031	0.065	0.483	0.629	0.18
Human signs	-0.033	0.068	0.482	0.630	0.18

The site Madjuh is used as reference category. Bold values indicate significance at $P < 0.05$. RVI, relative variable importance.

that the habitat closer to the river can host more species, although this warrants further research. It also indicates that, while the Dja River potentially facilitates access to the forest to hunters, it does not negatively affect species richness.

A reduction in animal abundance is typically associated with a loss of functional diversity (Flynn *et al.*, 2009; Chillo & Ojeda, 2012; Mouillot *et al.*, 2013; Wu *et al.*, 2016). Indeed, we found differences between sites for FDis and FOr. We found that the variety of functional roles (measured as FDis) decreases with increasing number of trails and higher levels of YSF. Accordingly, we found the lowest FDis in Madjuh, the site with the highest number of trails, and more YSF than in Ekoum, explaining the difference in FDis. Trails, which include old roads used by forest exploitation companies and human trails, are likely used by hunters to access forest patches and therefore facilitate hunting activities. Likewise, the high YSF proportions in Madjuh are the result of previous logging activities. Logging in Madjuh (and La Belgique) ceased 30 years ago, but it seems that the effect of these activities are still discernible via decreases in FDis levels, perhaps mediated by the higher proportion of YSF. As YSF is characterised by a discontinuous forest canopy and dense herbaceous undergrowth, it is possible that these forest patches are not suitable for species with certain trait combinations. For example, YSF may not be suitable for arboreal and frugivorous species (e.g. chimpanzees (Dupain *et al.*, 2004; Tagg *et al.*, 2013)) while terrestrial and herbivorous species may prefer YSF due to higher food abundances. In other words, historic logging activities, measured as a heightened proportion of YSF and a higher encounter rate of old logging roads, have long-term effects on the functional diversity of the remaining mammal communities via both an alteration in habitat composition and by facilitating access by humans to forest patches together reducing the variety of functional roles. We advocate that future studies focus on how functional diversity is affected in logging concessions and how recovery trajectories might help inform sustainable logging methods.

We also found that FOr levels are lower in Madjuh compared to Ekoum and La Belgique. FOr levels decrease when functionally unique species decline in abundance, or increase when functionally common species decline in abundance (Leitão *et al.*, 2016). As we observed a decline in abundance of several species in Madjuh, it is likely that FOr decreased in Madjuh, caused by a decline in the abundance of unique species in Madjuh, rather than an increase of FOr in Ekoum and La Belgique due to a decline in common species. Site was indeed a major driver affecting FOr values, with Ekoum having a positive effect and La Belgique a near significant positive effect. This indicates that mammal communities in these forests experience a positive effect from primary and secondary conservation efforts, resulting in higher levels of functional originality. We also found that FOr decreased with more trails, suggesting that increased human activity negatively affects the abundance of functionally unique species.

Despite differences in FDis and FOr, we did not find any between-site differences in FSpe, suggesting that the

abundance of specialist and generalist species are not affected by conservation type. This is remarkable given the differences in species abundance, community composition and FDis and FOrl between sites (Villéger *et al.*, 2010). More in-depth research is needed to understand why FSpe levels remain unchanged. Simultaneously, this confirms the idea that a single measure does not successfully represent changes in functional diversity, but that multiple indices are needed (Villéger *et al.*, 2008; Mouillot *et al.*, 2013).

As tropical forests provide ecosystem services of global relevance, conserving their ecological integrity is of high concern (Strassburg *et al.*, 2010; Gibson *et al.*, 2011). Overall, our results suggest that primary and secondary conservation efforts have a positive effect on mammal communities in terms of their structure and functional diversity and that a lack of conservation effort is associated with an impoverished mammal community structure and loss of functional diversity. Between sites with primary and secondary conservation efforts we found differences in the structure of mammal communities, but not in their functional diversity. This suggests that primary and secondary conservation efforts have different impacts on mammal communities but are nonetheless able to maintain relatively high levels of functional diversity. This highlights that measures of mammal community structure and functional diversity do not capture the same changes in mammal communities and should be used to complement each other. For effective future conservation management, it is essential to better understand the functional roles of animals within their ecosystem and how community dynamics respond to human activities and current conservation efforts.

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Conflict of interest

We declare no conflict of interest.

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Supporting information

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

Table S1. Traits regarding resource capture, use, release and energy flow used to measure mammal functional diversity indices

Table S2. Species-specific mean number of signs per 600 m stretch \pm SE per site with pairwise comparisons

Table S3. Trait data for all species included in functional diversity calculations