



CONVENTION ON MIGRATORY SPECIES

UNEP/CMS/COP13/Inf.35

11 December 2019

Original: English

13th MEETING OF THE CONFERENCE OF THE PARTIES
Gandhinagar, India, 17 - 22 February 2020
Agenda Item 11.6

LONG-TERM TRENDS IN WILDLIFE COMMUNITY STRUCTURE AND FUNCTIONAL DIVERSITY IN A VILLAGE HUNTING ZONE IN SOUTHEAST CAMEROON

(Prepared by Born Free Foundation)

Summary:

A recently published paper by Tagg *et al.* considers changes in wildlife abundance and diversity of functional traits related to resource use and energy flow, using data collected between 2002-2016, in a tropical forest wildlife community in southeast Cameroon which has been subject to escalating hunting activities over the past decade. The authors found that declines in wildlife abundances and species richness were followed by significant reductions in functional diversity, and concluded that by the end of the study, the area was likely to be experiencing the start of ecological decay. They concluded that hunting, particularly of large bodied mammals, which may represent the greatest threat to wildlife populations across the Congo basin, may consequently also be a driver of ecosystem breakdown.

This document has been submitted by Born Free Foundation to provide information on the unsustainable use of terrestrial and avian wild meat, in particular because of the methodology it offers for evaluating the threshold of alteration in wildlife communities, beyond which ecological functions are compromised and ecological decay begins.

Long-term trends in wildlife community structure and functional diversity in a village hunting zone in southeast Cameroon

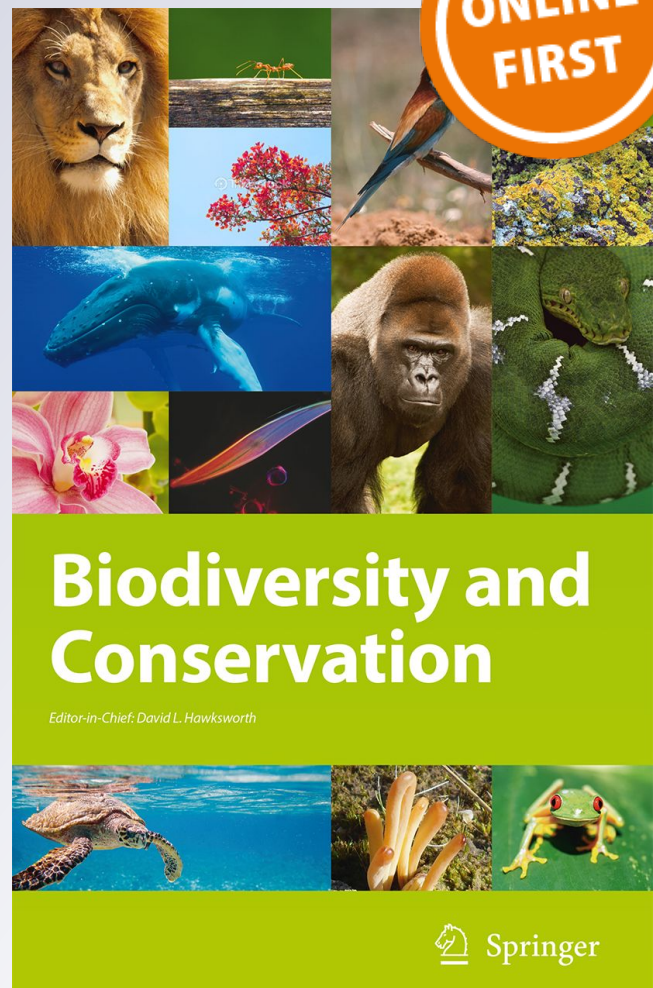
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Biodiversity and Conservation

ISSN 0960-3115

Biodivers Conserv

DOI 10.1007/s10531-019-01899-1



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Long-term trends in wildlife community structure and functional diversity in a village hunting zone in southeast Cameroon

Nikki Tagg^{1,2} · Jacques Keumo Kuenbou³ · Daan Willem Laméris⁴ · Fany Michelle Kamkeng Meigang⁵ · Sévilor Kekeunou⁵ · Manfred Aimé Epanda⁶ · Jef Dupain⁷ · Donald Mbohli² · Ian Redmond⁸ · Jacob Willie^{1,9}

Received: 14 January 2019 / Revised: 12 November 2019 / Accepted: 15 November 2019
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Abstract

Hunting may be the greatest threat to wildlife populations across the Congo basin. Large-bodied species are the most vulnerable; alterations in assemblages of such keystone species can affect many important ecological functions. There may be a reduction or loss of ecological services, such as seed dispersal. Monitoring functional diversity within a wildlife community alongside descriptions of wildlife community structure (abundances and species richness) increases understanding of how well a system can withstand disturbance, or recover following it (i.e., its ecological resilience). Between 2002 and 2016, changes in wildlife abundance and diversity of functional traits related to resource use and energy flow were monitored in a tropical forest wildlife community in southeast Cameroon, where hunting activities have escalated in the last decade. Wildlife abundances significantly decreased by 2009, and species richness and functional diversity declined by 2016. This reduction in functional diversity suggests that the wildlife community has been considerably altered, compromising ecological functions, and indicating the start of ecological decay. The study found a significant reduction in keystone species, such as great apes and elephants, suggesting that their decline as a result of hunting is leading to ecological imbalance. The results suggest that, beyond a certain threshold of wildlife decline, wildlife community collapse and ecological decay are likely. Identifying such thresholds can inform sustainable wildlife management and help monitor the health or integrity of the ecosystem, and its ability to provide globally significant ecosystem services, such as carbon sequestration and storage.

Keywords Wildlife abundance · Species richness · Ecological services · Ecological degradation

Communicated by Karen E. Hodges.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10531-019-01899-1>) contains supplementary material, which is available to authorized users.

✉ Nikki Tagg
 Nikki.tagg@kmda.org

Extended author information available on the last page of the article

Introduction

The tropical rainforests of the world's two biggest river basins, the Amazon and the Congo, have the highest biological diversity of all ecosystems on the planet (Mittermeier et al. 1998), supporting around three-quarters of all known species (Barlow et al. 2018). The integrity of these forest ecosystems is threatened by anthropogenic pressures, including the unsustainable use of forest resources, for example, hunting (Lewis et al. 2015; Malhi et al. 2014). Hunting may be the greatest cause of decline of many wildlife species in the tropics (Brashares et al. 2004; Fa et al. 2014; Milner-Gulland and Bennett 2003; Ripple et al. 2016). Modern humans have been hunting in these basins for hundreds of thousands of years (Stringer and Galway-Witham 2018). However, rapid population increases have led to dramatically increased hunting in recent decades (Abernethy et al. 2013; Castelletta et al. 2000; Robinson and Bennett 2000). This is exacerbated by recurrent or ongoing conflict or civil wars, and improved access into previously remote forest tracts (for example, as a result of logging activities; Ape Alliance 1998; Redmond et al. 2006; Ripple et al. 2016), which are now penetrated by up to 40 km from access points (Abernethy et al. 2013). The rapid increase in commercialisation of and demand for wild caught meat ('bushmeat') in recent decades has contributed to increased hunting. More than 5 million tons of wild meat, including primates, birds, rodents, carnivores, ungulates, amphibians and reptiles, are harvested from the tropical forests of Congo and Amazon basins annually (Fa et al. 2002, 2006; Muchaal and Ngandjui 1999).

The decline or loss of an animal population can affect all other animal and plant species with which it interacts ecologically (Dirzo et al. 2014). These effects may be greatest for keystone species, as they play important roles in determining the ecological functioning of a community (Mills et al. 1993). Keystone species include predators, which help maintain mammal, avian, invertebrate and herpetofauna abundance or richness (Estes et al. 2011; Ripple et al. 2014); and large herbivores and frugivores, which impact upon scavengers, mesoherbivores and small mammals (Ripple et al. 2015). Decline in a keystone species can lead to a boom in a species that it contributes to maintain; for example, a loss of large herbivores leads to an increase in rodents in Nigeria (Keesing and Young 2014). This is known as 'competitive release' (Linder and Oates 2011), and it further affects the balance of wildlife assemblage compositions. The abundance of rodents is higher in a hunted site as a result of competitive release, even though they are also hunted (Effiom et al. 2013).

As wildlife interactions are altered, ecological functions of the wildlife community are affected, reduced or lost (Cardinale et al. 2006). Species and communities contribute complex, diverse and critical ecological functions, also considered ecological 'services': direct and indirect functions that are advantageous or critical to human wellbeing (Chee 2004). Direct services include food production (Clough et al. 2011), which is crucial for livelihoods and food security of hundreds of millions of people around the globe (Nasi et al. 2011; Ripple et al. 2016); control of invasive species (Estes et al. 2011) and limiting the rise of zoonoses, which could increase through competitive release (Ripple et al. 2016). Most tropical tree species are animal-dispersed (Petre et al. 2013), and seeds can be cleaned, scarified (shallow cuts on the seed coat incurred during passage through the gut) or consumed, and deposited at some distance from the parent tree (Petre et al. 2015; Whitworth et al. 2016).

In some cases, when a species is lost, other sympatric species may fulfil (parts of) the same roles, thus rendering redundant the lost species' contribution and limiting the impact of its loss (Lawton and Brown 1994). In other cases, however, the role of a particular

species is not redundant, due to differing physical or behavioural characteristics (Ripple et al. 2016) and consequently, the function performed by the non-redundant species within the ecosystem will be lost (Bueno et al. 2013). This can result in a loss of certain tree species; a change in tree species compositions; a reduction in tree species richness; and a change in forest structure (Abernethy et al. 2013; Chillo and Ojeda 2012; Effiom et al. 2013; Nunez-Iturri et al. 2008; Poulsen et al. 2018; Vanthomme et al. 2010). For example, canopy-dwelling animal species and terrestrial frugivores contribute to pollination and seed dispersal in rainforests. This in turn results in the degradation or loss of many natural processes that underlie the ecosystem services of forests. These processes include regulating the dynamics of disease, and of wildfire, carbon sequestration and biogeochemical cycles (Brodie and Gibbs 2009; Bunker et al. 2005; Estes et al. 2011). Also affected are processes that limit the influence of natural disturbances (e.g., storms, floods and drought; Costanza et al. 1997), provide water and timber, or regulate the climate and the water cycle. Finally, cultural services, such as leisure and research, can be affected (Costanza et al. 1997). Each of these ecosystem services are of global concern, are relevant to health and wellbeing of all life, including humans, across the planet (Redmond, 2016; Redmond and Virtue 2008; Ripple et al. 2016) and are of high monetary value (Costanza et al. 1997).

Monitoring the diversity of different roles in the ecosystem ('functional diversity') helps us understand the mechanisms by which species diversity impacts upon ecological functions and ecosystem functioning (Cadotte et al. 2011; Chillo and Ojeda 2012). Functional traits of species are characteristics or habits that determine when and where a species can exist and how they interact (McGill et al. 2006). They can be phenotypic (e.g., gape size, tooth morphology) or behavioural (e.g., nocturnality, cannibalism; Cadotte et al. 2011). Monitoring of the presence or loss of critical functions in sites where wildlife abundances and species compositions are changing over time because of hunting pressures, can inform on how well a system can withstand disturbance, or recover following it (Abernethy et al. 2013; Wright et al. 2000). This can provide a measure of the degree of ecological resilience of the ecosystem at varying stages of defaunation (Mason et al. 2005), which can help us effectively conserve and restore habitats (Cadotte et al. 2011; Fukami et al. 2005). The focus should shift from species extinctions to ecological extinctions (Valiente-Banuet et al. 2015). Most studies to date on functional diversity have focussed on bird (Dehling et al. 2014; Flynn et al. 2009; Gasc et al. 2013; Monnet et al. 2014) or fish communities (D'Agata et al. 2014; Micheli et al. 2014). In Central African forest ecosystems, studies have focussed on arid and semi-arid environments (Chillo and Ojeda 2012), except for some studies in disturbed tropical forests investigating the functional diversity of amphibians (Ernst et al. 2006). However, empirical studies on mammal functional diversity in tropical forest hunting zones are few (Abernethy et al. 2013; Effiom et al. 2013; Laurance et al. 2012). All reveal that anthropogenic disturbance negatively affects functional diversity within the wildlife assemblage (Chillo and Ojeda 2012; D'Agata et al. 2014; Flynn et al. 2009; Micheli et al. 2014).

The objective of this paper, therefore, is to evaluate structural and functional change within a mammal community over a 14-year period in a site in southeast Cameroon, Central Africa, where hunting pressure has intensified over the years (Ávila et al. 2017), to assess how human pressure affects wild animal communities. The study describes mammal abundances, species richness and changes in functional diversity over time in the tropical forest mammal community of this hunting zone. The forest site has not been logged and lies within the buffer zone of a protected area (the Dja Faunal Reserve; IUCN 2014). The site is officially unprotected and is hunted by local people but receives some active management via a research programme and ongoing sensitisation of local people (Dupain

2001; Tagg et al. 2015). It was hypothesised that (1) mammals will significantly decrease in abundance over the 14-year period; (2) species diversity will subsequently decrease; and (3) functional diversity will decrease over time.

Methods

Study area

Research was carried out in the northern periphery of the Dja Reserve in southeast Cameroon in the traditional hunting forests of the communities of Malen V, Doumo Pierre and Mimpala, in the department of Abong-Mbang, East Region (Fig. 1). The hunting zone is about 110 km² (Epanda et al. 2005). There are two rainy seasons, February–July and August–November, and two dry seasons, November–February and July–August, and a mean annual precipitation of 1637.9 mm (SD=105.1 mm). The temperature in this area varies little throughout the year; average minimum and maximum daily values are 19.5 °C (SD=1.3 °C) and 26 °C (SD=2.4 °C) (Willie et al. 2014). Local communities have been involved in conservation, development and research activities of ‘Association de la Protection de Grands Singes’ (APGS), established in 2001 with the aim of preventing the extirpation of great apes and improving wildlife conservation efforts in the region (Dupain 2001; Tagg et al. 2015).

Data collection

In November 2002 (reference year), three sets of transects were established in the hunting zones of the villages Malen V, Doumo-Pierre and Mimpala, respectively (Fig. 1). All sets were located within 8 km of the nearest village and comprised 7–10 small transects totalling 20 km (average transect length \approx 2.35 km; range 1.5–4 km), therefore resulting in a total of 60 km of transects. Within each set, transects were placed parallel to each other, 1 km apart and perpendicular to the main trail. Transects traversed swamps, fallows

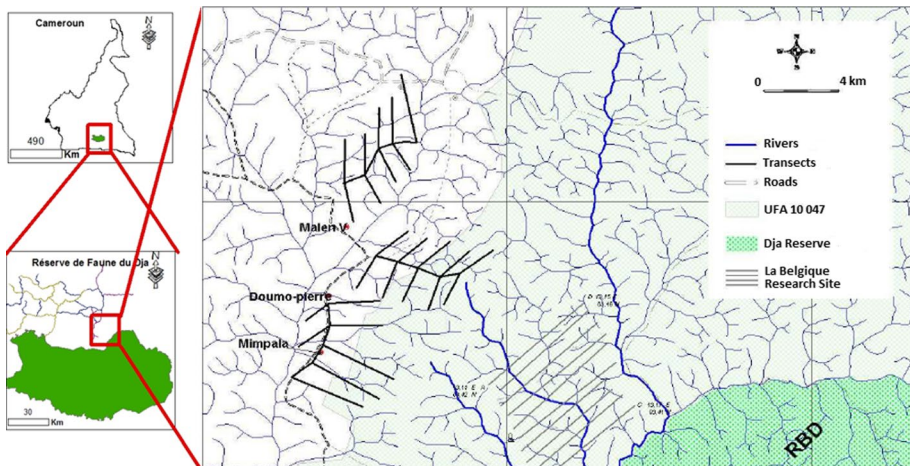


Fig. 1 Study area

and forests at various stages of stand development. The same transects were subsequently resurveyed in March 2006, February 2009 and November 2016. As the two rainy seasons span August to November and February to July, all surveys were performed in a rainy season, thus eliminating any seasonal bias in animal detection and enabling comparisons between study years. One-off surveys were conducted along transects in each study year within 2 weeks of transect establishment. Only mammals were recorded. Surveys were conducted by a researcher and three local assistants familiar with local wildlife and trained in wildlife data collection. In all years, surveys were carried out by people from the same villages (Malen V, Doumo-Pierre and Mimpala) using the same methodology. The team walked transects together but each member was assigned a particular role. Transect walks started in the morning around 0600–0700. Data on chimpanzee (*Pan troglodytes troglodytes*) and gorilla (*Gorilla gorilla gorilla*) nests and direct observations were not available for the year 2002, so only indirect observations such as footprints and dung (available for all study years) were used as proxy for abundance for all mammal species. Whenever a footprint or dung of any species was found, the location along the transect and the type of habitat were recorded. Additionally, for dung, the perpendicular distance from the transect line to the dung was measured, and dung age was estimated.

Data analysis

All data matrices were populated using abundance data for each mammal species. For each species, the encounter rate per kilometre (ERK) was calculated as the total number of indirect observations in all transects over the total length of all transects. Data did not meet the assumptions of normality and were therefore analysed using nonparametric statistical approaches. For each species, abundance across years was statistically compared using Median and Kolmogorov–Smirnov tests. Rarefaction curves were plotted to assess trends in wildlife species richness across years. Species richness was measured as the total number of species found. However, comparisons based on rarefaction (observed species richness) can be misleading (Chazdon et al. 1998; Loya and Jules 2008; Willie 2012). Rarefaction curves were therefore extrapolated beyond the reference sample size to estimate the expected number of species that could be found (estimated or asymptotic species richness) in a given year given observed patterns. This approach overcomes the shortcomings of traditional rarefaction curves and allows for more accurate estimations of richness and valid comparisons among groups (Colwell et al. 2012). Statistical inference is based conservatively on the extent to which confidence intervals overlap (Colwell et al. 2012). Extrapolations were done using the multinomial model (Chao et al. 2009; Colwell et al. 2012; Shen et al. 2003), and data were analysed in EstimateS Version 9.1.0 and SPADE (Chao and Shen 2009).

Wildlife composition between years was compared using a Multiple Response Permutation Procedure (MRPP), a multivariate testing method that assesses whether or not two or more groups differ significantly in composition (McCune and Grace 2002; Mielke and Berry 2001). Sampling units were transects, and the species data matrix measured 107 transects \times 29 species. Analyses were performed with the Bray–Curtis distance measure in PC-ORD 4.0 (McCune and Mefford 1999). In addition, an Indicator Species Analysis (Dufrene and Legendre 1997) was run in PC-ORD 4.0 to assess the extent to which each wildlife species separates among years. Information on each wildlife species' abundance and frequency in a particular year was combined to generate Indicator Values (I.V.s) for each species for that year. The highest I.V. of a given species across years was the overall

I.V. for that species. A Monte Carlo simulation of 1000 runs with a critical value of 0.05 was used to test I.V.s for statistical significance.

Functional diversity indices

To calculate functional diversity indices, species traits related to resource capture and use, and energy flow were chosen, given their relevance to the fitness of a species and its role in processing matter, which ultimately influences ecosystem functioning (Chillo and Ojeda 2012). Therefore, the following traits were selected for all functional diversity analyses: body mass, feeding guild (relevant to the type and amount of resources consumed and released), activity pattern (regarding the temporal distribution of resource use), habitat use, and home range (referring to the spatial distribution and extent of resource intake and release) (Chillo and Ojeda 2012; Flynn et al. 2009; Safi et al. 2011). Trait information for all surveyed species was collected from the literature (see Online Appendix 1 for references). Body mass was a quantitative variable measured on a continuous scale. Activity pattern (three attributes), feeding guild (nine attributes), and habitat use (three attributes) were categorical variables. Home range (four attributes) was a semi-quantitative, ordered variable (Online Appendix 1). Species trait information and species abundances were combined to generate functional diversity indices.

Functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv) were used as indices of functional diversity (Mouchet et al. 2010; Moullot et al. 2013; Villéger et al. 2008). In simple terms, FRic is the number of functional traits present in a community; FEve helps to ascertain whether certain functional traits are more abundant than others; and FDiv indicates the extent to which species are functionally dissimilar (Mason et al. 2005; Mouchet et al. 2010; Moullot et al. 2013; Villéger et al. 2008). In addition, functional β -diversity (which measures functional similarity between two communities) was calculated from presence/absence data to assess differences in functional diversity between study years, thus allowing for pairwise comparisons (Villéger et al. 2013). The lower the functional β -diversity value, the more functionally similar are two communities or study years.

The FD package in R 3.3.1 (R Core Team 2016) and the functions “quality_funct_space”, “plot_funct_space”, “multidimFD” and “multidimFbetaD” were used to compute functional diversity metrics and functional β -diversity (Laliberté and Legendre 2010; Villéger et al. 2008, 2013).

Results

Wildlife abundance

The earlier two study years (2002 and 2006) displayed similar wildlife abundances, but drastic declines were observed in 2009 and 2016, when abundances decreased by 56 and 82%, respectively, relative to the reference year, 2002 (Table 1). Of 29 wildlife species, 12 displayed significant differences across study years. Chimpanzee, otter (*Aonyx* spp.), forest elephant (*Loxodonta cyclotis*), bay duiker (*Cephalophus dorsalis*), blue duiker (*Cephalophus monticola*), Peter's duiker (*Cephalophus callipygus*), African brush-tailed porcupine (*Atherurus africanus africanus*), flat-headed kusimanse (*Crossarchus platycephalus*), leopard (*Panthera pardus*), cane rat (*Thyonomys swinderianus*) and long-nosed mongoose

Table 1 Wildlife abundance in different study years

	Descriptive statistics					
	2002	2006	2009	2016	Median test	P value
Mean	43.23 ± 27.32	48.63 ± 37.5	19.1 ± 8.79	7.93 ± 3.54	19.5	< 0.001***
	Pairwise comparisons based on Kolmogorov-Simonov test					
	2002 vs. 2006	2002 vs. 2009	2002 vs. 2016	2006 vs. 2009	2006 vs. 2016	2009 vs. 2016
Z	0.928	2.11	3.085	1.497	2.177	2.722
P-value	0.355	< 0.001***	< 0.001***	0.023*	< 0.001***	< 0.001***

Results were obtained using one-off wildlife survey datasets from each study year. In each study year, data were collected in transects of variable lengths, totalling about 60 km. Displayed results are encounter rates per kilometre, calculated based on the total number of sightings for all animal species. Evidence of animal presence included only footprints and dung as these indices were consistently recorded in all study years

Asterisks indicate significant differences. *Significant difference at $P < 0.05$; ***Significant difference at $P < 0.001$

(*Herpestes naso*) significantly declined, while yellow-backed duiker (*Cephalophus sylvicultor*) significantly increased (Online Appendix 2).

Wildlife species richness

Totals of 22, 23, 23 and 16 mammal species were recorded in 2002, 2006, 2009 and 2016, respectively (observed species richness; Online Appendix 2). Rarefaction curves were fitted based on wildlife sightings. Based on actual survey data, rarefaction curves did not stabilise, except in 2016. Hence, these curves were extrapolated using the Multinomial model. Extrapolation results indicated no significant differences in wildlife species richness among years 2002, 2006 and 2009 ($P > 0.05$; Fig. 2); this was also the case between years 2006 and 2016. However, years 2002 and 2009 statistically differed from year 2016 ($P < 0.05$). The stabilising curves of all study years indicated that no additional species would have been detected with additional sampling for all years.

Wildlife composition

The composition of the mammal community differed across time; the four study years formed four different clusters (Online Appendix 3). Compositional differences were more pronounced between years 2002 and 2016 but were minimal between years 2006 and 2009 (Online Appendix 4a). Overall, 29 different species were recorded in the four study years. Fifteen of these occurred in all years: chimpanzee, giant pangolin (*Smutsia gigantea*), yellow-backed duiker, forest elephant, bay duiker, blue duiker, Peter's duiker, African brush-tailed porcupine, flat-headed kusimanse, leopard, Emin's pouched rat (*Cricetomys emini*), cane rat, moustached monkey (*Cercopithecus cephus cephus*), tree pangolin (*Phataginus tricuspus*) and black-fronted duiker (*Cephalophus nigrifrons*) (Online Appendix 2). However, relative to the later study years, which each exhibited only one or two significant indicator species (2006: forest elephant and African brush-tailed porcupine; 2009: Emin's pouched rat and tree pangolin; 2016: yellow-backed duiker), six species were indicative of

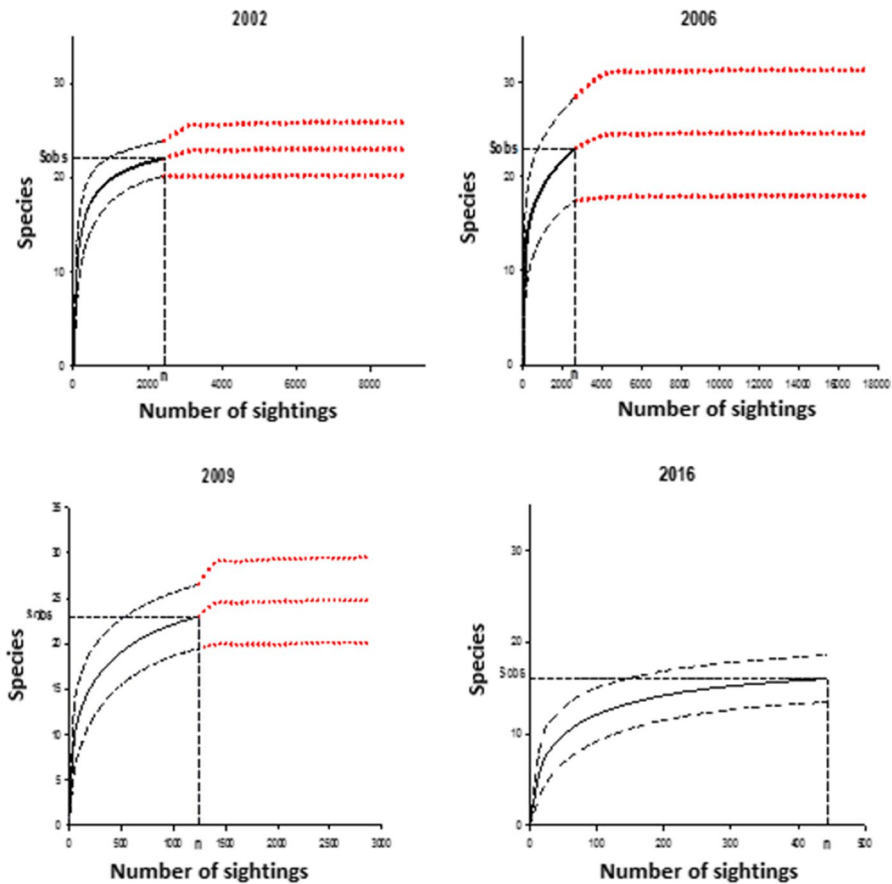


Fig. 2 Rarefaction and corresponding extrapolation curves based on the multinomial model. S_{est} is the estimated asymptotic number of wildlife species. S_{obs} is the observed number of wildlife species for a reference sample of n sightings. Curves initially rise quickly and then stabilize following adequate extrapolation. The 95% confidence intervals converge to 20–26, 18–31, 20–30 and 13–19 in 2002, 2006, 2009, and 2016 respectively. Differences are not significant when confidence intervals overlap

year 2002 (bay duiker, blue duiker, Peter's duiker, chimpanzee, agile mangabey [*Cercocebus agilis*] and flat-headed kusimanse; Online Appendix 4b).

Wildlife functional diversity

Functional diversity indices, such as functional richness, functional divergence and functional evenness, were calculated for the four study years (Fig. 3). Functional richness was comparable in 2002, 2006 and 2009, but was lower in 2016. A similar pattern emerged when comparing functional divergence. However, functional evenness was similar across the four study years. In addition, differences in functional diversity between years were assessed by calculating functional β -diversity indices. The highest functional β -diversity

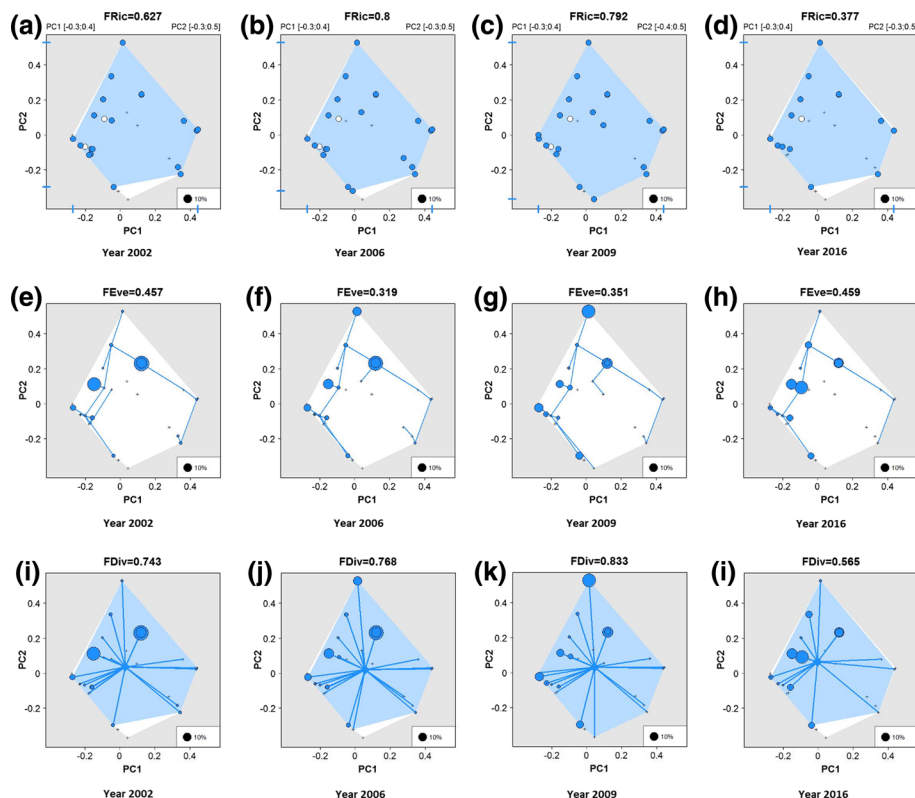


Fig. 3 Overall patterns of wildlife functional diversity indices for the four study years, based on the species pool present in each year. Graphs are plots of functional richness (a–d), functional evenness (e–h) and functional divergence (i–l) in the multidimensional functional space. The figure above each graph is the overall value of a functional diversity index for that particular year, expressed as a proportion. Dots indicate species characterised by their unique set of functional traits within the functional space. The size of the dots indicates relative abundances of species (and thus their corresponding set of functional traits) for graphs (e–l). Species occurring in other sites but absent in a given site are represented by plus signs. Changes in functional diversity are either due to species, and hence their set of functional traits, disappearing from the community, or due to changes in their relative abundances

was recorded in pairwise comparisons between the year 2016 and the other study years (Online Appendix 5), suggesting that functional diversity changed in 2016.

Discussion

Tropical rainforests are biologically diverse, yet most are heavily disturbed by human activities (Lewis et al. 2015; Malhi et al. 2014). Hunting is one of the most important factors causing wildlife loss and local extinctions in the tropics (Abernethy et al. 2013; Brashares et al. 2004; Castelletta et al. 2000; Fa et al. 2014; Milner-Gulland and Bennett 2003; Ripple et al. 2016). Simple measures of species abundance and diversity cannot adequately reflect the full picture of the impact on biodiversity of a changing wildlife community (Ernst et al. 2006). This study investigated changes in wildlife community structure and functional

diversity in a tropical rainforest ecosystem over a period of 14 years in a non-protected site with rapidly increasing hunting pressures (Ávila et al. 2017).

Wildlife community structure

Wildlife abundance, as measured by the transect approach, remained stable from 2002 through 2006 (Table 1). However, overall wildlife abundances then decreased to less than half the reference year abundances by 2009 and continued to decrease leading up to the 2016 surveys: data from 2016 show wildlife abundances at less than 20% of reference year abundances. Although standard line transect surveys are commonly used for monitoring several species in such ecosystems (Kühl et al. 2008), enabling comparative and replicable results, there are some limitations. For certain species living within the ecosystem, transect surveys may not be the most effective method; abundance measurements of some species in this study may therefore be underestimates, and some species present in the sites may not have been detectable at all via this method. Indeed, data from bushmeat offtake surveys in the same site in 2016 revealed a total of 27 different mammal species, whereas only 16 were detected in the transect data of 2016 (unpubl. data). However, this does not detract from the validity of the comparison between study years as standardised survey methods were used throughout and the same proportion of mammals present in the site were likely to be detectable each study year.

Interestingly, the yellow-backed duiker increased over the years. This species exhibited its lowest abundance in 2002, significantly increasing with time and in all year pairings except between 2006 and 2009. The observed increase in this large-bodied duiker in a hunting zone is of interest; there is no evidence of avoidance of this species by hunters nor of any retroviral outbreaks that may have caused a population dip in 2002. However, the observed increase may not be real; 2002 may have been an anomalous year. Fluctuations in abundances due to migrations in or out of the area may explain this, particularly because the site falls between a reserve and a village hunting zone where pressures vary.

When sampling wildlife abundances using line transects over time, some animals may be disturbed and may adjust their behaviour to human-induced environmental change. They may respond by dispersing, adjusting through phenotypic plasticity, or adapting through genetic changes; the former two processes being the most likely in the relatively short time-frame of rapid anthropogenic change (Wong and Candolin 2015). If animals become quieter or more elusive, or shift their ranging patterns, this can affect detectability. Therefore, lower wildlife abundances in later study years may be a result of altered animal behaviour, rather than a real ecosystem change. Behavioural studies could help elucidate the likelihood of such patterns. However, detectability of indirect signs of wildlife presence is less subject to changes in wildlife behaviour as is detectability of direct signs; evidence of presence will still persist even if behaviour patterns change. Behavioural changes in response to increasing human pressure may not be indicative of behavioural adaptations by animals, and may instead be maladaptive; for example, by restricting certain resources or leading to poor habitat choices (Wong and Candolin 2015).

Phenotypic plasticity or dispersal may enable animals to avoid hunting at local scales, but at wider scales wildlife species are depleted and extirpated as a result of increasing human pressures, such as hunting (de Araujo Lima Constantino 2016; Fa and Brown 2009; Peres and Palacios 2007). The lower wildlife abundances observed in this study therefore may reflect actual losses, as suggested in previous studies in the site (Luyten 2009). Given the increasing anthropogenic pressures in the area (Ávila et al. 2017; authors'

observations), intense hunting probably contributed to the observed abundance decreases. In 2005 and 2006, cheap imported motorbikes became widespread in the area, improving access into rural villages and forest tracts, and ownership and use of homemade guns in hunting practices increased (Ávila et al. 2017; Luyten 2009; Willie 2006; authors' observations). A growing demand for wild-caught meat from towns and cities has increased hunting pressures. Accessibility of bikes and guns enables traders and middlemen to place commands, supply ammunition, purchase and collect meat, etc. (Tagg et al. 2018). Therefore, increased hunting pressures in the region could have caused the decreases in wildlife abundance observed in the 2009 surveys and the continued decrease evidenced from the 2016 surveys (Ripple et al. 2016).

Despite the observed reduction in wildlife abundance from 2006 through 2009, wildlife diversity remained stable until 2009. However, by 2016, species richness also decreased. Again, certain animals may have adapted to the increased human activity making it difficult to detect certain species. However, behavioural changes cannot fully account for this evident reduction in species diversity by 2016, as not all individuals of a population exhibit the same degree of behavioural plasticity; some individuals would remain detectable. If, instead, this apparent loss in species diversity in 2016 is real, some species may have dramatically reduced in number, and possibly been locally extirpated. There are two points to note here: first, there appears to be a delay in this effect becoming apparent (i.e., a reduction in species diversity was not observed in 2009 but was observed by 2016). This may be due to the gradual loss in individuals eventually leading to loss of the population. Second, the disproportionate reduction or loss in some species supports previous evidence that hunting disturbance does not have the same effect on all species. Hunters disproportionately target certain species, sexes or size classes depending on their abundance, ease of capture, demand, value, taste, etc. (Arnhem et al. 2008; Linder and Oates 2011; Stokes et al. 2010). For example, human hunters select adult individuals more than do nonhuman predators (Darimont et al. 2015), because large-bodied animals provide more meat per cartridge (Abernethy et al. 2013; Macdonald et al. 2011; Ripple et al. 2016). In addition, species may respond differently to hunting pressures. Some species are more resilient and others, such as large-bodied animals, are more susceptible (Peres and Palacios 2007). For example, primates have relatively long lifespans and low rates of population increase, so sustainable annual offtake is only 1–4 per cent compared to some large-bodied rodents that can withstand up to 80 per cent (Robinson 2000). Even at low hunting pressures, large-bodied species cannot compensate for losses incurred by hunting, thus resulting in a decrease in number (Berryman 1992; Davidson et al. 2009; Dunn 2004; Ripple et al. 2016) and an alteration in the extinction order (Chillo and Ojeda 2012; Petchey and Gaston 2002). In the Congo Basin, more large-bodied primates, ungulates and carnivores are hunted than other taxa (Ripple et al. 2016). Furthermore, these are keystone species, with important and often unique roles in the ecosystem—their loss can have myriad detrimental knock-on effects (Effiom et al. 2013; Estes et al. 2011; Mills et al. 1993; Ripple et al. 2014, 2015). In this study, several keystone species decreased throughout the study (for example, chimpanzee, elephant and leopard). A bushmeat offtake study in the same site showed that relatively larger animals were taken by guns in more recent years (reflected in a rise in 'mean body mass indicator' [MBMI]—an indicator of defaunation—for gun-caught animals, which was not observed for trap-caught animals; Ávila et al. 2017). This suggests that guns are increasingly used to target larger game and supports the argument that the increase in gun hunting in the area may be directly causing the observed declines in wildlife.

In the present study, around half of wildlife species occurred in all study years. In contrast, the gorilla, crowned guenon (*Cercopithecus pogonias*), African civet (*Civettictis*

civetta), African palm civet (*Nandinia binotata*), otter, long-nosed mongoose and black-footed mongoose (*Bdeogale nigripes*) were not observed in the 2016 survey, having each been observed in at least two of the previous study years. Notably, the gorilla, African palm civet and long-nosed mongoose were observed in all three earlier years but not in 2016 (though the latter was the only one of those three species to present a significant overall decrease in abundance). This pattern may also explain the strong pairwise comparisons in species composition of the wildlife community between 2016 and each of the earlier study years (Online Appendix 4a). Furthermore, pairwise comparisons revealed strong significant differences between the reference year and the latter two study years (i.e., 2002 vs 2009 and 2002 vs 2016), probably because there was a greater overlap in species composition in the first two years, but the frequency of occurrence and the abundance of species strongly decreased in subsequent years. Furthermore, most primate ($n=5$) and carnivore ($n=9$) species present in the site were indicator species of year 2002 (60% and 66.67%, respectively); while—in contrast—by 2016, only two artiodactyls were indicator species. This is further evidence that the observed wildlife declines are real, as mammals are particularly susceptible to hunting (Fa and Brown 2009).

Functional diversity

If the observed loss in wildlife abundances and species diversity over the years is real, the implications are wide reaching. Hunting removes individuals from a population with obvious detrimental effects on the survival of the population (Bennett 2011; Fa and Brown 2009). However, there are a series of indirect effects on other species within the ecosystem. Keystone species are of importance in helping regulate top-down forces within the ecosystem, via processes related to prey, food resources, etc. (Estes et al. 2011; Ripple et al. 2014, 2015), and their functions can rarely be compensated for by smaller species. For example, forest elephants disperse seeds far from parent trees (Campos-Arceiz and Blake 2011), reducing the rate of seed predation and limiting the negative effects of pathogens. The loss of elephants would lead to a reduced recruitment of large trees (Poulsen et al. 2018). Similarly, gorillas have a large gape size, long daily path length and high frugivory, so they transport large seeds, undamaged, far from the parent tree, sometimes being the sole seed disperser for certain tree species (e.g., *Cola lizae*; Stoner et al. 2007a, b; Tutin et al. 1991). They also commonly deposit seeds in sites with suitable environmental conditions (e.g., light gaps) and passage through the gut can be beneficial, thus improving seedling survival and increasing plant recruitment (Harrison et al. 2013; Petre et al. 2015; Soares et al. 2015).

If there is non-redundancy in roles among the species being lost in the present study, then a loss in functional diversity would be expected. Indeed, there were strong functional dissimilarities between the wildlife communities present in 2016 and those of other years, as shown by the pairwise functional β -diversity indices (Online Appendix 5). Functional richness followed the same pattern as species richness, with a stable (and similar) number of functional traits present in the wildlife community in the first three years (2002, 2006 and 2009), then declining in 2016, as a lower value of functional richness was recorded (Fig. 3a–d). Because the selected functional traits concerned resource use and energy flow, the results reflect diversity and divergence of only certain relevant functions performed by the wildlife community. Quantitative trait selection procedures are still in development; until then, trait selection is subjective (Petchey and Gaston 2006). A finer resolution of trait data (using values for species measured in the same ecosystem) would enable the

identification of more subtle changes (Chillo and Ojeda 2012). However, the results are of great value to the field, as this represents the first investigation into changes in functional diversity over time in a Central African rainforest ecosystem that has undergone a rapid increase in hunting pressure during the study.

If the respective loss of species and interactions were ‘decoupled’, functional diversity would reduce before wildlife abundance and species richness reduces (Cadotte et al. 2011; Flynn et al. 2009; Mouillot et al. 2013; Nunez-Iturri et al. 2008; Valiente-Banuet et al. 2015). This is because different functional traits can respond differently to external pressures, perhaps more subtly, and with the potential to impact upon species diversity even with minimal change in species richness (Cadotte et al. 2011; Flynn et al. 2009; Nunez-Iturri et al. 2008). This is a further benefit of studying functional diversity because analyses of functional traits offer the potential for advanced warning (Mouillot et al. 2013). However, it ultimately means that ecological interactions can be lost at a higher rate—and therefore before—species disappear (Valiente-Banuet et al. 2015). ‘Decoupling’ was not observed in the present study, as abundances dramatically decreased by 2009, whereas changes in species richness and in functional diversity were not observed until 2016. This is to be expected in this case, as hunting causes active reduction in abundances. Also, redundancy in the functional roles of the species under decline may enable the ecosystem to withstand some degree of wildlife community alteration in the short term (Oliveira et al. 2016).

Functional divergence exhibited a similar pattern, remaining relatively high from 2002 through 2009 but drastically decreasing in 2016 (Fig. 3i–l), therefore indicating that the wildlife community in the first three years was composed of functionally more dissimilar species compared to the wildlife community in 2016. Functional divergence in a wildlife community informs us about niche differentiation and resource partitioning, thus providing insights into ecosystem functioning. Comparing functional divergence values across years means comparing resource use efficiency and ecosystem function. Thus, a lower niche differentiation between remaining species (and hence higher resource competition and decreased ecosystem function; Mason et al. 2005) was evident in 2016, further indicating that some functions might have been lost.

The functional diversity analyses therefore suggest that a moderate decrease in wildlife abundance may not affect the functioning or the ecological integrity of a wildlife community; however, beyond a certain threshold of wildlife decline, wildlife community collapse and ecological decay are likely. Firstly, these results indicate high ecosystem function in 2002, 2006 and 2009, compared to 2016, suggesting a compromise of the structure and function of this diverse tropical ecosystem and the subsequent delivery of economic and ecosystem services (Ripple et al. 2014). Secondly, identifying such thresholds can greatly inform sustainable wildlife management and help to monitor the health and integrity of an ecosystem.

Ecological degradation

This study demonstrates functional diversity being lost in this site. Functional diversity indices consider all functions together, as linked to the modalities of all selected traits. Therefore, the loss of functional diversity, as seen in the later year of the present study, suggests that not all functional roles are being fulfilled in the community and that functions and processes are being compromised. Given that this study considered traits relating to resource use and energy flow (Flynn et al. 2009), it indicates a loss of various functions,

including seed dispersal, fungi/lichen dispersal, browsing or grazing, carrion feeding and carnivore predation, structure builders (e.g., nests, burrows; Marcot and Van der Heyden 2001), etc. In this study, wildlife abundance decreased disproportionately, including that of several large keystone mammals, the chimpanzee and forest elephant. Furthermore, the gorilla was not observed at all in the 2016 survey. Consequently, unique seed removal and transport services of certain large-seeded species is likely to be compromised in this site (Beaune et al. 2013; Effiom et al. 2013; Petre et al. 2015), suggesting a reduction in seed dispersal effectiveness of the community. A loss in the 'top-down' control offered by large-bodied mammals can result in trophic cascades on globally important ecological processes (Estes et al. 2011). Eventual changes in floral composition and reductions or alterations in forest regeneration and maintenance are predicted (Petre et al. 2015, 2016). This is the start of a cycle of ecological degradation of this important tropical forest located within one of the two main river basins of the world. Such degradation will ultimately affect globally important ecosystem services (e.g., carbon storage; Brodie and Gibbs 2009) performed by these forests, in turn impacting upon global economy and health (Abernethy et al. 2013; Costanza et al. 1997). Rapid, widespread and potentially permanent ecosystem changes have the potential to result in enormous ecological and social costs (Ripple et al. 2016; Terborgh et al. 2001).

Conclusion

This paper presents the first investigation into changes in functional diversity in a tropical rainforest hunting zone over time. The study site lies in the buffer zone of the important Dja Faunal Reserve, which is highly threatened by human pressures and requires urgent action on the ground (IUCN 2014). The results display a reduction in wildlife abundances, species richness and functional diversity with time. It is possible that some species may behaviourally adapt to disturbance by human activity, rendering them more difficult to detect. However, the results likely reflect a real decrease in wildlife abundance as a direct result of increased hunting in the site over the years (Ávila et al. 2017; Nunez-Iturri et al. 2008). Several large mammals declined in the present study, suggesting a reduction, alteration or loss in complex and critical contributions to numerous ecological functions, and the start of trophic cascades (Estes et al. 2011; Ripple et al. 2014, 2015, 2016). For example, important processes related to seed dispersal are likely to be affected, impacting upon the seed dispersal services of the wildlife assemblage in the study sites (Abernethy et al. 2013; Effiom et al. 2013; Estes et al. 2011). Land use types with a more active conservation management status (and thus a higher degree of control or mitigation of hunting pressures) exhibit higher functional diversity (Laméris et al. 2019). If no action is taken, changes in forest and vegetation structure in the near future (within decades) may render the ecosystem unsuitable for mammals (e.g., they may be unable to sustain large fruit-eating vertebrates), suggesting that the loss in ecosystem integrity might be irreversible (Nunez-Iturri et al. 2008; Stoner et al. 2007a, b).

The study reveals a lag between wildlife abundance decreases and reductions in species richness and functional diversity, suggesting that the structure and functioning of a wildlife community can withstand some abundance decreases. The results of the 2016 survey suggest a threshold of wildlife decline (i.e., when certain species are lost and species richness reduces). Beyond this threshold, wildlife and functional trait assemblages can be dramatically altered, interactions affected and functions lost, triggering the start of

ecological collapse and decay (Abernethy et al. 2013). Examining how and when hunting pressures start to affect functional diversity can help identify and predict the thresholds after which functional diversity is lost. This can greatly assist sustainable wildlife management by informing as to whether repair and/or halting of the process may be possible (Cadotte et al. 2011). With evidence of loss in functional diversity, urgent and immediate action can be taken, preferably on a landscape scale, to fight to preserve large tropical mammals. Although it can take many decades to do so, wildlife species can often recuperate from losses (Dunn 2004). This way, complex species interactions and the myriad functions undertaken by these animals can be maintained, and ecosystem decay can be halted so that healthy ecosystems can continue to provide essential services. In this regard, unsustainable hunting is as much a concern for climate science as it is for biodiversity loss (Brodie and Gibbs 2009; Redmond 2016; Redmond and Virtue 2008). It is increasingly necessary to gather in-depth knowledge of the processes and mechanisms of changes caused by a number of external pressures (hunting, climate change, land use change, etc.) to safeguard tropical ecosystems in the future (Abernethy et al. 2013; Mouillot et al. 2013).

Acknowledgements We thank the Ministry of Economy, Science and Innovation of the Flemish government for its funding of the Centre for Research and Conservation, and all in-country logistic staff of Projet Grands Singes. We thank all villagers participating in the surveys since 2002, and the support and assistance of forest guides and research assistants.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Affiliations

Nikki Tagg^{1,2}  · **Jacques Keumo Kuenbou³** · **Daan Willem Laméris⁴** · **Fany Michelle Kamkeng Meigang⁵** · **Sévilor Kekeunou⁵** · **Manfred Aimé Epanda⁶** · **Jef Dupain⁷** · **Donald Mbohli²** · **Ian Redmond⁸** · **Jacob Willie^{1,9}**

¹ Centre for Research & Conservation (CRC), Royal Zoological Society of Antwerp (RZSA), Koningin Astridplein 20-26, 2018 Antwerp, Belgium

² Association de la Protection de Grands Singes (APGS), Yaoundé, Cameroon

³ Department of Forestry, Dschang University, Dschang, Cameroon

⁴ Animal Ecology Research Group, Utrecht University, Utrecht, The Netherlands

⁵ Department of Animal Biology and Physiology, Laboratory of Zoology, University of Yaoundé 1, Yaoundé, Cameroon

⁶ African Wildlife Foundation, Ngong Road, Karen, Nairobi, Kenya

⁷ Nairobi, Kenya

⁸ Ape Alliance, Lansdown, Stroud, UK

⁹ Terrestrial Ecology Unit, Ghent University, Ghent, Belgium

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