

Vertebrate community composition and diversity declines along a defaunation gradient radiating from rural villages in Gabon

Sally E. Koerner^{1*}, John R. Poulsen¹, Emily J. Blanchard¹, Joseph Okouyi² and Connie J. Clark¹

¹Nicholas School of the Environment, Duke University, P.O. Box 90328, Durham, NC 27708, USA; and ²Agence Nationale des Parcs Nationaux, Kalikak, BP, 20379 Libreville, Gabon

Summary

1. Anthropocene defaunation is the global phenomenon of human-induced animal biodiversity loss. Understanding the patterns and process of defaunation is critical to predict outcomes for wildlife populations and cascading consequences for ecosystem function and human welfare.

2. We investigated a defaunation gradient in north-eastern Gabon by establishing 24 transects at varying distances (2–30 km) to rural villages and surveying the abundance and composition of vertebrate communities. Distance from village was positively correlated with observations of hunting (shotgun shells, campfires, hunters), making it a good proxy for hunting pressure.

3. Species diversity declined significantly with proximity to village, with mammal richness increasing by roughly 1.5 species every 10 km travelled away from a village. Compared to forest far from villages, the wildlife community near villages consisted of higher abundances of large birds and rodents and lower abundances of large mammals like monkeys and ungulates.

4. Distance to nearest village emerged as a key driver of the relative abundance of five of the six taxonomic guilds, indicating that the top-down force of hunting strongly influences large vertebrate community composition and structure. Several measures of vegetation structure also explained animal abundance, but these varied across taxonomic guilds. Forest elephants were the exception: no measured variable or combination of variables explained variation in elephant abundances.

5. *Synthesis and applications.* Hunting is concentrated within 10 km around villages, creating a hunting halo characterized by heavily altered animal communities composed of relatively small-bodied species. Although the strongest anthropogenic effects are relatively distance-limited, the linear increase in species richness shown here even at distances 30 km from villages suggests that hunting may have altered vertebrate abundances across the entire landscape. Central African forests store >25% of the carbon in tropical forests and are home to 3000 endemic species, but roughly 53% of the region lies within the village hunting halo. Resource management strategies should take into account this hunting-induced spatial variation in animal communities. Near villages, resource management should focus on sustainable community-led hunting programmes that provide long-term supplies of wild meat to rural people. Resource management far from villages should focus on law enforcement and promoting industry practices that maintain remote tracts of land to preserve ecosystem services like carbon storage and biodiversity.

Key-words: abundance, Anthropocene defaunation, biodiversity, birds, Central Africa, hunting intensity, mammals, species richness, tropical forests

*Correspondence author. Department of Integrative Biology, University of South Florida, SCA 100, 4202 E. Fowler Ave., Tampa, FL 33620, USA. E-mail: koerner@USF.edu

Introduction

Twenty-eight per cent of the world's vertebrate species have declined in abundance over the last four decades, highlighting a pattern of Anthropocene defaunation that crosses both geographic and taxonomic boundaries (Colten *et al.* 2009; Dirzo *et al.* 2014). Overhunting is the major cause of defaunation in many parts of the world (Hoffmann *et al.* 2010), putting disproportionate pressure on large vertebrates – particularly mammals. The end result of overhunting is the loss of all vertebrate species (complete defaunation), creating a system analogous to an 'empty forest' (Redford 1992). Most forests, however, are not completely defaunated, instead lying somewhere along a gradient of vertebrate diversity and abundance. To understand the process of defaunation necessitates knowledge of how human activities progressively alter vertebrate community diversity and structure along a defaunation gradient (Galetti & Dirzo 2013).

People have harvested the diverse vertebrate community of Central African forests for millennia, depending on wild meat for protein and to improve their livelihoods (Wilkie & Carpenter 1999; Fa, Currie & Meeuwig 2003); however, recently human population growth, more efficient weapons and greater access to forests have yielded unprecedented rates of modern bushmeat hunting (Poulsen *et al.* 2009; Harrison 2011). Hunting alters the vertebrate community by selecting against prey species, resulting in some species 'losing' (decreasing in abundance) and others 'winning' (increasing in abundance) (Terborgh *et al.* 2008). Large-bodied, tropical mammal species with low reproductive rates, such as primates, are particularly sensitive to hunting pressures and are often 'losers' in this process (Nasi *et al.* 2008). On the other hand, smaller-bodied sympatric species such as rodents are often 'winners' and can come to dominate communities with release from predation and competition for resources (Nunez-Iturri, Olsson & Howe 2008; Effiom *et al.* 2013). Changes in vertebrate community structure can alter interactions among vertebrate species (Peres 1990; Bodmer, Eisenberg & Redford 1997) and modify many of the drivers of tree community dynamics such as seed dispersal, seed predation and herbivory (Dirzo & Miranda 1990; Harrison *et al.* 2013; Poulsen, Clark & Palmer 2013).

Due to their relative remoteness, Central African forests have been largely spared from large-scale defaunation compared to American, Asian and West African tropical forests. The era of relative isolation, however, is coming to an end as industry and agriculture – logging, palm oil, rubber – increasingly open human access to forests (Wich *et al.* 2014; Burton *et al.* 2016). Based on theory and previous studies, several *a priori* and mutually non-exclusive predictions can be made about how defaunation will proceed in Central Africa. First, large ungulates and monkeys should decline in abundance because they are the most commonly hunted forest animals (Fa & Brown 2009;

Poulsen *et al.* 2009). As a result, smaller mammals and birds, released from resource competition for fruits and seeds, could increase in abundance even if occasionally hunted (Peres & Dolman 2000; Rosin & Swamy 2013). Secondly, spatial variation in hunting pressure due to factors like forest access and local human population should create a spatial gradient of vertebrate community diversity and abundance. Finally, the top-down force of hunting should influence vertebrate community composition more strongly than bottom-up forces like vegetation characteristics (Estes *et al.* 2011; Muhly *et al.* 2013).

We test these three predictions by quantifying the effects of hunting and vegetation characteristics on the composition (both individual species and taxonomic guilds) and structure of tropical forest mammals and large birds, hereafter referred to as large vertebrates, in north-eastern Gabon. To do so, we established 24 transects across a range of distances from villages (Fig. 1) and then systematically sampled the diurnal large vertebrate community over 13 months. We use distance from village as an indicator of hunting pressure, with hunting intensity declining with distance away from villages (Peres & Lake 2003). In this way, we examine the effects of hunting pressure on large vertebrate populations and identify large-scale gradients in large vertebrate community composition and structure.

Materials and methods

STUDY AREA

We studied wildlife communities in the 5800 km² area surrounding the regional capital of Makokou in the Ogooué-Ivindo Province of north-eastern Gabon (Fig. 1). The region experiences bimodal rainfall with two relatively dry (January–March & June–August) and two rainy seasons (September–December & April–May). Mean annual precipitation is approximately 1700 mm, and mean annual temperature is 23.9 °C. The study area includes approximately 60 small villages located along three main roads, two active logging concessions and the northern section of Ivindo National Park. This arrangement of villages, logging concessions and protected forest creates a gradient of human activity, allowing for the evaluation of the effects of hunting pressure on large vertebrate communities in the area.

EXPERIMENTAL DESIGN AND DATA COLLECTION

J. Poulsen designed the study and data collection protocols, and field assistants collected the data. In October 2013, we established 24 2.5-km straight-line transects and surveyed them monthly from December 2013 to December 2014 for diurnal mammals (squirrel and larger mammals) and a suite of large bird species (a predetermined set of large frugivorous and insectivorous birds; Table S1, Supporting Information). Crews of 2–3 field assistants (or observers) walked the transects slowly (~1 km h⁻¹) and quietly in early morning, stopping every 50–100 m to listen for wildlife and every 200 m for 5 min to conduct point count surveys of large birds. In total, nine field assistants participated in data collection after receiving standard training in species identification and survey methods. Field crews were randomly assigned to

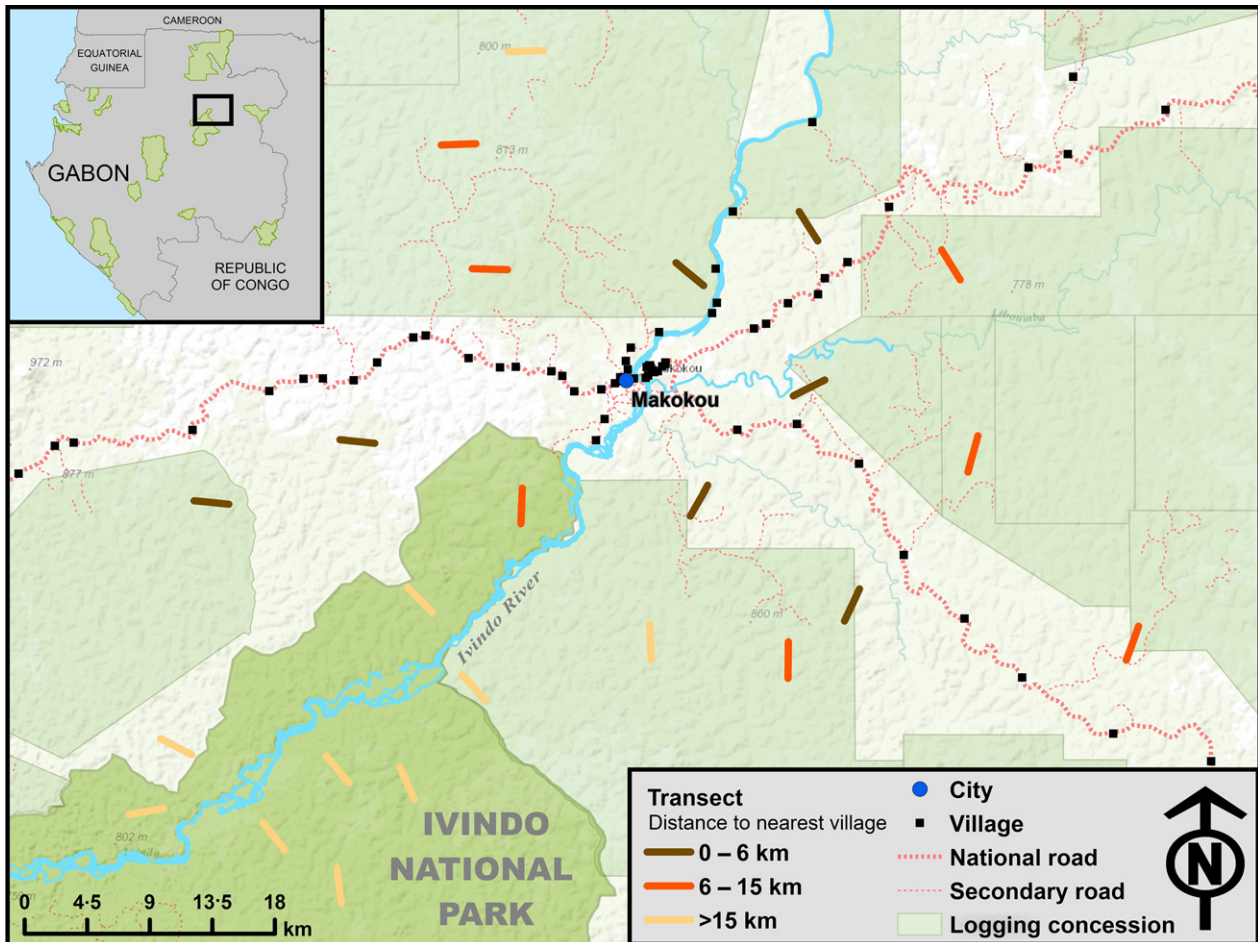


Fig. 1. (*inset*) Location of the study area within Gabon. (*main map*) The 6018 km² study area in north-eastern Gabon is centred around the regional capital of Makokou and includes numerous small villages (36–891 people per village), the Ivindo National Park and several logging concessions. Line segments represent the wildlife transects, coloured according to their distance from the nearest village, a proxy for hunting pressure, with forests closer to villages subjected to higher hunting pressure than those farther from villages.

transects, and each possible crew combination occurred so that there was no bias in the quality of data collection across time and space. Observers noted both direct (seen or heard) and indirect (dung or nests) observations of large vertebrates, measuring the perpendicular or radial distances from the centre of each observation to the transect line. For apes, monkeys and birds, they counted group size and recorded their confidence in the group size estimate. Observers considered groups of conspecific animals to be separate if they occurred more than 50 m apart. For indirect large vertebrate observations, they marked each observation with an individual number and recorded its age (fresh, recent, old, very old). In addition to observations of animals, they recorded all signs of human presence, including hunters, shotgun shells, wire snares and campfires.

To assess hunting pressure and environmental characteristics that might determine species abundance and distribution, we collected data on several transect characteristics. We calculated distance to the nearest village (km) as the distance from the mid-point of each transect to the mid-point of the nearest village (ESRI's ARCMAP 10.2 Near tool; Environmental Systems Research Institute, Redlands, CA, USA). The distance to the nearest village is an indicator of hunting pressure as it provides a measure of accessibility for people to the transect area. We censused households in the villages closest to our transects to

obtain current estimates of village population size. Transects were categorized into broad land use categories: national park, logging concession or neither. Field crews also surveyed the vegetation along transects, recording all saplings and trees over 2 m in height in eight circular plots (5 m radius; 78.5 m²) at equally spaced intervals along each transect. For each tree or liana, they recorded the species identity and diameter at breast height (DBH), from which we calculated the mean tree DBH of a plot. To determine understorey cover, we estimated the percentage of ground covered by undergrowth in each circular plot. To determine canopy cover, we estimated the percentage of sky blocked by the canopy in each circular plot. For both indices of cover, field assistants scored the percentage of cover, using the categories: 1 = 0–25%, 2 = 26–50%, 3 = 51–75% and 4 = 76–100%. We then averaged across the eight vegetation plots along a transect to derive a single value of tree richness (number of species), tree abundance (number of stems), mean tree DBH (cm), liana abundance (number of lianas), understorey cover and canopy cover for each transect.

ENCOUNTER RATES AND DENSITIES

To evaluate variation in species abundance across our study area, we calculated species encounter rate (observations km⁻¹) and

density (individuals km⁻²) for each transect. The encounter rate, E_i , for species i is the number of observations, N_i for the species divided by the total distance, L , walked along a transect, j .

$$E_{ij} = \frac{N_{ij}}{L_j}$$

We estimated mammal densities (individuals km⁻²) for the entire study area for nine species using DISTANCE 6.2 (Thomas *et al.* 2010), which requires a minimum of 60–80 observations to accurately estimate density (Table S2). The number of observations for each species was not high enough to calculate an effective stripe width (ESW) for each transect; therefore, we calculated species-specific ESWs for the study area and applied it to each transect (see Table S1 for species-level encounter rates near, intermediate and far from villages). Using a single ESW assumes no difference in detectability of animals across transects, which might not be the case if vegetation is denser along one transect than another. To test this assumption, we used linear regression to examine the relationships between vegetation characteristics and distance to the nearest village. Of six vegetation characteristics, only canopy cover increased significantly with distance away from village (Fig. S1), ranging from 75% to 100% over the distance gradient. Other factors, such as differences in animal behaviour across transects, could also influence detectability (e.g. if animals in hunted forest fled or hid, making them more difficult to observe). Thus, estimates of vertebrate densities should be treated with caution. Because we were only able to calculate animal densities for nine species, we use encounter rates, which do not incorporate the ESW, of all observed species for community-level analyses of relative abundance.

COMMUNITY DIVERSITY AND COMPOSITION

To assess whether the species composition of the large vertebrate community varies with environmental variables, we calculated the relative abundance of each species on each transect. The relative abundance, p , of species i for transect j is the encounter rate of the species divided by the sum of the encounter rates of all species on the transect.

$$p_{ij} = \frac{E_{ij}}{\sum_{i=1}^S E_{ij}}$$

where S is the total number of species encountered on transect j . We computed relative abundances for (i) the entire large vertebrate community, (ii) the mammal community, and (iii) the bird community, and then generated measures of species richness, S , evenness, J' , and Shannon–Weiner diversity, H' , for each of the communities (Magurran 2004). We also computed relative abundances for seven taxonomic guilds – ape, bird, carnivore, elephant, monkey, rodent and ungulate.

STATISTICAL ANALYSES

To evaluate whether distance from village is an effective indicator of hunting pressure, we first tested whether signs of human presence were positively related to distance from village using linear regression. We then examined the effects of hunting on individual species, the large vertebrate community and taxonomic guilds. In doing so, we evaluate how hunting affects (i) species encounter

rates, (ii) community richness, evenness, diversity and composition, and (iii) the relative abundances of the six taxonomic guilds (except carnivores for which there were only two observations).

We used linear regression to examine the relationships between the response variables, species encounter rates, S , J' and H' , and distance from village, which is a measure of hunting pressure. In addition, we employed NMDS based on the Bray–Curtis dissimilarity matrix to visualize the differences in community composition in multidimensional space for the entire measured large vertebrate community, the mammal community and the large bird community. Then, we examined the relationships between NMDS Axis 1 and distance from nearest village with linear regression. Additionally, we employed NMDS based on Sorenson's similarity index and presence/absence data to determine whether differences in multidimensional space were driven by species turnover or changes in species abundance.

At the taxonomic guild level, we employed two types of analyses. First, we used linear regression to determine how the relative abundance of each separate taxonomic guild changes with distance from village, again using NMDS based on Bray–Curtis dissimilarity matrix to visualize differences in the taxonomic guild community composition in multidimensional space. Secondly, to examine the relative importance of vegetation characteristics, distance to nearest village and size of nearest village to the relative abundance of taxonomic guilds, we took an information theoretic approach and implemented model averaging using the MUMIN package (Grueber *et al.* 2011; Bartoń 2016). Model averaging calculates multiple regression models for all possible combinations of variables and then ranks these models from best to worst according to their AIC score. We considered all models with $\Delta\text{AICc} < 4$ as equally informative and determined the importance of the explanatory variables for each response variable by calculating their frequency of occurrence in these models. Thirdly, we employed bivariate linear regression to visualize the effects of vegetation characteristics on the relative abundance of each taxonomic guild (shown in Table S3). To allow for nonlinearity, we also used general additive models (GAMs) to fit the above bivariate regressions. In all cases but one, linear regressions fit equally well or better, and therefore we only report the results of linear models. Unless otherwise specified above, all statistical analyses were conducted in R v3.1.2 (R Core Team, Vienna, Austria).

Results

SPECIES ENCOUNTER RATES AND DENSITIES

The encounter rate of human signs decreased significantly with distance from the nearest village ($F_{1,22} = 9.57$; $P = 0.005$; $R^2 = 0.303$), suggesting that distance to village is a good indicator of hunting pressure (Fig. S2) as other studies have shown (Peres & Lake 2003). We recorded 7041 direct observations of 41 species of diurnal mammals and large birds in 607 km of transects ($N = 245$ passages along transects, mean = 25.3 km per transect). Treating distance from village continuously, the encounter rates of three species decreased significantly and eight species increased significantly with distance from the nearest village (Table S1). In general, the encounter rates of bird and rodent species decreased with distance from village, while those of monkey, ape and ungulate species increased

with distance from village. Species densities for the nine mammals showed similar trends to encounter rates (Table S2).

COMMUNITY DIVERSITY AND COMPOSITION

Species richness of the mammal community increased significantly with distance from village ($F_{1,22} = 15.67$), while bird species richness ($F_{1,22} = 0.003$) did not vary significantly (Fig. 2). Approximately 1.5 species of mammal (or a 15% increase in richness) were gained with every 10 km from the nearest village. We expected species richness to saturate at some distance within 30 km from the nearest village, but a linear model fit the data better than nonlinear, saturating models (Fig. S3). Mammal and large bird diversity did not vary significantly with distance from village, whereas evenness of the mammal community decreased with proximity to nearest village (Fig. S4). Additionally, the composition of the large vertebrate, mammal and bird communities all varied significantly with distance from village in nonparametric multidimensional space (Fig. 3a–c; see Fig. S5a–c); these differences

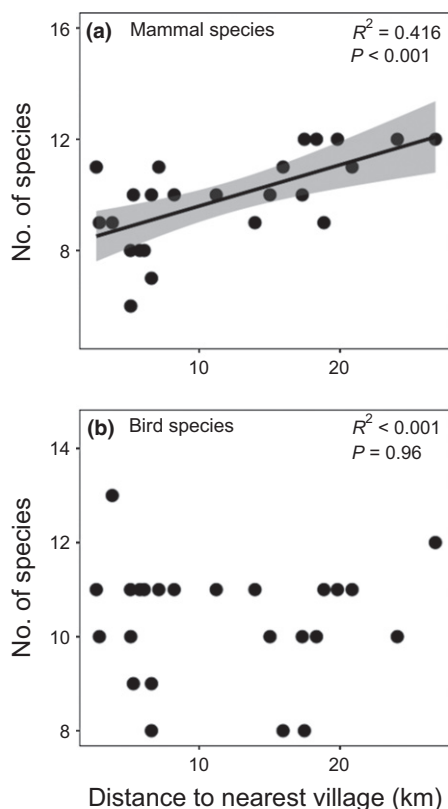


Fig. 2. Species richness of the (a) mammal and (b) bird communities in the Ivindo landscape in relation to distance from the nearest village. Distance to the nearest village is an indicator of hunting pressure, as encounter rates of human sign decrease with distance from villages. We fitted several models to species richness, expecting richness to saturate at some distance from the nearest village (Fig. S3); however, in all cases the linear model fit best. Shading around regression lines represents 95% confidence intervals.

were due to changes in the abundances of species, not species turnover as the identity of the species in these communities did not vary with distance from village in multidimensional space (presence/absence NMDS; data not shown).

The composition of the vertebrate community at the taxonomic guild level also differed significantly with distance from nearest village in nonparametric multidimensional space (Fig. 3d, Fig. S5d). Similarly, the relative abundance of monkeys (+10.1% per 10 km), apes (+2.3% per 10 km) and ungulates (+3.6% per 10 km) increased with distance from village, while birds (−15.3% per 10 km) and rodents (−1% per 10 km) decreased (Fig. 4, Table S3).

Model averaging identified distance to village as the most important or one of the most important drivers of relative abundance for all taxonomic guilds except elephants (Table 1; Tables S4 and S5). Bird relative abundance decreased with distance from nearest village and with increasing tree species richness; whereas monkey relative abundance showed the opposite pattern, increasing with distance from village and tree species richness (Table S5). Monkey relative abundance also decreased with increasing village size. Relative abundances of apes and rodents were primarily driven by distance from nearest village, with ape abundance being higher far from villages and rodent abundance being higher near villages. Relative abundances of ungulates increased with both distance from nearest village and understorey cover. None of the models or parameters strongly explained variation in elephant relative abundances across the landscape (Table S5).

Discussion

Our study highlights the landscape-level effects of small-scale hunting on the distribution and abundance of tropical vertebrate species and demonstrates the existence of a strong defaunation gradient in the forests of north-eastern Gabon. Hunting intensity, as measured by the number of human signs along transects, decreases significantly with distance from villages, resulting in a spatial gradient in animal species diversity, relative abundance and community composition. Following our predictions, the relative abundance of large prey species like primates and ungulates decreased significantly with proximity to villages, while the relative abundance of smaller species like rodents and birds increased near villages. The village halo, the roughly 10 km radius around villages where most hunting and human activities take place (Fig. S2), had highly degraded animal communities dominated by large birds and with high abundances of rodents. Importantly, while the relative abundance of birds increases near villages, the species composition of the bird community near villages is different than the bird community found far from villages; thus, hunting is beneficial for some bird species and detrimental for others.

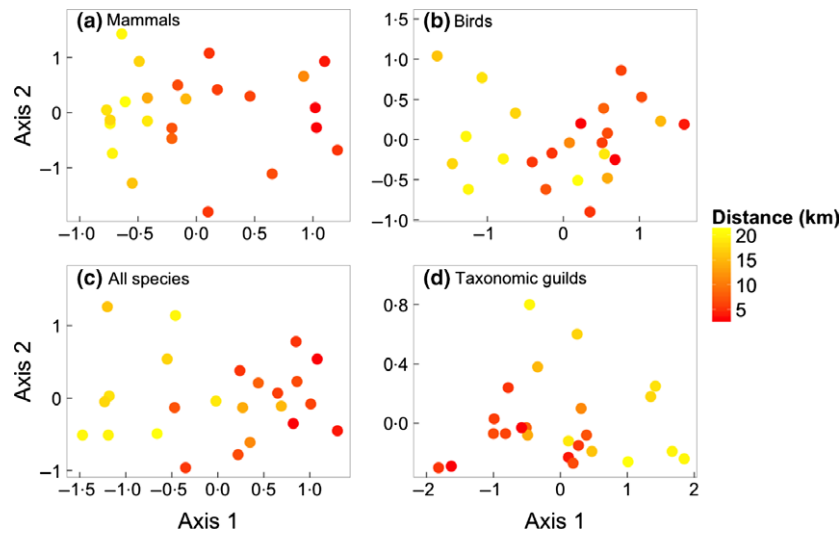


Fig. 3. Non-metric multidimensional scaling (NMDS) plots of the large vertebrate communities in the Ivindo landscape with distance from village represented by colours (red = near to villages; light yellow = far from villages). (a) Mammals, (b) birds and (c) all species (bird + mammal) ordinations incorporate relative abundance of species data, while the (d) taxonomic guild ordination uses the relative abundances of all species grouped in seven taxonomic guilds (birds, apes, monkeys, carnivores, elephants, ungulates, rodents). Stress levels for the NMDS were 0.19, 0.12, 0.16 and 0.04 for mammals, birds, all species and taxonomic guilds, respectively. Note that Axis 1 in all four ordinations is strongly correlated with distance to nearest village (see Fig. S5 for linear regressions of NMDS Axis 1 and distance to nearest village).

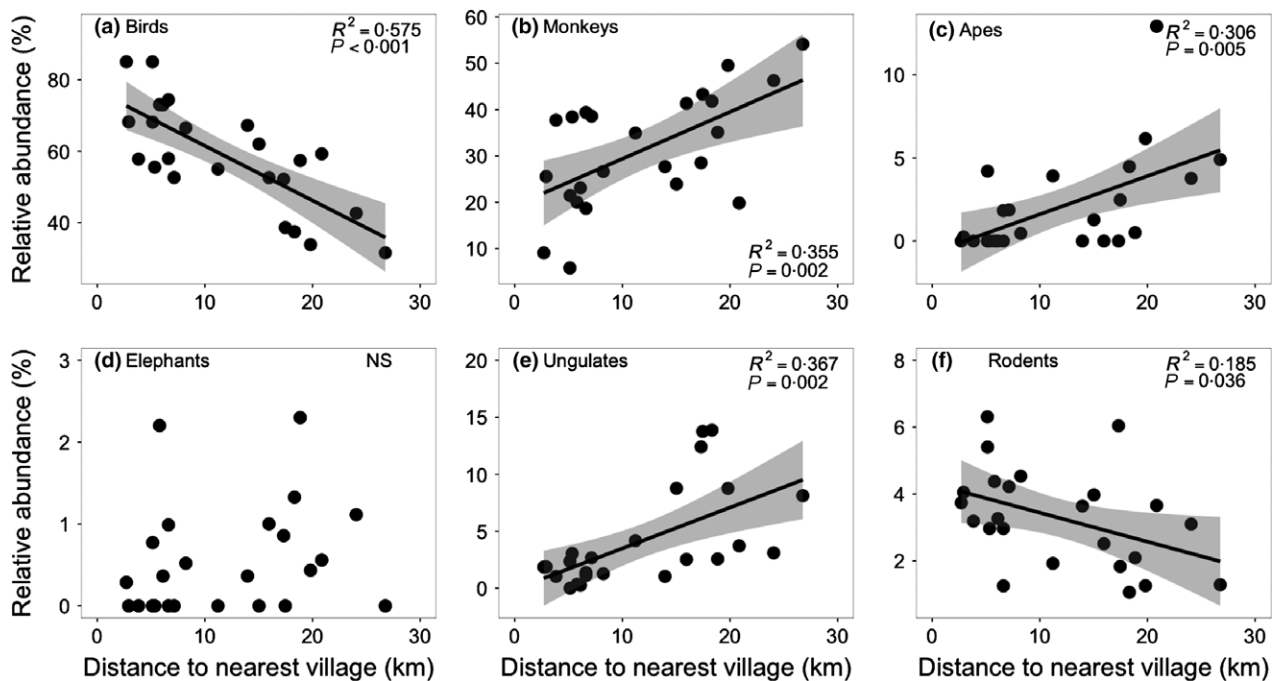


Fig. 4. The relative abundance of taxonomic guilds with distance from the nearest village in the Ivindo landscape. Distance to the nearest village is a proxy for hunting pressure, with hunting intensity decreasing with increasing distance from villages. Note that (a) birds ($F_{1,22} = 29.74$) and (f) rodents ($F_{1,22} = 4.98$) are significantly more common in the vertebrate communities close to villages, whereas (b) monkeys ($F_{1,22} = 12.09$), (c) apes ($F_{1,22} = 9.68$) and (e) ungulates ($F_{1,22} = 12.77$) are significantly more common farther from villages. (d) Elephants show no significant response to distance to nearest village ($F_{1,22} = 1.20$, $P = 0.28$). Shading around regression lines represents 95% confidence intervals.

Our study shows that vertebrate communities can change continuously along a gradient of hunting pressure, underscoring the idea that defaunation is a process, not a dichotomous state. Although many studies examine the

effects of hunting using a binary (hunted vs. non-hunted; e.g. Reyna-Hurtado & Tanner 2007) or categorical approach (high, medium, low pressure; e.g. Thiollay 2005; Laurance *et al.* 2006), a gradient approach enables the

Table 1. Akaike importance weights for model parameters predicting the relative abundance of six taxonomic guilds. We considered all models within 4 AICc of the best-fitting model (with the lowest AICc) as equally informative and determined the importance of the explanatory variables by calculating their frequency of occurrence in these models. Importance weights range from 0 (parameter with no explanatory weight) to 1 (parameter in all top models)

Model parameter	Importance weights (<i>N</i> containing models)					
	Birds	Monkeys	Apes	Elephant	Ungulates	Rodents
Dist. to nearest village	1.00 (8)	1.00 (6)	1.00 (14)	0.21 (8)	1.00 (8)	0.77 (18)
Size of nearest village	0.83 (6)	1.00 (6)	0.08 (2)	0.32 (12)	0.13 (8)	0.36 (10)
No. of tree species	1.00 (8)	1.00 (6)	0.11 (2)	0.34 (13)	0.71 (7)	0.07 (3)
No. of tree stems	0.07 (1)	0.08 (1)	0.10 (2)	0.11 (5)	0.11 (2)	0.05 (2)
Tree DBH	0.19 (2)	0.10 (1)	0.13 (2)	0.11 (5)	0.00 (0)	0.34 (9)
No. of lianas	0.10 (1)	0.07 (1)	0.11 (2)	0.48 (16)	0.18 (2)	0.08 (3)
Understorey cover	0.07 (1)	0.12 (1)	0.59 (7)	0.07 (4)	1.00 (1)	0.22 (6)
Canopy cover	0.08 (1)	0.22 (1)	0.09 (2)	0.08 (5)	0.74 (6)	0.07 (3)
Land use	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)

quantification of the vertebrate community response over all possible levels of hunting or other land use activities. In our study, we identify distances at which hunting has the strongest effect. In future studies, distance could be replaced with hunting intensity to identify acceptable thresholds of offtake to maintain game resources or conserve species.

The gradient of defaunation observed in northern Gabon may eventually result in a gradient in tree community composition, biodiversity and ecosystem responses through changes to underlying ecological processes (Poulsen, Clark & Palmer 2013). For example, monkeys and apes are seed dispersers of medium- and large-seeded tree species, and their relative abundances decreased by 40% and 84% over the 30 km gradient from nearly pristine forest to human-dominated forest. Rodents, on the other hand, are seed predators, and their relative abundance increased by 70%. The reduction of dispersal services and increase in seed predation could impede plant recruitment of primate-dispersed species, opening space for different plant species (Poulsen *et al.* 2002; Brodie *et al.* 2009). Under conditions of persistent hunting, this process could decrease the abundance of large-seeded, mammal-dispersed plant species common in the Ivindo landscape (Effiom *et al.* 2014) and increase the abundance of non-mammal-dispersed tree species (Terborgh *et al.* 2008). As a consequence, the relative abundance of large fruiting trees, which are food sources for both animal and human populations, could be reduced across the landscape.

In north-eastern Gabon, top-down forces of hunting seem to drive the relative abundance of all taxonomic guilds except elephants and influence mammal richness and community composition. Many vegetation characteristics, such as tree community richness or understorey density, have been shown to be important in habitat selection for different species (e.g. Feng & Zhang 2005; Abu Baker & Brown 2014; Carvalho *et al.* 2015). In our study, vertebrate abundances were occasionally related to our measured vegetation characteristics, but no single characteristic was important across taxonomic guilds and their

effect sizes tended to be lower than those of distance from village. Therefore, distance from village is likely the primary driver of large vertebrate animal communities as nearly every aspect (relative abundance, richness, composition) of the community responded to this gradient. Hunting remains overwhelmingly the greatest conservation threat to Afrotropical forest wildlife (Harrison 2011; Poulsen, Clark & Bolker 2011).

Unlike other taxonomic groups, the abundance and distribution of forest elephants were not related to distance to nearest village (see also Poulsen, Clark & Bolker 2011). Forest elephants range far and use large areas (2.5–21.6 km² core use areas; Schuttler, Blake & Eggert 2012), and therefore variation in elephant abundance may be better captured over larger scales than our transect design. Alternatively, forest elephants may not avoid villages. Crop raiding by forest elephants suggests they are attracted towards villages for food. At the same time, Gabonese law protects forest elephants from hunting; therefore, they are less likely to be hunted near villages for subsistence (where law enforcement is more conspicuous) and more likely to be poached for ivory in remote areas (Maisels *et al.* 2013). Thus, the combination of the high mobility of elephants and different types of threats to their populations likely create different patterns of elephant abundance and distribution relative to other taxa.

In the Ivindo landscape, heavy hunting is largely centred around villages. The clustering of most villages along roads and rivers may buffer remote forest from the effects of small-scale hunting. We expected that species richness would asymptote at some distance from the nearest village. Instead, species richness increased linearly with distance. We hypothesize that light levels of hunting may occur everywhere across our study area, affecting species relative abundances and composition into the national park. While increasing species richness across the 30-km distance gradient could be due to beta diversity, this is unlikely because the transects were all located in *terra firma* forest (not swamps or savannas) and historical records suggest that animal densities have declined over

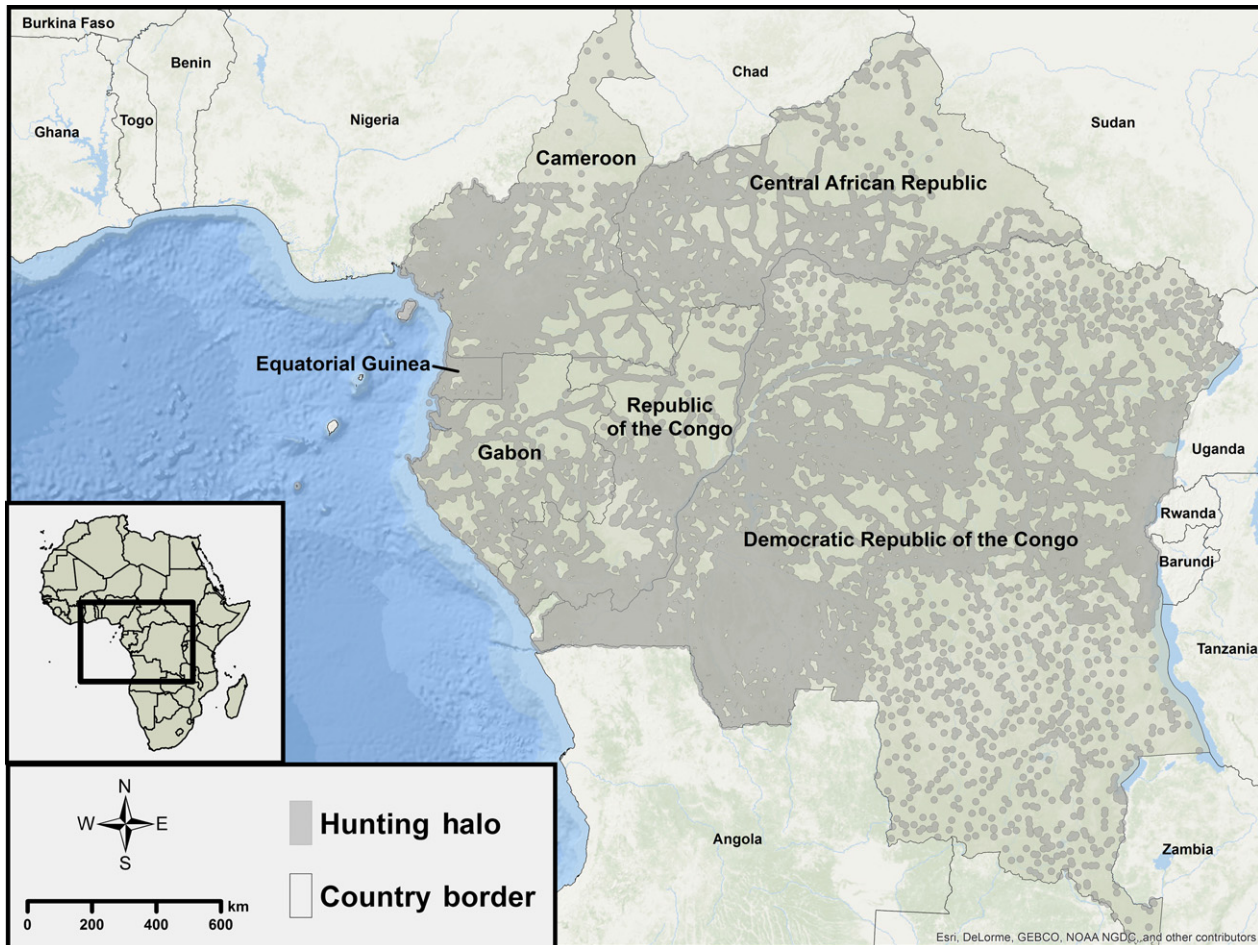


Fig. 5. Area within the hunting halo (10 km radius) around each village for Central Africa. Fifty-three per cent of the total area of the region (including six Central African countries) lies within the hunting halo (2.2 million km²). See Fig. S6 for a sensitivity analysis demonstrating variation in the total area affected with the size of the hunting halo. Data on village locations are taken from national population censuses between 2010 and 2013.

time. Encounter rates of game species within Ivindo National Park have decreased since 2002 (blue duiker: 8.05 individuals km⁻¹ to 4.24 individuals km⁻¹; white-noised guenon: 56.43 individuals km⁻¹ to 21.20 individuals km⁻¹ (Okouyi *et al.* 2002)). Therefore, even though most hunting is centred near villages, commercial hunters or fisherman hunting from camps along the Ivindo River could reduce animal populations over the entire landscape.

Our findings indicate that the effects of hunting decrease with distance from rural communities. Assuming a hunting halo around villages of 10 km (the point at which human sign dropped; Fig. S2), over 50% of the study area is composed of heavily altered vertebrate communities (15 km radius = 69% of study area). Alarming, 53% of Central Africa, where subsistence hunting is an important component of household economies (Wilkie & Carpenter 1999), lies within 10 km of a village and therefore is potentially home to heavily altered vertebrate communities (Fig. 5; see Fig. S6 for calculations based on several different sizes of the hunting halo).

Tropical forests are globally important for the ecosystem services they provide, including carbon storage, biodiversity conservation and the provision of resources like wild meat to rural people. Because the maintenance of different ecosystem services can sometimes be at odds with each other (e.g. conservation of biology and provision of wild meat), environmental management strategies must be adapted to the objectives of any site. Given the enormous impact that small-scale, village-based hunting is likely to have on wildlife communities region-wide, wildlife management strategies should account for the spatial gradients in anthropogenic pressure and species abundances. Near villages, management efforts should focus on limiting the growth of the village halo and maintaining ecologically functioning forests. By managing hunting, ecological processes could be preserved (even if not at their original levels) to facilitate forest regeneration. But the principal goal should be maintaining game populations for local people who depend on wildlife for protein and income. Village-based actions such as environmental education, citizen science, local wildlife management and

the development of community-led sustainable hunting programmes will be the most effective actions. Outside of the village halo, conservation efforts should focus on preventing biodiversity loss and maintaining intact animal communities. The detection of altered animal communities in our most remote transects suggests that distance alone will not be enough to completely maintain the vertebrate community. Landscape-level actions could include requiring industry cooperation (e.g. logging companies and other extractive resource operations) to prevent hunting in production forests as well as strict enforcement of hunting and poaching laws in contiguous forests (Clark *et al.* 2009).

Hunting reduces species diversity and shifts the species and functional composition to small-bodied vertebrates (Dornelas *et al.* 2014). These alterations of the vertebrate community can have cascading consequences for ecosystem function (Poulsen, Clark & Palmer 2013; Osuri *et al.* 2016), plant communities (Gaston & Fuller 2008; Harrison *et al.* 2013) and human livelihoods (Nasi, Taber & Van Vliet 2011; Gordon *et al.* 2012). Understanding the resulting patterns of defaunation is the first step to predicting the strength and distribution of defaunation effects; now management strategies must be tailored to these patterns to conserve biodiversity while simultaneously maintaining natural resources for the peoples of Central Africa.

Acknowledgements

We are grateful to the Gabonese government, in particular the Centre National de la Recherche Scientifique et Technologique (CENAREST) and the Agence Nationale des Parcs Nationaux (ANPN) for permission to conduct this work. Administrative and logistical support was generously provided by ANPN. For dedicated and skilled work in the field, we thank L. Amvame, E. Assadjola, K. Beals, A. Bedi, M. Belovitch, R. Harrison, B. Hayes, R. Kowe, J. Mbelassanga, J. Moore, G. Moussavou, M. Pendred and N. Yao. S. Moore created all maps and performed all GIS work shown in the manuscript. B. McLean, C. Rosin, A. Meier and C. Nunez provided helpful comments on early drafts of this manuscript.

Data accessibility

Taxonomic guild relative abundances, richness, evenness, diversity and environmental characteristics by transect are available from Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.vs97g> (Koerner *et al.* 2016).

References

- Abu Baker, M.A. & Brown, J.S. (2014) Foraging and habitat use of common duikers, *Sylvicapra grimmia*, in a heterogeneous environment within the Soutpansberg, South Africa. *African Journal of Ecology*, **52**, 318–327.
- Bartoń, K. (2016) *MuMIn: Multi-Model Inference*. R package version 1.15.6. The Comprehensive R Archive Network (CRAN), Vienna, Austria.
- Bodmer, R.E., Eisenberg, J.F. & Redford, K.H. (1997) Hunting and the likelihood of extinction of Amazonian mammals. *Conservation Biology*, **11**, 460–466.
- Brodie, J.F., Helmy, O.E., Brockelman, W.Y. & Maron, J.L. (2009) Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecological Applications*, **19**, 854–863.
- Burton, M.E.H., Poulsen, J.R., Lee, M.E., Medjibe, V.P., Stewart, C.G., Venkataraman, A. & White, L.J.T. (2016) Reducing carbon emissions from forest conversion for oil palm agriculture in Gabon. *Conservation Letters*, doi: 10.1111/conl.12265.
- Carvalho, J.S., Meyer, C.F.J., Vicente, L. & Marques, T.A. (2015) Where to nest? Ecological determinants of chimpanzee nest abundance and distribution at the habitat and tree species scale. *American Journal of Primatology*, **77**, 186–199.
- Clark, C.J., Poulsen, J.R., Malonga, R. & Elkan, J.P.W. (2009) Logging concessions can extend the conservation estate for Central African tropical forests. *Conservation Biology*, **23**, 1281–1293.
- Collen, B., Loh, J., Whitmee, S., McRae, L., Amin, R. & Baillie, J.E.M. (2009) Monitoring change in vertebrate abundance: the Living Planet Index. *Conservation Biology*, **23**, 317–327.
- Dirzo, R. & Miranda, A. (1990) Contemporary Neotropical defaunation and forest structure, function, and diversity – a sequel. *Conservation Biology*, **4**, 444–447.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014) Defaunation in the anthropocene. *Science*, **345**, 401–406.
- Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. & Magurran, A.E. (2014) Assemblage time series reveal biodiversity change but not systematic loss. *Science*, **344**, 296–299.
- Effiom, E.O., Nunez-Iturri, G., Smith, H.G., Ottosson, U. & Olsson, O. (2013) Bushmeat hunting changes regeneration of African rainforests. *Proceedings of the Royal Society B-Biological Sciences*, **280**, 20130246.
- Effiom, E.O., Birkhofer, K., Smith, H.G. & Olsson, O. (2014) Changes of community composition at multiple trophic levels due to hunting in Nigerian tropical forests. *Ecography*, **37**, 367–377.
- Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. *et al.* (2011) Trophic downgrading of planet Earth. *Science*, **333**, 301–306.
- Fa, J.E. & Brown, D. (2009) Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. *Mammal Review*, **39**, 231–264.
- Fa, J.E., Currie, D. & Meeuwig, J. (2003) Bushmeat and food security in the Congo Basin: linkages between wildlife and people's future. *Environmental Conservation*, **30**, 71–78.
- Feng, L. & Zhang, L. (2005) Habitat selection by Asian elephant (*Elephas maximus*) in Xishuangbanna, Yunnan, China. *Acta Theriologica Sinica*, **25**, 229–236.
- Galetti, M. & Dirzo, R. (2013) Ecological and evolutionary consequences of living in a defaunated world. *Biological Conservation*, **163**, 1–6.
- Gaston, K.J. & Fuller, R.A. (2008) Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution*, **23**, 14–19.
- Gordon, I.J., Acevedo-Whitehouse, K., Altwegg, R., Garner, T.W.J., Gompper, M.E., Katzner, T.E. *et al.* (2012) What the 'food security' agenda means for animal conservation in terrestrial ecosystems. *Animal Conservation*, **15**, 115–116.
- Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011) Multi-model inference in ecology and evolution: challenges and solutions. *Journal of Evolutionary Biology*, **24**, 699–711.
- Harrison, R.D. (2011) Emptying the forest: hunting and the extirpation of wildlife from tropical nature reserves. *BioScience*, **61**, 919–924.
- Harrison, R.D., Tan, S., Plotkin, J.B., Slik, F., Detto, M., Brenes, T. *et al.* (2013) Consequences of defaunation for a tropical tree community. *Ecology Letters*, **16**, 687–694.
- Hoffmann, M., Hilton-Taylor, C., Angulo, A., Boehm, M., Brooks, T.M., Butchart, S.H.M. *et al.* (2010) The impact of conservation on the status of the world's vertebrates. *Science*, **330**, 1503–1509.
- Koerner, S.E., Poulsen, J.R., Blanchard, E.J., Okouyi, J. & Clark, C.J. (2016) Data from: Vertebrate community composition and diversity declines along a defaunation gradient radiating from rural villages in Gabon. *Dryad Data Repository*, <http://dx.doi.org/10.5061/dryad.vs97g>.
- Laurance, W.F., Croes, B.M., Tchignoumba, L., Lahm, S.A., Alonso, A., Lee, M.E. *et al.* (2006) Impacts of roads and hunting on central African rainforest mammals. *Conservation Biology*, **20**, 1251–1261.
- Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing, Oxford, UK.
- Maisels, F., Strindberg, S., Blake, S., Wittemyer, G., Hart, J., Williamson, E.A. *et al.* (2013) Devastating decline of forest elephants in Central Africa. *PLoS ONE*, **8**, e59469.
- Muhly, T.B., Hebblewhite, M., Paton, D., Pitt, J.A., Boyce, M.S. & Musiani, M. (2013) Humans strengthen bottom-up effects and weaken trophic cascades in a terrestrial food web. *PLoS ONE*, **8**, e64311.

- Nasi, R., Taber, A. & Van Vliet, N. (2011) Empty forests, empty stomachs? Bushmeat and livelihoods in the Congo and Amazon Basins. *International Forestry Review*, **13**, 355–368.
- Nasi, R., Brown, D., Wilkie, D., Bennett, E., Tutin, C., van Tol, G. & Christophersen, T. (2008) Conservation and use of wildlife-based resources: the bushmeat crisis. *CBD Technical Series*, **33**, 1–50.
- Nunez-Iturri, G., Olsson, O. & Howe, H.F. (2008) Hunting reduces recruitment of primate-dispersed trees in Amazonian Peru. *Biological Conservation*, **141**, 1536–1546.
- Okouyi, J.O., Posso, P., Lepretre, A. & Scaps, P. (2002) Estimation of large mammal densities in the Ipassa-Makokou reserve (Gabon). *Bulletin De La Societe Zoologique De France*, **127**, 121–135.
- Osuri, A.M., Ratnam, J., Varma, V., Alvarez-Loayza, P., Hurtado Astaiza, J., Bradford, M. *et al.* (2016) Contrasting effects of defaunation on aboveground carbon storage across the global tropics. *Nature Communications*, doi: 10.1038/ncomms11351.
- Peres, C.A. (1990) Effects of hunting on Western Amazonian primate communities. *Biological Conservation*, **54**, 47–59.
- Peres, C.A. & Dolman, P.M. (2000) Density compensation in neotropical primate communities: evidence from 56 hunted and nonhunted Amazonian forests of varying productivity. *Oecologia*, **122**, 175–189.
- Peres, C.A. & Lake, I.R. (2003) Extent of nontimber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon basin. *Conservation Biology*, **17**, 521–535.
- Poulsen, J.R., Clark, C.J. & Bolker, B.M. (2011) Decoupling the effects of logging and hunting on an Afrotropical animal community. *Ecological Applications*, **21**, 1819–1836.
- Poulsen, J.R., Clark, C.J. & Palmer, T.M. (2013) Ecological erosion of an Afrotropical forest and potential consequences for tree recruitment and forest biomass. *Biological Conservation*, **163**, 122–130.
- Poulsen, J.R., Clark, C.J., Connor, E.F. & Smith, T.B. (2002) Differential resource use by primates and hornbills: implications for seed dispersal. *Ecology*, **83**, 228–240.
- Poulsen, J.R., Clark, C.J., Mavah, G. & Elkan, P.W. (2009) Bushmeat supply and consumption in a tropical logging concession in Northern Congo. *Conservation Biology*, **23**, 1597–1608.
- Redford, K.H. (1992) The empty forest. *BioScience*, **42**, 412–422.
- Reyna-Hurtado, R. & Tanner, G.W. (2007) Ungulate relative abundance in hunted and non-hunted sites in Calakmul Forest (Southern Mexico). *Biodiversity and Conservation*, **16**, 743–756.
- Rosin, C. & Swamy, V. (2013) Variable density responses of primate communities to hunting pressure in a Western Amazonian river basin. *Neotropical Primates*, **20**, 25–31.
- Schuttler, S.G., Blake, S. & Eggert, L.S. (2012) Movement patterns and spatial relationships among African forest elephants. *Biotropica*, **44**, 445–448.
- Terborgh, J., Nunez-Iturri, G., Pitman, N.C.A., Valverde, F.H.C., Alvarez, P., Swamy, V. *et al.* (2008) Tree recruitment in an empty forest. *Ecology*, **89**, 1757–1768.
- Thiollay, J.M. (2005) Effects of hunting on guianan forest game birds. *Biodiversity and Conservation*, **14**, 1121–1135.
- Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L. *et al.* (2010) Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, **47**, 5–14.
- Wich, S.A., Garcia-Ulloa, J., Kuhl, H.S., Humle, T., Lee, J.S.H. & Koh, L.P. (2014) Will oil palm's homecoming spell doom for Africa's great apes? *Current Biology*, **24**, 1659–1663.
- Wilkie, D.S. & Carpenter, J.F. (1999) Bushmeat hunting in the Congo Basin: an assessment of impacts and options for mitigation. *Biodiversity and Conservation*, **8**, 927–955.

Received 25 May 2016; accepted 26 September 2016

Handling Editor: Susan Cheyne

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Species-level encounter rates in relation to distance from village.

Table S2. Species-level densities in relation to distance from village.

Fig. S1. Vegetation characteristics of transects and lack of pattern with distance from village.

Fig. S2. Signs of human presence with distance to nearest village.

Fig. S3. Model fit exploration for richness relationship with distance from nearest village.

Fig. S4. Large mammal and bird community evenness and diversity in relation to distance from nearest village.

Fig. S5. Responses of NMDS Axis 1 (based on Bray–Curtis dissimilarity matrix) to distance from nearest village.

Table S3. General linear model results for the relative abundances of taxonomic guilds with environmental variables.

Table S4. Model comparison for taxonomic guild relative abundance.

Table S5. Results of model averaging to determine the effects of nine environmental variables.

Fig. S6. Sensitivity analysis of hunting halo size.