Hunting induced defaunation gradient in a Gabonese tropical forest

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Abstract:

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.

Article:

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 (Collen *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.
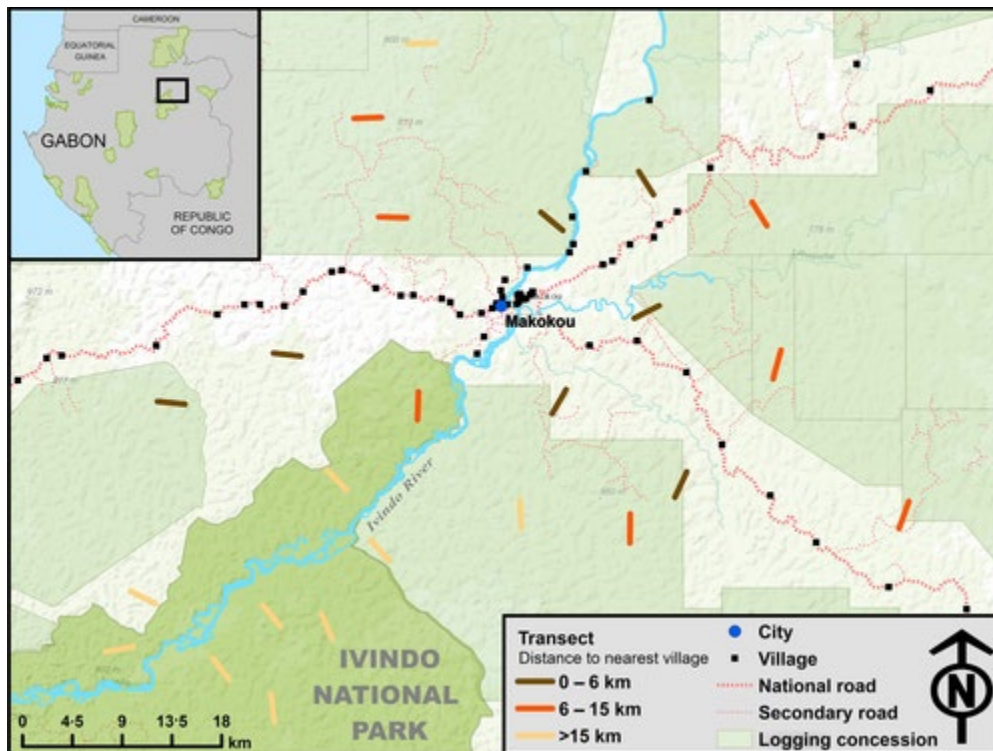
Figure 1. (*inset)* Location of the study area within Gabon. *(main map)* The 6018 km² study area in north-eastern Gabon is centred around the regional capital of Makokou and includes numerous small villages (36–891 people per village), the Ivindo National Park and several logging concessions. Line segments 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.

Materials and methods

Study Area

We studied wildlife communities in the 5800 km^2 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 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 m^2) 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.

$$E_{i,j} = \frac{N_{i,j}}{L_j}$$

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.

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

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 ΔAICc <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 ($F_{1,22} = 9{\cdot}57$; $P = 0{\cdot}005$; $R^2 = 0{\cdot}303$), 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 $= 25{\cdot}3$ 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).
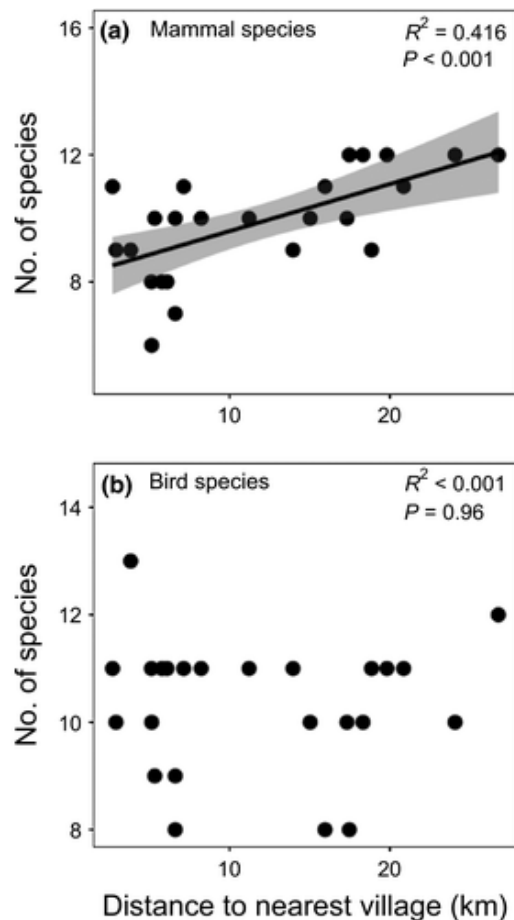
Figure 2. Species richness of the (a) mammal and (b) bird communities in the Ivindo landscape in relation to distance from the nearest village. Distance to the nearest village is an indicator of hunting pressure, as encounter rates of human sign decrease with distance from villages. We fitted several 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.

Community Diversity and Composition

Species richness of the mammal community increased significantly with distance from village ($F_{1,22} = 15 \cdot 67$), while bird species richness ($F_{1,22} = 0 \cdot 003$) did not vary significantly (Fig. 2). Approximately $1 \cdot 5$ 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 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).
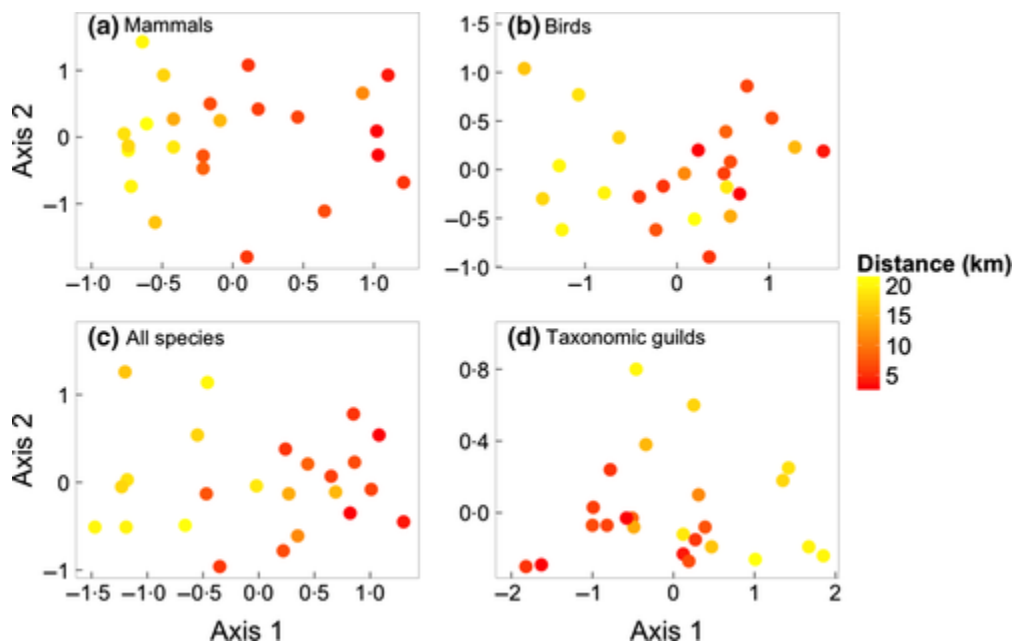

Figure 3. Non-metric multidimensional scaling (NMDS) plots of the large vertebrate communities in the Ivindo landscape with distance from village represented by colours (red = near to villages; light yellow = far from villages). (a) Mammals, (b) birds and (c) all species (bird + mammal) ordinations incorporate 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 $0 \cdot 19$, $0 \cdot 12$, $0 \cdot 16$ and $0 \cdot 04$ 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).

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).
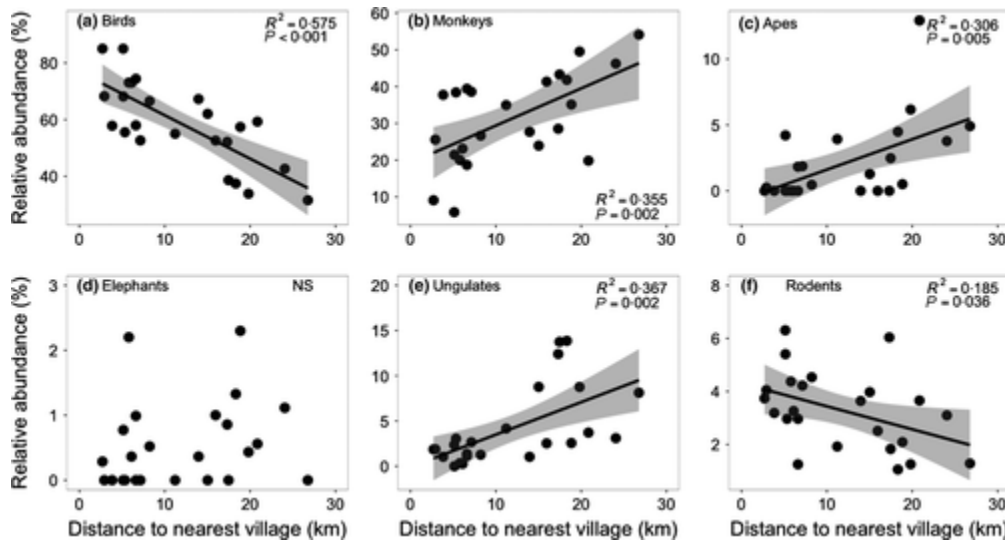

Figure 4. The relative abundance of taxonomic guilds with distance from the nearest village in the Ivindo landscape. Distance to the nearest village is a proxy for hunting pressure, with hunting intensity decreasing with increasing distance from villages. Note that (a) birds ($F_{1,22} = 29·74$) and (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.

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 (*N* 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)

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.

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 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 ($2·5–21·6$ km^2 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 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). Alarmingly, 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).
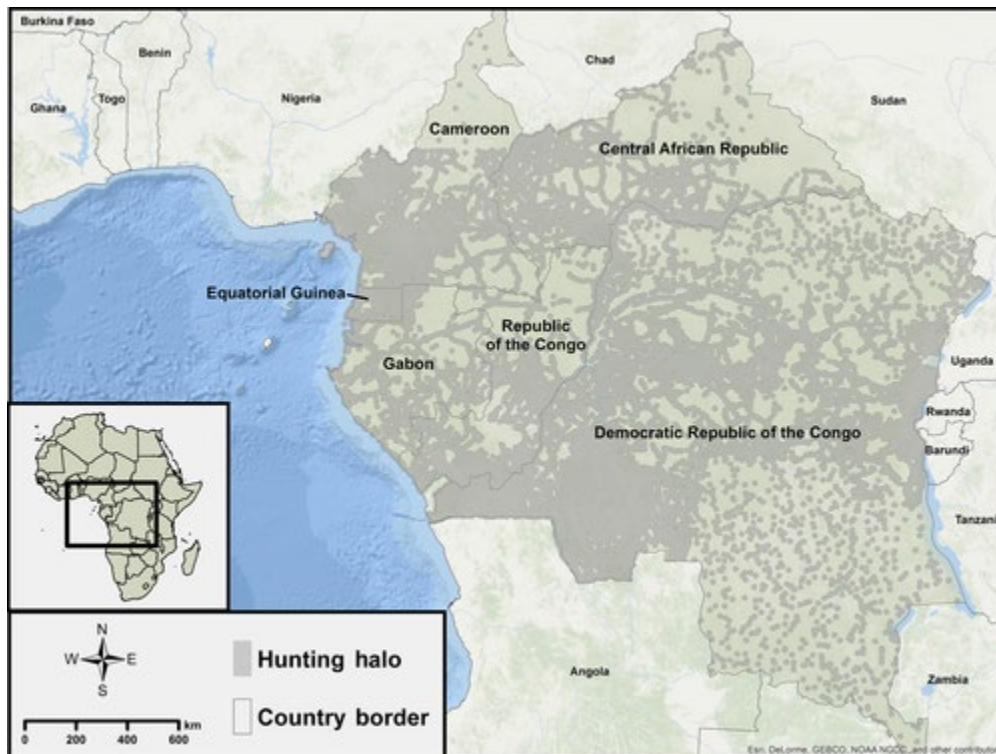

Figure 5. Area within the hunting halo (10 km radius) around each village for Central Africa. Fifty-three per cent of the total area of the region (including six Central African countries) lies within the hunting halo (2·2 million km^2). See Fig. S6 for a sensitivity analysis demonstrating variation 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.

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

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).

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1 ***** Corrected version in Aug 2017. Table S1 was altered to remove the Sun-tailed monkey**
2 **which does not occur in this region, likely an observer error. The removal does not affect**
3 **any results presented in the main manuscript or anywhere else in the supplemental**
4 **information. *****
5
6 **Supplemental Information**
7 **Table S1.** Species encounter rates (and standard error) at near, intermediate, and far distances
8 from villages. We assessed variation in encounter rates with distance from nearest village using
9 ANOVA to test for differences across distance categories and linear regression to evaluate the
10 relationship with continuous distances (slope). Bolded numbers indicate significant results, with
11 letters designating those distance categories that differ in encounter rates.

Species	Common Name	n	Encounter Rate (no. individuals/km) (SE)			Slope
			Near	Intermediate	Far	
Bird						
Agelastes niger	Black guineafowl	28	0.01 (0.01)	0.07 (0.03)	0.06 (0.03)	0.0032
Bycanistes albotibialis	White-thighed hornbill	134	0.40 (0.16)	0.23 (0.05)	0.12 (0.06)	**-0.0167**
Bycanistes fistulator	Piping hornbill	319	0.75 (0.10)	0.39 (0.12)	0.45 (0.09)	-0.0088
Ceratogymna atrata	Black-casqued hornbill	1501	**2.91 (0.48)[a]**	**3.34 (0.33)[a]**	**1.39 (0.15)[b]**	-0.1149
Corythaeola cristata	Blue-plantain eater	263	0.77 (0.28)	0.50 (0.14)	0.17 (0.07)	-0.0269
Francolinus lathami	Latham's forest francolin	22	0.03 (0.01)	0.03 (0.02)	0.06 (0.02)	0.0018
Guttera plumifera	Plumed guineafowl	5	0.03 (0.02)	0.00 (0.00)	0.00 (0.00)	-0.0014
Psittacus erithacus	African grey parrot	1092	1.74 (0.32)	1.62 (0.15)	2.05 (0.35)	-0.0022
Tauraco macrorhynchus	Yellow-billed turaco	41	0.07 (0.03)	0.10 (0.04)	0.04 (0.02)	-0.0024
Tauraco persa	Green turaco	124	**0.31 (0.06)[a]**	**0.24 (0.08)[ab]**	**0.08 (0.02)[b]**	**-0.0159**
Tockus camurus	Red-billed dwarf hornbill	247	**0.22 (0.04)[a]**	**0.34 (0.12)[ab]**	**0.60 (0.11)[b]**	0.0144
Tockus fasciatus	African pied hornbill	154	0.29 (0.06)	0.29 (0.05)	0.18 (0.04)	-0.0040
Tropicranus albocristatus	White-crested hornbill	64	0.06 (0.02)	0.11 (0.03)	0.14 (0.03)	**0.0049**
Monkey						
Cercocebus agilis	Agile mangabey	6	0.00 (0.00)	0.01 (0.01)	0.03 (0.03)	**0.0030**
Cercopithecus c. cephus	Mustached monkey	351	0.83 (0.37)	0.71 (0.27)	0.29 (0.05)	-0.0352
Cercopithecus mona pogonias	Crowned guenon	494	0.52 (0.19)	0.73 (0.25)	1.15 (0.29)	0.0375
Cercopithecus n. nictitans	White-nosed guenon	899	**0.73 (0.17)[a]**	**1.27 (0.13)[a]**	**2.26 (0.32)[b]**	**0.0922**
Colobus guereza occidentalis	Black and white colobus	3	0.01 (0.01)	0.00 (0.00)	0.01 (0.01)	0.0002
Lophocebus albigena	Grey-cheeked mangabey	503	**0.27 (0.13)[a]**	**0.63 (0.13)[ab]**	**1.41 (0.44)[b]**	0.0498
Mandrillus sphinx	Mandrill	18	0.10 (0.10)	0.00 (0.00)	0.00 (0.00)	-0.0037
Miopithecus ogouensis	Northern talapoin	7	0.04 (0.04)	0.01 (0.01)	0.00 (0.00)	-0.0022
Ape						
Gorilla gorilla	Gorilla	22	0.00 (0.00)	0.02 (0.01)	0.08 (0.04)	**0.0062**
Pan troglodytes	Chimpanzee	109	**0.05 (0.04)[a]**	**0.11 (0.06)[ab]**	**0.35 (0.11)[b]**	**0.0195**
Elephant						
Loxodonata cyclotis	Forest elephant	38	0.05 (0.04)	0.03 (0.02)	0.10 (0.03)	0.0023
Ungulate						
Cephalophus monticola	Blue duiker	45	0.08 (0.04)	0.07 (0.02)	0.09 (0.02)	0.0008
Cephalophus nigrifrons	Black-fronted duiker	5	0.01 (0.01)	0.00 (0.00)	0.02 (0.01)	0.0005
Cephalophus silvicultor	Yellow-backed duiker	7	0.00 (0.00)	0.01 (0.01)	0.03 (0.01)	**0.0016**
Cephalophus spp.	Medium duikers	75	**0.07 (0.03)[a]**	**0.07 (0.02)[a]**	**0.22 (0.04)[b]**	0.0081
Potamochoerus porcus	Red river hog	195	**0.03 (0.02)[a]**	**0.15 (0.09)[ab]**	**0.74 (0.28)[b]**	0.0379
Rodent						
Atherurus africanus centralis	African brush-tailed porcupine	4	0.01 (0.01)	0.01 (0.01)	0.00 (0.00)	-0.0008
Protoxerus stangeri	African giant squirrel	16	0.04 (0.03)	0.00 (0.00)	0.03 (0.01)	0.0001
Xerinae spp.	Other squirrels	220	0.43 (0.08)	0.37 (0.04)	0.29 (0.06)	-0.0090

12
13 [1]N is the sum of all direct (visual and auditory) observations for a species on all transects.
14 [2]Medium duikers include *Cephalophus callipygus*, *C. leucogaster*, and *C. dorsalis castaneus*.
15 Other species encountered (<3 observations) over the course of the study include: *Hyemoschus aquaticus*, *Tragelaphus spekei* (Ungulate);
16 *Civettictis civetta*, *Pantera pardus* (Carnivore); *Ceropithecus neglectus* (Monkey); *Francolinus squamatus* (Bird).

17 **Table S2.** The density of nine of the most common mammal species in the Ivindo landscape,
18 Gabon, including the 95% confidence intervals (CI), coefficient of variation (CV), and estimated
19 local population size. Density estimates were calculated from direct observations for monkey
20 species and indirect observations for other species (elephant and ungulate dung and ape nests).
21 Only newly discovered dung piles and nests were used for the analyses to avoid double counting.
22 Densities were analyzed by distance to nearest village category. Bolded numbers indicate
23 significant relationships between density and distance to nearest village. Letters after distance
24 category indicate significant differences in encounter rates between categories.

25

| Taxonomic Guild	Species	Density (no. animals km^{-2})	95% CI	df	CV (%)	Local Population Estimate	Mean Density by Distance Category (S.E.)		
							Near	Intermediate	Far
Ape	Chimpanzee[1]	0.12	0.08-0.16	25.2	16.8	696	**0.02 (0.01)[a]**	**0.03 (0.01)[ab]**	**0.06 (0.01)[b]**
Monkey	Mustached monkey	8.94	5.61-14.24	97.7	23.8	51,877	11.08 (5.26)	10.37 (4.28)	3.62 (0.64)
	White-nosed guenon	13.65	10.51 -17.71	77.7	11.8	79,207	**6.01 (1.43)[a]**	**11.19 (1.32)[ab]**	**17.42 (3.05)[b]**
	Crowned guenon	11.13	6.63-18.68	138.3	22.5	64,585	4.54 (1.82)	8.13 (2.85)	13.17 (3.43)
	Grey-cheeked mangabey	5.00	3.51-7.14	74.6	18.0	29,014	**2.14 (1.02)[a]**	**4.34 (1.07)[ab]**	**8.10 (1.60)[b]**
Elephant	Elephant[2]	0.33	0.24-0.45	63.2	15.9	1,898	0.32 (0.12)	0.32 (0.07)	0.45 (0.06)
Ungulate	Medium-sized duiker[3]	4.17	2.56-6.81	38.7	24.6	24,207	**1.20 (0.40)[a]**	**2.67 (1.15)[a]**	**7.33 (1.69)[b]**
	Blue duiker[4]	3.56	2.03-6.25	51.9	28.6	20,655	1.31 (0.39)	2.18 (0.75)	3.43 (1.50)
	Red river hog[5]	232.02	108.61-495.65	30.8	38.5	NA	**10.51 (7.29)[a]**	**36.50 (19.47)[a]**	**314.21 (100.45)[b]**

26
27 [1] Density of chimpanzee nests converted to chimpanzee group densities using a nest decay rate of 91.5 days and
28 assuming a production of one nest per night (Morgan et al., 2006). Nests found in trees were identified as
29 chimpanzee nests, while nests found on the ground were identified as gorilla nests.
30 [2] For elephants we used estimates of 18.07 defecations per day and dung lifespan of 44.63 days to translate dung
31 densities into densities of individual animals (Hedges et al. 2012; Barns and Barns 1992).
32 [3] Dung cannot be reliably distinguished by species, so medium-sized duikers includes *Cephalophus leucogaster*, *C.*
33 *nigrifrons*, *C. dorsalis castaneus*, and *C. callipygus*. For medium-sized duikers we used estimates of 4.4 defecations
34 per day and dung lifespan of 21 days to convert dung densities into densities of individual animals (Koster & Hart
35 1988)
36 [4] For blue duikers we used estimates of 4.9 defecations per day and dung lifespan of 18 days to convert dung
37 densities into densities of individual animals (Koster & Hart 1988)
38 [5] No reliable dung defecation and decay rate exists for red river hogs, thus the reported density is the density of dung
39 piles, not animals.
40

41
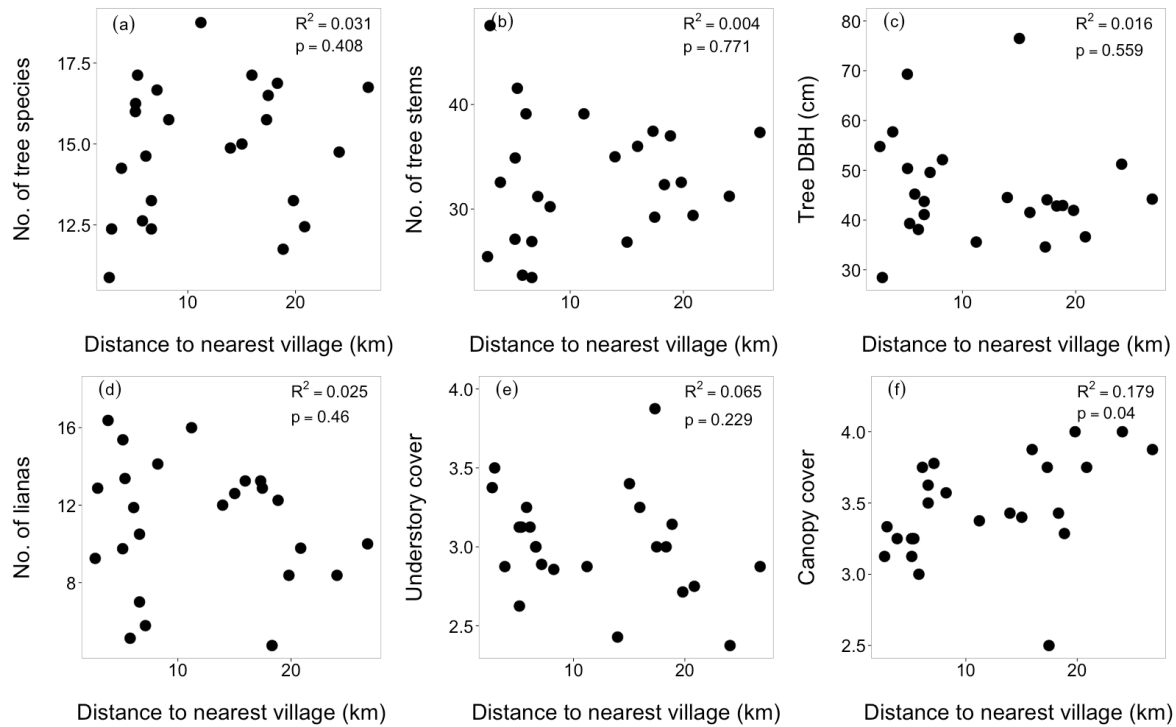
42
43
44
45 **Figure S1.** Average vegetation characteristics of transects in relation to distance to the nearest
46 village. Vegetation characteristics include (a) number of trees (>10 cm DBH), species richness,
47 (b) number of tree stems, (c), diameter at breast height (DBH; cm), (d) number of lianas, (e)
48 understory cover (scored on scale from 0 to 4, with 4 being completely closed), and (f) canopy
49 cover (same scale as understory cover). We show the mean vegetation characteristics of the 8
50 circle plots per transect (i.e., mean per 78. 5 m^2) with each transect representing a single point in
51 the linear regression. Note that none of the vegetation characteristics are significantly correlated
52 with distance to nearest village except for canopy cover(a: $F_{1,22} = 0.71$, b: $F_{1,22} = 0.09$, c: $F_{1,22} =$
53 0.35, d: $F_{1,22} = 0.57$, e; $F_{1,22} = 1.53$, f; $F_{1,22} = 4.78$), which goes from the already dense 75% cover
54 to 100% cover. This led us to conclude that detectability of wildlife was similar across the study
55 area. Residuals were checked for normality.
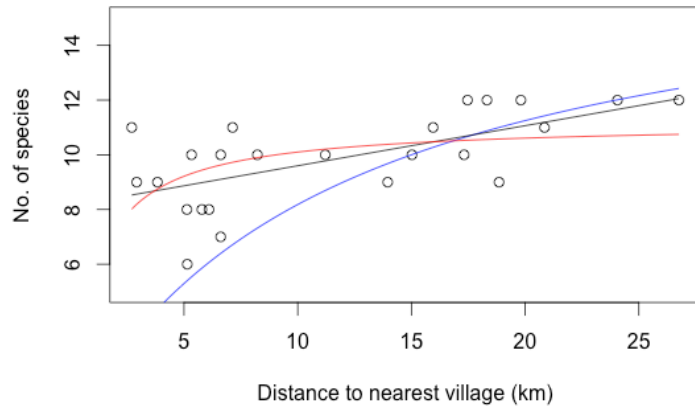
56
57
58 **Figure S2.** Richness of mammals in the Ivindo landscape with distance from the nearest village.
59 Three models were fit for this relationship: linear (black: M=aD+b), Beverton-Holt 1 (blue:
60 M=D * a/(b + D)), and Beverton-Holt 2 (red: M=((a*D)/(1 + (a*D/b)) where M=mammal
61 richness and D=distance to nearest village. The linear fit was the best fit (likelihood ratio test and
62 lowest AIC score). In all cases where regressions were fit, the linear model proved to be the best
63 fit.
64
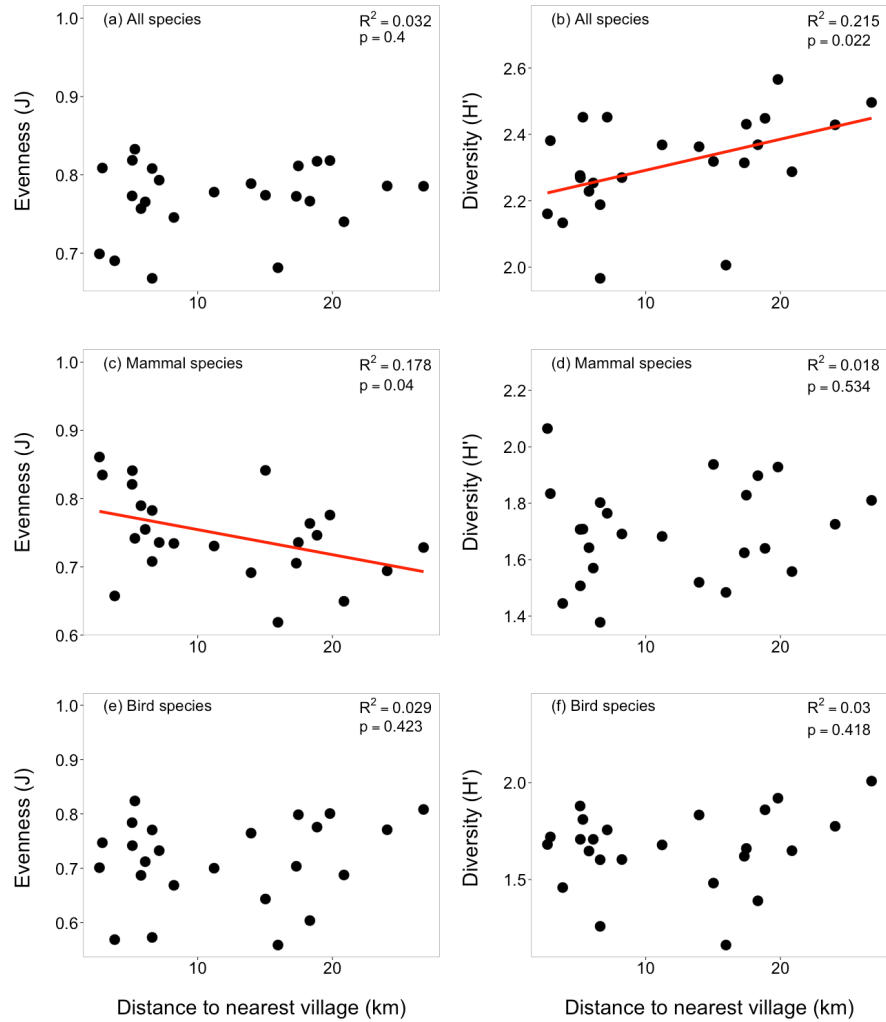
Figure S3. Evenness and diversity in relation to distance from the nearest village for all species, mammal species, and bird species in the Ivindo landscape. Distance to the nearest village is an indicator of hunting pressure, with hunting decreasing with increasing distance from the village. (a) $F_{1,22} = 0.738$, (b) $F_{1,22} = 6.035$, (c) $F_{1,22} = 4.766$, (d) $F_{1,22} = 0.399$, (e) $F_{1,22} = 0.667$, (f) $F_{1,22} = 0.681$.

74 **Table S3.** SIMPER results comparing near and far distance categories. The species shown here
75 contribute the most to the differences seen in community composition (see Fig. 3).
76

| Animal Community	Species	Average Abundance		Average Dissimilarity	Contribution %	Cumulative %
		Near	Far			
Mammals	Mustached monkey	21.05	3.97	9.01	17.37	17.37
	Grey-cheeked mangabey	5.96	18.57	7.31	14.09	31.46
	White-nosed guenon	24.9	34.16	7.25	13.96	45.42
	Other squirrels	16.54	4.64	6.44	12.41	57.83
	Crowned guenon	14.48	14.98	6.14	11.84	69.67
	Red river hog	1.9	8.21	4.08	7.86	77.52
	Chimpanzee	2	6.55	3.55	6.84	84.36
Birds	African grey parrot	23.6	36.49	7.56	22.79	22.79
	Black-casqued hornbill	39.05	25.96	7.28	21.96	44.75
	Red-billed dwarf hornbill	3.48	11.56	4.24	12.78	57.53
	Piping hornbill	10.61	8.79	3.33	10.03	67.57
	Blue-plantain eater	7.95	3.32	3	9.05	76.62
	White-thighed hornbill	4.65	2.43	2.03	6.12	82.74
All Species	Black-casqued hornbill	27.26	11.97	7.78	16.31	16.31
	White-nosed guenon	7.6	18.47	5.69	11.94	28.25
	Grey-cheeked mangabey	1.88	9.99	4.28	8.97	37.23
	Crowned guenon	4.65	9.01	3.87	8.12	45.34
	African grey parrot	16.61	16.57	3.73	7.83	53.17
	Piping hornbill	7.69	4.12	2.67	5.61	58.78
	Mustached monkey	6.55	2.18	2.64	5.53	64.3
	Red river hog	0.34	4.83	2.37	4.96	69.27
Functional Groups	Bird	70.41	45.07	12.78	43.92	43.92
	Monkey	22.59	39.98	9.79	33.64	77.55
	Ungulate	1.5	7.65	3.09	10.61	88.16
	Ape	0.64	3.92	1.88	6.44	94.6

77
78

79 **Table S4.** The general linear model results for the six taxonomic guilds of the vertebrate
80 community with eight environmental variables. Note that the best predictor of each taxonomic
81 guild abundance except elephants was always distance to village, a proxy for hunting pressure.
82 Relative abundances of birds and rodents are higher near villages, while relative abundances of
83 apes, monkeys and ungulates are higher farther away from villages.
84

Environmental Variable	df	Birds F	Birds P	Birds R^2	Monkeys F	Monkeys P	Monkeys R^2	Apes F	Apes P	Apes R^2
Dist. to nearest village	1, 22	**29.74**	**<0.001**	**0.575**	**12.09**	**0.002**	**0.355**	**9.68**	**0.005**	**0.306**
Size of nearest village	1, 22	0.94	0.343	0.041	2.17	0.155	0.090	<0.001	0.948	<0.001
No. of tree species	1, 22	**4.40**	**0.048**	**0.167**	3.93	0.060	0.152	0.00	0.988	0.000
No. of tree stems	1, 22	1.41	0.247	0.060	2.55	0.125	0.104	0.11	0.740	0.005
Tree DBH	1, 22	1.82	0.191	0.076	2.18	0.155	0.090	0.84	0.369	0.037
No. of lianas	1, 22	0.13	0.725	0.006	0.00	0.975	0.000	0.94	0.342	0.041
Understory cover	1, 22	1.53	0.229	0.065	2.39	0.137	0.098	**5.54**	**0.028**	**0.201**
Canopy cover	1, 22	2.54	0.125	0.104	2.95	0.100	0.118	1.95	0.176	0.081

Environmental Variable	df	Elephants F	Elephants P	Elephants R^2	Ungulates F	Ungulates P	Ungulates R^2	Rodents F	Rodents P	Rodents R^2
Dist. to nearest village	1, 22	1.20	0.285	0.052	**12.77**	**0.002**	**0.367**	**4.98**	**0.036**	**0.185**
Size of nearest village	1, 22	1.85	0.188	0.078	0.28	0.600	0.013	2.20	0.152	0.091
No. of tree species	1, 22	2.56	0.124	0.104	2.76	0.111	0.111	0.03	0.864	0.001
No. of tree stems	1, 22	0.65	0.430	0.029	0.01	0.912	0.001	0.16	0.691	0.007
Tree DBH	1, 22	0.58	0.458	0.025	0.05	0.822	0.002	2.72	0.113	0.110
No. of lianas	1, 22	3.21	0.087	0.128	0.38	0.545	0.017	0.46	0.505	0.020
Understory cover	1, 22	0.06	0.813	0.003	1.31	0.264	0.056	1.95	0.176	0.082
Canopy cover	1, 22	0.00	0.962	0.000	0.03	0.862	0.001	0.42	0.526	0.019

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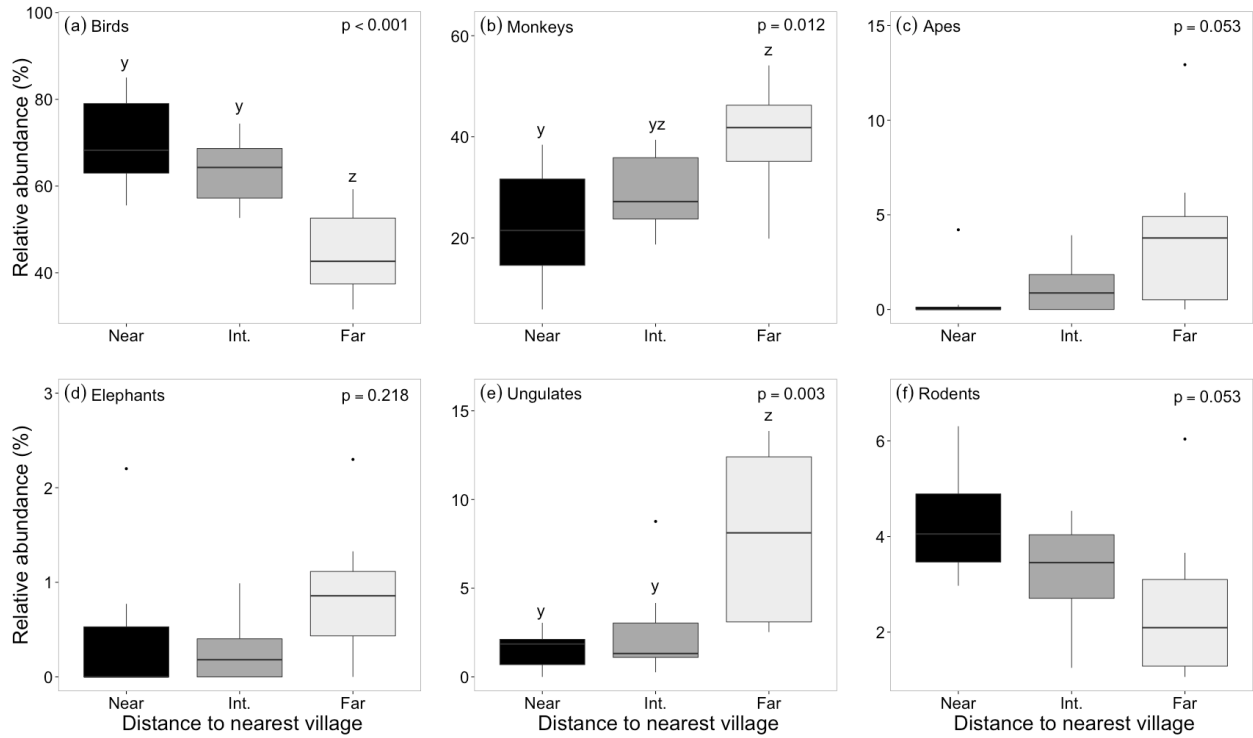
Figure S4. Effects of distance from nearest village on the relative abundance of taxonomic guilds of the Ivindo landscape. Carnivores were not included in the figures as only two individuals were sighted. Letters denote significant differences at $p<0.05$ (Tukey Tests). (a) $F_{2,21}$ = 13.780, (b) $F_{2,21}$ = 5.751, (c) $F_{2,21}$ = 3.382, (d) $F_{2,21}$ = 1.642, (e) $F_{2,21}$ = 7.523, (f) $F_{2,21}$ = 3.387.

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