Effect of protection status on mammal richness and abundance in Afromontane forests of the Udzungwa Mountains, Tanzania

Abstract

The effectiveness of Protected Areas (PAs) in reducing hunting pressure on mammal populations in tropical forests has rarely been examined at a community-wide level. In African forests, commercial and subsistence hunting are widespread, but assessments of mammal abundance and distribution patterns are often lacking. We investigated patterns of occupancy and abundance for 27 species of medium- to large-bodied mammals (>2 kg) within Tanzania's Udzungwa Mountains Afromontane forests, a global biodiversity hotspot. We sampled 22 forest sites within 10 forests under varying degrees of protection, elevation, distance to extractive communities, and levels of law enforcement. We sampled 251.7 km of recce line transects during dry seasons (July-November) between September 2007 and July 2010. We found a strong positive effect of protection status on species richness and on encounter rates of the most commonly encountered species. Consistent with the levels of resources and enforcement within each PA category, there was a significant progression in species richness and abundance from Forest Reserves through Nature Reserves to sites within Udzungwa Mountains National Park. Protective status closely reflected levels of disturbance. Snaring activity, and distance to ranger posts were identified as significant predictors of overall species richness and encounter rates for mammal species, including endemics. The species-area relationship for our study species was found to be largely overridden by levels of protection. Our findings demonstrate PA effectiveness in Afromontane forests and reinforce concerns over hunting pressures particularly the threat posed by snares.

Keywords:

Biodiversity hotspot, Hunting pressure, Protected area, Tropical forest

1. Introduction

Forest mammal populations are threatened by habitat loss and hunting pressure (Brodie et al., 2015; Fa and Brown, 2009), which are often synergistically linked (Peres, 2001). Larger-bodied animals are preferred prey for hunters (Harrison, 2011), and are highly vulnerable to human activities (Cardillo et al., 2005). Unsustainable hunting pressure on medium- to large-bodied vertebrate populations, as envisioned by the 'empty forest' concept (Redford, 1992), has potentially severe impacts on key ecosystem processes (Estes et al., 2011). Negatively impacted processes include seed dispersal (Wright et al., 2007), nutrient cycling (Nichols et al., 2009) and carbon storage (Bello et al., 2015). Protecting charismatic species and Protected Areas (PAs) have been the main tools employed to mitigate these threats but there remains much debate about their effectiveness in conserving biodiversity and ecosystem function (Caro et al., 2009; Geldmann et al., 2013; Le Saout et al., 2013; Watson et al., 2014). Assessment of PA effectiveness requires accurate information on species distributions and abundance in relation to anthropogenic pressures (e.g. hunting) and underlying environmental contexts. In mega-diverse regions, such as tropical forests, such information is hard to acquire (Cayuela et al., 2009) and there remains a shortage of multi-taxa surveys for larger-bodied terrestrial vertebrates in tropical Africa (Gardner et al., 2007).

Bushmeat hunting is important in rural African life (Abernethy et al., 2013; Knapp et al., 2017), and unsustainable harvests from mammal communities in African forests take a heavy toll on forest mammal populations (Fa and Brown, 2009), leading to local extinctions (Maisels et al., 2001; Milner-Gulland and Bennett, 2003) and an overall decline in many large-bodied mammal species, even inside protected areas (Craigie et al., 2010). The impact of hunting is well documented in West and Central Africa (Bowen-Jones et al., 2003; Fa et al., 2003) but has received less attention in East Africa. Studies in this region have focussed largely on open habitats such as the Serengeti (Lindsey et al., 2013). Yet, forests such as those within the Eastern Arc Mountains (EAM) support exceptional levels of species richness and endemism (Burgess et al., 2007; Myers et al., 2000; Rovero et al., 2014). Except for diurnal primates (Rovero et al., 2012, 2009, 2006), there has been limited quantitative assessment of the distribution, abundance or conservation status of large mammals across the critically important Udzungwa Mountains in Tanzania (Dinesen et al., 2001; Rovero et al., 2017). This mountain range, a major component of the Eastern Arc, spanning variations in altitudinal range, habitat type and forest area, contained within three categories of protective status: i) Forest Reserves (FR), with the lowest level of protection, permit regulated use of forest products and services e.g. medicinal plants, fungi, honey, some timber and wild animals; ii) Nature Reserves (NR) with more limited permitted use and a higher focus on tourism; and iii) the Udzungwa Mountains National Park (NP), which is strictly protected from extractive uses and devoted to tourism and nature conservation. This study assesses variation across the Udzungwa Mountains in the presence and relative density of medium- to large-bodied mammals.

Here, we evaluate environmental and anthropogenic factors, particularly PA status and hunting pressure, as predictors of mammal richness and abundance. We test the prediction that mammal species richness and abundance are higher in more strictly protected PAs. Variables related to habitat loss from deforestation and disturbance from hunting provide an overview of the biodiversity value and current threats to mammal communities in the Udzungwa Mountains. To our knowledge, this study is the first comprehensive assessment of the predictors of mammal distribution and abundance in eastern Afromontane forests.

2. Materials and methods

2.1. Study area

Our study was conducted within the Udzungwa Mountains in south-central Tanzania (7°15’S, 36°15’E), encompassing an area of 6,500 km^2 (Figure A1). This area contains PAs and village land (a mosaic of houses, roads, farmland, and plantations). There are three levels of legal protection in the Udzungwa mountains: Forest Reserves (FR); one (at the time of study) Nature Reserve (NR), with Kilombero NR formed from the merger of two FRs in 2007; and one National Park (NP), with the Udzungwa Mountains National Park (UMNP) formed from all or part of four existing FRs in 1992. The Uzungwa Scarp FR was upgraded to a NR in 2016 after this study concluded.

We selected 22 sites in 10 forests to cover all levels of protection and as wide a range of altitudes (Figure A2), topographies, habitat types, and human population density, as possible. All forests included in this study are within 7 km of human settlements. There are approximately 60 villages (20 administrative wards) within the districts of Kilombero (Morogoro Region) and Kilolo (Iringa Region), which contain the Udzungwa Mountains. Based on national censuses in 2002 and 2012 (Tanzania NBS, 2018) and assuming a mean annual national population growth rate of 2.8% (World Bank Group, 2017) the population at the time of study (2007-2010) was between 400-500,000 people.

2.2. Landscape, climate and habitat variables

The Udzungwa Mountains have a tropical, moist climate (Figure A3) and a single long dry season from May to November. Peak rainfall occurs in March and April. Mean annual rainfall ranges from 900 mm on the western plateau to 1,500-2,500 on the south-east-facing scarp. There is a substantial mist effect above 1,500 m. Temperatures vary with altitudinal gradient; seasonal maximums occur in December-January and minimums in June-July. We obtained climate variables for each of the 22 georeferenced sites: total annual precipitation (Tropical Rainfall Measuring Mission, TRMM) (Huffman et al., 2007), mean, minimum and maximum temperatures, and annual moisture index (AMI) (WorldClim) (Hijmans et al., 2005).

The area of each forest was determined from Landsat imagery (Landsat ETM1; Global Land Cover Facility/US Geological Survey; Oct 25 and Nov 1, 1999; Paths 167–8; Rows 65–6), with subsequent slight adjustments to polygons for two forests (Mwanihana and Nyanganie) based on a combination of ground-truthing, Google Earth, and aerial photos (WCS Flight Program). We determined altitude, slope and aspect for a circular buffer of radius 1 km around the centre of each site, using the 1 arc-second (~30 m) global SRTM DEM (USGS) in QGIS (version 2.14.22). We also calculated the shortest distance to the forest edge from the centre of each site using QGIS.

Habitats in the Udzungwa Mountains (Table A1) include altered village land, grassland and wooded grassland (WG; altitude range 300-1,500 m), woodland (W; 300-1,200 m), lowland forest (LF; 300-

800 m), sub-montane forest (SF; 800-1,400 m), and montane forest (MF, 1,400-2,600 m) (Rovero and De Luca, 2007). We only sampled forest (LF, SF and MF). Tree and pole density (within a 5 m radius), estimated canopy cover and height, and visibility i.e. the maximum distance to detectable mammal sign from the transect were recorded every 200 or 400 m along transects (depending on observed heterogeneity). Habitat variables were converted to categorical scales to include three sites with missing data using qualitative observations.

2.3. Anthropogenic variables

We quantified anthropogenic pressure from a range of variables: Wood extraction measured by the encounter rate (km^{-1}) of cut trees or poles within 5 m each side of the transect line; Snares (hunting pressure) also recorded as an encounter rate (km^{-1}) within 5 m each side of the transect line; Hunting pressure index (a 1-4 scale) determined by i) observations of people carrying meat, ii) snares and snared animals encountered off the transect but in the general area, iii) gunshots heard while walking transects or camping, iv) evidence of hunters' camps, and v) informal interviews with local guides and villagers. The distances to the nearest village, road and ranger post were calculated using QGIS (version 1.7.4). The protective status of each site was defined by the three categories of legal designation i) Forest Reserves, ii) Nature Reserve (KNR), or National Park (UMNP) (Table A2). Protection status was ordinal, with Forest Reserve being the lowest and National Park the highest protective designation (Dinesen et al., 2001; Nielsen, 2011; Rovero et al., 2012). All snares were removed and handed to the relevant forest managers, noting the size and type of snare (wire, rope or gin trap), and the targeted taxon (usually bushpig, duikers, or giant pouched rat).

2.4. Mammal surveys

We surveyed each site for medium- to large-bodied mammals (>2kg) between September 2007 and July 2010. We sampled only during dry seasons, (July to November), to minimise effects of seasonal variation in local abundance or differential rates of dung decay (Nowak et al., 2009). Surveys comprised diurnal line transects recording i) direct encounters (seen or heard) and ii) tracks and signs (footprints, feeding signs, dung, and burrows) (Kingdon, 2015). Sign surveys can be an effective method for monitoring vertebrates, particularly in hunted areas where under-detection can be common (Fragoso et al., 2016). Transects used a 'closed-circuit' recce design (Buckland et al., 2001; Waltert et al., 2008), where three approximately 1-km transects were completed per day in the shape of a triangle. This design is efficient in returning to the same location at the end of the day, and also reduces the potential biases of a single linear transect following an environmental gradient. Transects were walked at a slow (400 m/hr) pace between 7 am and 6 pm, measuring the transect by a hipchain which acts as the centre line for measuring perpendicular distances. We surveyed a total of 247 transects (251 km) across all sites (6-20 transects per site) (Table A2).

Mammals were identified from tracks and signs with the assistance of experienced local trackers. Field identification of forest antelopes from dung is unreliable, even for experienced observers (Bowkett et al., 2014, 2013, 2009). Observations of forest antelope dung were therefore pooled at the guild level. For other cases of uncertain identification e.g. medium-sized carnivores (mongooses and genets), dung were measured, photographed and checked against field guide books (Stuart and Stuart, 2000); <5% of cases were classified as 'unknown'.

2.5. Data analyses

Species occurrence and total richness per site were determined by the combination of direct and indirect (tracks and signs). As a measure of relative abundance, we used DISTANCE software (v6.0) to calculate encounter rates (km^{-1}) and density (km^{-2}) for mammal species along transects using indirect observations only. Indirect observations are more reliable in tropical forests where visibility is typically low and variable (Breuer and Breuer-Ndoundou Hockemba, 2012). We used encounters of dung piles for antelope (Table A3), buffalo (*Syncerus caffer*), bushpig (*Potamochoerus larvatus*), elephant (*Loxodonta africana*), and eastern tree hyrax (*Dendrohyrax arboreus*), and encounters of burrows for aardvark (*Orycteropus afer*). We measured the perpendicular distance from the centre of each dung pile/burrow to the transect line. Primates and carnivores were excluded from encounter rate analyses because of low samples sizes.

We used a GLM to model variation in mammal species richness in relation to climate, habitat, landscape and anthropogenic variables. We reduced the full list of variables measured based on co-linearity and biological relevance to produce a set of five variables for our global model: Distance to nearest village; Distance to ranger post; Forest area; Mean altitude; and Mean slope. We ranked all combinations of first-order models using Akaike Information Criterion for small sample sizes (AICc) values, averaging all models with ΔAICc < 2.0 from the best model, which were considered to be equivalent (Anderson, 2008). We also modelled variation in encounter rates for the most frequently observed species. We did not include PA status as a variable in GLMs but assessed its link to our responses and all other variables separately using one-way ANOVAs and Tukey's pair-wise comparisons. Finally, we performed cluster analyses and non-metric multidimensional scaling (NMDS), using a Bray-Curtis presence/absence similarity matrix to examine multivariate patterns in community composition across sites; we used an ANOSIM test to assess similarity between communities according to PA status, and a General Additive Model (GAM) to fit a surface of environmental parameters to the ordination. All analyses were conducted in R (R Core Team, 2016), using the packages 'glmulti' (Calcagno and Mazancourt, 2010), 'MuMIn' (Bartoń, 2016), and 'vegan' (Oksanen et al., 2013).

3. Results

3.1. Landscape, climate and habitat variables

The altitudinal gradient across sites (n = 22) spanned 346-2199 masl and slope varied between 7 and 23° (mean ± SD = 17.5 ± 4.4°) but sites were relatively uniform in mean aspect, with a south, south-south-east or south-south-west direction (mean ± SD = 175.8 ± 24.3°). Mean and variance of slope were positively correlated with each other (Pearson's: $r = 0.81$, $p < 0.001$) but not with altitude. We therefore excluded aspect and slope variance as variables in our models, retaining mean altitude and slope as an indicator of the complexity of topography within a site. Forest area ranged from 5 (Iwonde) to 522 km^2 (Matundu), with site distance to edge varying from 0.47 to 3.07 km. Distance to forest edge was positively correlated with forest area ($r = 0.48$, $p < 0.05$).

Variation in altitude across sites (Figure A2) is largely responsible for differences in mean climatic conditions across the year (Figure A3). Thus, mean altitude had a significant negative correlation with mean, minimum and maximum temperature ($r = -0.98$ – -0.99, $p < 0.001$), and a positive correlation with AMI ($r = 0.48$, $p < 0.05$). Mean temperature varied between 15.4 and 25.1° (mean ± SD = 19.7 ± 2.9°), with mean annual rainfall between 849 and 2236 mm (mean ± SD = 1455 ± 417 mm). Total annual precipitation was unimodal, peaking at intermediate altitude. AMI was significantly correlated with all other climatic variables, including a positive relationship with rainfall ($r = 0.84$, $p < 0.001$) and negative relationship with mean temperature ($r = -0.49$, $p < 0.05$).

Habitat variables were also influenced by altitude, including significant positive correlations between altitude and both tree (Spearman's: $r_s = 0.63$, $p < 0.01$) and pole density ($r_s = 0.48$, $p < 0.05$). Canopy cover and height were not significantly correlated with altitude, despite plant community transitions with increasing elevation (from deciduous woodland to lowland forest to montane forests) (Table A1). Canopy cover was negatively correlated with forest area ($r_s = -0.62$, $p < 0.01$). Larger forests often had natural canopy openings and temporary or permanent clearings caused by elephants, selective logging or agriculture. Visibility, an inverse measure of herb layer density, was positively correlated with canopy height ($r = 0.45$, $p < 0.05$), although all surveyed forest sites had relatively low vegetation biomass at ground level. There were no significant differences in any landscape, climate or habitat variables between protected area categories (Figure A4).

3.2. Anthropogenic variables

Measures of anthropogenic disturbance were closely related with each other. There was a significant positive correlation of our qualitative index of hunting pressure with the detection of snares ($r_s = 0.73$, $p < 0.001$) and wood extraction ($r_s = 0.69$, $p < 0.001$). The cut pole encounter rate was not correlated with tree or pole density. Hunting pressure was higher with increased proximity to villages (r_s = -0.48, $p < 0.05$) and with greater distance from forest edges (r_s = 0.60, $p < 0.01$) and from ranger posts (r_s = 0.42, $p < 0.05$). The effect of distance to ranger posts was very clear for snares (r = 0.73, $p < 0.001$). Distance to the nearest road, and landscape variables including altitude, were not significantly correlated to any measure of disturbance. PA status explained much of the variation in anthropogenic disturbance. Hunting with snares and with guns was significantly higher in Forest Reserves with low-level protection (Snares: ANOVA, $F_{2,19}$ = 5.99, $p < 0.01$; Guns: $F_{2,19}$ = 10.82, $p < 0.001$), compared to the Nature Reserve and the National Park with higher levels of protection (Figure A4). There were no significant differences between PA categories in distance to nearest road or village but Forest Reserve sites were significantly further from the nearest ranger post ($F_{2,19}$ = 14.49, $p < 0.001$; Figure A4).

3.3. Mammal richness and abundance

We recorded the presence of 27 medium- to large-bodied mammal species from our 251 km of line transect surveys across 22 sites (Table A3). Species richness (mean ± SD = 14.7 ± 4.85) ranged from 7 species at Matundu W1 (NR) to 22 species at Ng'ung'umbi (NP). Distribution across sites also varied greatly (mean ± SD = 12.0 ± 6.84); Angolan colobus (*Colobus angolensis*) and Harvey's duiker (*Cephalophus natalensis harveyi*) were found at all 22 sites, whereas kipunji (*Rungwecebus kipunji*) and hippopotamus (*Hippopotamus amphibius*) were found at only one site each (Vikongwa and Matundu Ruipa, respectively).

Model averaging, using the reduced set of five predictor variables, showed a negative effect on species richness with distance to the nearest ranger patrol post (Figure 1). Altitude, slope, distance to the nearest village, and forest area were relatively unimportant in predicting species richness. Species richness was highest inside the National Park, intermediate in Nature Reserves, and lowest in Forest Reserves (ANOVA: $F_{2,19}$ = 8.88, $P < 0.01$; Figure 2a), consistent with levels of legal protection. Distance to the nearest village, a general disturbance variable encompassing pressure from snaring and other forms of hunting, and habitat disturbance through tree felling, predicted presence or absence of the five largest species (aardvark, buffalo, bushbuck [*Tragelaphus scriptus*], elephant and crested porcupine [*Hystrix cristata*]), but not the three smallest (blue duiker [*Philantomba monticola*], eastern tree hyrax and giant pouched rat [*Cricetomys gambianus*]). Distance to nearest ranger post significantly predicted mammal species richness across all body sizes (Figure 2b).

For species where encounter rates could be calculated, PA status had a variable effect (Figure 3). There was no significant effect of PA status on encounter rates of aardvark, antelope, or tree hyrax. Encounter rates for buffalo (ANOVA: $F_{2,19} = 5.90$, $P < 0.05$) and elephant ($F_{2,19} = 9.73$, $P < 0.01$) were significantly higher within Udzungwa Mountain NP sites than either NR or FR sites. Bushpig encounter rates were significantly higher in both NR and NP sites than in Forest Reserves ($F_{2,19} = 11.73$, $P < 0.001$). Model averaging showed a negative effect of distance to the nearest ranger post on encounter rates for antelope, bushpig, and hyrax, but not for aardvark, buffalo and elephant (Figure A5, Table A4).

The three PA designations supported distinct mammal communities based on presence/absence data, with FR communities nested within NR communities, which were in turn nested within NP communities (ANOSIM: $R = 0.185$, $p < 0.05$; Figure A6a). Elephants were present at all NP sites, but only four out of seven NR, and three out of eight FR sites. Leopard (*Panthera pardus*) were present at all NP sites, but only four NR and two FR sites. Buffalo were present at all but one NP sites, but only four NR and one FR sites. Bushbuck were present at all but one NP sites, but only four NR and three FR sites. African civet (*Civettictis civetta*), crested porcupine, hippopotamus, kipunji, lion (*P. leo*), and spotted hyena (*Crocuta crocuta*) were all absent from Forest Reserves, with presence of hippopotamus and lion only recorded within the National Park. Distance to the nearest ranger patrol post was the only variable significantly related to community composition across sites ($R^2 = 0.51$, $p = 0.004$; Figure A6b).

4. Discussion

4.1. Drivers of mammal abundance and richness

The geologic age, biogeographical isolation, natural fragmentation and patchy distribution of higher altitude forests in Eastern Arc (Lovett and Wasser, 1993) enabled the evolution of endemics. However, size, isolation and patchy distribution also makes forests vulnerable to local extinctions and loss of biodiversity (Newmark, 2002). Mammal populations are especially vulnerable to extirpation in tropical forests (Redford, 1992) and populations in isolated fragments, such as those in our study, are more vulnerable to hunting (Peres, 2001). Hunting has been and remains widespread in the Udzungwas (Hegerl et al., 2017; Nielsen, 2006; Topp-Jørgensen et al., 2009) and hunting pressure outside the National Park and Nature Reserves is reported to be increasing over time (De Luca and Mpunga, 2005; Rovero et al., 2012; Topp-Jørgensen et al., 2009).

In our study, hunting pressure was the best predictor of mammal abundance and richness. Ranger post proximity predicted encounter rates for heavily hunted antelope, bushpig and hyrax, and snare density was significantly and negatively related to abundance of several species. Bushpig encounter rates were negatively affected by human disturbance, probably due to snares. Forest antelopes were also negatively affected by snaring, leading to the absence or low density of certain species (e.g. Endangered Abbott's duiker, *Cephalophus spadix*) in poorly protected forests. Wherever there is more snaring, there is also a higher occurrence of hunting with guns and dogs.

Forest area is important in relation to the species-area relationship (MacArthur and Wilson, 1967) and has been identified as a contributor to primate species richness in Udzungwa, in relation to habitat heterogeneity (Marshall et al., 2009). Across a wider range of species, effects of patch area were overridden by the level of protection from hunting pressure. Hyrax was the only species assessed for which forest area was a significant factor in determining encounter rates. The lack of species-area relationships is striking, although it is important to recognise that not all mammal species we recorded are forest interior specialists.

4.2. Species of conservation concern

The Udzungwas hold endemic and other species of particular conservation concern. These include: the Tanzania-endemic Abbott's duiker (Bowkett et al., 2014; Jones and Bowkett, 2012; Rovero et al., 2005); the endemic subspecies of the Zanzibar galago, *Galago zanzibaricus udzungwensis*, and at least one undescribed galago (A. Perkin, pers. comm.); two endemic monkeys, the Sanje mangabey and Udzungwa red colobus; and the Kipunji monkey a near-endemic genus and species (Jones et al, 2005; Davenport et al, 2006).

Conservation action frequently focuses on charismatic, endangered and/or endemic species (Morse-Jones et al., 2012) but attention is increasingly focussed on the importance of biodiversity in terms of ecosystem function, Fruits in tropical forests are important food resources and many plants rely upon frugivorous mammals for seed dispersal (Fleming and Kress, 2011; Howe and Smallwood, 1982). Within African forest systems, rodents (Beaune et al., 2013a; Nyiramana et al., 2011), bushpig (Beaune et al., 2012), primates (Chapman et al., 1994) and elephants (Beaune et al., 2013b; Campos-Arceiz and Blake, 2011) are all important seed dispersers. Preventing declines of mammal populations within remaining forests may be crucial in arresting habitat loss and biodiversity decline (Terborgh et al., 2008; Wright et al., 2007) as well as maintaining carbon stocks (Bello et al., 2015; Peres et al., 2016).

Other behavioural and ecological factors such as habitat preferences are also important. Forest interior species may be differentially affected by hunting pressure compared to species common in open habitats. Similarly, smaller-bodied species are typically less affected (or at least not extirpated) by hunting pressure (Cardillo et al., 2005). We found that distance to ranger posts – which correlates strongly with levels of snaring – did not significantly predict the presence of larger, wide ranging mammals (buffalo, elephant), or the nocturnal aardvark which may be subject to lower hunting pressure by local people. The relationships between body size, biology and behavioural ecology are likely to influence responses to, and tolerance of, the different types of disturbance they experience (Davidson et al., 2009; Laurance et al., 2006; Lawes et al., 2000). Our results will hopefully contribute to behaviourally and ecologically appropriate conservation initiative design.

4.3. Conservation management implications

Protected Areas are the principle tool for global biodiversity conservation but PA effectiveness has been the subject of scrutiny and debate (Bruner et al., 2001; Craigie et al., 2010; Geldmann et al., 2018, 2013; Nagendra, 2008). Our results support the effectiveness of PAs as a conservation strategy. National Parks are most effective at maintaining wild mammal populations, while biodiversity remains affected by hunting in reserves with lower protective status. There is a clear hierarchical pattern in relation to PA status, with Nature Reserves intermediary in their effectiveness and Forest Reserves providing the lowest protection. It is possible that hunting is at a higher level in the Forest Reserves because more people are allowed inside for limited legal resource extraction, though our data are not able to confirm this. Our findings are however consistent with the level of resources and law enforcement available (Geldmann et al., 2018; Keane et al., 2008) – National Parks have more and better equipped rangers and infrastructure – and further supports evidence for the effectiveness of East African PAs in preventing forest loss (Green et al. 2013; Pfeifer et al., 2012).

The strongest predictor of large mammal species richness in Udzungwa Mountain forests was distance to nearest ranger post. This is evidence for law enforcement effectiveness against exploitation of mammal populations. (Caro et al., 1998; Hilborn et al., 2006). Our results are consistent with studies showing greater richness and abundance of large mammal species in Tanzanian national parks than in game reserves (Stoner et al., 2007). Our models addressed possible bias from area and topography differences by the inclusion of environmental variables, describing climate, elevation and forest structure. These variables were not biased across PA status and distance to the nearest ranger patrol post still emerged as the major influence on species richness and on encounter rates. Our findings also illustrate the particular threat posed by snares (Becker et al., 2013; Noss, 1998). Snares are a highly effective but unselective and kill or injure, a wide range of species. Easily and cheaply made (Lindsey et al., 2011), snares are difficult to control, even within PAs. That distance to ranger post was a significant predictor of large mammal presence/absence and species richness, shows that active protection and enforcement are effective means of protecting mammal populations from snares and other forms of hunting.

This study expands evidence of PA effectiveness to the Afromontane forest context and provides an initial baseline for conservation design. However, enforcement alone is unlikely to be sufficient for successful long-term conservation (Challender and MacMillan, 2014). There is clearly a need to consider the wider social setting. An encompassing approach that addresses underlying issues such as poverty reduction, provision of alternative livelihoods and protein sources (Brashares et al., 2011; Lindsey et al., 2011), and environmental education (Keane et al., 2011) is needed, of which PAs will be a critical part.

5. Conclusion

The National Park in the Udzungwa Mountains is significantly more effective in conserving mammals than the Forest Reserves. Hunting pressure, especially the use of snares, has had a negative impact on diversity and richness of larger bodied mammal populations. Megaherbivores and large predators are now largely absent from forest reserves due to hunting and reduction of prey bases. Smaller mammals are affected by human disturbance in terms of density but still persist at most sites. The strong influence of protection level on mammal populations appears to drown out species-area relationships in these forests but, large forests are vital for viable populations of larger mammals. Our results provide an initial baseline for understanding the conservation needs of medium- and large-bodied mammals in the Udzungwas and identifying predictors of animal abundance in forests across fragmented landscapes.

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Figures

Figure 1.

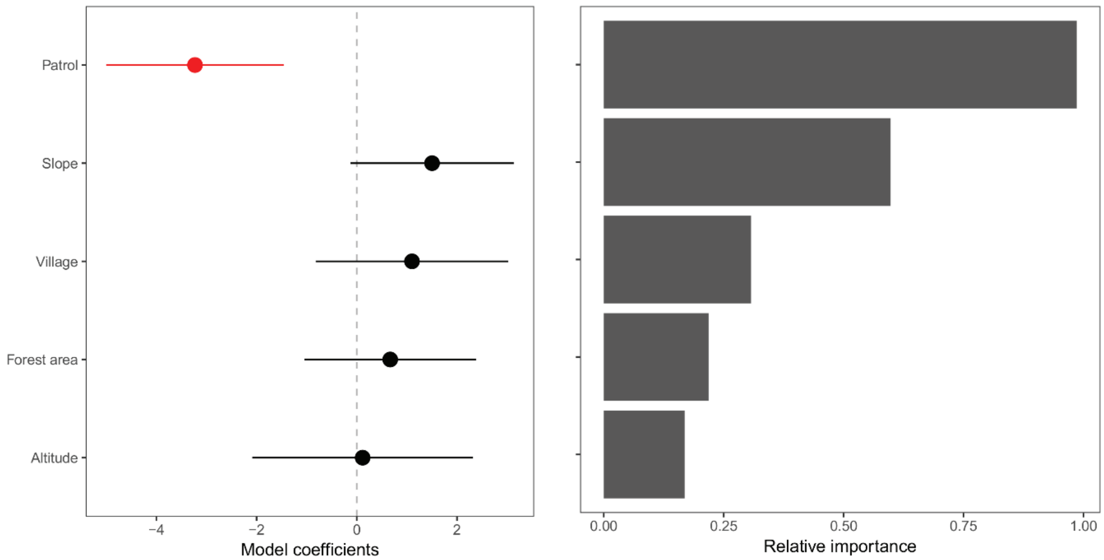

Figure 1. Coefficients and relative importance from model averaging process (all candidate models) for species richness of medium- to large-bodied mammals. Error bars represent 95% confidence intervals.

Figure 2.

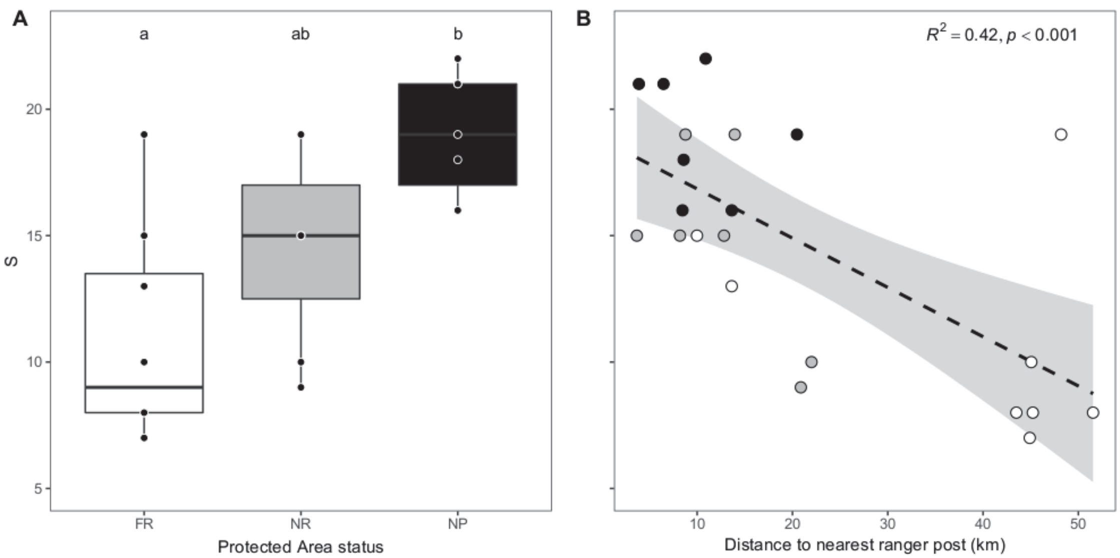

Figure 2. Effectiveness of protection in maintaining mammal species richness (S) as shown by (A) the effect of Protected Area status, and (B) the relationship with distance to the nearest ranger post (km). FR = Forest Reserve (white), NR = Nature Reserve (grey), NP = National Park (black). Letters above boxplots represent Tukey subsets.

Figure 3.

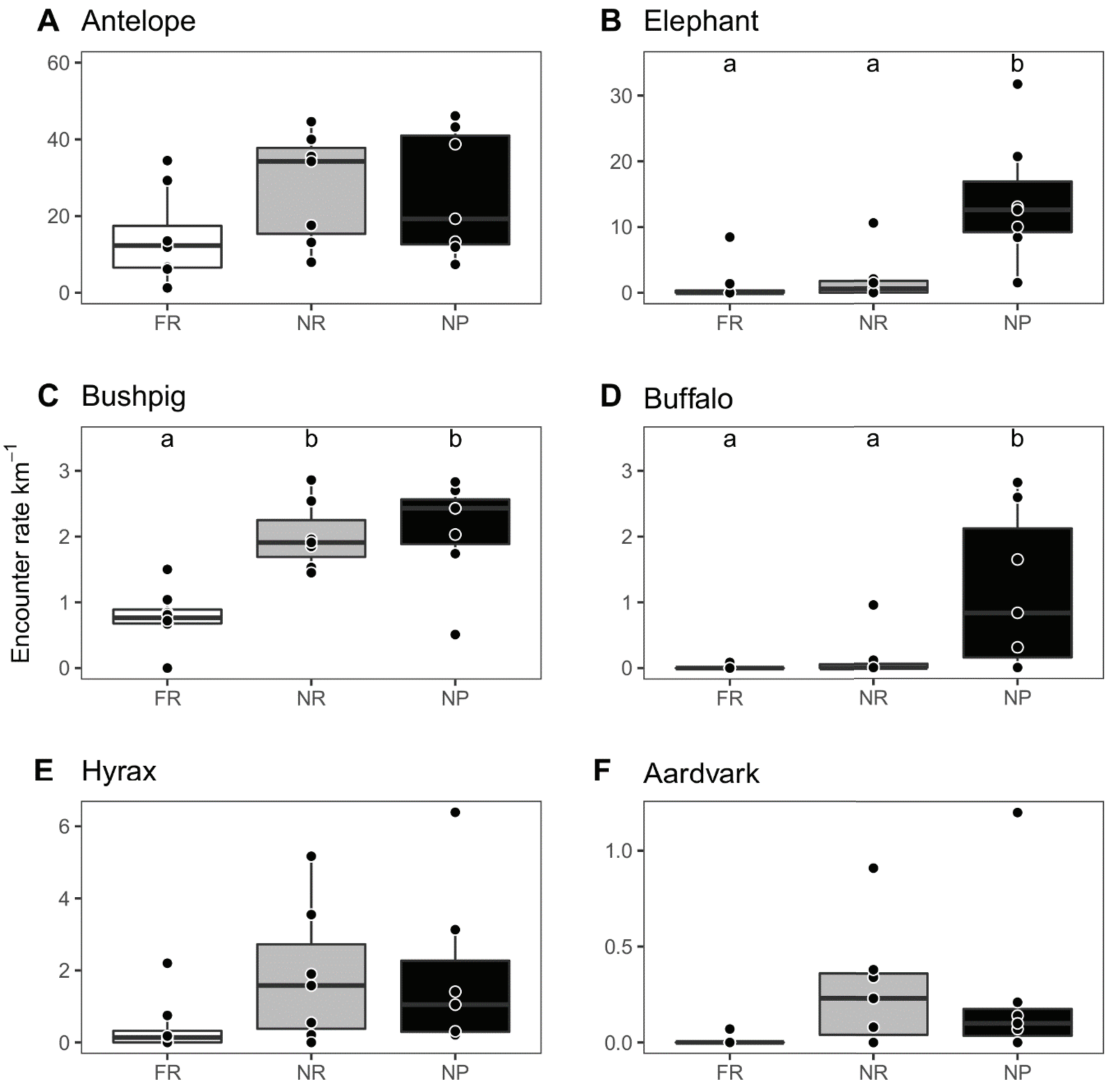

Figure 3. Effect of Protected Area status on mammal species encounter rates (km^{-1}) of (A) antelope, (B) elephant, (C) bushpig, (D) buffalo, (E) hyrax, and (F) aardvark. FR = Forest Reserve (white), NR = Nature Reserve (grey), NP = National Park (black). Letters above boxplots represent Tukey subsets where ANOVA results showed a significant effect of PA status.

Appendix A

Effect of protection status on mammal richness and abundance in Afromontane forests of the Udzungwa Mountains, Tanzania

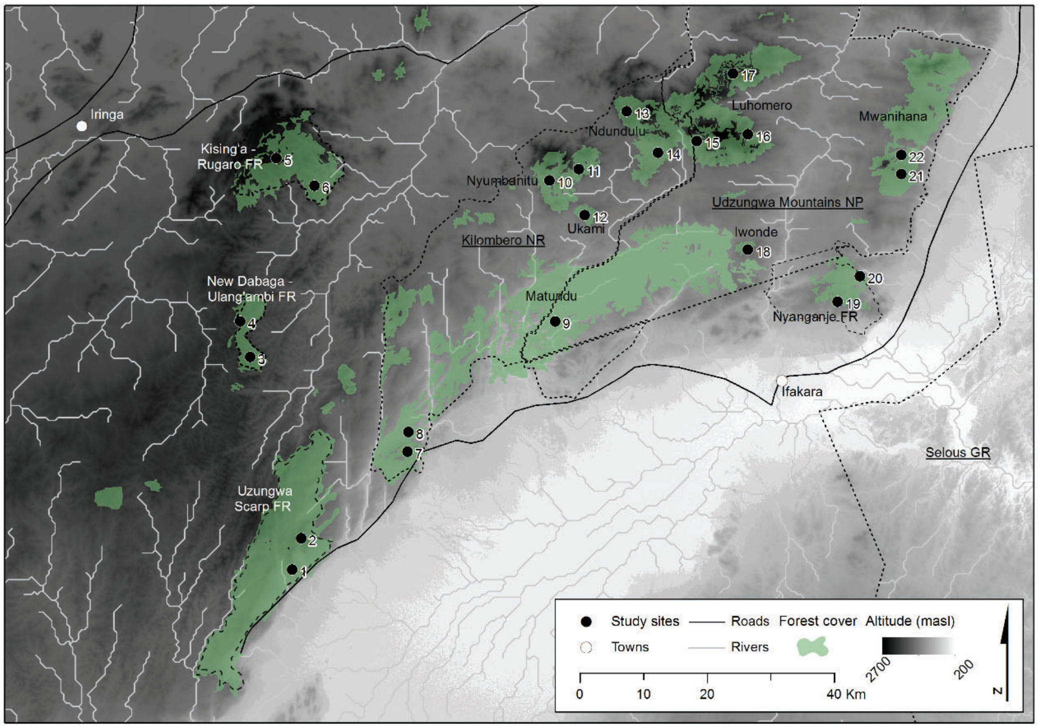

Figure A1. Map of Udzungwa Mountains, showing the ten study forests (Ndundulu and Luhomero being contiguous) and 22 study sites. Dashed lines represent PA boundaries: FR = Forest Reserve; NR = Nature Reserve; NP = National Park; GR = Game Reserve. Forest cover refers to lowland, submontane and montane forest (Table S1). Site codes refer to list in Table A2.

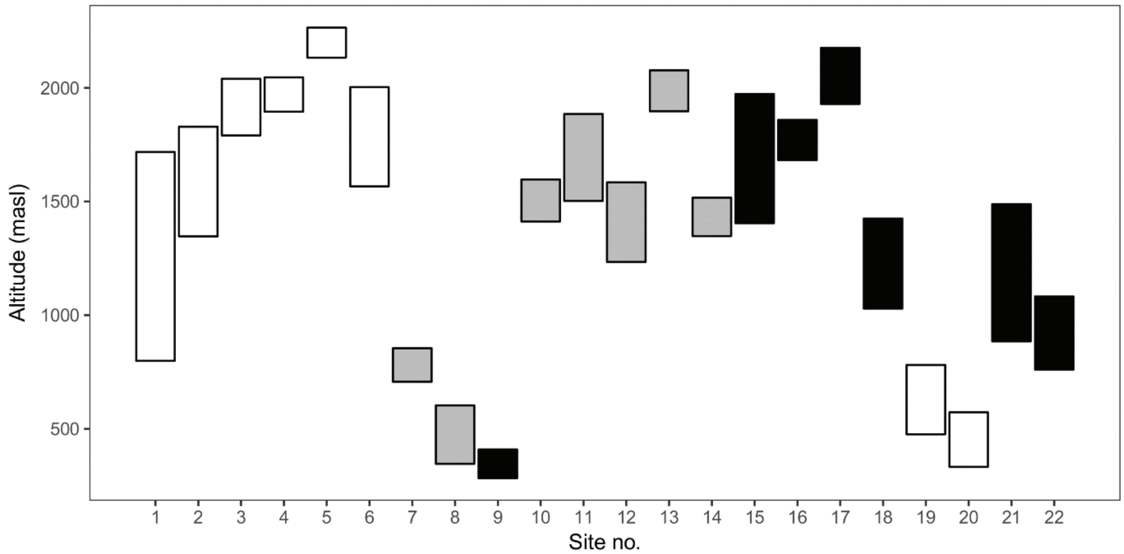

Figure A2. Altitudinal range (masl) of the 22 study sites sampled in the Udzungwa Mountains, Tanzania. FR = Forest Reserve (white), NR = Nature Reserve (grey), NP = National Park (black).

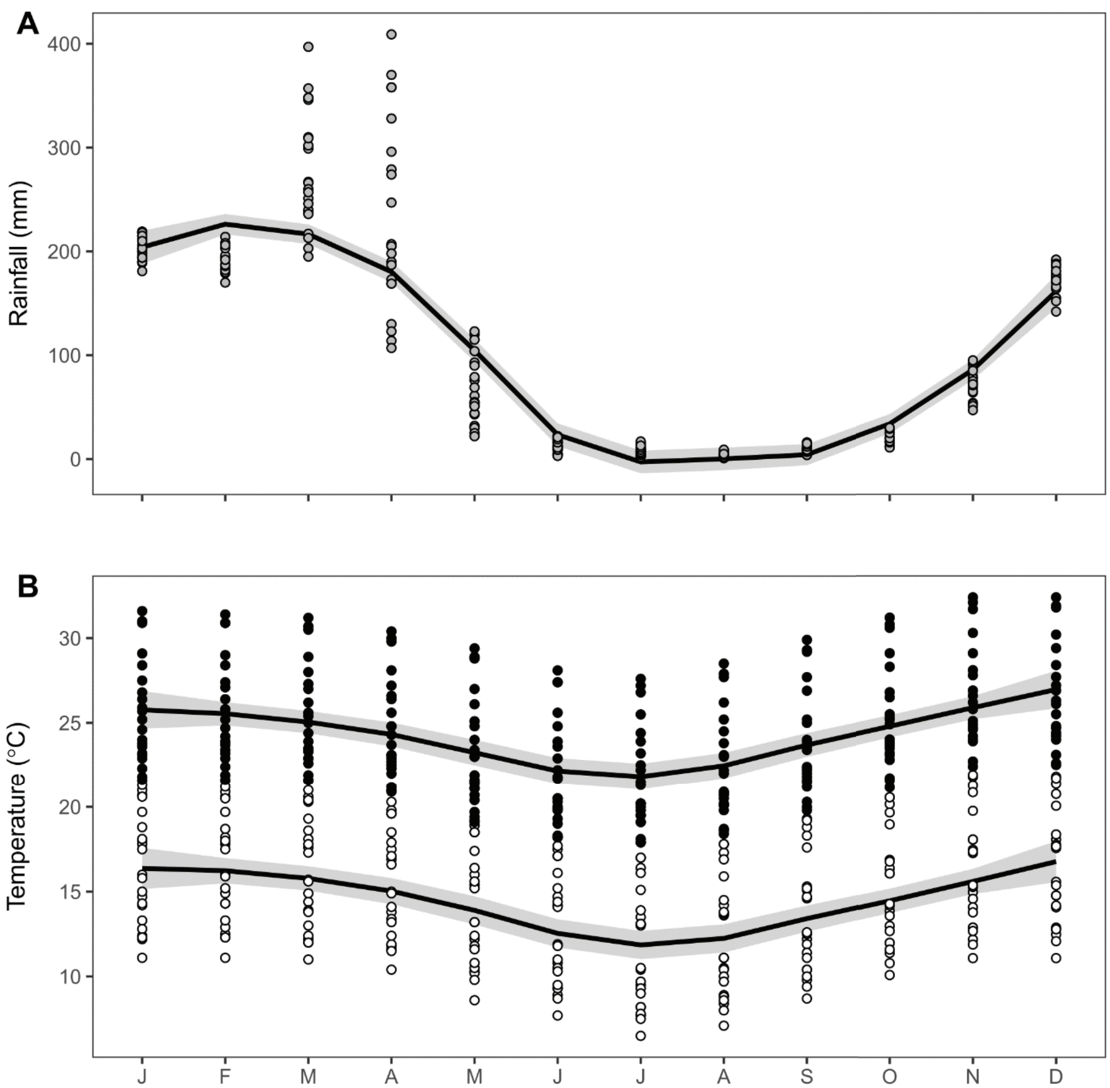

Figure A3. Average monthly WorldClim 2.0 data (1970-2000; 30 second resolution; http://www.worldclim.org/) for (a) precipitation (mm) and (b) temperature (°C) from the 22 study sites sampled in the Udzungwa Mountains, Tanzania. White and black points represent minimum and maximum temperatures, respectively; grey fill represents 95% confidence intervals.

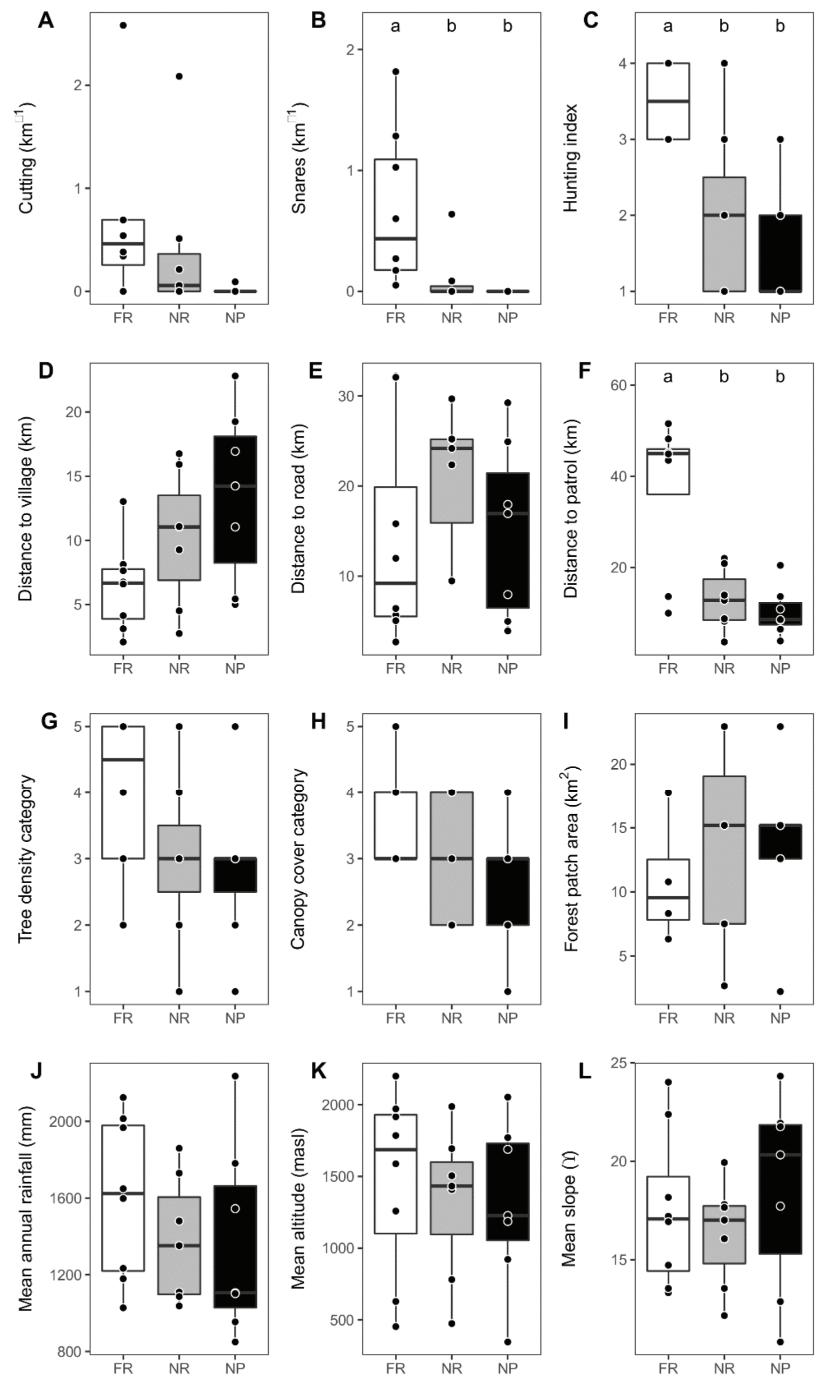

Figure A4. Effect of Protected Area status on anthropogenic (A-F) and environmental (G-L) variables. FR = Forest Reserve (white), NR = Nature Reserve (grey), NP = National Park (black). Letters above boxplots represent Tukey subsets where ANOVA results showed a significant effect of PA status.

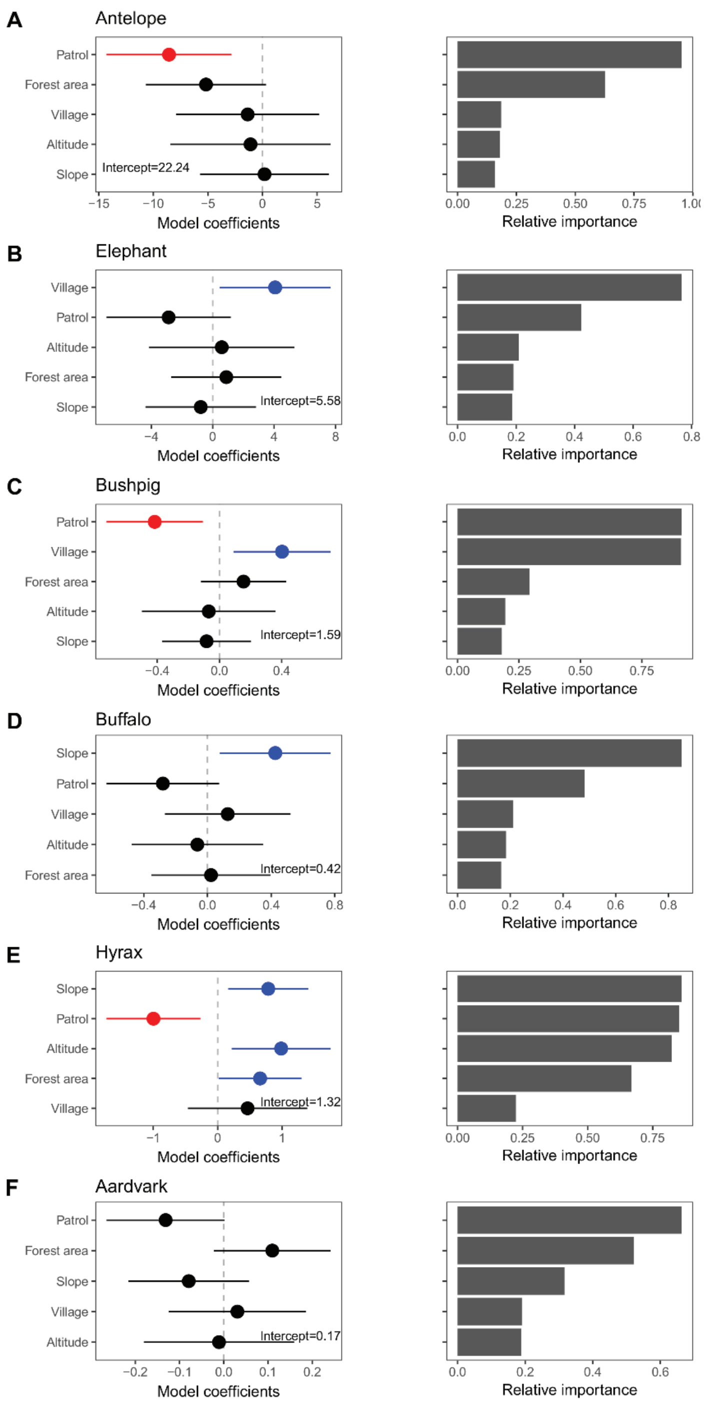

Figure A5. Coefficients and relative importance from model averaging process (all candidate models) for encounter rates of (A) antelope, (B) elephant, (C) bushpig, (D) buffalo, (E) hyrax, and (F) aardvark. Error bars represent 95% confidence intervals; blue and red represent significant positive and negative effects, respectively.

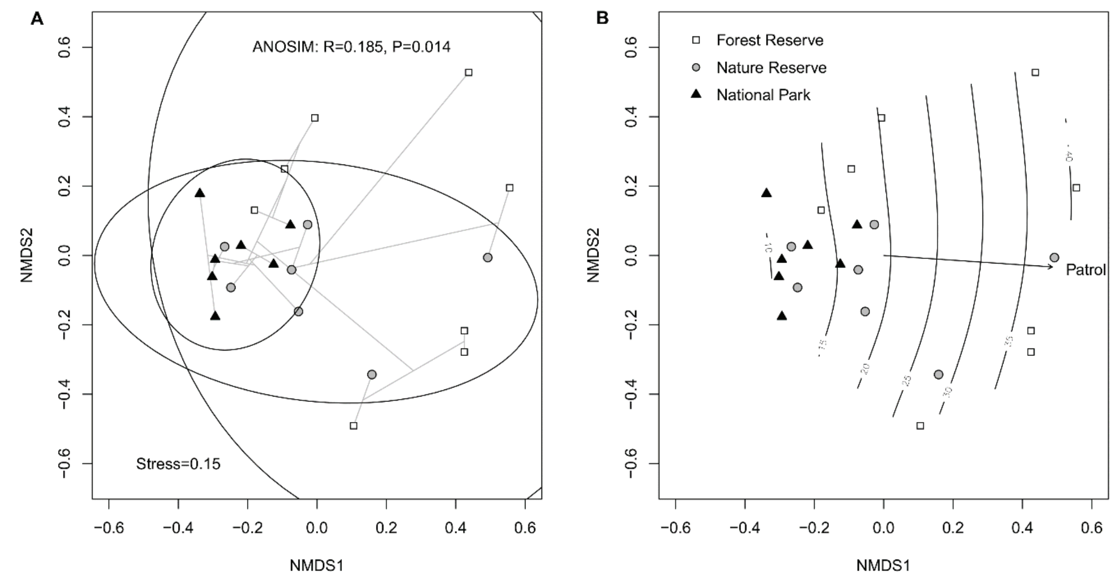

Figure A6. Non-metric multidimensional scaling (NMDS) plot (based on presence-absence data) for mammal communities at the 22 study sites. In (A), black lines represent dispersion ellipses for each protected area status based on 95% confidence intervals, grey lines represent hierarchical cluster dendrograms overlaid into the ordination space; In (B), the arrow and contours represent the gradient in relation to distance to the nearest patrol (km). FR = Forest Reserve (white squares), NR = Nature Reserve (grey circles), NP = National Park (black triangles).

Table A1. Features of the main habitat types in the Udzungwa Mountains, Tanzania (Rovero and De Luca, 2007).

Habitat type	Altitude range (m)	Dominant tree species	Description
Grassland and wooded grassland (WG)	300–1,500	*Acacia* spp., *Brachystegia* spp.	Bracken and grassland with scattered trees
Woodland (W)	300–2,000	Low elevation: *Commiphora* spp., *Adansonia digitata* Low to mid elevation: *Brachystegia* spp., *Pterocarpus angolensis* Mid to high elevation: A*cacia* spp., *Uapaka kirkiana*	Deciduous woodland with low canopy (to 20 m) variable from very dense to open
Lowland forest (LF)	300–800	*Funtumia africana*, *Erythrophleum suaveolens*, *Treculia africana*, *Lettowianthus stellatus*, *Anthocleista grandiflora*, *Sorindeia madagascariensis*, *Parkia filicoidea*, *Pteleopsis myrtifolia*	Forest with deciduous and semi-deciduous trees, canopy 15–25 m with emergents to 50 m
Sub-montane forest (SF)	800–1,400	*Parinari excelsa*, *Felicium decipiens*, *Harungana madagascariense*, *Allanblackia stuhlmannii*, *Trilepsium madagascariense*, *Isoberlinia scheffleri*	Moist forest with mainly evergreen species, canopy 25–40 m with emergents to 50 m
Montane forest (MF) [a]	1,400–2,600	*Parinari excelsa, Ocotea usambarensis, Hagenia abyssinica*, *Syzygium* sp., *Macaranga kilimandscharica,* *Caloncoba welwitschii*	Evergreen moist forest, with canopy height progressively lower with altitude

[a] MF includes upper montane forest (*sensu* Lovett 1993), which is above 1800 m and often contains bamboo towards the peaks of the mountains.

Table A2. Summary information, including sampling effort, for the 22 sites sampled in the Udzungwa Mountains, Tanzania.

Forest, forest area (km^2)	**Site no.**	**Site name**	**Altitude (masl)**	**Area sampled (km^2)**	**Status [a]**	**Habitat [d]**	**Survey date**	**No. recce transects**	**Total transect length (km)**
Uzungwa Scarp, 17.73									
	1	US Chini (lower)	799-1718	4.27	FR [b]	SF	Jul-08	15	14.6
	2	US Juu (upper)	1347-1829	3.16	FR [b]	MF	Jul-08	10	10.5
New Dabaga, 6.32									
	3	New Dabaga S	1791-2040	2.43	FR [b]	MF	Oct-09	12	11.2
	4	New Dabaga N	1895-2046	3.57	FR [b]	MF	Oct-09	9	10.0
Kising'a-Rugaro, 10.78									
	5	K-Rugaro W	2133-2265	3.52	FR	MF	Oct-07	6	10.1
	6	K-Rugaro SE	1567-2003	5.09	FR	MF	Oct-07	12	19.8
Matundu, 22.94									
	7	Matundu W1	707-855	2.50	NR	SF	Jul-08	9	9.4
	8	Matundu W2	346-603	2.66	NR	LF	Jul-08	12	11.7
	9	Matundu Ruipa	283-409	4.85	NP	LF	Jul-09	12	10.9
Nyumbanitu, 7.52									
	10	Nyumbanitu W	1412-1597	1.04	NR [c]	SF	Sep-07	6	5.2
	11	Nyumbanitu E	1503-1885	5.59	NR [c]	SF	Sep-07	20	17.6
Ukami, 2.68									
	12	Ukami	1234-1584	1.60	NR	SF	Sep-07	12	9.2
Ndundulu-Luhomero, 15.19									
	13	Ndundulu N	1897-2077	2.95	NR [c]	MF	Nov-08	12	11.0
	14	Vikongwa	1348-1517	2.61	NR [c]	SF	Nov-08	12	12.1
	15	Luhomero W	1405-1973	2.46	NP	SF	Oct-08	10	10.1
	16	Luhomero E	1682-1859	3.34	NP	SF	Oct-08	12	12.1
	17	Ng'ung'umbi	1929-2176	18.13	NP	MF	Jul-10	7	9.7
Iwonde, 2.24									
	18	Iwonde	1029-1425	2.37	NP	SF	Sep-09	11	9.6
Nyanganje, 8.32									
	19	Nyanganje W	476-781	2.65	FR	LF	Sep-09	12	11.5
	20	Nyanganje E	333-573	2.67	FR	LF	Aug-09	12	11.1
Mwanihana, 12.58									
	21	Three Rivers	885-1488	3.86	NP	SF/W	Aug-08	15	15.2

22	Mizimu	761-1082	1.76	NP	SF/W	Sep-08	9	8.5
	Total						**247**	**251.0**

[a] Protected Area status: FR = Forest Reserve; NR = Nature Reserve; NP = National Park.

[b] FR at time of the study, but subsequently raised to NR status in 2016.

[c] Reserve under Joint Forest Management (JFM) with adjacent village communities since February 2002.

[d] Habitat: WG = grassland and wooded grassland; W = woodland; LF = lowland forest; SF = sub-montane forest; MF = montane forest.

Table A3. Status and ecological variables for the 27 medium- to large-bodied mammal species surveyed in the Udzungwa Mountains, Tanzania. All species are included in analyses of species richness; species in bold are further analysed in relation to encounter rates.

Order Species	**Common name**	**Red List status** [a]	**Body mass (kg)** [b]	**Forest specialist**	**Habitats in Udzungwa** [c]	**Functional guild**
Primates						
Cercopithecus mitis moloneyi	Sykes' monkey	LC	4.9	N	LF, SF, MF	Monkey
Cercocebus sanjei	Sanje mangabey	EN	6	Y	LF, SF, MF	Monkey
Rungwecebus kipunji	Kipunji	CR	6.2	Y	MF	Monkey
Procolobus gordonorum	Udzungwa red colobus	EN	6.6	Y	LF, SF, MF	Monkey
Colobus angolensis palliatus	Angolan colobus	LC	6.9	N	LF, SF, MF	Monkey
Papio cynocephalus	Yellow baboon	LC	13	N	W, LF	Monkey
Artiodactyla						
Cephalophus natalensis harveyi	**Harvey's duiker**	LC	9	Y	W, LF, SF, MF	Herbivore
Cephalophus spadix	**Abbott's duiker**	EN	40	Y	LF, SF, MF	Herbivore
Neotragus moschatus	**Suni**	LC	4	Y	LF, SF, MF	Herbivore
Philantomba monticola	**Blue duiker**	LC	4	Y	SF, MF	Herbivore
Tragelaphus scriptus	**Bushbuck**	LC	34.2	N	W, LF, SF, MF	Herbivore
Potamochoerus larvatus	**Bushpig**	LC	60	N	W, LF	Herbivore
Syncerus caffer	**African buffalo**	LC	502.4	N	Throughout	Herbivore [d]

	Hippopotamus amphibius	Hippopotamus	VU	1520	N	LF	Herbivore [d]
Proboscidea							
	Loxodonta africana	**African elephant**	VU	2000	N	Throughout	Herbivore [d]
Hyracoidea							
	Dendrohyrax arboreus	**Eastern tree hyrax**	LC	2.5	Y	LF, SF, MF	Herbivore
Rodentia							
	Cricetomys gambianus	Giant pouched rat	LC	2.1	N	Throughout	Semi-fossorial
	Hystrix cristata	Crested porcupine	LC	16	N	Throughout	Semi-fossorial
	Thryonomys swinderianus	Cane rat	LC	2.1	N	WG, LF, MF	Semi-fossorial
Tubulidentata							
	Orycteropus afer	**Aardvark**	LC	42	N	W, WG, LF, SF	Semi-fossorial
Carnivora							
	Aonyx capensis	African clawless	NT	10	N	LF, SF	Carnivore
	Mellivora capensis	Honey badger	LC	8.8	N	Throughout	Carnivore
	Civettictis civetta	African civet	LC	10.4	N	Throughout	Carnivore
	Atilax paludinosus	Marsh mongoose	LC	2.8	N	LF, SF, MF	Carnivore
	Crocuta crocuta	Spotted hyena	LC	48.9	N	Throughout	Carnivore
	Panthera pardus	Leopard	VU	40	N	Throughout	Carnivore
	Panthera leo	Lion	VU	138.8	N	Throughout	Carnivore

[a] http://www.redlist.org, accessed 31st January 2018: LC = Least Concern; NT = Near Threatened; VU = Vulnerable; EN = Endangered; CR = Critically Endangered.

[b] Body mass (Kingdon, 2015).

[c] Habitat: WG = grassland and wooded grassland; W = woodland; LF = lowland forest; SF = sub-montane forest; MF = montane forest.

[d] Also classed as a Megaherbivore (Owen-Smith, 1992).

Table A4. Summary showing Akaike weight (ω) of models with ΔAICc < 2 for site-scale species richness and encounter rates for the most common species of medium- to large-bodied mammals in the Udzungwa Mountains, Tanzania.

	No. of models <2.0	Model rank	Model details	Int. [a]	Patrol	Slope	Village	Altitude	Forest	K	AICc	ΔAICc	ω
Species richness													
S	2	1	1 + S + P	12.19	-0.2	0.05				4	124.12	0	0.643
		2	1 + P	18.8	-0.19	0.01				3	125.31	1.19	0.355
		NULL	1	14.68						2	135.55	11.434	0.002
Encounter rates													
Antelopes	2	1	1 + F + P	22.24	-8.53				-5.02	4	177.15	0	0.63
		2	1 + P	22.24	-8.45					3	178.31	1.157	0.353
		NULL	1	22.24						2	184.39	7.237	0.017
Elephant	2	1	1 + V	5.58			4.27			3	155.12	0	0.584
		2	1 + V + P	5.58	-2.21		3.48			4	156.21	1.09	0.339
		NULL	1	5.58						2	159.17	4.046	0.077
Bushpig	2	1	1 + V + P	1.59	-0.41		0.37			4	44.7	0	0.674
		2	1 + F + V + P	1.59	-0.4		0.4		0.16	5	46.16	1.46	0.325
		NULL	1	1.59						2	58.42	13.714	0.001
Buffalo	2	1	1 + S + P	0.42	-0.29	0.44				4	55.09	0	0.517
		2	1 + S	0.42		0.41				3	55.6	0.507	0.401
		NULL	1	0.42						2	58.78	3.683	0.082
Hyrax	1	1	1 +F + A + S + P	1.32	-1.07	0.81		1.07	0.69	6	82.27	0	0.99
		NULL	1	1.32						2	91.43	9.16	0.01
Aardvark	3	1	1 + F + P	0.17	-0.13				0.11	4	12.25	0	0.417
		2	1 + P	0.17	-0.13					3	12.95	0.704	0.293
		3	1 + S + P	0.17	-0.13	-0.08				4	14.04	1.794	0.17
		NULL	1	0.17						2	14.73	2.482	0.12

[a] Model parameters: Int. = intercept; A = mean altitude; F = forest area; P = nearest patrol; S = mean slope; V = nearest village.
[b] K
[c] Model