Biodivers Conserv (2017) 26:1103–1119
DOI 10.1007/s10531-016-1288-2

ORIGINAL PAPER

Camera trapping surveys of forest mammal communities in the Eastern Arc Mountains reveal generalized habitat and human disturbance responses

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Received: 26 January 2016 / Revised: 2 December 2016 / Accepted: 21 December 2016 /
Published online: 29 December 2016

Abstract Large-bodied mammals are a rich and diversified faunal group in tropical rainforests. However, knowledge on community size and composition, and on species' distribution and ecology remains often scant and inadequate against their chronic status of threats. We used camera trapping to detect mammals in the forests of the Eastern Arc Mountains (EAM) of Tanzania, a world renowned region for biodiversity comprised by a series of distinct and ancient mountain ranges partially covered in moist montane forest. We conducted surveys from 2003 to 2011 in eight of the 12 mountain blocks in Tanzania, and, through an overall sampling effort of 11,500 camera days, we detected 43 species. We normalized species richness and species' detection events by effort, and used these metrics to assess the effect of habitat and human disturbance variables. We found that rarefied richness is positively affected by forest area at the block level, and that richness at forest patch level is also affected by forest area as well as surrounding human density (negative effect). For a subset of 17 species, we found consistent patterns of avoidance or tolerance of human disturbance and forest edges, and increased occurrence in areas at higher elevation, matching the historical forest loss that in most mountains occurred at lower elevation. Our study provides ecological insights that are novel for most species and sites, and reveals a general trend of negative impact of human disturbance on both community size and species' relative abundance. Increased protection of the EAM forests in Tanzania is of urgent importance for the persistence of diversified mammal communities.

Communicated by Iain James Gordon.

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Keywords Camera trap · Community ecology · Population ecology · Rainforest · Species richness · Tanzania

Introduction

Medium to large-sized mammals are a rich and diversified faunal group in rainforest ecosystems, accounting for a large portion of animal biomass, however they are chronically threatened by hunting and by habitat loss and degradation (Ceballos et al. 2005; Visconti et al. 2011; Beaudrot et al. 2016). Hence, assessing these communities and the factors affecting their presence and abundance are of increasing conservation relevance (Schipper et al. 2008; Rovero et al. 2014a). Yet, there remains scant knowledge on this group, probably because it is composed mainly of species that are difficult to detect due to their elusiveness, nocturnal habits and/or rarity. In recent years, camera trapping (i.e. the use of remotely-set, automatic cameras taking pictures of passing animals) has rapidly become the tool of choice for studying ground-dwelling, medium-to-large bodied mammals (O'Connell et al. 2011; Ahumada et al. 2011). Besides being very efficient for inventorying mammal communities (e.g. Tobler et al. 2008; Rovero et al. 2014a), camera trapping provides an event count of species' detection at the site that can be used as an index of relative abundance, which in turn can be modelled to determine environmental factors influencing the index (e.g. Bowkett et al. 2008; Martin et al. 2015).

In this study, we analysed the results of several camera trapping surveys conducted over a span of almost 10 years that were aimed at assessing the diversity of medium-to-large forest mammals in the Eastern Arc Mountains (EAM) of Tanzania. The region is well known for its exceptional biological richness and endemism (e.g. Burgess et al. 2007), and a recent assessment has updated and analysed the diversity of endemic vertebrates that includes 11 endemic or regional-endemic, medium to large mammals (Rovero et al. 2014b). However, there remains scant knowledge on forest mammals among EAM blocks. Notable exceptions are a number of forests in the Udzungwa Mountains, the southern and largest range within the EAM, for which there has been intense camera trapping sampling, and other species-specific, or block-specific studies (e.g. Rovero and De Luca 2007; Bowkett et al. 2008; Jones 2013; Rovero et al. 2014a), including unpublished reports for surveys in a number of mountain ranges, which contributed the data used in our analysis. Generally, these studies raise conservation concern over the protection status of the EAM forests, pointing to alarming levels of threats from hunting and habitat degradation that have a direct impact on mammals (e.g. Hegerl et al. 2015). Such evidence of increasing threats to EAM mammals, combined with the general poor level of knowledge on the diversity of mammals and associated environmental and anthropogenic factors, triggered the surveys we conducted for this study. We aimed to (1) present the checklist of species detected over the entire period of surveys by mountain block and forest patch therein, (2) assess community composition by trophic guilds and determine broad patterns of habitat and human disturbance drivers of species richness and species composition, and (3) determine the relative abundance and ecological traits for the pool of most-detected species.

Materials and methods

Study area

The EAM of Kenya and Tanzania (Fig. 1) consist of 13 mountains blocks from southern Kenya (Taita Hills 3°25′S, 38°20′E) to south-central Tanzania (Udzungwa 7°15′S, 36°15′E) that are under the climatic influence of the Indian Ocean favouring the persistence of moist forest on the mountain slopes. These forests are currently isolated from each other by drier lowland vegetation and heavily settled and farmed zones. In early prioritization analysis, the EAM and coastal forests ranked as the biodiversity hotspots with highest density of endemic vertebrates on earth (Myers et al. 2000). With the exception of the larger forests in Udzungwa, that have maintained a protected gradient of forest habitat type with elevation (from deciduous lowland to montane evergreen), most of the forest cover in the areas surveyed are left in the mid- to upper elevation zone of the mountains and consist of sub-montane or montane evergreen forest with large tracts degraded by selective logging in the past and/or current degradation. The majority of target forests are protected under the Tanzania Forest Service as either Catchment Forest Reserve or Nature Reserve, while only a handful of forests in Udzungwa are part of the Udzungwa Mountains

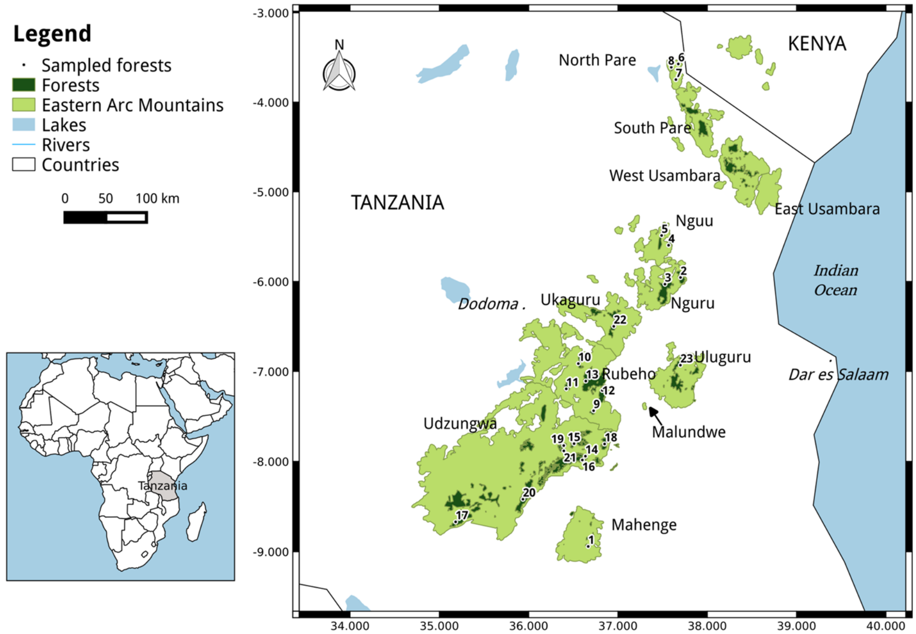

Fig. 1 Map of the study area, the Eastern Arc Mountains in Tanzania where camera trapping surveys of forest mammals were conducted during 2005–2011. In *light green shade* are the Eastern Arc Mountains (remaining closed forest in *dark green*), with mountain limits that follow Platts et al. (2011). Surveys were conducted in eight mountain blocks and within these in the following forests (indicated by *numbers*): *1* Sali (Mahenge mountains). *2* Kanga, *3* Nguru south (Nguru mountains). *4* Kilindi and *5* Nguru north (Nguu mountains). *6* Minja, *7* Kindoroko and *8* Mramba (North Pare mountains). *9* Ilole, *10* Mafwomero, *11* Mangalisa, *12* Pala Ulanga and *13* Ukwiva (Rubeho mountains). *14* Iwonde, *15* Ndundulu-Luhomero, *16* Matundu, *17* Mufindi, *18* Mwanihana, *19* Nyumbanitu, *20* Uzungwa Scarp, *21* Ukami (Udzungwa mountains). *22* Mamiwa Kisara (Ukaguru mountains). *23* Uluguru North (Uluguru mountains). (Color figure online)

National Park. Being for most formally protected, no legal extraction of timber and non-timber forest products is allowed, however some forests have been logged in the past until 1960s and 1970s before becoming reserves, and some illegal logging of valuable timber trees such as *Ocotea usambarensis* and *Milicia excelsa* is reported until today (e.g. Burgess et al. 2007).

Data collection

Camera trap surveys were conducted in eight of the 12 EAM blocks in Tanzania (Fig. 1). The total forest area of these eight blocks varies between 41 and 1726 km^2 (Platts et al. 2011) and, within each block, the forest patches we targeted for surveys had an area of 5–520 km^2 and an elevation range of 400–1950 m a.s.l. We collected data from 2003 to 2011 with the bulk of data collected during 2005–2007 through a series of distinct camera trap sessions, each consisting of an array of camera trap sites (5–25), each camera trap sampling for 30–120 days (mean 48.6 days) within a forest patch (Table 1). Surveys were aimed at compiling inventories, so most did not involve the deployment of a robust and systematic sampling design. Single camera traps were placed opportunistically along presumed wildlife trails to maximize trapping rates. The typical design consisted of choosing one or more focal areas for sampling within each forest, and deploying camera traps within each focal area at a spacing of 500 m to 1 km (Doggart 2006). The area effectively sampled by camera traps ranged from 2 to 148 km^2 per forest. We sampled mainly in the dry season (June–October) and secondarily in the low rainfall months (November–January) before the heavy rains, that generally occur during March–May.

We used analog, film camera traps (Deercam DC300, Non-Typical Inc., Park Falls, Wisconsin, USA) set tight to a tree at approximately 50 cm height and 2–3 m from the target trail. Cameras were set to take pictures with a minimum interval of 1 min between consecutive triggers, to not saturate the film too quickly. Cameras were left unattended in the field except when we planned survey efforts greater than 60 days, in which case we checked camera traps once to replace the film roll; we then retrieved cameras at the end of the survey. For each camera trap photo, we scored on a spreadsheet the animal species present, number of individuals, geographic coordinates of the camera trap site, elevation, time and day of image, start and end day of sampling, geographic location of the site (EAM block, forest patch, and forest site when more than one site in each forest was surveyed). The database is publicly available at https://figshare.com/s/85fb49bf23d3a9abce57.

Data analysis

For each camera trap site, we quantified the sampling effort in camera days, defined as the number of cameras multiplied by the number of days they effectively sampled (i.e. until they were retrieved or the film was full). Image records were screened to derive detection ‘events’ according to a standard temporal separation criterion of 1 h between consecutive images of the same species. This is a commonly used approach (e.g. Bowkett et al. 2008) that avoids repeated counting of images related to the same individual pausing in front of the camera trap. We then computed the camera trapping rate, or RAI (Relative Abundance Index) as the number of events divided by the sampling effort (e.g. Bowkett et al. 2008). While this metric does not account for imperfect detection (O’Connell et al. 2011), it has showed to be useful to understanding the ecological factors that may influence relative abundance (Carbone et al. 2001; O’Brien et al. 2003; Rowcliffe et al. 2008; Rovero and Marshall 2009). We did not aim to compare this index among species as we either analysed

Table 1 Sampling details and summary of results (number of images, events and species) of terrestrial mammals obtained per Eastern Arc Mountains (EAM) block (forest area, protected forest area and elevation range sampled are also indicated)

EAM Block	Forest area (km^2)[a]	Protected forest area (km^2)[a]	Forest elevation range sampled (m a.s.l.)	Num forest	Num surveys	Num cameras set	Num cameras working	Camera days	Num images (events)	Num species	Sampling period[b]
Mahenge	20.2	11.3	1155–1400	1	1	10	6	290	170 (170)	13	Oct–Dec 2005
Nguru	326.7	271.4	860–2020	2	3	18	14	564	177 (171)	15	Jun 2005–Sept 2006
Nguu	357.1	183.0	900–1450	2	1	22	19	660	219 (209)	17	Nov 2007–Jan 2008
North Pare	40.7	21.7	1573–1800	3	1	16	16	265	208 (202)	15	Oct–Dec 2005
Rubeho	520.9	296.9	1320–2161	5	2	47	40	1081	487 (478)	20	Sept 2006–Jul 2007
Udzungwa	1764.6	1415.6	290–1890	8	21	213	185	8239	5075 (4863)	41	Dec 2003–Jan 2011
Ukaguru	191.0	150.9	1750–2020	1	1	5	5	118	9 (9)	6	Feb 2007
Uluguru	308.6	259.2	1310–1550	1	1	12	6	245	99 (94)	7	Oct–Dec 2005

See map in Fig. 1 for the list of forests where camera trapping was conducted

[a] From Platts et al. (2011)

[b] For EAM blocks where multiple surveys were conducted the period indicates the overall temporal span taken by the study

species-specific habitat associations or we pooled RAI among species to assess effects on community composition (see below for details).

We analysed data at the community-, trophic guild- (i.e. community composition), and species-level and performed analysis at the block-, forest-, and camera trap site-level, as hereafter described. We built species accumulation curves for data pooled by mountain block to assess sampling completeness in each block. We used a randomized curve (see e.g. Rovero et al. 2014a) and visually assessed the levelling of the accumulation curves. To investigate the potential environmental drivers of observed richness, we standardized this metric using a rarefaction function as proposed by Hurlbert (1971; see also Colwell et al. 2004). This yields the expected number of species in a community normalizing the bias due to sample size. We derived standardized richness at both block and forest levels, using the packages ‘reshape’ (Wickham 2007) and ‘vegan’ (Oksanen et al. 2008) in the statistical software R (R Development Core Team 2015). We analysed the effect of habitat and human disturbance covariates (see below) on rarefied species richness at the block level ($N = 8$) by means of Generalized Linear Models with Quasi-Poisson error distribution (Maindonald and Braun 2003)—given the response variable is a count and we detected overdispersion—with a stepwise backward model selection based on minimizing AIC. At the forest level ($N = 23$), given the possible dependency structure of data, with forests variably ‘nested’ within the eight blocks, we used Generalized Linear Mixed Models (GLMM; Zuur et al. 2009) with a random intercept to account for the ‘block’ effect. As we detected over-dispersion, we used a negative binomial GLMM. We used the package ‘lme4’ in R to fit GLMMs (Bates et al. 2015) and conducted a manual model selection based on minimizing AIC.

We studied differences in community composition among blocks and forests by lumping species according to their trophic habit (i.e. carnivores, omnivores, herbivores, insectivores). We categorized species by trophic guild using Kingdon (2015). At the forest level, we derived the cumulative RAI for all species in each guild and correlated it with a set of covariates to assess how guilds’ relative abundance relate to environmental and human disturbance factors. We did not perform multiple regression because of low sample size for the least represented guilds. At the species level, we used the species’ RAI derived at each camera trap site as the response variable to regress against covariates by means of GLMM with Poisson or negative binomial error distribution to determine best habitat and human disturbance drivers of species’ relative abundance. Because camera trap sites were nested within forests (and blocks), we set ‘forest’ as a random intercept in these GLMMs. We did not use ‘block’ as an additional random effect because there were not enough forests in each block to do so; we considered the forest effect more justified because ecological processes at the camera trap site may vary among forests (e.g. due to protection level and other features), irrespective of the block. For this analysis, we targeted a subset of species that overall had at least 40 detections to ensure adequate convergence of GLMs. The sample size for this analysis varied (see “Results” and Table 4), as we excluded the camera trap sites of forests where the species was completely undetected.

Habitat and human disturbance covariates

At the block level, we derived from Rovero et al. (2014b) the following set of covariates for the analysis described above: (1) average annual rainfall, based on analysis of 1997–2006 data from the Tropical Radar Measuring Mission (TRMM; Mulligan 2006) as derived by Platts et al. (2010); (2) total forest area (Platts et al. 2011); (3) forest elevation range (Platts et al. 2011); (4) estimated % forest loss during 1955–2000 (Hall et al. 2009);

(5) human disturbance, derived from disturbance data collected along c. 500 km of 10 m wide transects that recorded all cutting of trees and poles; compiled by Ahrends et al. (2011); following Rovero et al. (2014a, b) we only used the % of trees cut (i.e. stems ≥15 cm diameter at breast height with ≥3 m straight stem length); (6) mean human population density around each block (Platts et al. 2011); and (7) funding for zoological surveys, as a proxy of overall research effort involved (see Rovero et al. 2014b for details).

At the forest level, we derived ex-novo: (1) forest area, calculated with the QGIS software 1.8 (QGIS Development Team 2014) following the boundaries updated at 2014 found at http://www.easternarc.or.tz or digitized from satellite imagery using Google satellite maps as a base; (2) perimeter of the forest; (3) perimeter-area ratio, as a simple measure of forest shape complexity; (4) mean human population density around each forest (Platts et al. 2011); however, we did not use perimeter and perimeter-area ratio due to collinearity with forest area. We also averaged the following variables available for each camera trap site: (5) elevation (m a.s.l.); (6) distance to the nearest forest edge (m); (7) distance from the reserve boundary (m). These three variables were also used at the camera trap site level for investigating their effect on species' RAI, after being standardized to a normal distribution with mean = 0 and standard deviation = 1. Covariates were checked for collinearity before running models, and were deemed redundant when correlated with other variables with a Pearson's correlation coefficient of $r > 0.6$. In particular, elevation and distance to reserve border were significantly correlated ($r = 0.59$, $P < 0.001$) but both retained; elevation and distance to forest edge, and distance to edge and distance to border both had a weaker and non-significant correlation ($r = 0.11$, $P = 0.07$ and $r = 0.03$, $P = 0.63$).

Results

We realized a survey effort that varied from 118 to 1081 camera days among EAM blocks when excluding Udzungwa, where the effort was 5075 camera days. Such discrepancy reflects the number of forests surveyed per block and the number of camera trapping sessions conducted in each forest. We accumulated 11,462 camera days. Out of 343 camera traps set, 291 worked reliably while the remaining failed, i.e. a failure rate of 15.2% (Table 1). Camera traps yielded 6444 images of ground-dwelling, medium-to-large mammals (Table 1).

Community-level results

We detected 43 species of medium-to-large mammals overall (Table 2). Observed richness varied markedly among blocks, reflecting the disparity in survey efforts: rarefied species richness ranged from 7 in Uluguru to 20 in Rubeho, and peaked in Uzungwa, with 35 species. Species accumulation curves were generally steep for the first 200 camera days then progressively tended to flatten out, however only for Udzungwa the curve approximated to an asymptote (Fig. 2). Variation of rarefied species richness among EAM blocks was positively and significantly predicted by forest area (Table 3); forest loss was also retained by the best model but was not significant. The deviance explained by the best model was 67.4%. At forest level, the best model showed that rarefied richness was significantly predicted by forest area (positive effect) and surrounding human population

Table 2 Checklist of species detected by camera trapping in the Eastern Arc Mountains of Tanzania

Taxonomic group	Common name	Scientific name	Body mass (kg)	Feeding guild	Relative Abundance Index (RAI) per mountain block							
					Mahenge	Nguru	Nguu	North Pare	Rubeho	Udzungwa	Ukaguru	Uluguru
Primates	Udzungwa red colobus*	*Procolobus gordonorum*	8.33	H						0.02		
	Angolan Colobus	*Colobus angolensis palliatus/sharpei*	9.85	H		0.53				0.02		
	Sanje mangabey*	*Cercocebus sanjei*	8.00	O						1.81		
	Yellow baboon	*Papio cynocephalus*	18.40	O						0.23		
	Sykes' monkey	*Cercopithecus mitis*	5.00	O	0.34	0.71	0.91	2.64	1.48	0.33	1.69	
	Small-eared galago	*Otolemur garnettii*	0.76	H				1.89				
Rodents	Swynnerton's bush squirrel	*Paraxerus vexillarius*	0.35	H	0.34	2.66				0.57	1.69	14.29
	Tanganyika mountain squirrel	*Paraxerus lucifer*	0.68	H	1.03		0.61		4.07	0.87		
	Zanji sun squirrel	*Heliosciurus undulatus*	0.35	H					0.09			
	Smith's bush squirrel	*Paraxerus cepapi*	0.18	H						0.01		
	Cape porcupine	*Hystrix africaeaustralis*	8.00	O			0.15	0.38		0.64		
	Crested porcupine	*Hystrix cristata*	2.00	H						0.02		
	Lesser pouched rat	*Beamys hindei*	0.75	O	1.72			0.38	0.09	0.29	0.85	
	Giant pouched rat	*Cricetomys gambianus*	1.29	O	16.55	3.19	2.12	50.57	2.31	6.40	0.85	12.65
Carnivores	Honey badger	*Mellivora capensis*	9.00	C		3.90			0.37	0.55		
	Marsh mongoose	*Atilax paludinosus*	3.30	C		0.18	0.15		0.46	0.24		0.41
	Slender mongoose	*Herpestes sanguinea*	0.50	C	0.69							
	Banded mongoose	*Mungos mungo*	1.93	I						0.11		
	Bushy-tailed mongoose	*Bdeogale crassicauda*	1.55	C	11.72	4.08	1.97	0.75	8.79	5.73		5.31
	Egyptian mongoose	*Herpestes ichneumon*	2.85	C				0.38				

Table 2 continued

Taxonomic group	Common name	Scientific name	Body mass (kg)	Feeding guild	Relative Abundance Index (RAI) per mountain block							
					Mahenge	Nguru	Nguu	North Pare	Rubeho	Udzungwa	Ukaguru	Uluguru
	Jackson's mongoose	*Bdeogale jacksoni*	2.50	C						0.28		
	Spotted hyena	*Crocuta crocuta*	62.99	C						0.33		
	Central African large spotted genet	*Genetta maculata*	2.23	C	1.38			3.40	0.09		0.85	
	Lowe's servaline genet	*Genetta servalina*	1.06	O		1.42	1.52		3.79	1.46		0.82
	African palm civet	*Nandinia binotata*	2.00	O			0.15	0.38	0.37	0.35		
	African civet	*Civettictis civetta*	12.00	O			0.15	2.26		0.36		
	Serval	*Felis serval*	12.00	C					0.09			
	Leopard	*Panthera pardus*	52.04	C		0.71	0.45			0.50		
Afrotheria	Aardvark	*Orycteropus afer*	52.35	I			0.61			0.33		
	Eastern tree hyrax	*Dendrohyrax validus*	2.95	O		0.18	0.15			0.28		
	Elephant	*Loxodonta africana*	3940.03	H						1.29		
	Four-toed sengi	*Petrodromus tetradactylus*	0.22	H				3.40	0.09	1.27		
	Chequered sengi	*Rhynchocyon cirnei*	0.49	I	3.79				3.79	1.15		
	Grey-faced sengi*	*Rhynchocyon udzungwensis*	0.70	I						1.95		
	Black and rufous sengi	*Rhynchocyon petersi*	0.42	O		3.01	1.82	1.51				4.08
Ungulates	Hippo	*Hippopotamus amphibius*	1417.49	H						0.39		
	Bushpig	*Potamochoerus larvatus*	48.78	O		2.84	5.30	1.13	1.39	1.48		
	Abbott's duiker	*Cephalophus spadix*	56.00	O					0.37	0.86		

Table 2 continued

Taxonomic group	Common name	Scientific name	Body mass (kg)	Feeding guild	Relative Abundance Index (RAI) per mountain block							
					Mahenge	Nguru	Nguu	North Pare	Rubeho	Udzungwa	Ukaguru	Uluguru
	Buffalo	*Syncerus caffer*	580.00	H						0.16		
	Blue duiker	*Cephalophus monticola*	6.25	H						3.79		0.82
	Red duiker	*Cephalophus harveyi*	12.00	H	8.62	7.62	10.45	5.28	3.33	17.26		
	Bushbuck	*Tragelaphus scriptus*	43.25	H	0.34	0.71	1.21		3.05	0.62		
	Suni	*Neotragus moschatus*	6.25	H	11.72	0.18	3.94	1.89	9.16	5.86		

Values are relative abundance index (RAI; detection events per camera trap days) per mountain block where the species was detected (see text for details). Species' biological traits are also indicated (body mass and feeding guild: *C* carnivore, *H* herbivore, *I* insectivore, *O* omnivore). Asterisks after common name indicate block-endemic species

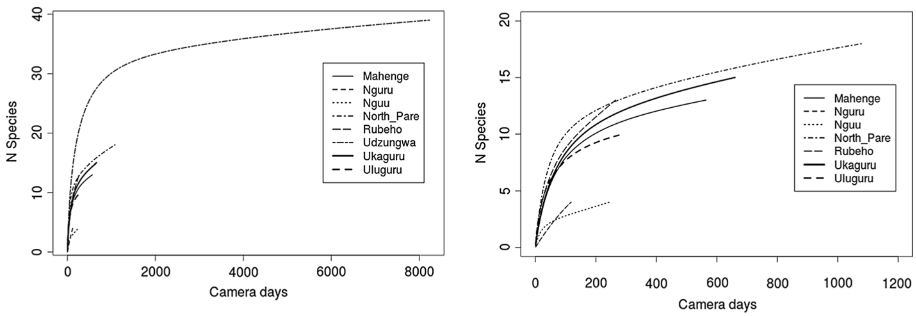

Fig. 2 Randomized accumulation curves of forest mammal species for the eight mountain blocks in the Eastern Arc Mountains in Tanzania where camera trapping was conducted during 2005–2011 (*left chart*; see Table 1 for details on survey effort); the chart on the right excludes Udzungwa to better visualize the curves for the remaining blocks where sampling effort was lower

Table 3 Results of Generalized Linear Models and Generalized Linear Mixed Models testing the effect of habitat and disturbance factors on the rarefied species richness of communities of large mammals camera trapped in the Eastern Arc Mountains of Tanzania at block and forest levels; predictors retained by the best models are shown (see text for details)

Level of analysis	Variable	Estimate	SE	Z	*P*
EAM block	Forest area	0.0007	0.0018	3.530	<0.02
	Forest loss	0.0202	0.0228	0.884	0.417
EAM forest[a]	Log (forest area)	0.1377	0.065	2.115	<0.05
	Human population	−0.0022	0.0009	−2.376	<0.02

[a] Estimated variance of random intercept ('block' effect) = $1.427e^{-10}$

density (negative effect) (Table 3). The estimated variance of the random intercept (block effect) was negligible, i.e. $1.427e^{-10}$.

Overall, community composition by trophic guild was almost equally dominated by herbivores and omnivores (16 and 14 species, respectively), followed by carnivores (9 species) and insectivores (4 species). This pattern was maintained when trophic guild representation is assessed at forest level, with herbivores (maximum number of species per forest was 10 species, mean 3.6), and omnivores (max. 11 species, mean 4.9) being the most represented, followed by carnivores (max 5 species, mean 2.6) and insectivores (max 4 species, mean 0.8), which were not detected in 4 of the 8 EAM blocks surveyed (Table 2). Correlations between cumulative RAI for each feeding guild and environmental covariates at forest level indicated that RAI increased with forest size for herbivores and insectivores, decreased for omnivores and did not vary for carnivores. In addition, omnivores' RAI increased with human density while it decreased for the other three guilds. The omnivorous RAI with human density was the only significant relationship ($R^2 = 0.73$, $P < 0.05$).

Species-level results

Mean RAI per species when pooling data for all EAM blocks varied substantially, with 20 species scoring a RAI > 1, five species 0.5–1, 13 species >0.1–0.5, and the remaining five species had RAI < 0.1 (Table 1). The five most detected species in terms of RAI were: giant pouched rat, bushy-tailed mongoose, suni, Harvey's duiker and chequered sengi. We could fit GLMMs successfully for 17 species, and because we consistently detected overdispersion, we used the negative binomial error distribution. For four additional species (bush squirrel, honey badger, marsh mongoose and African civet) no covariate was retained with statistical significance by the best model. The estimated random intercept's variance (i.e. 'forest' effect) varied markedly among species' best models (range 0–29.97) but overall was <1 for 11 of the 17 species' models. We found the following, statistically significant patterns of responses, as listed by predictor and species (Table 4): distance from forest edge positively affected RAI of bushy-tailed mongoose, while for blue duiker, bush pig, four-toed sengi and Sanje mangabey the effect was negative. Distance from protected area border positively affected the RAI of elephant and leopard, while it negatively affected the RAI of blue duiker, four-toed sengi and Sanje mangabey. Elevation had a significant, positive effect on the RAI of Abbott's duiker, blue duiker, chequered sengi, Lowe's servaline genet, Sanje mangabey, suni, Swynnerton's bush squirrel and Sykes' monkey, and a negative effect on the RAI of bushy-tailed mongoose, elephant, four-toed sengi, Harvey's duiker and leopard (Table 4).

Discussion

In this study we analysed a large database of camera trapping images of ground-dwelling forest mammals detected in 23 discrete forests belonging to eight EAM blocks, and aimed to assess ecological patterns at community- and species-level. Despite the lack of a systematic sampling design in our study, our findings provide important data on mammals in the EAM as well as insights into how communities and selected taxa may be influenced by environmental factors and human-driven disturbance. A species-by-species discussion of the results is beyond the scope of this analysis given that earlier accounts have reported on most of the range-restricted or endemic species such as Abbott's duiker, Jackson's mongoose, Lowe's servaline genet (*G. servalina lowei*) and the grey-faced sengi, or elephant-shrew (*R. udzungwensis*) (De Luca and Rovero 2006; Rovero et al. 2006, 2008; Bowkett et al. 2014).

The significant relationship we found between rarefied species richness and forest area at the block-level is an ecologically important result, consistent with the Island Biogeography Theory (MacArthur and Wilson 1967) and empirical studies (e.g. Harcourt and Doherty 2005), including some in the EAM (Marshall et al. 2010; Burgess et al. 2007). The conservation relevance of this result is mirrored by the analysis at forest-level, showing that rarefied richness is affected by forest area at this level of analysis too, and, additionally, it is negatively affected by human population density. The community composition analysis yielded qualitative results due to the small sample size when assessing trophic guild representation. However, the results provide interesting indication of increased representation of herbivores and insectivores with forest size, and a positive correlation between omnivores and human density in the areas surrounding the forest. These findings are in general agreement with other studies (Henle et al. 2004; Vetter et al. 2011), including a standardized assessment of tropical forest mammal communities that reports greater imbalance among trophic guilds in smaller and/or more fragmented sites, with loss of insectivores (Ahumada et al. 2011). The increase in omnivores with disturbance we report matches findings by Hegerl et al. (2015) in Udzungwa, where rodents

Table 4 Model coefficients from Generalized Linear Mixed Models testing the influence of a set of habitat and human disturbance predictors on the relative abundance index (RAI) for selected species of mammals (alphabetic order) detected through camera trapping in the Eastern Arc Mountains in Tanzania

Species	Num. sites	Num. sites where present (proportion on total sites)	Distance from forest edge	Distance from reserve border	Elevation	Random intercept variance
Abbott's duiker	121	40 (0.33)			0.840*	2.67e−10
Blue duiker	124	35 (0.28)	−1.413*	−5.310*	3.427*	17.640
Bushbuck	125	37 (0.30)	−0.037	0.485	0.337	1.095
Bush pig	144	68 (0.47)	−0.370*			0.594
Bushy-tailed mongoose	149	126 (0.85)	0.304*		−0.363*	0.314
Cape porcupine	121	19 (0.16)	−0.980		1.623*	3.970
Chequered sengi	130	42 (0.32)		0.146	0.775*	0
Elephant	111	22 (0.20)		4.731*	−2.258*	29.970
Four-toed sengi	111	15 (0.14)	−0.318*	−2.572*	−2.225*	27.090
Giant-pouched rat	167	130 (0.78)		−0.219	0.144	4.753 e−11
Harvey's duiker	174	147 (0.84)			−3.192*	0.029
Leopard	117	25 (0.21)		1.875*	−1.215*	1.764
Lowe's servaline genet	153	84 (0.55)			0.570*	1.498 e−05
Sanje mangabey	101	38 (0.38)	−0.638*	−2.792*	1.931*	6.05e−08
Suni	161	111 (0.69)	−0.242		0.247*	3.16e−08
Swynnerton's squirrel	102	25 (0.25)			2.737*	2.06e−12
Sykes' monkey	127	37 (0.29)			0.520*	3.3e−09

Values are parameters' estimates and the asterisk indicates significant outcome ($P < 0.05$). No value indicates that the best model did not retain the corresponding covariate

The grey-faced sengi, *Rhynchocyon udzungwensis*, is not included because a focal habitat association study has been conducted earlier (Rovero et al. 2013)

especially (which in ours and Ahumada et al. (2011)'s studies are included among the omnivores) dominated at the expenses of other trophic guilds in the disturbed forest significantly more than in the undisturbed forest.

Given the relatively modest sampling effort allocated to some of the EAM blocks, our observed species richness is likely an underestimate of true richness. Yet, it is very realistic that forests under heavy human pressure, as documented during the surveys themselves, such as Uluguru, Nguru, Rubeho and North Pare, do not hold communities of medium-to-large mammals with more than 10–15 species. A recent study in Udzungwa compared the species richness in Mwanihana and Uzungwa scarp, two of the largest forest blocks in the area, the former being in the National Park and therefore benefiting of relatively effective ground protection, while the latter is a Forest Reserve (recently upgraded to Nature Reserve) that was unprotected. Through a systematic assessment with 30 camera traps in each forest, Hegerl et al. (2015) found 23 and 15 species in these forests, respectively. Yet most of the other forests surveyed in our study are smaller than these two forests, have a narrower elevation range, and do not have the baseline, high level of mammal diversity documented in Udzungwa (Rovero and De Luca 2007). This lends support to evidence for a generally decreased diversity and poor conservation status of mammals in the EAM.

The species-specific analyses aimed to determine generalized patterns of effects of habitat and human disturbance on selected species. The variance of the estimated 'forest' effect in the mixed-effects models was relatively little, indicating that the relationships found between species' relative abundance and covariates are generally similar among forests. The significant relationships that emerged broadly indicate that elevation is a significant predictor, for most species, with a positive effect. This is likely an indication of preference for interior portion of the forest, and, in turn, of disturbance-avoidance; indeed elevation and distance to reserve border were significantly correlated, while elevation and distance to forest edge had a weaker correlation. This pattern may be due to the fact that a number of EAM blocks (e.g. Ukaguru, Uluguru, North Pare, Rubeho) have their residual forest cover at high elevation. Distance from reserve border and, even more so, distance from forest edge were retained in the best models and at significant level for a relatively smaller number of species, with a predominantly negative effect. This is generally concordant with the notion that habitat edges are beneficial to wildlife given the diversity of vegetation increases in their proximity (e.g. Yahner 1988). Such pattern is plausible, for example, for Sanje mangabey and bush pig, a frugivore and omnivore species, respectively, both occurring with higher relative abundance within the secondary forest found near forest edges. When forest edge coincides with protected area border, distance to edge may also reflect disturbance-avoidance. Indeed distance from reserve border has a positive effect for larger, 'landscape' species such as elephant and leopard that need large and protected areas. Elephants in EAM have a stable presence only in Udzungwa, the mountain block with largest forests and protected areas (Jones 2013).

A comparison of our results with available data on presence of mammals in the EAM confirms that an impoverishment of larger mammals has occurred in these forests. The Tanzania Mammal Atlas Project database (Tanzania Wildlife Research Institute, unpublished data) include camera trapping data from Ukaguru and Uluguru mountains: bush pig, bushbuck and honey badger are additional records relative to our study for the former block, while only palm civet was found in Uluguru relative to our study. Cordeiro et al. (2005) surveyed forests in Nguu, North Pare and South Pare (the latter not being surveyed by us) and the only records of larger species that we did not record are bushbuck recorded in North (and South) Pare, and leopard still occurring in North Pare and confirmed in Nguu. It is also worth noting that we recorded signs of elephant and buffalo in Kanga Forest Reserve (Nguru mountains), Sali Forest Reserve (Mahenge mountains), Ilole forest and Pala Ulanga Forest Reserve (Rubeho mountains; also reported in Ukwiva and Mafwomero forests; Doggart et al. 2006, this study), which, in addition to where we camera trapped them, they seem the only sites in the EAM where these large species are still found.

While data on historical presence of large mammals in the EAM are very scant, there is consistent evidence that extirpation of larger species has occurred from the 1960s. For example, Rovero et al. (2012) interviewed villagers living around Uzungwa Scarp that reported hunting in this forest had been most intensive in the period 1965–1975 and oriented towards commercial trade. The disappearance of elephant, buffalo and leopard in this forest happened by the early 1970s, thereafter hunters shifted to primarily using snares, traps and dogs and hunted mainly for subsistence with limited trade within villages. Similarly, Wilson (2001) reported Abbott's duiker as having been quite common until the early 1960s in montane forests across Tanzania, and mentioned frequent records of hunted animals from several sites until the late 1980s. Thus, increasing hunting and habitat destruction may have caused a dramatic decline in the last few decades of this Tanzanian endemic species.

In conclusion, in this study we analysed forest mammal occurrences in the EAM of Tanzania that include a bulk of data not published before, and provides broad-scale ecological patterns which are of conservation relevance. From a methodological point of view, besides generally confirming the usefulness of camera trapping for inventorying elusive mammals in tropical forests (e.g. Ahumada et al. 2011), we showed how heterogeneous data can provide robust ecological assessments. Our results reinforced the urgent need for boosting the ground protection of EAM forests in Tanzania. Most of these forests have not gained from the same level of protection allocated to National Parks (Caro and Davenport 2015; see Hegerl et al. 2015 for a specific example), with Udzungwa being the only EAM block a portion of which is protected as a National Park. However, a number of Forest Reserves have recently been upgraded, or are in process of being upgraded, to Nature Reserve status, a higher ranked category of protected area that should be accompanied by greater efficiency in ground protection allocated to these globally important sites.

Acknowledgements We thank four anonymous reviewers for their constructive comments on earlier versions of the manuscript. Permits for surveys were granted by Tanzania Wildlife Research Institute, Tanzania Commission for Science and Technology, the former Forestry and Beekeeping Division (now Tanzania Forest Service) and Tanzania National Parks. Funding was from the Critical Ecosystem Partnership Fund, a joint initiative of l'Agence Francaise de Developpement, Conservation International, the Global Environment Facility, the Government of Japan, the MacArthur Foundation and the World Bank. Additional funding was from MUSE-Museo delle Scienze and Tanzania Forest Conservation Group (TFCG). We are grateful to Nike Doggart of TFCG for coordinating surveys implemented by MUSE/TFCG, and Charles Leonard of TFCG for logistic support and fieldwork during data collection for MUSE/TFCG surveys.

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