

**PATTERNS OF TEMPORAL AND SPATIAL VARIATIONS OF A FOREST  
MAMMAL COMMUNITY IN THE UDZUNGWA MOUNTAINS  
NATIONAL PARK, TANZANIA**

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**A THESIS SUBMITTED IN FULFILLMENT OF THE  
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OF SOKOINE UNIVERSITY OF AGRICULTURE. MOROGORO,  
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## EXTENDED ABSTRACT

In tropical forests, mammals represent particularly rich communities of species with a variety of trophic groups and wide range of life history traits. This diversity plays a significant role in the functioning of the ecosystems. Yet, tropical forest mammals are negatively affected by a number of factors caused by both natural and anthropogenic activities. However, limited and often not-consistent information is available on the status or trends of mammal communities in tropical forests. For that reason, this study employed systematic camera trapping during 2009 – 2014 to determine the temporal and spatial variations of forest mammal communities. The study was conducted in Mwanihana forest within the Udzungwa Mountains National Park, south-central Tanzania, an outstanding area in Africa for biological richness and endemism, particularly the mammals. Camera trapping data were collected together with field- and remote sensing-based environmental and human disturbance variables considered influential of species' occurrence. State-of-the-art occupancy analytical framework was used to investigate the relationships between species abundance and environmental covariates, including seasonal variations. Occupancy requires repeated temporal replications to resolve the ambiguity between species absence and non-detection when species are unobserved at sample locations. Such analysis was complemented by more classic, multiple regression analysis such as Generalized Linear Models used to analyze effects of covariates on a raw index of abundance, the camera trapping rate (RAI). Results show that a minimum of 32 mammal species are present in the target forest, and the species-specific occupancy modelling revealed novel ecological knowledge for the 11 most detected species, highlighting patterns such as 'montane forest dwellers', e.g. the endemic Sanje mangabey (*Cercocebus sanjei*), and 'lowland forest dwellers', e.g. suni antelope (*Nesotragus moschatus*). Furthermore, the habitat associations in relation with the raw index of abundance was found to be positively correlated with distance to the park border for IUCN-Endangered

Abbott's duiker (*Cephalophus spadix*), indicating preference for interior forest habitat and avoidance of disturbance while that of Eastern Arc-endemic Lowe's servaline genet (*Genetta servalina lowei*) was positively correlated with the diversity of large trees but negatively correlated with visibility and herbaceous cover, indicating preference for mature forest habitat. As for the analysis of seasonal variation (as especially related to rainfall), only bush pig (*Potamochoerus larvatus*) showed a significant decrease in detectability from dry to wet season. Analysis of the variation of relative abundance with space *and* time revealed that anthropogenic activity such as firewood collection had a negative impact, by lowering relative species' abundance for a number of species such as Harvey's duiker (*Cephalophus harveyi*). Moreover, the relative abundance of the pooled species most targeted by poaching increased with decreased poaching activities over time.

Overall this study shows that the analysis of camera trap data deployed using systematic and standardized protocols - and with account for imperfect detection - can provide robust ecological assessments of mammal communities. It further shows how these assessments can determine the various drivers of change of mammals' occurrence (both natural and anthropogenic), hence providing insights that are of clear potential relevance to mammals' conservation management.

## THESIS ORGANIZATION

This thesis starts with an extended abstract followed by declaration statement, copyrights statement, acknowledgements, and dedication. The extended abstract summarises briefly the study objectives, approaches to sampling, main findings, conclusions and recommendations. The core of the thesis consists of three chapters. The first chapter covers introduction which includes background information, problem statement, hypotheses and study objectives. It also includes a sub-section on methods with descriptions of study area, sampling, and data analysis. Chapter two contains a series of three original papers published in international, peer-reviewed journals (*Paper 1*, *Paper 2* and *Paper 3*) and one manuscript which is under submission at the time of writing (*Paper 4*). Chapter three presents in summary the major findings, conclusion and recommendations.

**DECLARATION**

I, EMANUEL HENRY MARTIN, do hereby declare to the Senate of Sokoine University of Agriculture that this thesis is my own original work, done within the period of registration and that it has neither been submitted nor being currently submitted in any other institution.



11/11/2016

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Emanuel Henry Martin  
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Date

The above declaration is confirmed by:



11/11/2016

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Prof. V.G. Ndibalema  
(Supervisor)

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Date

11/11/2016

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Dr. F. Rovero  
(Supervisor)

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Date

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## ACKNOWLEDGEMENTS

First and foremost I would like to thank the Almighty God, the source of all knowledge, understanding and wisdom. From him I owe all that I have and all that I am.

I would also like to thank Tropical Ecology Assessment and Monitoring (TEAM) Network project (a collaboration between Conservation International, the Missouri Botanical Garden, the Smithsonian Institution, and the Wildlife Conservation Society, partially funded by these institutions, the Gordon and Betty Moore Foundation and other donors) for providing the scholarship for this Ph.D. and MUSE – Museo delle Scienze (Trento, Italy) for additional funding.

I am deeply indebted to my employer, College of African Wildlife Management Mweka (CAWM) for granting me study leave to pursue my Ph.D. studies in Morogoro.

Special gratitude is extended to my main supervisor and also the Head of Department of Wildlife Management at Sokoine University of Agriculture (SUA), Professor Vedasto G. Ndibalema for his insights, patience, commitment and guidance whenever I needed his assistance throughout the research period. Further thanks are extended to my co-supervisor, Curator for the Tropical Biodiversity Section at MUSE and Director of the Udzungwa Ecological Monitoring Centre (UEMC), Dr. Francesco Rovero, for both his moral support and his in-depth knowledge on camera trapping and ecological modelling. I further thank him for spearheading and organising trainings on statistics and Geographical Information System (GIS) that I undertook in Tanzania (Arusha) and abroad, particularly in Italy and United Kingdom.

Adhering to the rules and regulations governing research activities in Tanzania are important components for successful accomplishment of studies. I therefore would like to extend my gratitude to the Tanzania Wildlife Research Institute (TAWIRI) and Tanzania National Parks (TANAPA) for the research permits. I also thank Park wardens and staff from Udzungwa Mountains National Park (UMNP) and UEMC for their valuable logistic support during fieldwork. Several field assistants helped invaluablely in the field, especially R. Mwakisoma, A. Mwakisoma, S. Shinyambala, D. Msoffe, N. Masenge and A. Uisso, without forgetting our best ever field cook, I. Ndyamukama.

The support, love and care of my wife, Yuster; daughters, Miranda and Michelle; son, Milan; together with my parents, my in-laws and relatives, inspired me during all stages of my four year studies. “Thank you for your endlessly support, encouragement and patience during these trying moments”.

Emanuel Henry Martin

November, 2016



## **DEDICATION**

This Ph.D. work is dedicated to God almighty; my dear wife, Yuster; daughters, Miranda & Michelle; son, Milan and my parents.

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## LIST OF PAPERS

### ***Paper 1:***

Rovero F., **Martin E.**, Rosa M., Ahumada J. A. and Spitale D. (2014). Estimating Species Richness and Modelling Habitat Preferences of Tropical Forest Mammals from Camera Trap Data. *PLoS ONE* 9(7): e103300.

### ***Paper 2:***

**Martin E. H.**, Cavada N., Ndibalema V.G. and Rovero F. (2015) Modeling fine scale habitat associations of medium to large size forest mammals in Udzungwa Mountains National Park, Tanzania. *Tropical Zoology* 28 (4):137-151.

### ***Paper 3:***

**Martin E. H.**, Ndibalema V.G. and Rovero F. (2016) Does variation between dry and wet seasons affect tropical forest mammals' occupancy and detectability by camera traps? Case study from the Udzungwa Mountains, Tanzania. *African Journal of Ecology* doi:10.1111/aje.12312

### ***Paper 4:***

**Martin E. H.**, Ndibalema V.G. and Rovero F. (in submission) The effect of human disturbance on the spatial and temporal patterns of relative abundance of medium to large bodied forest mammals in the Udzungwa Mountains of Tanzania.



### **DECLARATION OF THE PAPERS**

I, Emanuel H. Martin, do hereby declare to the Senate of Sokoine University of Agriculture that the above listed papers comprising this thesis, summarise my independent efforts and they constitute my own original work and they will not be part of another thesis in any other University.

**LIST OF ABBREVIATIONS AND ACRONYMS**

|        |                                                       |
|--------|-------------------------------------------------------|
| AIC    | Akaike Information Criterion                          |
| ANCOVA | Analysis of Covariance                                |
| CAWM   | College of African Wildlife Management, Mweka         |
| CF     | Compact Flash                                         |
| CT     | Camera traps                                          |
| DBH    | Diameter at Breast Height                             |
| ETM+   | Enhanced Thematic Mapper plus                         |
| GAM    | Generalised Additive Model                            |
| GIS    | Geographical Information Systems                      |
| GLM    | Generalised Linear Model                              |
| GPS    | Geographical Positioning System                       |
| IUCN   | International Union for Conservation of Nature        |
| MBA    | Mean Basal Area                                       |
| MUSE   | Museo delle Scienze                                   |
| RAI    | Relative Abundance Index                              |
| SD     | Stem density                                          |
| SUA    | Sokoine University of Agriculture                     |
| TANAPA | Tanzania National Parks                               |
| TAWIRI | Tanzania Wildlife Research Institute                  |
| TBA    | Total Basal Area                                      |
| TEAM   | Tropical Ecological Assessment and Monitoring Network |
| TM     | Thematic Mapper                                       |
| UEMC   | Udzungwa Ecological Monitoring Centre                 |
| UMNP   | Udzungwa Mountains National Park                      |
| VD     | Very deep                                             |

## CHAPTER ONE

### 1.0 GENERAL INTRODUCTION

#### 1.1 Factors Associated with Temporal and Spatial Variations of Terrestrial Mammal Communities

The word ‘temporal’ is derived from the Greek word ‘tempo’ which means time whereas spatial is a term that refers to space (White, 2012). Both terms are of relevance when determining the variations of the tropical forest mammal communities. As observed by Thomas *et al.* (2001), there is poor understanding of how species of vertebrates are distributed across mosaic landscape, and yet this information is basic to any research on community dynamics or conservation biology. Globally, there is a general deterioration on the status of mammals, and tropical forest mammals are the least studied and the most threatened (Schipper *et al.*, 2008) when compared to those of temperate regions (Cayuela *et al.*, 2009). Several factors such as hunting, habitat fragmentation, deforestation and agricultural expansion are considered to be the major drivers of spatio-temporal variation (Kinnaird *et al.*, 2003; O’Brien *et al.*, 2003; Ahumada *et al.*, 2011).

In addition other factors such as vegetation structure and composition, intra and interspecies composition, geographical range, climate change (see Post *et al.*, 2009) and food availability (O’Brien *et al.*, 2003) are also drivers of variation. The degree to which these factors affect the forest mammal species may vary but little work has been done to assess the relative importance of these factors to forest mammal species’ long term persistence (Tilson *et al.*, 1994).

## 1.2 Species Richness and Abundance

Species richness is defined as the total number of species occurring in a location (Schluter and Ricklefs, 1993; Lande, 1996) whereas species abundance refers to the relative representation of a species in a particular community (Wright, 1991) and it is usually measured as the number of individuals found per sample. Quite often, the objective of determining species richness is to have baseline information upon which focal studies can be established (Rovero *et al.*, 2010). Notably, linking forest mammal species richness and their abundance is very critical in determining the quality of habitat. For example, Ahumada *et al.* (2011) observed that areas with intact or continuous forests have higher levels of mammal species diversity and abundance compared to fragmented forests. Similar observation was noted by O'Brien *et al.* (2003) in Indonesia on which both the abundance of Sumatran tiger and its preys was higher in areas with no or low human disturbances compared to the areas with high human disturbances.

Arguably, wildlife management and conservation require unbiased information about population size and about how species richness and abundance is shaped by environmental factors and human activity. Such knowledge is especially important for managing rare and vulnerable species to ensure that actions aimed at addressing apparent population declines or protecting habitats are well informed (Buckland *et al.*, 2005). As Tobler *et al.* (2008) correctly observe knowledge of the presence and distribution of species is critical to planning and evaluating strategies for conservation of biodiversity. However, Balmford *et al.* (2005) noted that one of the greatest hindrances to understanding and conserving biodiversity is our inability to determine exactly how many

species we have and how fast that number is changing with time. As one of the responses to that the indices are being used as alternative to true abundances. For example Bowkett *et al.* (2008) and Rovero *et al.* (2013) used trapping rate from camera trap data as an index of relative abundance to study mammal species' habitat associations. Trapping rate is obtained as the number of images filtered by 1 hour divided by the number of sampling days for each photographed species (Rovero *et al.*, 2013). However, O'Brien (2011), observed that this metric does not account for imperfect detection and therefore is of limited inference. Conversely, various studies have shown that the metric can be correlated with true abundance (Carbone *et al.*, 2001; O'Brien *et al.*, 2003; Rowcliffe *et al.*, 2008), including the study by Rovero and Marshall (2009) on Harvey's duiker in the Udzungwa Mountains.

### **1.3 Species Distribution Models and Mapping**

Predictive species distribution models are empirical models relating field observations to environmental variables, based on statistically or theoretically derived response surfaces (Guisan and Thuiller, 2005). The most common strategy for estimating the potential geographic distribution of a species is to characterize the environmental conditions that are suitable for that species (Cayuela *et al.*, 2009). The spatial distribution of environments that are suitable for a species can then be estimated across a given study region. A wide variety of modeling techniques have been developed for this purpose including occupancy modeling. Occupancy is defined as the proportion of sites where a species is expected to occur, with detection probability, being the probability that a species is detected given it is present (Mackenzie *et al.*, 2002). Various studies have used occupancy modeling in their approaches including a study by Mackenzie *et al.* (2002) in

estimating occupancy rates for anurans in Michigan; Ahumada *et al.* (2011) in determining the global structure and diversity of tropical forest mammals and Rovero *et al.* (2013) in determining distribution and habitat association for grey faced sengi (*Rhynchocyon udzungwensis*) in Udzungwa Mountains.

Apart from using occupancy which is regarded as a true surrogate of species abundance (Ahumada *et al.*, 2011), there are other approaches that rely on the use of raw data such as trapping rates (Relative Abundance Index – RAI) as a proxy of relative abundance. Trapping rate with regard to camera trap data is defined as the number of events of each photographed species filtered by 1 hour divided by the number of sampling days (Rovero and Marshall, 2009). While this metric is an index that does not account for imperfect detection (O’Brien, 2011), and therefore is of limited inference, this approach is supported by studies that show how this index is correlated with true abundance (Carbone *et al.*, 2001; O’Brien *et al.*, 2003; Rowcliffe *et al.*, 2008). Applications of species distribution model methods include a study by Bowkett *et al.* (2008) that used generalized linear model (GLM) to determine the correlations between trapping rate and habitat associations of forest antelopes in Udzungwa Mountains.

#### **1.4 Problem statement and study justification**

In the tropical forests, mammals comprise rich communities of species from a variety of diverse trophic groups and a wide range of body sizes (Robinson and Redford, 1986). This diversity plays a significant role in the functioning of the ecosystems (Struhsaker, 1997). Seldom is information available on the status or trends of mammal communities, in tropical forests (Ahumada *et al.*, 2011). Several studies that have attempted to study

terrestrial mammals in tropical forests have been focusing to either fauna inventories (see Srbek-Aruajo and Garcia, 2005; Azlan and Lading, 2006; and Tobler *et al.*, 2008), that led to a new range of records (De Luca and Rovero, 2006; Sanderson, 2007), discovery of new species such as the new giant elephant-shrew (*Rhynchocyon udzungwensis*) (Rovero *et al.*, 2008) or studying abundance of ungulates particularly duikers (Rovero and Marshall, 2009), and studying carnivores (De Luca and Mpunga, 2005). Furthermore, most studies that focused on long term monitoring that involves both temporal and spatial distributions of forest terrestrial mammals have been restricted to single and charismatic species, e.g. tiger (*Panthera tigris*) (Karanth *et al.*, 2011), leopard (*Panthera pardus*) (Henschel and Ray, 2003), and certain mammal groups, e.g. primates (Rovero *et al.*, 2012). However, little is still known on how terrestrial mammal communities in the tropical forests are being distributed spatially and changing with respect to time.

This study aimed to fill this gap by studying mammal community of Mwanihana forest in Udzungwa Mountains National Park (UMNP) as a case study, with the focus on medium to large bodied ground dwelling forest mammals. The findings from this study will help the Park management to support biodiversity conservation in the tropics, by supporting the development of conservation strategies and plans, identifying knowledge gaps, and providing a tool to examine various threats facing tropical forest mammal community. Furthermore, the study will add to the existing body of knowledge and stimulate further research in the field of conservation.

## **1.5 Objectives**

### **1.5.1 General objective**

The main objective of this study was to assess patterns of temporal and spatial variations of species and guilds of the mammal community of Mwanihana forest in UMNP.

### **1.5.2 Specific objectives**

The specific objectives were:

- i. To determine species richness and estimate abundance.
- ii. To determine temporal and seasonal variation of the forest mammal community.
- iii. To assess factors associated with the patterns of variations in forest mammal community.
- iv. To map species distribution using remote sensing and ground data on relevant habitat features.

## **1.6 Hypotheses**

The following hypotheses were developed:

**Hypothesis 1:** The mammal community in Mwanihana forest would not show significant changes in species richness within the time frame of the study.

**Hypothesis 2:** The forest-dwelling species would not experience colonization or extinction between dry and wet seasons, and therefore their occupancy levels would not change significantly, while detectability could change.



**Hypothesis 3:** A number of forest mammal species (those with enough records for analysis) would show significant spatial variations due to species-specific habitat preferences.

**Hypothesis 4:** Some of the forest mammals would tend to recolonize the eastern side of Mwanihana forest after firewood collection ban, and species' relative abundance would vary with poaching pressure, while overall mammals species' relative abundance would increase due to decreased poaching activities with time.

## **2.0 MATERIALS AND METHODS**

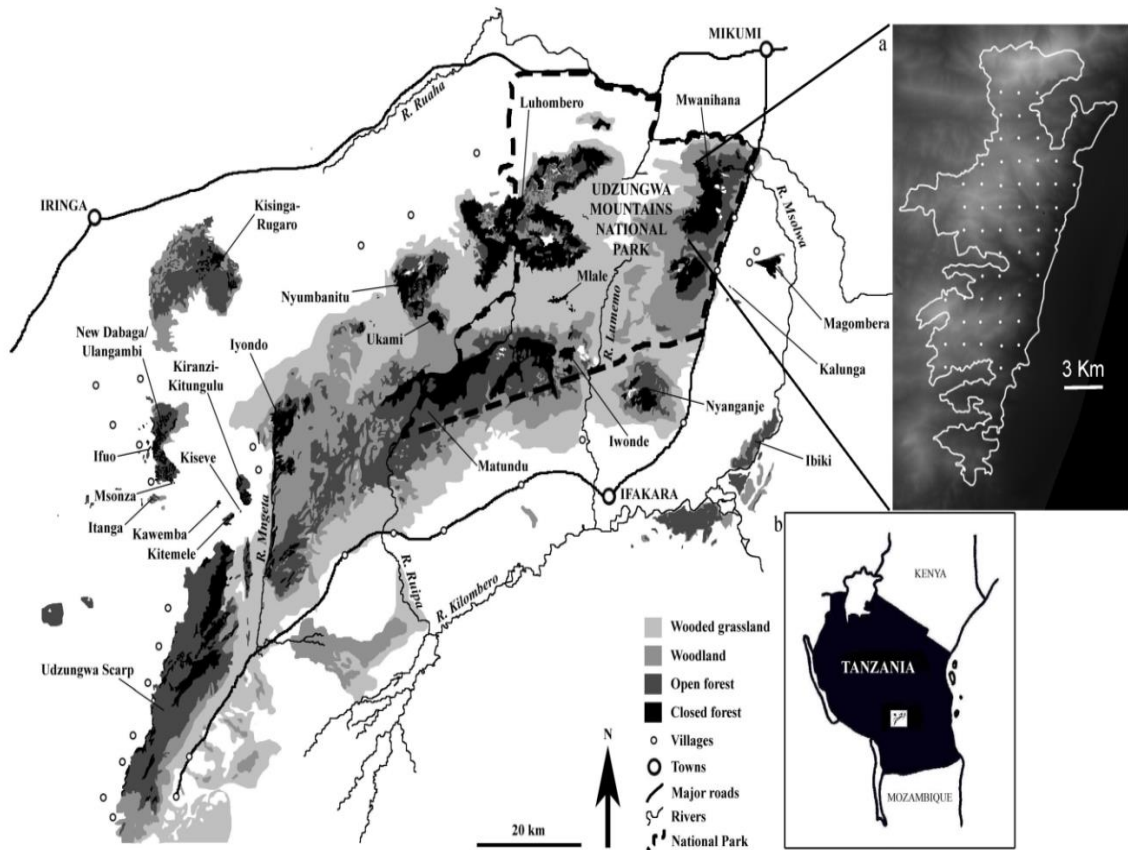
### **2.1 Study Site**

All four studies (*paper 1, 2, 3 and 4*) were conducted in Mwanihana forest, located on the eastern side of UMNP (Fig.1). UMNP is centred on 7°46'S, 36°51'E has a size of 1990 km<sup>2</sup> and is also on the eastern part of the Udzungwa Mountains. The Udzungwa Mountains are a part of Eastern Arc Mountains characterized by a mosaic of moist forest blocks interspersed with drier habitats found in south-central Tanzania (Rovero *et al.*, 2014a). Mwanihana is one of the largest forest blocks in the range (192 km<sup>2</sup> of closed forest habitat) with continuous vegetation cover from 300 to over 2000 m above sea level (Bowkett *et al.*, 2008).

The forest habitat broadly ranges east-west from lowland deciduous forest to montane evergreen forest (Lovett *et al.*, 2006). The habitats at lower altitudes is mostly comprised of dry forest, followed by semi-deciduous forest of moderate to old-growth (transitional) forest and evergreen old growth montane forest (Lovett *et al.*, 2006 ; Rovero *et al.*, 2006; Martin *et al.*, 2015). The estimated mammal species richness in Mwanihana forest ranges

between 32 to 34 species which include endemic species to the Eastern Arc Mountains such as Sanje mangabey (*Cercocebus sanjei*) and Udzungwa red colobus (*Procolobus gordonorum*) (Rovero *et al.*, 2014b).

Temperature in Udzungwa varies according to the pronounced altitudinal gradient while there is also modest seasonal variation, with the maximum in November (mean 24.2°C), and minimum in July (mean 19.4°C; data from [www.worldclim.org](http://www.worldclim.org) in Dubois *et al.*, 2015). The total annual rainfall in Mwanihana forest is around 1500 mm, with light and heavy rainy seasons from November to February and March to May, respectively, and the dry season from June to October (TEAM Network unpublished data; Dubois *et al.*, 2015).



**Figure 1:** Map of the Udzungwa Mountains showing the main forest blocks with closed-canopy forest darker in colour (source: Rovero *et al.*, 2014b). The study forest

was Mwanihana (top right in set) where the 60 camera trap sites are shown as white dots and the background is a black with Digital Elevation Model

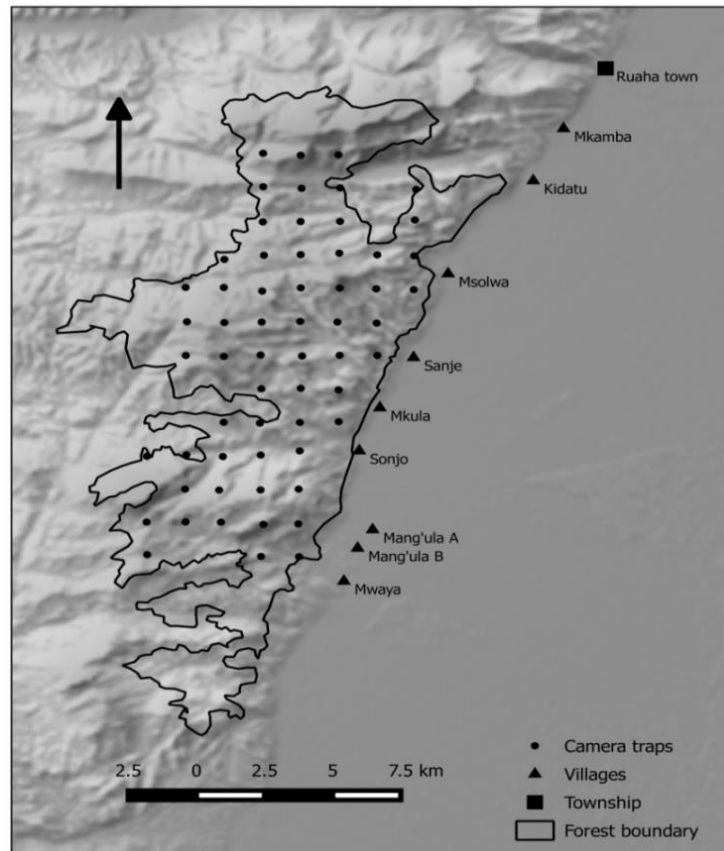
## **2.2 Sampling and Measurements**

Various sampling techniques were used for data collection. Two sets of data that addressed all the four specific objectives/papers were obtained. The first set of data was obtained from camera trap data and was used to determine the species richness in *paper 1*, and also occupancy estimates in *paper 1* and *3*. Furthermore, camera trap data were used to determine trapping rate (also regarded as an index of relative abundance) in *paper 2* and *4*. The second set of data which mainly formed the covariates that deemed to explain the factors responsible for both temporal and spatial variations of forest mammals. The data include fine scale vegetation data obtained from vegetation sampling technique adopted from Bowkett *et al.* (2008); major habitat data obtained from ArcGIS geo processing tools; climate data from weather stations and poaching data from field surveys.

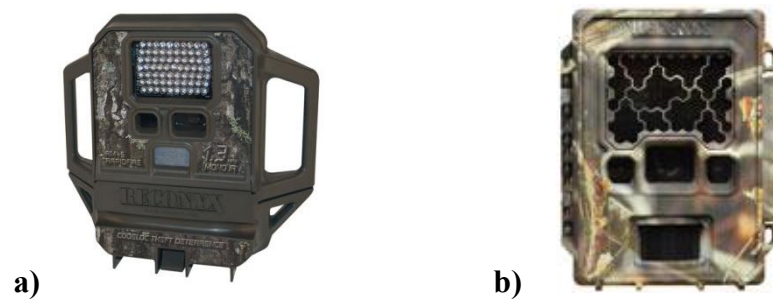
### **2.2.1 Camera trap data**

The use of camera trap as a sampling tool yielded pictures of different species including information such as date, time and camera trap site. Identification of species was done using a field guide book on African mammals (Kingdon, 2003). Species abundance was determined by using occupancy (O'Brien and Kinnaird, 2011). Camera trapping data were collected annually in dry seasons from year 2009 to 2014. However, in year 2014, besides the usual 60 camera traps set during the dry seasons, more 20 camera traps were set during the wet season. Sixty camera trap points regularly arranged on a grid covering most of Mwanihana forest (one camera every 2 km<sup>2</sup>), thus covering an area of 120 km<sup>2</sup>, (Fig. 2) was covered. Each camera was left on site for a minimum of 30 days as

recommended standard period (O'Brien, 2008). Because of material constraints (availability of only 20 cameras and time needed to set and retrieve cameras in the forest), sequential sampling of three arrays of 20 camera-trap sites was done. Digital camera-traps with an infrared flash (model Reconyx RM 45 and HC 500 (Fig.3)) were used. Field locations of camera traps sites were guided by the use of a Global Positioning System (GPS) hand-held unit with pre-loaded sampling points. The actual locations of the camera-traps at the required sites were determined by the presence of wildlife trails and other animal signs. Cameras were set to work continuously without delay between consecutive photos. The Reconyx models are able to take consecutive photos with intervals of about 1 second between shots. Rechargeable batteries (6 C-size each for RM 45 and AA for HC 500) were used as a source of power and the data captured were stored in Compact Flash (CF) memory cards (of at least 2 GB).



**Figure 2:** Mwanihana forest showing camera traps points and surrounding villages  
Adapted from TEAM Network (2011)



**Figure 3:** Camera traps (a) Reconyx Model RM45 and (b) Reconyx Model HC 500

## 2.2.2 Data on potential covariates of variations in forest mammal community

### 2.2.2.1 Vegetation sampling

A detailed and quantitative habitat assessment at all 60 camera trap locations was conducted.

A vegetation assessment protocol previously developed in Udzungwa for a camera trapping study on forest ungulate was adapted (Bowkett *et al.*, 2008). Thus, measurements of vegetation at three spatial scales were taken including small, mid and broadest scales (see *paper 2* for more details). The variables that were obtained and used in the analysis under this method are listed in Table 1.

**Table 1:** Vegetation variables measured in plots centred on camera-trap sites, and used to analyse habitat associations of forest mammals in the Udzungwa Mountains of Tanzania. Redundant variables that were not used in the regression analysis are reported in the footnotes

| Type of plots for the measurements | Variables used in the regression analysis (abbreviation)  |
|------------------------------------|-----------------------------------------------------------|
| 20 large trees (> 10 cm DBH)       | Stem density (SD1)                                        |
|                                    | Mean basal area (MBA1)                                    |
|                                    | Diversity (Simp1) <sup>a</sup>                            |
| 20 small trees (5- 10 cm DBH)      | Mean basal area (MBA2)                                    |
|                                    | Diversity (Simp2) <sup>b</sup>                            |
| 3 x 3 m plots                      | Small trees stem density (SD3)                            |
|                                    | Diversity (LogSimp3) <sup>c</sup>                         |
| 1 x 1 m plot (forest floor cover)  | Herbaceous layer and seedlings (Herbs_Seedl) <sup>d</sup> |
|                                    | Sum of deep and very deep leaf litters (Sum Depth D_VD)   |
|                                    | Visibility*                                               |

<sup>a</sup>Simp1 correlated with richness1 ( $r = 0.9$ ,  $P < 0.01$ ,  $n = 59$ )

<sup>b</sup>Simp2 correlated with richness 2 ( $r = 0.8$ ,  $P < 0.01$ ,  $n = 59$ )

<sup>c</sup>LogSimp3 correlated with richness 3 ( $r = 0.8$ ,  $P < 0.01$ ,  $n = 59$ )

<sup>d</sup>Herbs\_Seedl correlated with leaves ( $r = -0.7 < 0.01$ ,  $n = 59$ )

\*Measured 20 m from the centre of the plot

### 2.2.2.2 Spatial data

A number of spatial environmental covariates deemed relevant to explain both the spatial variations of species' richness, occupancy and relative abundance of the species were determined by using geo processing tools available in ArcGIS. The following variables were calculated: (1) distance from eastern park border ('border'), (2) distance from forest

edge ('edge'), (3) forest habitat type, i.e. montane forest and lowland forest ('habitat'), (4) slope and (5) distance to rivers. The distance from each camera trap point to the nearest 'border', 'edge', or river segment was calculated in ArcGIS. Forest habitat type was mapped using a supervised classification approach on Landsat TM and ETM+ satellite imagery (30 m resolution). Habitats were categorized into three forest types: 1) Montane, 2) Deciduous, and 3) Regenerating.

#### **2.2.2.3 Climate data**

Climate variables especially temperatures and rainfall for a period of six years (2009 – 2014) were obtained from TEAM Udzungwa Climate Station which is located within the Mwanihana forest block. Other climate data records in the area for the past 50 years were obtained from Global Climate Data ([www.worldclim.org](http://www.worldclim.org)). The climate data were mainly used for *paper 3* that addressed the effects seasonality (rainfall) on species occupancy.

#### **2.2.2.4 Anthropogenic factors**

Data on the effects of poaching activities on the forest mammal species' relative abundance was obtained based on the survey aimed to determine the number of snares in the forest. The survey was done alongside camera trap setup and removal exercises from July to November each year from 2009 – 2014 based on three camera trap arrays i.e. array I "South", II "Centre" & III "North" comprised of 20 camera sites each. During the survey the number of active snares that were found per each camera trap array was recorded (and removed by park rangers) every year. Each survey lasted for 20 days per array.

### **2.3 Data Analysis**

All statistical analyses were carried out in R software versions 3.1.1 and 3.2.2 (R Core Team, 2013). Detailed analyses are provided in each respective paper in chapter two. Here, a summary of major analysis used is given but I refer to methods section for details.

### 2.3.1 Occupancy estimates and modeling

Occupancy is an example of a state variable, i.e. a numerical value that indicates the status of a wildlife population. Since occupancy analysis is based on the detection history of a particular species (see below), a special script is needed in R to match the correct format of the ‘unmarked’ package used for the analysis. In this case, the study used scripts already developed by Ahumada *et al.* (2011) for TEAM data, to arrange the species’ detection/non-detections data into species’ occupancy matrices. Data for each species were arranged as matrices of sites by surveys (i.e. sampling occasion). Each entry indicated if the species was observed at site  $i$  on survey  $j$  or not. If the species was observed at site  $i$  on survey  $j$ , then the entry was given a score of 1. If the species was not observed, then the entry was given a score of 0. NA indicated site  $i$  was not sampled on survey  $j$ . A resolution of five days was used for the species-specific occupancy matrix.

In order to run the models with all the covariates that deemed necessary to explain the spatial distributions of the forest mammals, the following models were performed: For *paper 1*, a single season occupancy model was used as it involved data collected during the dry season only. Under this the model was first performed without the covariates and referred to as null model. This is the default model which specifies that  $\Psi$  and  $p$  are constant across all the study sites and surveys, and do not vary with environmental covariates i.e.  $\Psi(.)$ ,  $p(.)$ . This model was then compared with the ones with all the selected covariates. A second model with all the covariates used was then performed on



which was allowed to vary. The covariates used included (1) distance to the eastern National Park border (border), (2) distance to the forest edge (edge), (3) distance to rivers (river) and (4) forest habitat type, i.e. montane forest and lowland forest (habitat).

For *paper 3*, a dynamic occupancy model was used. Unlike single-season models, the dynamic occupancy model allows to estimate the parameters governing changes in occupancy state variable in addition to  $p$ , namely colonization ( $\gamma$ ) and extinction ( $\epsilon$ ) probability (MacKenzie *et al.*, 2003) (For details, see paper 3).

### **2.3.2 Habitat associations for the selected mammal species**

Occupancy modeling was used to determine species distribution based on major habitat covariates as described in subsection 2.3.1. However, other habitat variables at a fine scale levels for the selected species were determined by using GLM (For details see *paper 2*). Under this, predictor variable was event count (trapping rate) and explanatory variables included covariates obtained from habitat analysis. The event counts were computed as the number of images filtered by 1 hour for each photographed species (Rovero *et al.* 2013; Rovero *et al.*, 2014b).

Hence, instances where the same species were captured by the same camera more than once within 1 hour were excluded from the analysis as a compromise between scoring the same individual multiple times and missing individuals (e.g. Kinnaird *et al.* 2003). While this metric is an index that does not account for imperfect detection (O'Brien 2011), and therefore is of limited inference, the choice is supported by studies that show how this index is correlated with true abundance (Carbone *et al.*, 2001; O'Brien

*et al.*, 2003; Rowcliffe *et al.*, 2008), including the study by Rovero and Marshall (2009) on Harvey's duiker in the Udzungwa Mountains. The GLM can be presented by the following equation:

$$Y = X_1\beta + X_2\beta_2 \dots X_n$$

Y=dependent (event counts)

$\beta$  = constant (Y-intercept)

X=Mean basal area (MBA), total basal area (TBA) and diversity (Simp 1) for large trees (DBH > 10cm); Mean basal area (MBA2) and Diversity (Simp 2) for medium trees (DBH = 5-10cm); small trees stem density (SD3) and diversity (logsimp3) for the under story and herbaceous layer, seedling and leaf litters for the forest floor.

Since the response variables were counts, which are always non-negative and that tend to be heterogeneous, Poisson GLM was chosen owing to its ability to deal with both aspects (Zuur *et al.*, 2010). Whenever over-dispersion was detected in the model (i.e. over-dispersion > 1.5), standard errors were corrected using a quasi-Poisson GLM, adding an over-dispersion parameter  $\phi$  to the variance of the response variable ( $Y$ ). Following Zuur *et al.* (2009) a stepwise backward selection was employed to derive the best model.

### 2.3.3 Anthropogenic factors

After determining the major habitat variables described in subsection 2.3.2 for *paper 1*, habitat associations at fine scale levels described in subsection 2.3.2 for *paper 2* and seasonality with respect to rainfall described in *paper 3*, other factors included in the study were related to human activities. These activities included firewood collection and poaching. To determine the effects of anthropogenic factors, the following analyses were performed: A paired sample t-test was used to determine the effects of firewood

collection before and after it was banned in UMNP. An independent sample t-test was then used to determine the effects of poaching between the northern and southern sides of the Park on which different poaching pressures were experienced. To determine if the differences in relative abundance between forest portions changed with time, analysis of covariance (ANCOVA) was used to compare the slopes of the regression between years and trapping rates for north and southern areas. Also Pearson's correlation test was used to determine the relation between mammals species relative abundance with the number of snares removed (For details see *paper 4*).

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## **CHAPTER TWO**

### **PAPER ONE**

#### **Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data**

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# Estimating Species Richness and Modelling Habitat Preferences of Tropical Forest Mammals from Camera Trap Data

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## Abstract

Medium-to-large mammals within tropical forests represent a rich and functionally diversified component of this biome; however, they continue to be threatened by hunting and habitat loss. Assessing these communities implies studying species' richness and composition, and determining a state variable of species abundance in order to infer changes in species distribution and habitat associations. The Tropical Ecology, Assessment and Monitoring (TEAM) network fills a chronic gap in standardized data collection by implementing a systematic monitoring framework of biodiversity, including mammal communities, across several sites. In this study, we used TEAM camera trap data collected in the Udzungwa Mountains of Tanzania, an area of exceptional importance for mammal diversity, to propose an example of a baseline assessment of species' occupancy. We used 60 camera trap locations and cumulated 1,818 camera days in 2009. Sampling yielded 10,647 images of 26 species of mammals. We estimated that a minimum of 32 species are in fact present, matching available knowledge from other sources. Estimated species richness at camera sites did not vary with a suite of habitat covariates derived from remote sensing, however the detection probability varied with functional guilds, with herbivores being more detectable than other guilds. Species-specific occupancy modelling revealed novel ecological knowledge for the 11 most detected species, highlighting patterns such as 'montane forest dwellers', e.g. the endemic Sanje mangabey (*Cercocebus sanjei*), and 'lowland forest dwellers', e.g. suni antelope (*Neotragus moschatus*). Our results show that the analysis of camera trap data with account for imperfect detection can provide a solid ecological assessment of mammal communities that can be systematically replicated across sites.

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**Data Availability:** The authors confirm that all data underlying the findings are fully available without restriction. Data used for this study, along with all TEAM data, are available for public download at <http://www.teamnetwork.org/data/query>.

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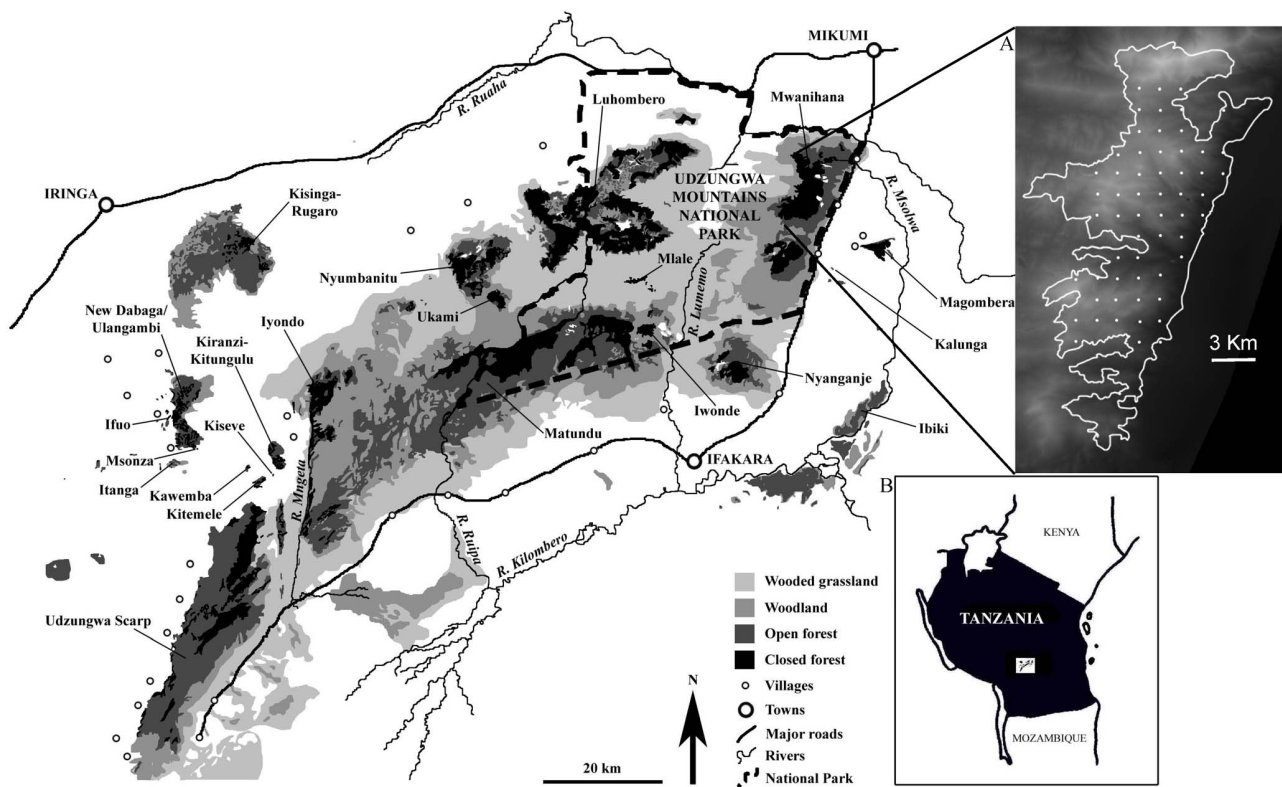
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## Introduction

Profiling large-bodied animal communities, such as mammals, fundamentally implies assessing species richness and composition. Determining a state variable of species' abundance is also required to make inferences on species distribution, habitat associations, and trends over time [1–4]. In this context, medium-to-large mammals in tropical forests are of priority because they represent a rich and functionally diversified component of this biome, and yet they are universally threatened by hunting, and habitat loss and fragmentation [5–8]. The removal, or decrease in abundance, of tropical mammals will likely impact forest dynamics [11,12] due to their direct involvement in seed predation, seed dispersal, herbivore control, nutrient cycling and other ecosystem functions [9,10]. Systematic assessments that allow inference of tropical forest mammal communities in space and time remain limited and a chronic gap persists in standardized data collection.

The Tropical Ecology, Assessment and Monitoring (TEAM) network was set-up to fill this gap by establishing a network of field stations, scientists and partners across the tropics for long-term monitoring of mammal communities using a standardized and annually repeated sampling protocol [13]. The excellent potential of TEAM network data for answering questions on the status and trends of mammals has already been shown both through the first pan-tropical analysis from seven sites, which compared communities' richness and composition against forest area and fragmentation [8], as well as the first assessment of temporal changes at one particular site in Costa Rica using dynamic occupancy analysis [14]. In the present study, we used data from the first TEAM site established in Africa in 2009, the Udzungwa Mountains of south-central Tanzania, to propose a standardized approach for assessing the community of medium-to-large mammals detected through camera-trapping during the first, baseline year of the long-term programme.



**Figure 1. Map of the study area, the Udzungwa Mountains of south-central Tanzania.** The map shows the main habitat types and blocks with closed-canopy forest (adapted from [53]). The study forest was Mwanihana in the northeastern portion of the range, which is zoomed in inset (A) where the 60 camera trap sites are shown as white dots and the background is a Digital Elevation Model (dark is lower elevation); (B) shows the position of Udzungwa in Tanzania.  
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The use of camera trapping for wildlife studies has increased exponentially in the last decade as it is an efficient, cost-effective and easily replicable tool to study and monitor ground-dwelling terrestrial mammals and birds [15,16]. Camera trapping is particularly suited to collect standardized data because sampling effort can be easily controlled for and sampling design can be replicated across time and space [15]. In addition, sampling can be considered as multiple occasions during a discrete season, hence data are suited for analyses that account for imperfect detection, such as occupancy [17,18]. Occupancy ( $\psi$ ) is defined as the proportion of area, patches or sites occupied by a species [19] and can be used as a surrogate for abundance [20]. Detection probability ( $p$ ) is defined as the likelihood of detecting an individual, or species, during a sampling occasion [18]. With the inclusion of covariates, occupancy models provide a robust statistical framework for testing scientific hypotheses. For example, one can test for differences in occupancy rates between study sites that contrast by habitat type, hunting level, distance to key resources, climate conditions and vegetation features [21,22]. In addition, the same approach used for occupancy analysis can also be used for estimating species richness and accumulation [23].

The Udzungwa Mountains are an area of outstanding importance for biodiversity endemism and conservation in Africa [24], and are particularly rich in forest dwelling mammals [25]. Through our assessment we aimed to (1) evaluate sampling effort and estimate species' richness, (2) determine drivers of variation in species richness and detection probability ( $p$ ) using an occupancy framework [17], (3) estimate species' occupancy ( $\psi$ ), and (4)

determine the best habitat and human disturbance predictors of both  $\psi$  and  $p$  to identify major patterns of species' responses to these predictors.

## Materials and Methods

### Ethics Statement

Data collection used non-invasive, remotely set camera traps and hence did not involve direct contact or interaction with the animals. Fieldwork was done under research permit number 2009-139-NA-2009-49 to FR, issued by the Tanzania Commission for Science and Technology (COSTECH).

### Study area

The Udzungwa Mountains of south-central Tanzania (over 10,000 km<sup>2</sup>; 7°40'–8°40'S, 35°10'–36°50'E) are a mosaic of moist forest blocks interspersed with drier habitats. The study was conducted in Mwanihana forest, which at 180 km<sup>2</sup> is one of the largest forests in the area and with the widest, continuous forest elevation range (290–2250 m a.s.l.; Fig. 1). The forest is inside the Udzungwa Mountains National Park (1990 km<sup>2</sup>). The eastern border of the forest coincides with the eastern boundary of the park. The forest habitat broadly ranges east-west from lowland, deciduous forest to montane, evergreen forest [26]. The lower elevation habitats, which include deciduous, semi-deciduous and riverine evergreen forest, have been degraded historically and have large portions of secondary, regenerating vegetation. The interior forest is mainly undisturbed with large chunks of pristine,

closed-canopy moist forest. Anthropogenic disturbance in the form of firewood collection occurred at the lower elevations, a practice likely coupled with illegal bush meat hunting done using snares. The upper elevation zone has lower canopy and bamboo forest with rocky and very steep areas, especially in the northern part. Total rainfall in Mwanihana forest is around 1500 mm per year (data from Udzungwa Mountains National Park); rainfall measured at 1200 m a.s.l. by an automatic rainfall gauge was 1387 and 1451 mm in 2011 and 2012, respectively (FR/TEAM Network, unpublished data). The dry season spans from June to November, while two rainy seasons occur during November–June. In 2012, mean monthly air temperature at 1200 m a.s.l. ranged 17.2–22.6°C. (FR/TEAM Network, unpublished data).

## Data collection

Camera trapping was conducted from July to November 2009, as the baseline year of the TEAM programme [13]. We used digital cameras (Reconyx RM45, Reconyx Inc., Holmen, Wisconsin, USA) set to take photos without delay between consecutive triggers. Using ESRI's ArcGIS 10 software, we designed a regular grid of 60 camera trap locations at a density of one camera per 2 km<sup>2</sup>, and placed at random across the forest. We then conducted a ground survey to select the final camera positions, and locations that fell in excessively steep, open canopy or rocky areas were repositioned no more than 100 m from the original location (Fig. 1).

Camera traps were positioned so the field of view included an active wildlife trail and then secured to a tree about 2–3 m away from the trail at an average height of 50 cm and left running for 30 days. Since cameras can run automatically over such period, we did not check them to avoid unnecessary disturbance. Due to limits in the number of cameras available and the time needed for the field team to set cameras, we sampled the 60 points by deploying three consecutive arrays of 20 camera traps (south, central and northern Mwanihana, respectively). Therefore, the data collection lasted 133 days from July 24 to December 4, 2009.

At sampling completion, memory cards were recovered and images were identified using specialized software (DeskTEAM, [27]; see also [www.teamnetwork.org/en/help-deskteam](http://www.teamnetwork.org/en/help-deskteam)). A single taxonomic authority [28] was used across all TEAM sites for species identification, except for species that were not included in this reference or species that were re-assessed. The validated and publicly available data were downloaded from the TEAM portal (data package id: TV-2011116005138\_3515).

## Data analysis

We derived standard descriptors of mammal community by filtering the image records for each species of mammal to derive the number of events per hour, hence avoiding that multiple images of the same individual pausing in front of the camera trap were scored as multiple events [29]. We then computed a relative abundance index (RAI) as the number of events divided by sampling effort and multiplied by 100 (i.e. events per 100 days of camera trapping). We also computed the naïve occupancy as the number of camera trap sites occupied on sites sampled.

We derived a number of spatial environmental covariates deemed relevant to explain both the spatial variations of species' richness and occupancy of selected species using geoprocessing tools available in ArcGIS. We calculated the following variables: (1) distance from eastern park border ('border'), (2) distance from forest edge ('edge'), (3) forest habitat type, i.e. montane forest and lowland forest ('habitat'), (4) slope and (5) distance to rivers. The distance from each camera trap point to the nearest 'border', 'edge', or river segment was calculated in ArcGIS. Forest habitat

type was mapped using a supervised classification approach on Landsat TM and ETM+ satellite imagery (30 m resolution). Habitats were categorized into three forest types: 1) Montane, 2) Deciduous, and 3) Regenerating. Forest habitat type was then extracted for each camera trap point in ArcGIS. 'Border' correlated highly with elevation at camera trap sites given the forest morphology of an east-west escarpment (Pearson's  $r = 0.802$ ,  $P < 0.001$ ) and it is considered a proxy of decreasing anthropogenic disturbance, which may be mainly associated to firewood collection and pole/timber cutting [30]. After checking that no collinearity existed among the covariates used, these were standardized to have mean 0 and unit variance before estimating the model coefficients.

As a fundamental measure of the community structure, we analysed species richness under three different perspectives and with different aims. (1) Species accumulation curve with cumulative camera trap days was used to check if data collection lasted a sufficient number of days to virtually capture the total number of species. The order in which samples (they consisted of number of events per day) were included in the curve was randomized 1000 times and results were used to derive 95% confidence intervals around the mean [31]. Even though this approach ignores imperfect detection of individual species, it is useful for comparison with other studies [32,33]. (2) Analysis of species richness that accounts for imperfect detection was studied using the model by Dorazio and colleagues [23], which requires repeated temporal replications to resolve the ambiguity between species absence and non-detection when species are unobserved at sample locations. This Bayesian approach combines community-level and species-level attributes in the same framework, allowing either community-level or species-level parameters to be evaluated. Such flexibility is not matched by other methods for estimating species richness [23]. The frequentist approach to the same problem is possible, but computationally intensive to implement [23]. The model was specified in BUGS language and fitted to data using WinBUGS and the package 'R2WinBUGS' in R software [34,35]. Simulations were executed with five Markov chains; 55,000 iterations for each chain, discarding 5,000 iterations at the beginning (burn-in) and setting the thinning rate to 50. This returned 5,000 samples from the posterior distributions. (3) We used the occupancy analysis framework to investigate possible relationships between species richness and environmental covariates [19,36]. In particular, we compared two sets of models: (1) testing the effect of environmental covariates on the occupancy of all the species (species richness), and (2) testing if trophic guild (carnivores, herbivores, omnivores, insectivores) and body mass (data from [37]) were related to detection probability. Akaike Information Criterion (AIC) was used to rank all the candidate models and calculate their Akaike weights [38]. To achieve intra-guild homogeneity, we discarded elephant (*Loxodonta africana*) and buffalo (*Syncerus caffer*) among the herbivores for their large body mass and movement habits (i.e. they periodically move into the forests from drier habitats in the park). Among the carnivores, the bushy-tailed mongoose (*Bdeogale crassicauda*) was discarded because it is a common, non-elusive, and partially omnivorous species; hence it effectively represents an outlier in the carnivore guild.

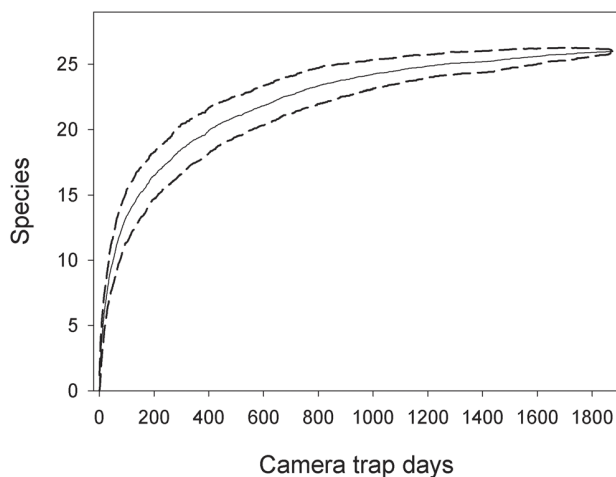
We also used occupancy [17] as the species-specific state variable of abundance to assess differences across species under an unbiased framework and determine covariates of both occupancy and detection probability for a set of species. We used scripts already developed [8] and implemented in R to arrange the TEAM data (<http://www.teamnetwork.org/>) into a list of species' occupancy matrices. Data for each species were arranged as

**Table 1.** List of mammals camera trapped in Mwanihana forest, Udzungwa Mountains, Tanzania, reporting species traits (body mass from Smith et al. (2003) and functional guild from IUCN (2013)) and three raw indices of abundance: hourly events, relative abundance index (RAI) and naïve occupancy (number of sites that are positive to species' presence divided by the total number of sites sampled).

| #  | Taxonomic group | Common name                  | Latin name                       | Mass (kg) | Functional guild | Events per hour | RAI (events/100 days) | Naïve occupancy |
|----|-----------------|------------------------------|----------------------------------|-----------|------------------|-----------------|-----------------------|-----------------|
| 1  | Afrotheria      | Tree hyrax                   | <i>Dendrohyrax arboreus</i>      | 2.95      | Omniv            | 23              | 1.27                  | 0.241           |
| 2  |                 | African elephant             | <i>Loxodonta africana</i>        | 3900      | Herbiv           | 11              | 0.61                  | 0.121           |
| 3  |                 | Four-toed sengi              | <i>Petrodromus tetradactylus</i> | 0.19      | Insectiv         | 3               | 0.17                  | 0.017           |
| 4  |                 | Chequered sengi              | <i>Rhynchocyon cirnei</i>        | 0.49      | Insectiv         | 4               | 0.22                  | 0.052           |
| 5  |                 | Grey-faced sengi             | <i>Rhynchocyon udzungwensis</i>  | 0.80      | Insectiv         | 45              | 2.48                  | 0.259           |
| 6  | Carnivores      | Marsh mongoose               | <i>Atilax paludinosus</i>        | 3.30      | Carniv           | 3               | 0.17                  | 0.052           |
| 7  |                 | Bushy-tailed mongoose        | <i>Bdeogale crassicauda</i>      | 1.55      | Carniv           | 130             | 7.15                  | 0.741           |
| 8  |                 | African civet                | <i>Civettictis civetta</i>       | 12        | Omniv            | 1               | 0.06                  | 0.017           |
| 9  |                 | Lowe's servaline genet       | <i>Genetta servalina lowei</i>   | 1.06      | Omniv            | 18              | 0.99                  | 0.259           |
| 10 |                 | Honey badger                 | <i>Mellivora capensis</i>        | 8.50      | Carniv           | 7               | 0.39                  | 0.103           |
| 11 |                 | Banded mongoose              | <i>Mungos mungo</i>              | 1.93      | Insectiv         | 2               | 0.11                  | 0.034           |
| 12 |                 | African palm civet           | <i>Nandinia binotata</i>         | 1.90      | Carniv           | 2               | 0.11                  | 0.034           |
| 13 |                 | Leopard                      | <i>Panthera pardus</i>           | 52        | Carniv           | 8               | 0.44                  | 0.052           |
| 14 | Primates        | Sanje mangabey               | <i>Cercocebus sanjei</i>         | 8         | Omniv            | 73              | 4.02                  | 0.517           |
| 15 |                 | Sykes' monkey                | <i>Cercopithecus mitis</i>       | 5         | Omniv            | 22              | 1.21                  | 0.241           |
| 16 |                 | Yellow baboon                | <i>Papio cynocephalus</i>        | 18.4      | Omniv            | 3               | 0.17                  | 0.052           |
| 17 |                 | Udzungwa red colobus         | <i>Procolobus gordonorum</i>     | 10        | Omniv            | 5               | 0.28                  | 0.069           |
| 18 |                 | Angolan colobus              | <i>Colobus angolensis</i>        | 8.6       | Omniv            | 1               | 0.06                  | 0.017           |
| 19 | Rodents         | Giant pouched-rat            | <i>Cricetomys gambianus</i>      | 1.24      | Omniv            | 276             | 15.18                 | 0.534           |
| 20 |                 | Cape porcupine               | <i>Hystrix africaeaustralis</i>  | 14.94     | Omniv            | 11              | 0.61                  | 0.086           |
| 21 |                 | Tanganyika mountain squirrel | <i>Paraxerus vexillarius</i>     | 0.68      | Herbiv           | 46              | 2.53                  | 0.328           |
| 22 | Ungulates       | Harvey's duiker              | <i>Cephalophus harveyi</i>       | 12        | Herbiv           | 367             | 20.19                 | 0.862           |
| 23 |                 | Abbott's duiker              | <i>Cephalophus spadix</i>        | 56        | Herbiv           | 60              | 3.30                  | 0.466           |
| 24 |                 | Suni                         | <i>Neotragus moschatus</i>       | 6.5       | Herbiv           | 114             | 6.27                  | 0.448           |
| 25 |                 | Bush pig                     | <i>Potamochoerus larvatus</i>    | 48.78     | Omniv            | 18              | 0.99                  | 0.190           |
| 26 |                 | African buffalo              | <i>Syncerus caffer</i>           | 580       | Herbiv           | 4               | 0.22                  | 0.052           |

Trophic guilds: Herbiv = herbivores, Omniv = omnivores, Insectiv = insectivores, Carniv = carnivores.  
doi:10.1371/journal.pone.0103300.t001

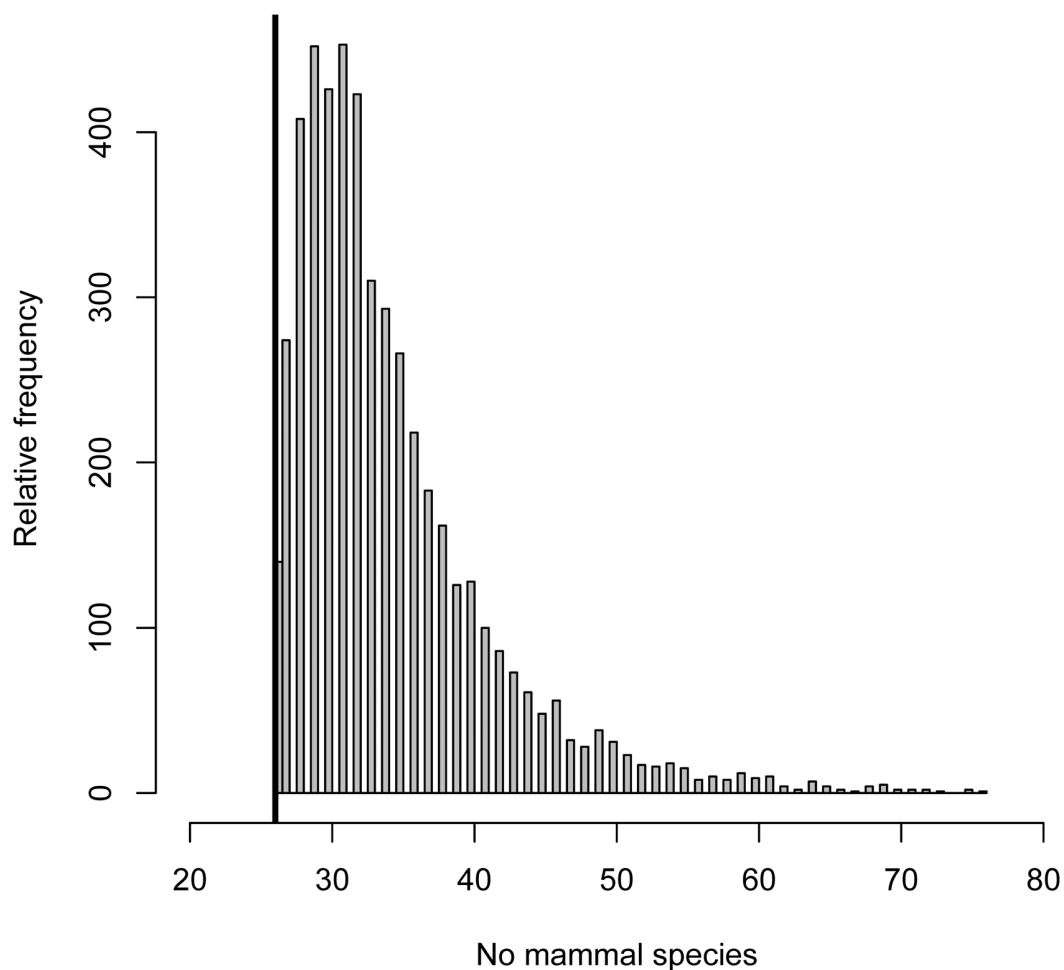




**Figure 2. Species accumulation curve for the community of medium-to-large mammals detected by camera trapping.** Detection of species is randomized 1000 times and results used to derive the 95% confidence intervals of the mean. doi:10.1371/journal.pone.0103300.g002

matrices of sites by surveys (i.e. sampling occasion). Each entry indicated if the species was observed at site  $i$  on survey  $j$  or not. If the species was observed at site  $i$  on survey  $j$ , then the entry was given a score of 1. If the species was not observed, then the entry was given a score of 0. NA indicated site  $i$  was not sampled on survey  $j$ . The species-specific occupancy matrix had a resolution of five days.

We used these matrices as the input for the single-season occupancy model [19]. We modelled both estimated occupancy ( $\Psi$ ) and detection probability ( $p$ ) with and without covariates. A common set of models was used for all the species. In addition to the null model, that assumes constant  $\Psi$  and  $p$  (i.e.  $\Psi(\cdot)$ ,  $p(\cdot)$ ), for other models  $p$  was allowed to vary by distance to border and distance to edge. In both cases, our hypothesis was that animals would be more elusive near the border and/or the edge because of greater disturbance [30]. Four covariates for  $\Psi$  were the following: (1) 'border', (2) 'edge', (3) 'river' and (4) 'habitat'. Numerical covariate were standardized into z-scores and included both individually and in combination. We used the Akaike Information Criterion (AIC) to rank candidate models and calculate their Akaike weights [38]. In the case of top-ranked models with similar AIC (and weight  $>0.01$ ), we applied a model-averaging technique to estimate occupancy from these multiple models [38]. Occu-



**Figure 3. Posterior distribution of species richness.** The analysis follows Dorazio et al. (2006). The posterior probability that the community comprises only 26 species (vertical line is the observed species richness) is essentially zero, and the estimated median and mean values of species richness are 32.0 ( $\pm 7.04$  SD) and 34.3, respectively (26–54 CRI 95%; CRI = credible intervals). doi:10.1371/journal.pone.0103300.g003

**Table 2.** Summary of model selection outcome for predictions of mammal species' richness in the Udzungwa Mountains of Tanzania.

| Model                                                 | Number of parameters | AIC     | Delta  | AIC weight | Cumulative weight |
|-------------------------------------------------------|----------------------|---------|--------|------------|-------------------|
| $\psi(\cdot) p(\text{mass, guild})$                   | 6                    | 1151.59 | 0.00   | 0.410      | 0.410             |
| $\psi(\cdot) p(\text{guild})$                         | 5                    | 1152.57 | 0.98   | 0.250      | 0.660             |
| $\psi(\text{habitat, species}) p(\text{mass, guild})$ | 7                    | 1153.59 | 2.00   | 0.150      | 0.810             |
| $\psi(\text{border}) p(\text{guild})$                 | 6                    | 1154.56 | 2.97   | 0.093      | 0.910             |
| $\psi(\text{habitat}) p(\text{guild})$                | 6                    | 1154.56 | 2.98   | 0.093      | 1.000             |
| $\psi(\cdot) p(\cdot)$                                | 2                    | 1323.63 | 172.04 | 0.000      | 1.000             |

The top-ranked models are shown (delta AIC <3) followed by the null model.  
doi:10.1371/journal.pone.0103300.t002

pancy analysis was performed using the package 'unmarked' in R [39]. The relative importance of the model parameters were calculated with the R package AICmodavg [40]. Once we identified the best occupancy model (or the average of the best models), we mapped occupancy probability across Mwanihana forest by deriving occupancy estimates from covariates computed on a spatial grid with a cell size of 100 m.

## Results

Of the 60 camera traps set, two malfunctioned and the remaining 58 accumulated 1,818 camera days (mean 31.34) yielding 10,647 images of mammals. The list of 26 species recorded and standard descriptors are reported in Table 1. The range of species captured per camera was 3–10 (median 6). Four species were recorded with >100 events in this order: (1) Harvey's duiker (*Cephalophus harveyi*), (2) giant-pouched rat (*Cricetomys gambianus*), (3) bushy-tailed mongoose and (4) suni. Six species scored >20 and ≤100 events: (1) Abbott's duiker (*Cephalophus spadix*), (2) Tanganyika mountain squirrel (*Paraxerus vexillarius*), (3) grey-faced sengi (*Rhynchocyon udzungwensis*), (4) Sykes' monkey (*Cercopithecus mitis*) and (5) tree hyrax (*Dendrohyrax validus*). The remaining 16 species scored ≤20 events, of which 10 species scored ≤5 events. The accumulation of species detected with sampling effort was initially steep, but by 1,000 camera days the majority of species were detected (24 species, or 92%; Fig. 2). The estimated size of the community according to [23] exceeds the number of species observed in the sample by a substantial margin, with median and mean values being 32 and 34.3, respectively (Fig. 3).

The modelling of species richness using a sub-set of 23 species revealed no support for the null model, with several models having lower AIC, and five that were top-ranked with delta AIC<3 (Table 2). Model averaging using these first five models shows that no environmental covariates affected relative species richness. However, there is a significant influence of the functional guild on the detection probability (Table 3). Herbivores had the highest detection probability ( $0.52 \pm 0.03$  SE), followed by omnivores ( $0.20 \pm 0.02$  SE), insectivores ( $0.09 \pm 0.02$  SE) and carnivores ( $0.06 \pm 0.02$  SE; Fig. 4).

We could fit occupancy models for the 11 most recorded species. We initially considered 14 species with ≥10 events or naïve occupancy ≥0.1; however, for three of these (*Genetta servalina*, *Loxodonta africana*, *Hystrix africaeaustralis*) the models did not converge. For these 11 species,  $\psi$  ranged from 0.25–0.86 and  $p$  ranged from 0.10–0.51. The null model was not supported for any of these species, and at least one of the covariates considered affected significantly or marginally significantly  $\psi$  and  $p$  (Table 4). Details of model selection for each species are shown in Table S1.

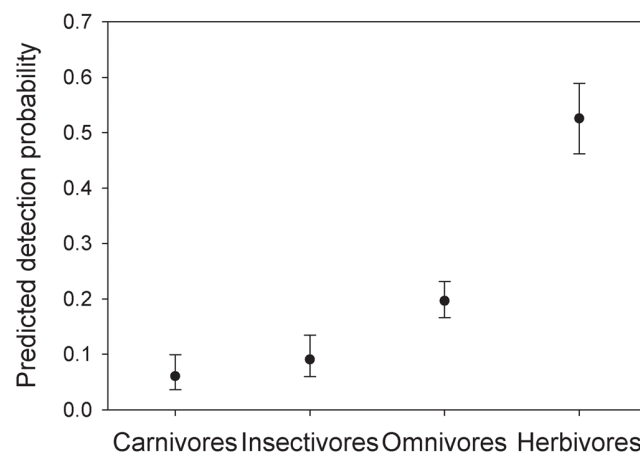
The main patterns of predicted  $\psi$  and the functional relationships of  $\psi$  with the dominant covariate represented by the four species shown in Fig. 5 are as follows:

- (1) As a 'montane forest dweller', Sanje mangabey's  $\psi$  is positively associated with montane forest habitat and not affected by any of the other variables. Hence, predicted occupancy falls in two values of  $0.34 \pm 0.12$  SE in lowland, deciduous forest and  $0.76 \pm 0.10$  SE in montane, evergreen forest.
- (2) In contrast with the above, suni is a 'lowland forest dweller', with  $\psi$  being negatively related to montane forest habitat; hence,

**Table 3.** Summary of model averaging for the effect of environmental covariates on species richness ( $\psi$ ) and detection probability ( $p$ ) of the mammal community in the Udzungwa Mountains of Tanzania.

| Model                                   | Estimate | SE     | Z     | P(> z ) |
|-----------------------------------------|----------|--------|-------|---------|
| $p(\text{mass})$                        | -0.136   | 0.08   | 1.704 | 0.089   |
| $p(\text{herbivores})$                  | 2.860    | 0.31   | 9.345 | <0.001  |
| $p(\text{insectivores})$                | 0.380    | 0.37   | 1.040 | 0.298   |
| $p(\text{omnivores})$                   | 1.327    | 0.30   | 4.497 | <0.001  |
| $\psi(\text{habitat} - \text{montane})$ | 2.814    | 292.60 | 0.010 | 0.992   |
| $\psi(\text{border})$                   | 1.273    | 628.75 | 0.002 | 0.998   |

See Table 2 for the covariates modelled with both  $\psi$  and  $p$ .  
doi:10.1371/journal.pone.0103300.t003



**Figure 4. Detection probability by functional guild.** Values are from the model averaging of relative species richness of the mammal community in the Udzungwa Mountains of Tanzania. Bars are 95% confidence intervals.  
doi:10.1371/journal.pone.0103300.g004

indicating preference for lowland forest. In addition, the species'  $\psi$  is marginally affected by distance to park border, with predicted occupancy decreasing in the proximity of park border relative to more interior zones of lowland forest. Its detection probability also significantly increased with distance to edge.

(3) The Harvey's duiker is a typical 'edge lover' species, as  $\psi$  is negatively affected by distance to edge, which is clearly seen in the spatially-explicit model. Therefore, the species avoids interior forest, with predicted  $\psi$  declining sharply and non-linearly after 1.5–2 km from the forest edge.

(4) An opposite pattern is shown by the grey-faced sengi, which seems to be an 'edge avoider' with  $\psi$  being positively affected by distance from edge and preference for montane habitat and both associations being marginally significant ( $0.05 < P < 0.1$ ).

For approximately half of the species, detection probability varied with distance to the park border and/or distance to the forest edge (Online Resource 1). We portray two limiting cases (Fig. 6): (1) the bushy-tailed mongoose, where  $p$  decreased linearly with the distance to park border, and (2) the Abbott's duiker, where  $p$  exponentially increased with distance to border.

## Discussion

Our study shows how camera trap data collected using a robust, standardized field methodology, and analysed with statistical approaches that account for imperfect detection and incorporate ecological factors, can provide a robust baseline assessment of mammal communities in tropical forests. In particular, we estimated species richness using a sampling protocol requiring repeated observations at sample locations. This approach provided information needed to resolve the ambiguity between species absence and non-detection. The Bayesian analysis used [23] is a flexible alternative to the classic frequentist approach, which is computationally complex, and combines community-level and species-level attributes in the same modelling framework. We also determined how simple ecological covariates such as gross habitat, distance to forest edge and distance to park border explain the occupancy of most species in the community. Finally, we provided a framework for deriving spatially-explicit, fine resolution models of estimated species occupancy in relation to covariates, which represent a valuable tool for conservation management of threatened and/or poorly known species.

The efficiency of camera trapping for inventorying species has already been indicated by other studies of tropical mammal communities [33,41]. In the Udzungwas, additional camera trapping effort and scattered sighting reports indicate that at least four species have been 'missed' by the present survey (bushbuck *Tragelaphus scriptus*, spotted hyena *Crocuta crocuta*, cane rat *Thryonomys swinderianus* and serval cat *Leptailurus serval*; FR unpublished data). Other small, elusive carnivores may also be present in the target forest [42]. This observation is supported by our models, which estimate that  $>30$  species occur. It is worth noting that the classic species richness estimators, parametric and non-parametric, asymptotic and non-asymptotic, rely on extrapolations of the species accumulation curve and do not account for imperfect detection [31,43]. The explicit incorporation of detection probability in the models we used is particularly important in estimating species richness of communities that contain a preponderance of rare, or difficult to detect, species [44]. In these cases, using traditional approaches may yield incorrect inferences if heterogeneity in detectability exists among species or if the effects of environmental covariates on occurrence differ among species.

In terms of species composition, the pool of ten most-detected species ( $>20$  events) reveals the relative high occurrence of a number of species that are poorly known, and poorly detected using alternative methods. For example, the Abbott's duiker is a IUCN-Endangered 'giant' duiker endemic to and found only in a handful of montane forests in Tanzania, including the Udzungwa population considered to be the stronghold, and was the third most common species in terms of occupancy,  $\psi = 0.72$  [28,45]. Similarly, the fourth most common Sanje mangabey ( $\psi = 0.62$ ) is a predominantly terrestrial forest monkey endemic to only two forests in the Udzungwa mountains and classified as Endangered [28]. Being terrestrial and elusive, this monkey is poorly sighted from line-transects despite living in large groups of up to 50 individuals [46], and hence it is so far regarded as rarer than our data reveal. Among other commonly detected species, the relatively high ranking of tree hyrax ( $\psi = 0.48$ ) is also surprising given this is known as an arboreal dweller [47]. Our data show that tree hyraxes spend more time on the ground than previously thought. It is also worth mentioning the 11<sup>th</sup> position in the occupancy ranking of the Udzungwa-endemic and IUCN Vulnerable grey-faced sengi (or elephant-shrew), a species described in 2008 which is very rarely seen despite being diurnal,

**Table 4.** Summary of species-specific occupancy estimates for 11 mammals that had adequate detection for the analysis, ordered by decreasing estimated occupancy ( $\psi$ ).

| Species                         | Naïve $\psi$ | SE( $\psi$ ) | $p$   | SE( $p$ ) | $\rho$ (border) | $\rho$ (edge) | $\psi$ (border) | $\psi$ (edge) | $\psi$ (river) | $\psi$ (habitat [type]) |
|---------------------------------|--------------|--------------|-------|-----------|-----------------|---------------|-----------------|---------------|----------------|-------------------------|
| <i>Cephalophus harveyi</i>      | 0.862        | 0.876        | 0.432 | 0.046     | (+)             | -             | -               | -             | (-)            |                         |
| <i>Bdeogale crassicauda</i>     | 0.741        | 0.815        | 0.298 | 0.039     | -               |               |                 |               |                |                         |
| <i>Cephalophus spadix</i>       | 0.466        | 0.716        | 0.171 | 0.040     | +               | +             |                 |               |                |                         |
| <i>Cercocebus sanjei</i>        | 0.517        | 0.615        | 0.234 | 0.057     |                 |               |                 |               |                | + [montane]             |
| <i>Cricetomys gambianus</i>     | 0.534        | 0.539        | 0.118 | 0.033     |                 |               |                 |               | +              |                         |
| <i>Cercopithecus mitis</i>      | 0.241        | 0.503        | 0.198 | 0.039     | -               |               |                 |               |                |                         |
| <i>Dendrohyrax validus</i>      | 0.241        | 0.480        | 0.116 | 0.039     | (+)             | (+)           |                 |               | +              |                         |
| <i>Neotragus moschatus</i>      | 0.448        | 0.472        | 0.105 | 0.057     | +               | +             | (+)             |               |                | - [montane]             |
| <i>Paraxerus vexillarius</i>    | 0.328        | 0.400        | 0.203 | 0.040     |                 |               |                 | +             |                |                         |
| <i>Potamochoerus larvatus</i>   | 0.190        | 0.387        | 0.150 | 0.055     | (-)             |               |                 |               |                |                         |
| <i>Rhynchocyon udzungwensis</i> | 0.259        | 0.278        | 0.114 | 0.048     |                 |               |                 | (+)           |                | (+) [montane]           |

This is the average value of predicted occupancy at the 58 camera trap localities from the final models. Significant outcomes of the effects of covariates on  $\psi$  and detection probability ( $p$ ) are also indicated with their directionality (positive/negative effect), which is in parenthesis when the significance is marginal ( $0.05 < p < 0.1$ ). Naïve occupancy values are also shown to appreciate the differences with  $\psi$ , which are particularly remarkable for species with  $p < 0.2$ .

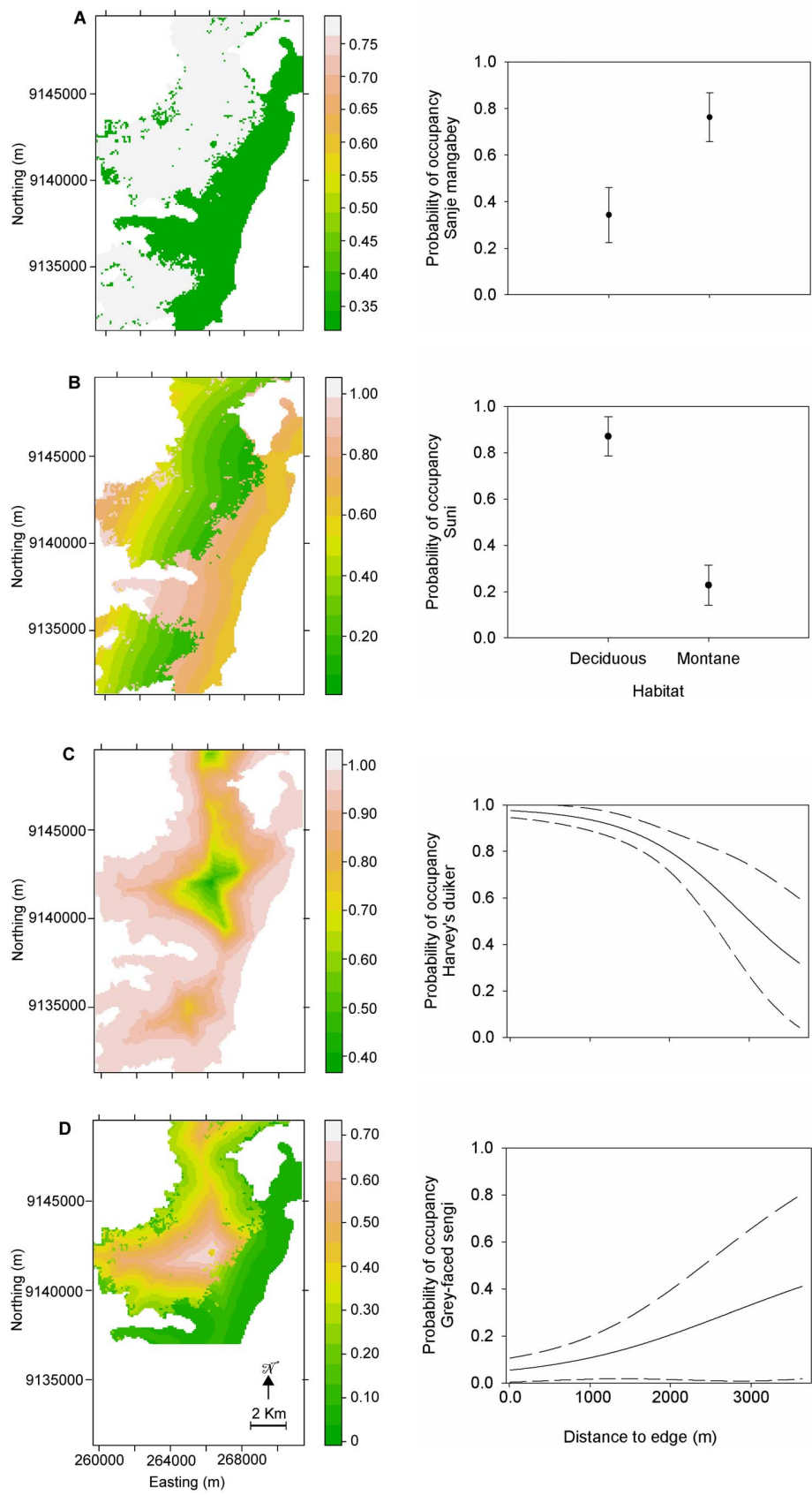
doi:10.1371/journal.pone.0103300.t004

and for which Mwanihana holds approximately half of the global population [48]. The pool of least-detected species contains a number of truly arboreal mammals, typically the two colobine monkeys that are common in high densities across the forest [46], which are completely explained by their habit. Besides these 'exceptions', the other least-detected species are a diverse suite of less common (e.g. bush pig, Lowe's servaline genet), or rare animals for the target forest (e.g. leopard, marsh mongoose), in addition to species that are mainly found in savannah and/or in the deciduous woodland occurring at the lower edge of Mwanihana forest (e.g. yellow baboon, African civet, banded mongoose, honey badger).

It is not surprising that we did not find any significant pattern of variation of estimated species richness across camera trap sites because Mwanihana forest has continuous forest cover without drastic habitat changes, except for the gradual variation in habitat type that broadly follows altitudinal and edge versus interior gradients. Whilst the species-specific occupancy models do highlight clear patterns of ecological preference by a suite of species, these preferences do not hold across the whole community. Interestingly, we found that the trophic guilds have significantly different detection probabilities. The low detectability of carnivores and insectivores matches their generally greater elusiveness relative to omnivores and herbivores. In contrast to our expectations, detection probability of species decreases with body mass, although the relationship is marginally significant (Table 3). Previous studies examining the effect of body mass on the animal detection process by camera traps suggest that small species are more likely to be missed due to the sensitivity and dimensions of the detection zone of the camera sensor [33,49]. However, this aspect did not appear to have a statistical effect within the range of body mass in our study, perhaps because of the high sensitivity of the camera model we used. The relationship we found may rather reflect inter-specific behavioural differences, with larger species being less detected because of their greater elusiveness.

The species-specific occupancy analysis generally revealed novel ecological knowledge for roughly half of the species included in the analysis, excluding the strictly arboreal ones and those that are not typical forest-dwellers (see considerations above). The need to include corrections for imperfect detection in the modelling process is clearly shown by the remarkable variation of  $p$  among species (range 0.096–0.505; see Table 4). Because of this variation, the difference between naïve and estimated occupancy is also varying, and for the least-detectable species ( $p < 0.2$ ), the increment between naïve and estimated occupancy is 54–109% the naïve occupancy (see Table 4). The importance of allowing  $\psi$  and  $p$  to vary with covariates is shown by the fact that the null model was the least supported for any species. This is shown by a number of previous studies that investigated habitat associations from camera trapping data in an occupancy framework [21,22,36,50]. To achieve similar inference for the remaining half of the species ( $p < 0.1$ ), a large number of sites should be surveyed [44]. Alternatively, one could pool data for more than one season under the assumption of a closed community (e.g. occupancy status does not change among survey seasons [22]).

The four limiting cases we highlighted show the particularly relevant ecological and conservation implications of our approach. For example, ecological knowledge on the Sanje mangabey was limited to results from a single, long-term focal group study located in the lower part of the forest [46,51] before our analyses. There also was a lack of general understanding of their occurrence across the entire forest, which includes about half of the global population. Our results indicate that the species' occupancy in montane forest is more than double than in lowland forest, which



**Figure 5. Spatially-explicit occupancy models.** Maps of predicted occupancy (left) and functional relationship between the most relevant covariate and  $\psi$  (right, with confidence intervals indicated by dashed lines) for four mammals in the Udzungwa Mountains of Tanzania, representing limiting cases in occupancy pattern: (A) Sanje mangabey, a montane evergreen forest species; (B) suni, a lowland deciduous forest species; (C) Harvey's duiker, an edge-lover and disturbance-tolerant species; (D) grey-faced sengi, an edge-avoider and disturbance-sensitive species. doi:10.1371/journal.pone.0103300.g005

in turn suggests the vulnerability of this species to both human-induced (e.g. logging and forest degradation), stochastic (e.g. fires) and climate change impacts. The limit of using a categorical and broad classification of habitat type for this and other habitat-sensitive species may be overcome in future studies by collecting fine-scale vegetation and human disturbance data at camera trap sites for consideration in the modelling [22,52]. Similar considerations apply to the results for the grey-faced sengi, whose preference for forest interior and edge avoidance matches the results from a recent focal study on habitat associations [22].

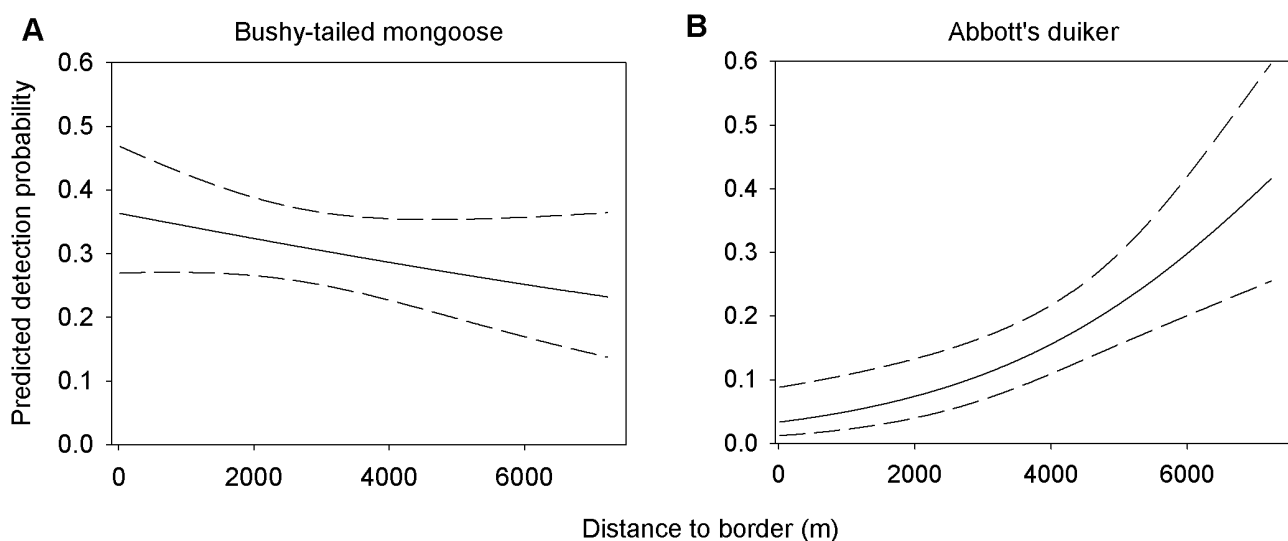
While the forest antelope community has been previously studied using camera trapping [29,52] the fine grain occupancy models we derived shed new light into the occurrence of these species. Suni and Harvey's duiker occur predominantly in the lower forest with the latter occurring across the forest edges. This is relevant to the need to protect the full array of forest cover, including the lower elevation areas, which border densely populated settlements. The preference of Harvey's duiker for edges also indicates its suitability as an indicator of connectivity between forest blocks across marginal, often riverine habitat, which is important in highly heterogeneous areas such as the Udzungwas.

Despite a minority of species whose detection probability did not vary significantly with the covariates used (e.g. distance from edge and from border), the general finding is assuming that constant detection is broadly incorrect. Care needs to be taken when choosing covariates for  $p$  to ensure they are meaningful, which may be related to assumptions on the differences in the density of vegetation across camera trap sites. This assumption, in turn, may affect the efficiency of camera traps to capture an image of passing animals. In addition, variation in detectability may be due to differential animals' shyness in relation to human disturbance and/or density of vegetation on the forest floor

compressing the field of view of camera traps. These results may indicate a pattern of lower detectability in areas that are closer to human disturbance (e.g. border) and/or habitat 'disturbance' (e.g. border and edge), where forest floor vegetation is generally denser due to higher canopy degradation than in forest interior, and include animals that are more shy. The few cases of a negative relationship between  $p$  and one of the two covariates may also be explained by species-specific habits. For instance, the Sykes' monkey's  $p$  is negatively related to edge, which fits with the habit of this opportunistic primate to move easily among dense, degraded and regenerating vegetation in forest edge [30]. Similar considerations may also be valid for the bushy-tailed mongoose, a small, nocturnal and opportunistic carnivore that is often sighted by the park border and forest edge (FR unpublished data).

## Conclusions

Our study applied a robust analytical framework to profiling tropical mammal communities detected by the standard camera trapping protocol adopted by the TEAM Network. With the network currently made of 16 sites across three continents and progressively expanding (<http://www.teamnetwork.org>), and a number of studies adopting similar designs outside the network [36], there emerges a growing need for standardized analytical procedures to facilitate and enhance the sound use of the large data-sets being accumulated. In turn, detailed and site-specific baseline analysis will help interpreting patterns of community composition and changes from multi-site comparisons [8]. Similarly, with data collected from a number of sites for >5 years, baselines such as ours are relevant to the interpretation of temporal trends in species and community occupancy, for which robust and standardized analytical procedures have recently been proposed, including the Wildlife Picture Index [2,14].



**Figure 6. Graphs of predicted detection probability.** Values are modelled with distance from the park border for (A) the bushy-tailed mongoose, and (B) the Abbott's duiker, in the Udzungwa Mountains of Tanzania. Confidence intervals are indicated by dashed lines. doi:10.1371/journal.pone.0103300.g006



The ultimate relevance of standardizing tropical mammal community assessments rests in the need to develop indicators for distribution and abundance of pan-tropical species, as outlined by the Convention on Biological Diversity [2,14]. In this context, our study offers an example of how analysis of species' richness in occupancy framework, focal species' occupancy and their spatial variation relative to a suite of covariates, represents a useful approach for comparing data from several sites, and hence for deriving indicators for these global targets.

## Supporting Information

### Table S1 Model selection details for the 11 species for which occupancy and detection probability were modelled with covariates.

(DOCX)

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## Author Contributions

Conceived and designed the experiments: FR JAA. Performed the experiments: FR EM MR. Analyzed the data: FR MR JAA DS. Contributed to the writing of the manuscript: FR EM MR JAA DS.

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**PAPER TWO**

**Modelling fine scale habitat associations of medium-to-large forest mammals in the  
Udzungwa Mountains of Tanzania using camera trapping**

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## Modelling fine-scale habitat associations of medium-to-large forest mammals in the Udzungwa Mountains of Tanzania using camera trapping

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We used camera trap data collected in 2013 from 60 locations in the Udzungwa Mountains of Tanzania to determine fine-scale habitat associations for medium-to-large mammal species. The area is outstanding for biodiversity and endemism in Africa, particularly for mammals. Each camera trap sampled for 30 days and the survey yielded 12,911 images of 26 species. We used generalized linear modelling to determine relationships between camera-trapping events and vegetation and other habitat variables, and obtained satisfactory model fit for 9 out of the 11 most recorded species, with explained model deviance up to 63.7%. Results provide novel insights into the ecology of target species. For example, the event count of the IUCN-endangered Abbott's duiker (*Cephalophus spadix*) was positively correlated with distance to the park border, indicating preference for interior forest and avoidance of disturbance. The event count of the Eastern Arc-endemic Lowe's servaline genet (*Genetta servalina lowei*) was positively correlated with diversity of large trees but negatively correlated with visibility and herbaceous cover, indicating preference for mature forest habitat. Our study validates the usefulness of camera trapping to assess communities of forest mammals, especially as related to habitat associations, providing data that are of relevance to their conservation management.

**Keywords:** camera traps; Eastern Arc; habitat modelling; habitat preferences; tropical forest

### Introduction

Forest mammals are a key component of tropical forests in terms of biomass and as indicators of ecosystem health (Ahumada et al. 2011). They are also among the most threatened faunal groups due to habitat loss and degradation (Schipper et al. 2008). Hence, knowledge on their occurrence and factors determining their habitat associations are important for defining conservation strategies (e.g. Wasserman and Chapman 2003; Tobler et al. 2008; Rovero, Zimmerman et al. 2013). Despite such widely recognized importance, however, tropical forest mammals are generally poorly known partly because they are difficult to detect, owing to their nocturnal behaviour, elusiveness and rarity (e.g. Linkie et al. 2007).

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In this context, remotely set, automatic cameras taking pictures of passing animals (camera trapping) have been increasingly used in the last decade for studying mammals all over the world (Karanth and Nichols 1998, 2002; reviews in O'Connell et al. 2011; Fleming et al. 2014). Camera traps are non-invasive, relatively easy to use and cost-efficient (e.g. Rovero, Zimmerman et al. 2013; Fleming et al. 2014). A number of studies (e.g. O'Brien 2008; Ahumada et al. 2011; Ahumada et al. 2013; Rovero, Martin et al. 2014; Rovero, Menegon et al. 2014) have proved the efficiency of camera traps in mammal studies, with a more limited set of studies focusing on habitat associations (e.g. Linkie et al. 2007; Bowkett et al. 2008; Rovero, Collett et al. 2013). These studies have considered single species, or groups of species, to investigate habitat associations (e.g. Bowkett et al. (2008) targeted forest antelopes in the Udzungwa Mountains). Here, we present the results of a study on a community of medium-to-large forest mammals assessed by camera trapping in mountain forest habitat in Tanzania with a focus on fine-scale habitat modelling.

Our study area, the Udzungwa Mountains, is one of the most outstanding sites for biodiversity endemism and conservation in Africa (Rovero, Menegon et al. 2014). The area is particularly rich in mammalian forest fauna (Rovero and De Luca 2007). Forest mammals have been the subject of a number of studies that deployed camera trapping (De Luca and Mpunga 2005; Bowkett et al. 2008; Ahumada et al. 2011; Rovero, Collett et al. 2013; Rovero, Martin et al. 2014). Our study objective was to assess the community of medium-to-large forest mammals as detected through an extensive camera-trapping effort, derive a proxy of species' relative abundance and determine the best predictors of this response variable among a suite of fine-scale vegetation and other habitat factors as potential covariates of relative abundance. In turn, we aimed to provide new insights on habitat associations of several poorly known and/or rare species which are relevant to their conservation management.

## **Material and methods**

### ***Study area***

The Udzungwa Mountains in south-central of Tanzania are a system of moist forest blocks interspersed with drier habitats. We conducted the study in Mwanihana forest, eastern Udzungwa Mountains National Park (UMNP; Figure 1). UMNP is centred on 7°46'S, 36°51'E, has a size of 1990 km<sup>2</sup> and is in the eastern part of the Udzungwa Mountains. Mwanihana is one of the largest forest blocks in the range (192 km<sup>2</sup> of closed forest habitat) with continuous vegetation cover from 300 to over 2000 m above sea level (Rovero, Collett et al. 2013). The forest habitat is characterized by deciduous forest at lower altitude on the eastern side while evergreen forests are found at higher altitudes on the western side (Lovett et al. 2006). In addition, the lower elevation habitat contains large portions of secondary, regenerating forest as a result of past human activities including logging. The northern part of the upper elevation zone has lower canopy and bamboo forest with rocky and very steep areas. Total rainfall in Mwanihana forest is around 1500 mm per year (data from UMNP). The dry season spans from June to November, with light rains typically falling from November to February and heavy rains from March to June (Tropical Ecology Assessment Monitoring (TEAM) Network, unpublished data).

### ***Data collection: camera trapping***

We conducted the camera-trapping survey from 3 July to 11 November 2013 by sampling 60 camera trap locations. Sampling was part of a long-term biodiversity

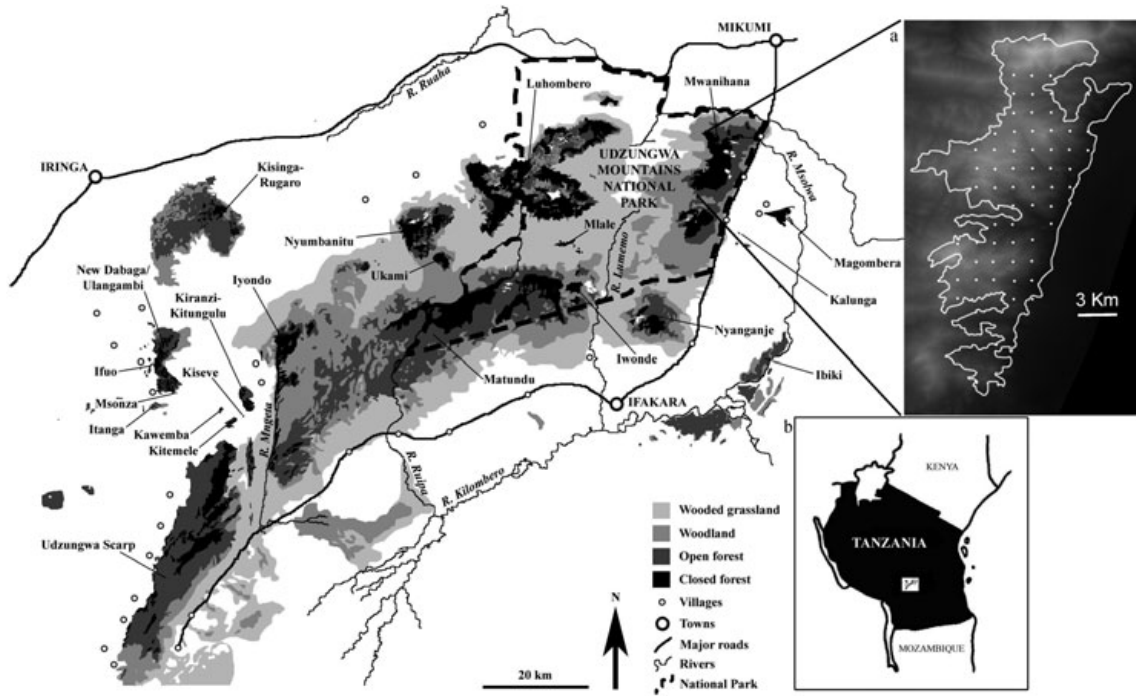


Figure 1. Map of the Udzungwa Mountains showing the main forest blocks with closed canopy forest darker in colour. The study forest was Mwanihana (top right inset) (A) where the 60 camera trap sites are shown as white dots and the background is a black with Digital Elevation Model; (B) shows the location of Udzungwa Mountains in Tanzania. *Source:* Rovero, Martin et al. 2014.

monitoring programme, the TEAM network, of which Udzungwa has been a part since 2009. However, we here used only data for year 2013, as we conducted habitat analysis during the same year. While pooling data for multiple years will have increased the sample size, we preferred not to introduce in our analysis the potential bias due to temporal discordance between animal and habitat data, as well as those due to habitat differences between years. Using ArcGIS 10 (Environmental Systems Research Institute (ESRI) Redlands, CA, USA), we placed camera traps in a pre-designed, regular grid of 60 locations across the forest, at a density of one camera per 2 km<sup>2</sup>. We selected the final camera position as on active wildlife trail located within a maximum of 100 m from the original location using a handheld GPS unit (Figure 1). Due to the number of cameras available and the time needed for the field team to set cameras, we sampled the 60 points by deploying three consecutive arrays of 20 cameras traps (south, central and northern Mwanihana). We used automated digital cameras with infrared flash (Reconyx RM 45 and HC 500 models, Reconyx Inc., Holmen, WI, USA). Cameras were set to take photos with no delay between consecutive triggers and tied to a tree about 2–3 m away from the wildlife trail at an average height of 50 cm and left running for 30 days. As cameras can operate autonomously over such periods, we did not check them so as to avoid unnecessary disturbance. At sampling completion, memory cards were recovered and mammal images extracted for identification using specialized software (DeskTEAM, Fegraus et al. 2011). A single taxonomic authority ([IUCN] International Union for Conservation of Nature, 2014) was used for species identification. Once validated by the TEAM Network secretariat, we downloaded the data package from the open-access repository at <http://www.teamnetwork.org> (data package ID: TV-20140227231705\_4591).

**Data collection: vegetation sampling**

We conducted habitat assessment at all 60 camera trap locations. We adapted a vegetation assessment protocol previously developed in the same area for a camera-trapping study on forest ungulates (Bowkett et al. 2008; Table 1). Thus, we took measurements of vegetation at three spatial scales. At the broadest scale, the 20 nearest trees were measured starting with the tree closest to the camera trap location and moving clockwise until the 20th tree was reached.

Trees were split into two categories: trees with a diameter at breast height (DBH) of 5–10 cm and those greater than 10 cm. For mid-scale, four 3 × 3 m plots were randomly placed within 10 m radius of each camera and the number of stems >5 cm DBH and taller than 1 m recorded within each plot. At the smallest scale, the percent cover of leaves, seedlings and herbs, and bare soil and dead logs was recorded within four, 1-m<sup>2</sup> plots positioned at the corners of each 3 × 3 m plot, resulting in a total of 16, 1-m<sup>2</sup> plots around each camera trap.

We recorded the proportion of leaf litter that was at least 5 cm deep in the plots as measured with a ruler. A visibility index of the plot around each camera trap location was calculated by estimating percentage visibility of a 1 × 1 m plastic sheet at a distance of 20 m from the middle of the plot (Bowkett et al. 2008). We randomly repeated this exercise four times by placing the plastic sheet at four different bearings, i.e. north, east, south and west to give a mean value of visibility for each plot. This method was adopted to quantify the density of forest floor vegetation growth not measured by stem density (SD). In addition, the shortest linear distances from each camera trap point to National Park border and forest edge were calculated using geo-processing tools available in ArcGIS 10 software. The distance to the National Park border is negatively correlated with elevation at camera trap sites given the landscape morphology of an east–west escarpment and, together with the distance from forest edge, is considered a proxy of decreasing anthropogenic disturbance (Rovero et al. 2012).

Table 1. Vegetation variables measured in plots centred on camera-trap sites, and used to analyse habitat associations of forest mammals in the Udzungwa Mountains of Tanzania. Redundant variables that were not used in the regression analysis are reported in the footnotes.

| Type of plots for the measurements | Variables used in the regression analysis (abbreviation)                                                                                                                                                                                                                           |
|------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 20 large trees (>10 cm DBH)        | Stem density (SD1)<br>Mean basal area (MBA1)<br>Diversity (Simp1) <sup>a</sup>                                                                                                                                                                                                     |
| 20 small trees (5–10 cm DBH)       | Mean basal area (MBA2)<br>Diversity (Simp2) <sup>b</sup>                                                                                                                                                                                                                           |
| 3x3 m plots                        | Small trees stem density (SD3)<br>Diversity (LogSimp3) <sup>c</sup>                                                                                                                                                                                                                |
| 1x1 m plot (forest floor cover)    | Herbaceous layer and seedlings (Herbs_Seedl) <sup>d</sup><br>Sum of deep and very deep leaf litters (SumDepthD_VD)<br>Visibility <sup>e</sup><br>Distance to the National Park border (DistToNPBorder) <sup>f</sup><br>Distance to the Forest Edge (DistToForestEdge) <sup>f</sup> |

<sup>a</sup>Simp1 correlated with richness 1 ( $r = 0.9$ ,  $p < 0.01$ ,  $n = 59$ ).

<sup>b</sup>Simp2 correlated with richness 2 ( $r = 0.8$ ,  $p < 0.01$ ,  $n = 59$ ).

<sup>c</sup>LogSimp3 correlated with richness 3 ( $r = 0.8$ ,  $p < 0.01$ ,  $n = 59$ ).

<sup>d</sup>Herbs\_Seedl correlated with leaves ( $r = -0.7$ ,  $p < 0.01$ ,  $n = 59$ ).

<sup>e</sup>Measured 20 m from the centre of the plot.

<sup>f</sup>Calculated by using ArcGIS version 10.



### **Data analysis**

TEAM data are.csv files that we analysed using ad-hoc codes in R (R Development Core Team, 2013; see also Ahumada et al. 2011). We derived for each photographed species the number of camera-trapping events as the number of images filtered by 1 h (Rovero, Collett et al. 2013; Rovero, Martin et al. 2014). Hence, instances where the same species were captured by the same camera more than once within 1 h were excluded from the analysis as a compromise between scoring the same individual multiple times and missing individuals (e.g. Bowkett et al. 2008). Following the analytical approach in Bowkett et al. (2008) and Rovero, Collett et al. (2013), we used the number of events, which is standardized by sampling effort as this was constant among sites, as a proxy of relative abundance to determine habitat associations. While this metric is an index that does not account for imperfect detection (O'Connell et al. 2011), and therefore is of limited inference, our choice is supported by studies that show how this index is correlated with true abundance (Carbone et al. 2001; O'Brien et al. 2003; Rowcliffe et al. 2008), including the study by Rovero and Marshall (2009) on Harvey's duiker in the Udzungwa Mountains. We did not oversight the limited value of such index as especially associated with the failure of accounting for potential differences between species due to factors such as trail use, body size, daily range and behaviour (Trolle and Kéry 2003; Kelly and Holub 2008; Rowcliffe et al. 2008; Sollmann et al. 2013); however, we did not aim to compare this index among species. We aimed to analyse species-specific habitat associations; hence, we considered our approach sound for a descriptive assessment of how vegetation features may influence relative abundance.

We derived a species accumulation curve to check if data collection lasted a sufficient number of days to capture the species in the community. The order in which samples were included in the curve was randomized 1000 times and results were used to get confidence intervals around the mean using the package “vegan” in R (Gotelli and Cowell 2001). Even though this approach ignores imperfect detection of individual species, it is useful for comparison with other studies (e.g. Silveira et al. 2003; Tobler et al. 2008).

We derived the following covariates from vegetation data. For the two plots of trees 5–10 and >10 cm DBH, we calculated mean basal area (MBA), total basal area (TBA) and (SD = number of stems divided by the area approximated by a circle of radius equivalent to the distance from camera-trap site of the farthest tree). For the 3 × 3 m plots, we only computed SD. For the 1-m plots, we computed the mean estimated cover of the forest-floor categories and the proportion of plots with deep leaf litter. We used Simpson's reciprocal diversity index (1/D) to calculate plant diversity in each plot.

We then used generalized linear models (GLMs, McCullagh and Nelder 1989) to determine which variables best accounted for variation between the selected species trap events and the habitat covariates at the camera locations. We implemented models in R (www.r-project.org) version 3.1.1 using the packages “lattice” for graph visualizing and “nlme” for running the model (Sarkar 2008; Pinheiro et al. 2014). Before applying the model, we first performed data exploration to check for outliers and collinearity among the explanatory variables (Zuur et al. 2007).

We used dot charts to identify presence of outliers in the explanatory variables. In order to obtain a normalized distribution for explanatory variables, a log transformation was done to correct for the extreme values found for the parameter of SD. Co-plots were used to highlight collinearity among some of the variables. For the covariates that showed high autocorrelation (correlation coefficient  $r > 0.6$ ), only one variable from each

pair was considered for further analysis and this yielded a final set of 12 variables that were used for the model formulation (Table 1).

Since the response variables were counts, which are always non-negative and that tend to be heterogeneous, we chose Poisson GLM owing to its ability to deal with both aspects (Zuur et al. 2010). Whenever over-dispersion was detected in the model (i.e. over-dispersion  $>1.5$ ), standard errors were corrected using a quasi-Poisson GLM, adding an over-dispersion parameter  $\phi$  to the variance of the response variable ( $Y_i$ ). Following Zuur et al. (2009), we employed a stepwise backward selection to derive the best model. Since we first performed accurate data exploration and addressed collinearity among the explanatory variables, we were then assured that the algorithm employed could not affect the model selection process.

In order to determine which variable to drop, “Chi” and “ $F$ ” tests were applied when using a Poisson GLM and quasi-Poisson GLM, respectively (Zuur et al. 2010). The final model, containing only the variables showing significance at 0.05 level, was then validated, looking at the homogeneity of the residuals; these were further plotted against the fitted values and against each explanatory variable in the model, as well as against those covariates that were excluded from the model. In case patterns were found in the variables not included in the models, further analysis was required in order for them to be included in the model (Zuur et al. 2010).

## Results

Of the 60 camera traps set, one was stolen, and the remaining accumulated 1818 camera days (mean 30.8), yielding 12,911 images of mammals. Twenty-six species were recorded from all the 59 sites (Table 2). The range of species captured per camera was 1–12 (median 7). Five species were recorded with  $>100$  events in this order: giant pouched rat (*Cricetomys gambianus*), bushy-tailed mongoose (*Bdeogale crassicauda*), red duiker (*Cephalophus harveyi*), suni (*Nesotragus moschatus*) and Sanje Mangabey (*Cercocebus sanjei*). Six species namely grey-faced sengi (*Rhynchocyon udzungwensis*), Tanganyika mountain squirrel (*Paraxerus vexillarius*), tree hyrax (*Dendrohyrax validus*), Abbott's duiker (*Cephalophus spadix*), servaline genet (*Genetta servalina*) and bush pig (*Potamochoerus larvatus*) scored  $>20 \leq 100$  events, while the remaining 15 species scored  $\leq 20$  events, of which seven species scored  $\leq 5$  events (Table 2). The accumulation of species detected with increasing sampling effort was at first steep, but by 1000 camera days 24 species were recorded, representing 92% of the total number of species detected (Figure 2).

We could only model habitat association for the 11 most camera trapped species (i.e. minimum of 20 events recorded). Out of these, the models did not converge for red duiker and tree hyrax. The deviance explained by the models ranged from 5.8 to 63.7%, and for nearly half of the mammal species deviance explained was  $>30\%$  (Table 3; see Appendix 1 for full results of GLMs).

The trapping events for the two carnivore species modelled, servaline genet and bushy-tailed mongoose, were found to be influenced by different variables. For the bushy-tailed mongoose, leaf litter depth and SD were found to be negatively correlated with species' trapping events, with the latter variable being more significant (Table 3). For the servaline genet, instead, the herbaceous cover and visibility index were found to be negatively correlated with its trapping events, while the diversity of large trees was the most significant variable positively correlated. The explained deviances were 21.9 and 43.5% for bushy-tailed mongoose and servaline genet, respectively (Table 3). For the Afrotheria, the model explained 29.8% of deviance of grey-faced sengi's trapping

Table 2. Checklist of mammals camera-trapped in Mwanihana forest, Udzungwa Mountains, Tanzania ordered by decreasing number of events. Naïve occupancy is computed as the number of sites the species was trapped divided by all sites sampled ( $n = 59$ ).

| Latin name                                             | Common name                  | Events per hour | Naïve occupancy |
|--------------------------------------------------------|------------------------------|-----------------|-----------------|
| <i>Cricetomys gambianus</i> Waterhouse, 1840           | Giant pouched rat            | 443             | 0.712           |
| <i>Bdeogale crassicauda</i> Peters, 1852               | Bushy-tailed mongoose        | 419             | 0.831           |
| <i>Cephalophus harveyi</i> (Thomas, 1893)              | Red duiker                   | 394             | 0.763           |
| <i>Nesotragus moschatus</i> Von Dueben, 1846           | Suni                         | 165             | 0.492           |
| <i>Cercocebus sanjei</i> Mittermeier, 1986             | Sanje mangabey               | 129             | 0.695           |
| <i>Rhynchocyon udzungwensis</i> Rathbun & Rovero, 2008 | Gray-faced sengi             | 69              | 0.288           |
| <i>Paraxerus vexillarius</i> (Kershaw, 1923)           | Tanganyika mountain squirrel | 59              | 0.322           |
| <i>Dendrohyrax validus</i> True, 1890                  | Tree hyrax                   | 57              | 0.305           |
| <i>Cephalophus spadix</i> True, 1890                   | Abbott's duiker              | 52              | 0.458           |
| <i>Genetta servalina</i> Pucheran, 1855                | Lowe's servaline genet       | 37              | 0.356           |
| <i>Potamochoerus larvatus</i> (F. Cuvier, 1822)        | Bush pig                     | 24              | 0.203           |
| <i>Cercopithecus mitis</i> Wolf, 1822                  | Sykes monkey                 | 19              | 0.220           |
| <i>Petrodromus tetradactylus</i> Peters, 1846          | Four toed sengi              | 15              | 0.034           |
| <i>Mellivora capensis</i> (Schreber, 1776)             | Honey budger                 | 12              | 0.153           |
| <i>Loxodonta africana</i> (Blumenbach, 1797)           | African elephant             | 9               | 0.119           |
| <i>Nandinia binotata</i> (Gray, 1830)                  | Palm civet                   | 9               | 0.119           |
| <i>Syncerus caffer</i> (Sparman, 1779)                 | African buffalo              | 7               | 0.068           |
| <i>Atilax paludinosus</i> (G.[Baron] Cuvier, 1829)     | Marsh mongoose               | 6               | 0.085           |
| <i>Colobus angolensis</i> (P. Sclater, 1860)           | Black & white colobus monkey | 3               | 0.068           |
| <i>Panthera pardus</i> (Linnaeus, 1758)                | Leopard                      | 3               | 0.034           |
| <i>Procolobus gordonorum</i> (Matschie, 1900)          | Udzungwa red colobus monkey  | 3               | >0.051          |
| <i>Mungos mungo</i> (Gmelin, 1788)                     | Banded mongoose              | 2               | 0.034           |
| <i>Tragelaphus scriptus</i> (Pallas, 1766)             | Bush buck                    | 2               | 0.034           |
| <i>Papio cynocephalus</i> (Linnaeus, 1766)             | Yellow baboon                | 1               | 0.017           |
| <i>Rhynchocyon cirnei</i> Peters, 1847                 | Chequered sengi              | 1               | 0.017           |
| <i>Thryonomys swinderianus</i> (Temminck, 1827)        | Marsh cane rat               | 1               | 0.017           |

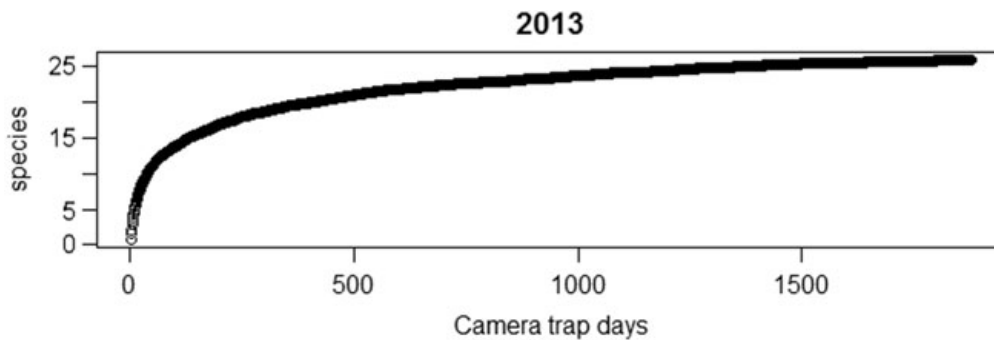


Figure 2. Species accumulation curve with sampling effort for the community of medium-to-large mammals detected by camera trapping in the Udzungwa Mountains of Tanzania.



Table 3. Results of generalized linear models with Poisson error distribution habitat predictors of abundance of nine mammals that had adequate camera trapping events for the analysis (>20). Both the deviance and the significant outcomes of the effects of covariates on trap events are indicated, along with their directionality. See Table 1 for abbreviations of covariates.

| Species                      | Significant covariates | Estimates (SE)      | <i>p</i> -value | Deviance (%) |
|------------------------------|------------------------|---------------------|-----------------|--------------|
| Sanje Mangabey               | MBA2                   | − 510.933 (280.192) | 0.074           | 5.8          |
| Bushy-tailed mongoose        | LOGSD3                 | − 1.675 (0.490)     | < 0.05          | 21.9         |
|                              | Simp1                  | 0.088 (0.048)       | 0.072           |              |
|                              | SumDepthD_VD           | − 1.365 (0.691)     | 0.053           |              |
| Lowe's servaline genet       | DistToNPBorder         | 0.000 (0.000)       | < 0.05          | 43.5         |
|                              | LOGSD1                 | 1.937 (1.036)       | 0.067           |              |
|                              | Simp1                  | 0.239 (0.067)       | < 0.001         |              |
|                              | Visibility             | − 0.030 (0.015)     | < 0.05          |              |
|                              | Herbs_Seedl            | −0.052(0.021)       | < 0.05          |              |
| Giant pouched rat            | Simp1                  | 0.110 (0.066)       | 0.098           | 30           |
| Tanganyika mountain squirrel | LOGSD1                 | − 2.260 (1.312)     | 0.091           | 14.5         |
|                              | LOGSD3                 | 3.214 (1.472)       | < 0.05          |              |
| Gray-faced sengi             | Simp2                  | 0.165 (0.080)       | < 0.05          | 29.8         |
|                              | Simp3                  | 0.190 (0.073)       | < 0.05          |              |
| Abbott's duiker              | DistToNPBorder         | 0.000 (0.000)       | < 0.001         | 14.5         |
| Suni                         | DistToForestEdge       | − 0.000 (0.000)     | < 0.05          | 30.9         |
|                              | DistToNPBorder         | − 0.000 (0.000)     | 0.08            |              |
|                              | LOGSD3                 | − 1.860 (0.846)     | < 0.05          |              |
|                              | Visibility             | 0.030 (0.009)       | < 0.01          |              |
| Bush pig                     | DistToNPBorder         | 0.000 (0.000)       | 0.055           | 63.7         |
|                              | DistToForestEdge       | − 0.000 (0.000)     | < 0.05          |              |
|                              | LOGSD1                 | 2.221 (1.307)       | 0.089           |              |
|                              | LOGSD3                 | −6.141 (1.814)      | < 0.001         |              |
|                              | Simp2                  | −0.468 (0.129)      | < 0.001         |              |
|                              | Simp3                  | −0.316 (1.286)      | < 0.05          |              |
|                              | MBA1                   | 2.150 (0.552)       | < 0.001         |              |
|                              | Herbs_Seedl            | −0.089 (0.034)      | < 0.01          |              |

events and showed significant positive correlation with small tree diversity (Table 3). For the primates, the model selected MBA of large trees as the only variable negatively correlated with trapping events of Sanje mangabey with explained deviance of 5.8% (Table 3). For the ungulates, distance to the national park border was the only and most significant variable positively correlated with the trapping event of Abbott's duiker (14.5% of deviance explained), while for suni, with the exception of the visibility index which was positively correlated with the species trapping event, the remaining variables, i.e. SD of small trees, distance to forest edge and National Park border, had negative correlations. Bush pig showed the highest number of variables significantly influencing its trapping events, with 63.7% of explained deviance. These were, from the most significant to the least significant, plant diversity and SD of small trees, distance to the forest edge and herbaceous cover (negative correlation); and MBA of large trees, distance to the National Park border and SD of large trees (positive correlation; Table 3). For the rodents, giant pouched rat's trapping event was positively correlated with large trees diversity, with 30% of deviance explained, while for the Tanganyika mountain squirrel herbaceous cover and SD of large trees negatively correlated with the species-trapping events (14.5% deviance explained; Table 3).

## Discussion

We undertook a considerable and systematic camera trap effort comprehensively covering the target area to define the community of medium-to-large forest mammals in the Udzungwa Mountains, and determined habitat associations of selected species based on fine-scale modelling of habitat features at camera trap sites. Our study confirms the usefulness of camera trapping for studying elusive forest mammals, as shown by previous studies in the area (e.g. Rovero, Martin et al. 2014) and elsewhere in the tropics (e.g. Tobler et al. 2008; Ahumada et al. 2011). Our sampling effort was adequate to detect a large (i.e. 87%) proportion of species in the community, as additional camera trapping and complementary knowledge indicates approximately 30 species may in fact be present in the area (Rovero and De Luca 2007; Rovero, Martin et al. 2014). This in turn confirms the need for more than 1000 camera days to describe a complex forest-dwelling community of larger mammals (Tobler et al. 2008; Rovero et al. 2010). While our image event score is an index and does not inform on differences in abundance among species (see Methods), that approximately half of the species were detected with < 10 events does indicate their relative rarity and/or poor detectability by camera traps. Among these are the canopy dwellers such as the two colobine monkeys, namely Udzungwa red colobus and black and white colobus, that rarely come to ground and for which, therefore, camera traps are not a suitable detection method. The remaining species in the forest community were either only detected at low relative abundance, such as leopard, buffalo and elephant, or only live in the marginal areas of the forest, such as yellow baboon and banded mongoose (Kingdon 2008).

The limit of our approach of using an index of relative abundance (see Methods and O'Connell et al. 2011) bears the consequence that we could only implement habitat models for 11 species, while studies adopting inferential approaches that consider detectability may allow extending the analysis to some of the least-detected species. However, Rovero, Martin et al. (2014) used occupancy modelling for a different analysis on the same study system and found that for species with less than 10 events occupancy models did not converge (see also Ahumada et al. 2011). Future analysis, with larger sample size, should capitalize on our results by adopting inferential analytical approaches that account for imperfect detection.

For small carnivores such as the Lowe's genet and bushy-tailed mongoose, we found a strong relationship of their trapping events with plant species diversity. Higher tree diversity occurs in the interior and at mid-elevation forest (Lovett et al. 2006) where prey availability may be optimal for these two forest dwelling species (De Luca and Mpunga 2005). In addition, SD of large trees positively correlated with trapping events of Lowe's genet, indicating their preference for closed canopy, highly sheltered areas (Rovero, Collett et al. 2013). For bushy-tailed mongoose, instead, the model predicted a negative correlation with small SD, which is also concordant with preference for mature, old-growth forest with relatively open lower canopy and understory (Rovero et al. 2012).

Plant diversity of both medium and small trees (i.e. those forming the lower canopy) had a positive and significant effect on the grey-faced sengi's trapping events. This rare species, endemic to Udzungwa Mountains, was described in 2008 (Rovero et al. 2008) and is listed as vulnerable by the International Union Conservation for Nature – IUCN ([IUCN] International Union for Conservation of Nature 2014). Being diurnal, this species may prefer more dense vegetation to avoid detection from aerial predators (Rovero, Collett et al. 2013). For the Sanje mangabey, another Udzungwa-endemic and

IUCN-endangered species ([IUCN] International Union for Conservation of Nature 2014), our model predicted a negative correlation between trapping events and MBA of lower canopy trees. This suggests that the species probably avoids areas with few lower canopy stems, indicative of limited food availability particularly fruits, and high predation risk by raptors particularly African crown eagle (*Stephanoaetus coronatus*) (Rovero et al. 2009). Indeed, the Sanje mangabey's preference for steep, low canopy and densely covered areas is supported by focal group studies (T. Jones, pers. comm.).

For two of the forest ungulates for which the model converged, Abbott's duiker and bush pig, results show that their trapping events were positively correlated with distance to the National Park border, a factor considered as a proxy of anthropogenic disturbance (Rovero et al. 2012). For the endangered and Tanzania-endemic Abbott's duiker, this is an interesting and conservation-relevant finding, and we note that a previous study on forest antelope in the area could not determine the drivers of relative abundance for this species due to insufficient data (Bowkett et al. 2008).

Conversely, Harvey's duiker had a negative association with distance to National Park border, indicating possible tolerance towards disturbance events (Rovero, Martin et al. 2014). The different results found by Bowkett et al. (2008), who found decreasing index of relative abundance with distance from villages, may be partly due to the fact that the latter study had the bulk of its data collected in Matundu, a lowland forest which was reported to be more disturbed with possible hunting from nearby villages. Moreover, in Mwanihana forest local communities were allowed to collect firewood inside the National Park border although this activity was stopped in 2011 (UMNP unpublished data). Our result for Harvey's duiker may also therefore indicate greater use and re-colonization of the lower elevation of Mwanihana by this species to the findings in Bowkett et al. (2008). In contrast, for suni, another forest antelope, trapping events were negatively correlated both with the distances to National Park border and forest edge, and with small SD, which is probably indicative of the species avoidance of the areas where human disturbances are likely to be high such as along the park border and/or forest edge. Comparable results were found by Mugerwa et al. (2012) in Bwindi Impenetrable National Park, Uganda, where higher detection of the yellow-backed duiker (*Cephalophus silvicultor*) from camera trapping was found in the interior forest where human activities were lower than along the park edge. The fact that we found a positive relationship between suni's trapping event and visibility index but negative relationship with small SD does also support this species' sensitivity to disturbances. Poor visibility will likely occur in areas dominated by dense vegetation and lianas along the Park's border due to canopy degradation and predominance of secondary, regenerating forest (Bowkett et al. 2008; Rovero, Martin et al. 2014). Our results also showed negative correlations of bush pig trapping events with sub-canopy tree diversities and stem densities; this response may reflect their opportunistic habits with preference for lower elevation areas, with regenerating vegetation and relatively low tree species' diversity (Simoons 1953). Furthermore, the model predicted the species' habitat preferences to the areas with high percentage of leaf litter coverage, where the content of invertebrates, small vertebrates, insect larvae and carrion constitutes the species' main food (Maberly 1967; Smithers 1983; Kingdon 2008). Only one variable, large tree diversity positively correlated with the trapping events of giant pouched rat. This may likely indicate the species' preference for highly sheltered areas with complex habitat which may in turn mean more food abundance. In contrast, Tanganyika mountain squirrel's trapping events showed a positive relationship with small SD, indicating the species dependence on the

dense forest floor and/or bushy areas not only for food searching but also providing perfect refuges when fleeing from predators particularly raptors.

In general, we found that a number of potential covariates both as proxies of gross habitat, namely the distance to the National Park border, and as fine-scale vegetation features, namely the SD of small trees, appeared to influence habitat associations for most of the selected species. Conversely, few species such as bush pig and Lowe genet appeared to be influenced by a greater set of covariates while a small number of species were only affected by one covariate, such as the Udzungwa-endemic Sanje mangabey (MBA for understory forest) and the Eastern Arc-endemic Abbott's duiker (distance to the National Park border). These species–habitat specific relationships may be of particular relevance to the need of protecting the full array of forest habitat, including the interior in which moist montane forest is found but also the forest edge preferred by other species. Particular emphasis should indeed be given to the areas along the Park border where human activities resulting in severe habitat degradation are higher (Rovero et al. 2012).

### **Conclusion and recommendations**

Our study confirms the usefulness of camera trapping in studying habitat–species associations for elusive forest mammals. Our analytical approach, i.e. the use of an event-based index, has the limits described in the methods, and these should be considered in future studies by adopting inferential approaches. We have provided insights using a habitat sampling approach, i.e. measuring vegetation features at the fine scale that was previously only conducted on forest antelope and on the grey-faced sengi (Bowkett et al. 2008; Rovero, Martin et al. 2014). Our results are of particular conservation relevance for the range-restricted species, such as the Lowe's servaline genet and Abbott's duiker, for which limited ecological data existed before this study. We acknowledge that greater effort would be required to adequately determine habitat associations for a greater portion of species in the community.

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**Appendix 1**

|                               |                      |                   |                    |         |             |
|-------------------------------|----------------------|-------------------|--------------------|---------|-------------|
| <i>Bdeogale crassicauda</i>   |                      |                   |                    |         |             |
| Estimate                      | SE                   | <i>t</i> value    | Pr (>  <i>t</i>  ) |         |             |
| (Intercept)                   | – 4.7153             | 2                 | 2.07066            | – 2.277 | 0.0267*     |
| LOGSD3                        | – 1.67528            |                   | 0.49020            | – 3.418 | 0.0012**    |
| Simpl                         | 0.08793              |                   | 0.04785            | 1.838   | 0.0715      |
| SumDepthD_VD                  | – 1.36536            |                   | 0.69129            | – 1.975 | 0.0533      |
| <i>Cricetomys gambianus</i>   |                      |                   |                    |         |             |
| Estimate                      | Std. Error           | <i>t</i> value    | Pr(>  <i>t</i>  )  |         |             |
| (Intercept)                   | 1.25240              |                   | 0.52363            | 2.392   | 0.0201*     |
| Simpl                         | 0.11045              |                   | 0.06562            | 1.683   | 0.0978      |
| <i>Cephalophus harveyi</i>    |                      |                   |                    |         |             |
| (Intercept)                   | 2.3895473            |                   | 0.36 23282         | 6.595   | 1.5e-08***  |
| Edge                          | – 0.0005083          |                   | 0.0003376          | – 1.505 | 0.138       |
| <i>Cercocebus sanjei</i>      |                      |                   |                    |         |             |
| Estimate                      | SE                   | <i>t</i> value    | Pr (>  <i>t</i>  ) |         |             |
| (Intercept)                   | 2.828                |                   | 1.112              | 2.544   | 0.0137*     |
| MBA2                          | – 510.933            |                   | 280.192            | – 1.824 | 0.0735      |
| <i>Cephalophus spadix</i>     |                      |                   |                    |         |             |
| Estimate                      | SE or <i>z</i> value | Pr(>  <i>z</i>  ) |                    |         |             |
| (Intercept)                   | – 1.178e+00          |                   | 3.556e-01          | – 3.314 | 0.000919*** |
| DistToNPBorder                | 2.674e-04            |                   | 7.361e-05          | 3.632   | 0.000281*** |
| <i>Dendrohyrax validus</i>    |                      |                   |                    |         |             |
| Estimate                      | SE                   | <i>t</i> value    | Pr (>  <i>t</i>  ) |         |             |
| (Intercept)                   | – 5.478              |                   | 3.366              | – 1.628 | 0.109       |
| LOGSD1                        | 2.058                |                   | 1.234              | 1.667   | 0.101       |
| <i>Genetta servalina</i>      |                      |                   |                    |         |             |
| Estimate                      | SE                   | <i>t</i> value    | Pr (>  <i>t</i>  ) |         |             |
| (Intercept)                   | – 6.5538390          |                   | 2.8101742          | – 2.332 | 0.023522*   |
| Border                        | 0.0002665            |                   | 0.0001043          | 2.555   | 0.013524*   |
| LOGSD1                        | 1.9368203            |                   | 1.0363583          | 1.869   | 0.067171    |
| Simpl                         | 0.2792012            |                   | 0.0672681          | 4.151   | 0.000121*** |
| Visibility                    | – 0.0304681          |                   | 0.0147306          | – 2.068 | 0.043501*   |
| Herbs_Seedl                   | – 0.0524114          |                   | 0.0213909          | – 2.450 | 0.017614*   |
| <i>Potamochoerus larvatus</i> |                      |                   |                    |         |             |
| Estimate                      | SE                   | <i>z</i> value    | Pr (>  <i>z</i>  ) |         |             |
| (Intercept)                   | – 3.170e+01          |                   | 1.083e+01          | – 2.927 | 0.003422**  |
| DistToNPBorder                | 2.792e-04            |                   | 1.453e-04          | 1.921   | 0.054723    |
| DistToForestEdge              | – 9.146e-04          |                   | 4.485e-04          | – 2.039 | 0.041427*   |
| LOGSD1                        | 2.221e+00            |                   | 1.307e+00          | 1.699   | 0.089269    |
| LOGSD3                        | – 6.141e+00          |                   | 1.814e+00          | – 3.385 | 0.000711*** |
| Simp2                         | – 4.675e-01          |                   | 1.286e-01          | – 3.636 | 0.000277*** |
| Simp3                         | 3.159e-01            |                   | 1.316e-01          | 2.401   | 0.016333*   |
| MBA1                          | 2.150e+00            |                   | 5.517e-01          | 3.897   | 9.73e-05*** |
| Herbs_Seedl                   | – 8.885e-02          |                   | 3.433e-02          | – 2.588 | 0.009641**  |
| <i>Paraxerus vexillarius</i>  |                      |                   |                    |         |             |
| Estimate                      | SE                   | <i>t</i> value    | Pr (>  <i>t</i>  ) |         |             |
| (Intercept)                   | 6.412                |                   | 3.411              | 1.880   | 0.0654      |
| LOGSD1                        | – 2.260              |                   | 1.312              | – 1.722 | 0.0906      |
| LOGSD3                        | 3.214                |                   | 1.472              | 2.183   | 0.0332*     |

(Continued)

*Rynchocyon udzungwensis*

Coefficients:

Estimate SE *t* value Pr ( $>|t|$ )

|             |           |         |         |           |
|-------------|-----------|---------|---------|-----------|
| (Intercept) | − 2.68711 | 0.86516 | − 3.106 | 0.00298** |
| Simp2       | 0.16537   | 0.08000 | 2.067   | 0.04337*  |
| Simp3       | 0.19016   | 0.07308 | 2.602   | 0.01184*  |

*Nesotragus moschatus*Estimate SE *t* value Pr ( $>|t|$ )

|             |             |           |         |           |
|-------------|-------------|-----------|---------|-----------|
| (Intercept) | 0.6440157   | 0.6224449 | 1.035   | 0.30544   |
| Border      | − 0.0002310 | 0.0001025 | − 2.253 | 0.02833*  |
| Edge        | − 0.0005118 | 0.0002880 | − 1.777 | 0.08124   |
| LOGSD3      | − 1.8602366 | 0.8458175 | − 2.199 | 0.03216*  |
| Visibility  | 0.0304017   | 0.0094714 | 3.210   | 0.00224** |

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**PAPER THREE**

**Does variation between dry and wet seasons affect tropical forest mammals' occupancy and detectability by camera traps? Case study from the Udzungwa Mountains, Tanzania**

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# Does variation between dry and wet seasons affect tropical forest mammals' occupancy and detectability by camera traps? Case study from the Udzungwa Mountains, Tanzania

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## Abstract

The increasing use of camera trapping coupled to occupancy analysis to study terrestrial mammals has opened the way to inferential studies that besides estimating the probability of presence explicitly consider detectability. This in turn allows considering factors that can potentially confound the estimation of occupancy and detection probability, including seasonal variations in rainfall. To address this, we conducted a systematic camera trapping survey in the Udzungwa Mountains of Tanzania by deploying twenty camera traps for 30 days in dry and wet seasons and used dynamic occupancy modelling to determine the effect of season on estimated occupancy and detection probability for species with >10 capture events. The sampling yielded 7657 and 6015 images in dry and wet seasons, respectively, belonging to 21 mammal species. Models with no season dependency and with season-dependent detectability were best supported, indicating that neither colonization nor extinction varied with seasons and hence occupancy did not vary. Only bush pig (*Potamochoerus larvatus*) showed a significant decrease in detectability from dry to wet seasons. Our study indicates that seasonal variation in rainfall may have limited effect on occupancy and detectability of resident mammals in Udzungwa rainforests; however, it remains a factor to consider when designing future studies.

**Key words:** detection probability, occupancy estimates, seasonal variation, tropical forest mammals, Udzungwas

## Résumé

Pour étudier les mammifères terrestres, l'utilisation de plus en plus fréquente des pièges photographiques, associée à l'analyse de l'occupation, a ouvert la voie à des études inférentielles qui, en plus d'estimer la probabilité de présence, tiennent compte de la détectabilité. Ceci permet alors d'estimer des facteurs qui peuvent confondre estimation du taux d'occupation et probabilité de détection, comme des variations saisonnières de chutes de pluie. Pour répondre à cela, nous avons mené une étude systématique par pièges photos dans les Monts Udzungwa, en Tanzanie, en déployant 20 pièges photographiques pendant 30 jours en saison sèche et en saison des pluies, et nous avons utilisé une modélisation dynamique de l'occupation pour déterminer l'effet de la saison sur l'occupation estimée et sur la probabilité de détection pour des espèces avec plus de 10 cas de capture. L'échantillonnage a récolté 7657 et 6015 images respectivement en saison sèche et en saison des pluies, pour 21 espèces de mammifères. Les modèles non dépendants de la saison et avec une détectabilité dépendant de la saison étaient les plus adaptés, indiquant que ni la colonisation ni l'extinction ne varient avec les saisons et que l'occupation ne varie pas non plus. Seul le potamochère (*Potamochoerus larvatus*) présentait une diminution significative de détectabilité entre la saison sèche et la saison des pluies. Notre étude indique que la variation saisonnière des chutes de pluies peut n'avoir qu'un effet limité sur l'occupation et la détectabilité des mammifères résidents des forêts pluviales d'Udzungwa,

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mais elle reste un facteur dont il faudra tenir compte lors de la conception de futures recherches.

## Introduction

Tropical rainforests generally experience relatively little seasonal changes in temperature and photoperiod compared to temperate habitats; however, seasonal fluctuations in rainfall (i.e. moisture stress occurring regularly during the year as a consequence of monsoonal circulation; Ghazoul & Sheil, 2010) are pronounced (Primack & Corlett, 2005; Williams & Middleton, 2008; Ghazoul & Sheil, 2010). Indeed, the most extensive rain forest formations, including in most of the African wet tropics, experience alternating wetter and drier seasons to a varying degree (Kato *et al.*, 2000; Primack & Corlett, 2005; Ghazoul & Sheil, 2010). This, in turn, has important implications on the resource availability, and hence on the activity patterns and movements, of forest-dwelling animals, including mammals (e.g. Babaasa, 2000; Shannon *et al.*, 2010; Djagoun *et al.*, 2013; Gaidet & Lecomte, 2013; White, 2013; Gould & Gabriel, 2014). In spite of these implications, the effect of variations in rainfall remains surprisingly little considered in ecological assessments of mammals. However, the recent, increasing application of camera trapping to the study of ground-dwelling, medium-to-large-sized mammals using statistically robust, inferential frameworks (such as occupancy, *sensu* Mackenzie *et al.*, 2002; see also Mackenzie *et al.*, 2006), has opened the way to studies that explicitly consider animal's detectability in the estimation of the state variable of interest, such as abundance or relative abundance. Specifically, occupancy is defined as the proportion of sites where a species is expected to occur, with detection probability, or detectability, being the probability that a species is detected given it is present (Mackenzie *et al.*, 2002). Hence, such approach allows us to determine how factors such as seasonal variation affect detectability and occupancy. As detectability relates to the observation process, with camera trapping it is known to vary with camera sensitivity due to climate parameters, including temperature and wetness (Rowcliffe *et al.*, 2011), providing a rationale for potential variation with seasons. Potentially, moreover, detectability could vary with

behavioural changes in movement patterns between seasons (e.g. due to varying patterns of trail use by animals; Trolle & Kéry, 2003). More intuitive is the potential variation of occupancy with season, which may be a result of variation in detectability (upon which occupancy estimation is conditional) and a direct effect of temporary movements outside the sampling area.

We aimed to provide a contribution to this topic by conducting a systematic camera trapping study replicated in wet and dry seasons in the Udzungwa Mountains of the south-central Tanzania. This area contains the largest forested blocks in the Eastern Arc Mountains of Kenya and Tanzania (Rovero *et al.*, 2014a) and is particularly important for mammal diversity and endemism (Rovero & De Luca, 2007; Burgess, Fjeldsa & Botterweg, 1998; Burgess *et al.*, 2007; Newmark 2002; Dimitrov, Nogués-Bravo & Scharff 2012 & Rovero *et al.*, 2014a). Camera trapping has been used extensively in Mwanihana forest (e.g. Rovero, Jones, & Sanderson, 2005; Rovero & De Luca, 2007; Bowkett, Rovero & Marshall, 2008; Rovero *et al.*, 2013, 2014b; Martin *et al.*, 2015); however, this is the first study to address seasonality effects on mammals. We used a dynamic occupancy framework (Mackenzie *et al.*, 2003, 2006), which allows occupancy estimation over multiple 'seasons' with the explicit incorporation of detection probability. Our specific objective was to determine whether the marked seasonal variation in rainfall had any effect on estimated occupancy and detection probability of forest-dwelling, medium-to-large mammals in the Udzungwa Mountains. The majority of mammals found in the study site are residents in the forest throughout the year. An exception, however, may be represented by species such as Harvey's duiker (*Cephalophus harveyi*) that were found to prefer forest edges (Rovero *et al.*, 2014b) and that may temporarily migrate outside the forest determining site extinction/colonization and hence, potentially, changes in occupancy; the same may apply to large herbivores (i.e. elephants (*Loxodonta africana*) and buffaloes (*Syncerus caffer*)) who are not forest specialists but may spend most of the time in the forest. Our general hypothesis was that (i) for forest-resident mammals, estimated occupancy does not vary between dry and wet seasons, and, in contrast; (ii) estimated detectability does vary between dry and wet seasons due to the above mentioned, potential differences in camera sensitivity and/or in movement patterns within the study area.

## Material and methods

### Study area and seasonal variability

The Udzungwa Mountains of south-central Tanzania are a mosaic of moist forest blocks interspersed with drier habitats (Dinesen *et al.*, 2001; Marshall *et al.*, 2010). This study was carried out in Mwanihana forest, on the eastern side of Udzungwa Mountains National Park (UMNP, 7°46'S, 36°51'E; Fig. 1). Mwanihana is one of the largest forest blocks in the range (192 km<sup>2</sup>, Rovero *et al.*, 2013) of closed forest habitat with continuous vegetation covering most of the forest elevation range spanning from 290 to 2279 m above sea level (a.s.l.). The habitat types in the area contain deciduous forest on the low altitude to montane evergreen forest in the high altitude and ranges from east to west (Lovett, Marshall & Carr, 2006). Temperatures vary according to the pronounced altitudinal gradient while seasonally they experience modest variation, with maximum in November (mean 24.2°C), and minimum in July (mean 19.4°C; data from [www.wordclim.org](http://www.wordclim.org) in Dubois *et al.*, 2015).

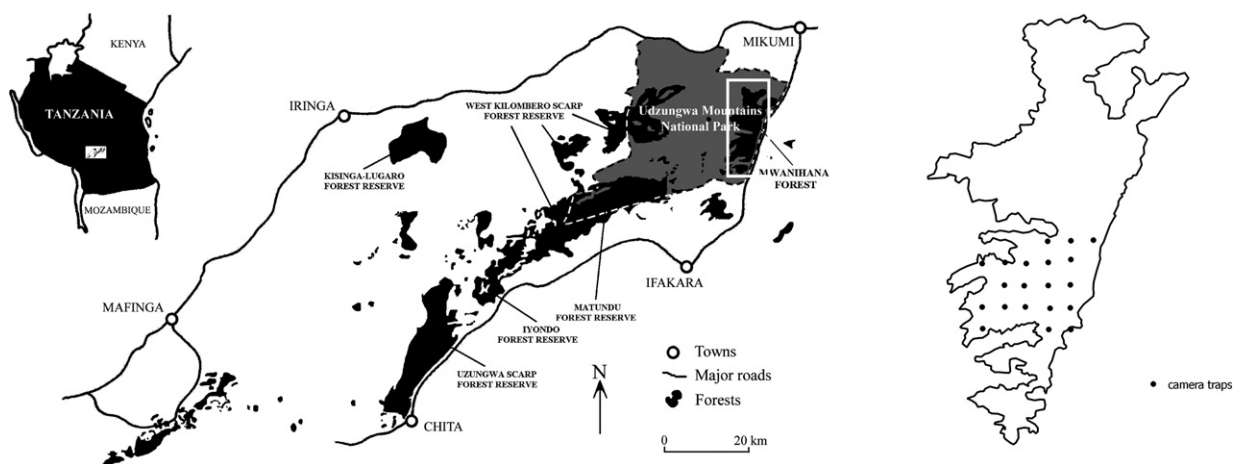
The total annual rainfall in Mwanihana forest is around 1500 mm from the two rainy seasons, with light and heavy rainfall seasons occurring during November to February and March to May, respectively, while the dry season spans from June to October (Burgess, Fjeldsa &

Botterweg, 1998; TEAM Network, unpublished data; Dubois *et al.*, 2015). Climate data records in the area for the past 50 years show that dry seasons received 5–25 mm of rainfall per month (June–October) while wet seasons received 168–271 mm of rainfall (December–April; [www.wordclim.org](http://www.wordclim.org) in Dubois *et al.*, 2015). These data concur with rainfall data recorded recently by the Tropical Ecology Assessment and Monitoring (TEAM) automatic weather station located within Mwanihana forest at 1200 m a.s.l., whereby during the dry season, that is July to October 2013 mean monthly rainfall was recorded at 10, 5, 12 and 8 mm of rains, respectively, while during the wettest months in 2014 (i.e. March to May), it was 150, 165 and 180 mm, respectively (TEAM Network, unpublished data).

The area is home to about 45 endemic or near-endemic vertebrate species to the Eastern Arc Mountains such as Sanje mangabey (*Cercocebus sanjei*) and Udzungwa red colobus (*Procolobus gordonorum*) (Burgess *et al.*, 2007; Rovero & De Luca, 2007; Rovero *et al.*, 2009, 2014a).

### Data collection

We conducted systematic camera trapping surveys in the dry and wet season, by deploying twenty camera traps for 30 days at the very same sampling locations. In the dry season, the data were collected from 3 July to 13 August



**Fig 1** Map of the Udzungwa Mountains of south-central Tanzania (adapted from Marshall *et al.*, 2010 and Rovero *et al.*, 2014b) showing the main blocks with closed-canopy forest. The study forest was Mwanihana in the north-eastern portion of the range; this forest is zoomed in the right inset where the twenty camera trap sites on the south-central part of the forest are shown as black dots.

2013, while in the wet season, the survey was conducted from 1 April to 8 May 2014, hence falling within the main rainfall season (see 'Study area and seasonal variability'). Therefore, we choose these periods assuming they would capture adequate variation in rainfall. Camera traps were placed on a regular grid in the southern part of the forest covering part of the full forest elevation gradient, that is from 525 to 1468 m a.s.l., at a density of one camera per 2 km<sup>2</sup> following the standardized TEAM Network protocol (TEAM-Network, 2011; Rovero *et al.*, 2014b). All camera traps were set within the area of occurrence of targeted forest-dwelling mammals as deduced from earlier work (e.g. Rovero *et al.*, 2014b). Automated digital cameras with infrared flash (Reconyx RM 45 and HC 500 models, Reconyx Inc., Holmen, WI, U.S.A.) were used. Cameras are well camouflaged to reduce the chances of them being detected by animals in daytime; in addition, they mount a low-glow, LED flash that is almost invisible at night. Cameras were set to take photographs without delay between consecutive triggers and tied to a tree about 2–3 m away from the wildlife trail located within a 100 m of radius in a proposed camera trap position at an average height of 50 cm. The cameras were angled to be parallel to the slope of the ground to maximize capture rate. As cameras can operate on such period in autonomy, they were not checked to avoid unnecessary disturbance. At sampling completion, memory cards were recovered and mammal images extracted for identification using specialized software DeskTEAM (Fegraus *et al.*, 2011). A single taxonomic authority was used for species identification by following IUCN (2014). The data package for dry season was downloaded from the TEAM Network open-access repository (<http://www.teamnetwork.org>; ID: TV-20140227231705\_4591).

#### Data analysis

We first assessed differences between seasons based on two descriptors from raw data in each season: (i) the observed species richness; and (ii) the camera trapping rates of species detected in both seasons. To compute camera trapping rate, we scored events as the number of images filtered by 1 h that compromises between scoring the same individual multiple times and missing individuals (e.g. Mugerwa *et al.*, 2012; Rovero *et al.*, 2013, 2014b). We measured sampling effort as the number of 24-h periods from setting a camera trap in the field up until the camera was retrieved. We then calculated RAI as the ratio of

events on camera days and multiplied by 100. We used Wilcoxon signed rank tests for paired samples to compare camera trap rates between seasons.

We then used dynamic occupancy modelling (Mackenzie *et al.*, 2003) applied to species with enough trapping events for the analysis (i.e. >10 events). We defined occupancy ( $\psi$ ) as the proportion of sites where a species is expected to occur, with detection probability ( $p$ ) being the probability that a species is detected given it is present; these two parameters are estimated using a likelihood-based method (Mackenzie *et al.*, 2002). Specifically, the analysis of detection/nondetection data is described by a hierarchical, or state-space model that contains one submodel for the only partially observed true state (occurrence, the result of a biological process), and another submodel for the actual observations, whereby the actual observations result from both the particular realization of the biological process and the observation process (see Kéry, 2010 for full details of modelling formulation). In practice, for the species that were captured by camera traps, we modelled presence/absence data at each sampling site and considered three potential outcomes: (i) the species is detected at the site; (ii) the species is not detected at the site because it is absent; and (iii) the species is not detected but it is present. Thus, for each species, we built a matrix of detections (1, i.e. at least one image obtained by the camera trap within the sampling occasions) and nondetections (0, i.e. no images obtained) that aligned data for wet and dry seasons, made of camera trap sites by sampling occasions (eight for each of the two seasons), each sampling occasion being 5 days (Rovero *et al.*, 2014b). Unlike single-season models, the dynamic occupancy model allows to estimate the parameters governing changes in occupancy state variable in addition to  $p$ , namely colonization ( $\gamma$ ) and extinction ( $\epsilon$ ) probability (Mackenzie *et al.*, 2003). As described in Introduction, we assumed that the majority of targeted, forest-dwelling populations would not experience colonization or extinction between seasons and therefore that occupancy levels would not change significantly, while we did assume that detectability could change (see Introduction). However, because the different seasons being compared were in different years, with a time span of about 8 months in between (dry 2013 to wet 2014), we also considered models with time-dependent  $\gamma$  and  $\epsilon$ . Thus, we evaluated four basic dynamic occupancy models as follows: (i) null model, with no time dependence (M0):  $\psi(.)\gamma(.)\epsilon(.)p(.)$ , where (.) indicates that no effect of covariates is tested;

(ii) model with season-dependent detectability (M1):  $\psi(.)\gamma(.)\epsilon(.)p(\text{season})$ ; (iii) model with season-dependent colonization and extinction (M2):  $\psi(.)\gamma(\text{season})\epsilon(\text{season})p(.)$ ; and (iv) fully season-dependent model (M3):  $\psi(.)\gamma(\text{season})\epsilon(\text{season})p(\text{season})$ . To prepare data for the analysis and to run models, we followed a data management procedure described by Ahumada *et al.* (2011) and Rovero *et al.* (2013, 2014b) conducted in R software (R Development Core Team 2011). We implemented the modelling using package 'unmarked' in R (Fiske & Chandler, 2011; Fiske *et al.*, 2015). We used the Akaike information criterion (AIC) to rank candidate models and calculate their Akaike weights and considered  $\text{AIC} < 2$  as the criterion to determine the best supported model/s (Burnham & Anderson, 2012). We derived  $\psi$  and  $p$  for both seasons by means of bootstrapping (Kéry & Chandler, 2012).

## Results

All twenty camera traps in the dry season worked successfully, while only fifteen cameras worked in the wet season,

due to either camera failure or production of blurred images preventing identification. Hence, we limited the analysis to data from the fifteen camera sites that were sampled in both seasons, for a sampling effort of 466 (mean 31) and 449 (mean 30) camera days in dry and wet season, respectively. Sampling yielded a total of 7657 and 6015 images in dry and wet seasons, respectively. A total of 21 species of mammals from both seasons were photographed by the camera traps, of which fifteen in both seasons, and three in each season only (Table 1). The number of species captured per camera was 2–9 (median 6) and 4–9 (median 6.5) in dry and wet season, respectively. The species with the greatest difference in camera trapping events between seasons were the following (Table 1): suni (*Nesotragus moschatus*) with 98 and 51 events in dry and wet season, respectively, bushy-tailed mongoose (*Bdeogale crassicauda*) with 164 and 77 events, red duiker (*Cephalophus harveyi*) with 185 and 215 events, Sanje mangabey with 26 and 66 events, tree hyrax (*Dendrohyrax validus*) with 29 and two events and bush pig (*Potamochoerus larvatus*) with 15 and 34 events in dry and wet seasons, respectively (Table 1).

**Table 1** Checklist of mammals camera trapped in Mwanihana forest, Udzungwa Mountains, Tanzania, in dry and wet seasons with three raw descriptors of occurrence: photographic events, relative abundance index (RAI) and naïve occupancy. Outcomes of Wilcoxon paired-sample test for differences in events between seasons are also indicated

| Scientific name                  | Common name                  | Events by hours |     | RAI   |       | Naïve occupancy |      | Wilcoxon test |         |
|----------------------------------|------------------------------|-----------------|-----|-------|-------|-----------------|------|---------------|---------|
|                                  |                              | Dry             | Wet | Dry   | Wet   | Dry             | Wet  | V value       | P Value |
| <i>Atilax paludinosus</i>        | Marsh mongoose               | 3               | 5   | 0.64  | 1.11  | 0.13            | 0.13 | 3.5           | 0.7127  |
| <i>Bdeogale crassicauda</i>      | Bushy-tailed mongoose        | 164             | 77  | 35.19 | 17.15 | 0.93            | 0.8  | 49            | <0.05   |
| <i>Cephalophus harveyi</i>       | Harvey's duiker              | 184             | 215 | 39.48 | 47.88 | 0.8             | 0.93 | 50.5          | 0.6083  |
| <i>Cephalophus spadix</i>        | Abbott's duiker              | 6               | 8   | 1.29  | 1.78  | 0.27            | 0.4  | 5             | 0.5827  |
| <i>Cercocebus sanjei</i>         | Sanje mangabey               | 26              | 66  | 5.58  | 14.7  | 0.6             | 0.73 | 25            | 0.1544  |
| <i>Cercopithecus mitis</i>       | Sykes' monkey                | 3               | 3   | 0.64  | 0.67  | 0.13            | 0.13 | 3             | 1       |
| <i>Cricetomys gambianus</i>      | Giant pouched rat            | 119             | 142 | 25.54 | 31.63 | 0.8             | 0.73 | 27.5          | 0.3862  |
| <i>Dendrohyrax validus</i>       | Tree hyrax                   | 29              | 2   | 6.22  | 0.45  | 0.33            | 0.13 | 19.5          | 0.07314 |
| <i>Genetta servalina</i>         | Lowe's servaline genet       | 6               | 6   | 1.29  | 1.34  | 0.27            | 0.2  | 12            | 0.8421  |
| <i>Hystrix africae australis</i> | Crested porcupine            | NA              | 1   | NA    | 0.22  | NA              | 0.07 |               |         |
| <i>Loxodonta africana</i>        | African elephant             | 3               | NA  | 0.64  | NA    | 0.13            | NA   |               |         |
| <i>Mellivora capensis</i>        | Honey badger                 | 4               | 11  | 0.86  | 2.45  | 0.2             | 0.47 | 2.5           | 0.1058  |
| <i>Mungos mungo</i>              | Banded mongoose              | NA              | 1   | NA    | 0.22  | NA              | 0.07 |               |         |
| <i>Nandinia binotata</i>         | Palm civet                   | 2               | NA  | 0.43  | NA    | 0.13            | NA   |               |         |
| <i>Nesotragus moschatus</i>      | Suni                         | 98              | 51  | 21.03 | 11.36 | 0.8             | 0.6  | 61            | 0.09031 |
| <i>Panthera pardus</i>           | Leopard                      | 2               | 1   | 0.43  | 0.22  | 0.07            | 0.07 | 1.5           | 1       |
| <i>Papio cynocephalus</i>        | Yellow baboon                | 2               | 1   | 0.43  | 0.22  | 0.07            | 0.07 | 1.5           | 1       |
| <i>Paraxerus vexillarius</i>     | Tanganyika mountain squirrel | 6               | 7   | 1.29  | 1.56  | 0.2             | 0.2  | 5             | 1       |
| <i>Petrodromus tetradactylus</i> | Four-toed sengi              | NA              | 2   | NA    | 0.45  | NA              | 0.13 |               |         |
| <i>Potamochoerus larvatus</i>    | Bush pig                     | 15              | 34  | 3.22  | 7.57  | 0.47            | 0.53 | 9             | 0.2223  |
| <i>Syncerus caffer</i>           | African buffalo              | 1               | NA  | 0.21  | NA    | 0.13            | NA   |               |         |



The Wilcoxon paired-sample test for differences between seasons was significant ( $P < 0.05$ ) only for the bushy-tailed mongoose and marginally significant ( $P < 0.1$ ) for tree hyrax and suni (Table 1).

For the six species that had enough events in each season for dynamic occupancy modelling ( $>10$ ), model selection based on minimizing AIC showed that the best candidate models were both M0 and M1, that is models with no season dependency and with season-dependent detectability (Table 2; see also Fig. 2). The only exception was bush pig, for which M3 and M1 were best models with almost identical AIC, indicating a significant variation (decrease) of detectability (Table 2; Fig. 2).

## Discussion

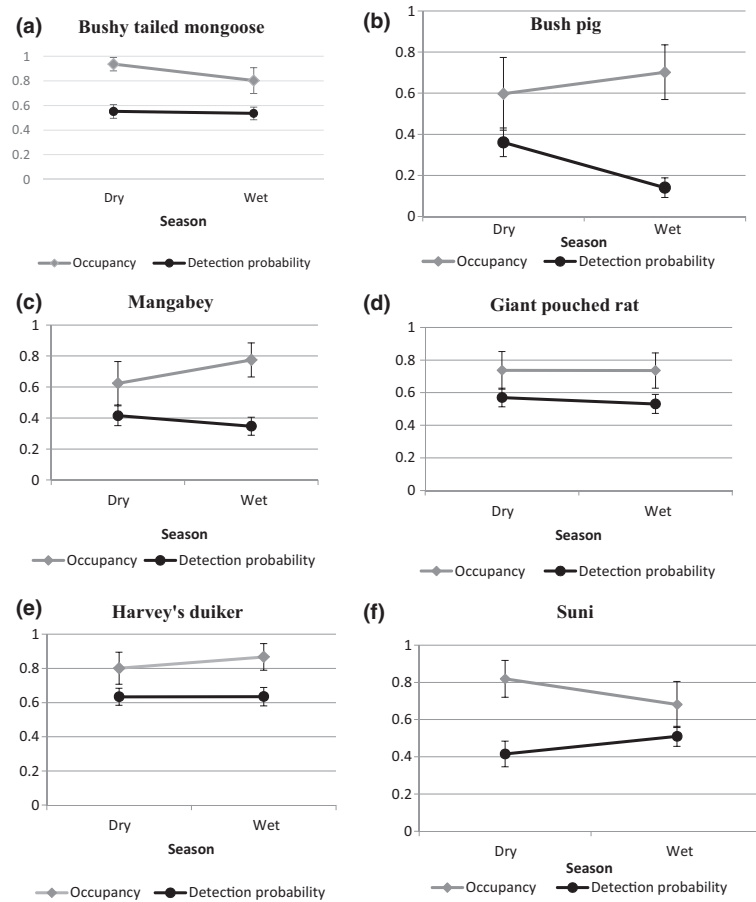
We used camera trapping coupled with dynamic occupancy modelling to test whether seasonal variation had

any effect on estimated occupancy and detectability of forest-dwelling mammals in the Udzungwa Mountains of Tanzania. We consider the marked changes in rainfall (and moisture) as the key driver of seasonality of relevance in our study, while both historical and current data show that variation in temperature between seasons is little. The regular occurrence of a wet period due to monsoonal periodicity of rainfall is indeed the main feature of seasonal rain forests (Ghazoul & Sheil, 2010). For the six species for which we had enough data for dynamic occupancy modelling, we found that neither occupancy nor detectability varied significantly between seasons, with the exception of bush pig for which detectability decreased significantly from dry to wet season. Furthermore, the results from this modelling approach that explicitly considers imperfect detection and therefore corrects the estimation of occupancy for the bias associated with the observation process (Mackenzie *et al.*, 2006) are broadly

**Table 2** Outcome of model selection applied to four dynamic occupancy models testing for the effect of seasonal variation in estimated occupancy and detectability of six species of mammals camera trapped in Mwanihana forest, Udzungwa Mountains, Tanzania. See text for methodological details

| Species                       | Model <sup>a</sup> | Number of parameters | AIC    | Delta | AIC weight | Cumulative weight |
|-------------------------------|--------------------|----------------------|--------|-------|------------|-------------------|
| <i>Bdeogale crassicauda</i>   | M0                 | 4                    | 272.26 | 0.00  | 0.063      | 0.62              |
|                               | M1                 | 5                    | 274.22 | 1.96  | 0.234      | 0.86              |
|                               | M3                 | 7                    | 277.80 | 3.53  | 0.039      | 1.00              |
|                               | M2                 | 6                    | 275.84 | 3.58  | 0.104      | 0.96              |
| <i>Potamochoerus larvatus</i> | M1                 | 5                    | 171.59 | 0.00  | 0.441      | 0.44              |
|                               | M3                 | 7                    | 171.60 | 0.01  | 0.439      | 0.88              |
|                               | M2                 | 6                    | 175.00 | 3.41  | 0.08       | 0.96              |
|                               | M0                 | 4                    | 176.43 | 4.84  | 0.039      | 1.00              |
| <i>Cephalophus harveyi</i>    | M0                 | 4                    | 256.85 | 0.00  | 0.641      | 0.64              |
|                               | M1                 | 5                    | 258.85 | 2.00  | 0.236      | 0.88              |
|                               | M2                 | 6                    | 260.79 | 3.93  | 0.09       | 0.97              |
|                               | M3                 | 7                    | 262.79 | 5.94  | 0.033      | 1.00              |
| <i>Nesotragus moschatus</i>   | M0                 | 4                    | 247.49 | 0.00  | 0.473      | 0.47              |
|                               | M1                 | 5                    | 248.30 | 0.81  | 0.316      | 0.79              |
|                               | M2                 | 6                    | 250.11 | 2.62  | 0.128      | 0.92              |
|                               | M3                 | 7                    | 250.96 | 3.47  | 0.084      | 1.00              |
| <i>Cercocebus sanjei</i>      | M0                 | 4                    | 229.89 | 0.00  | 0.519      | 0.52              |
|                               | M1                 | 5                    | 231.26 | 1.37  | 0.262      | 0.78              |
|                               | M2                 | 6                    | 232.46 | 2.56  | 0.144      | 0.93              |
|                               | M3                 | 7                    | 233.77 | 3.87  | 0.075      | 1.00              |
| <i>Cricetomys gambianus</i>   | M0                 | 4                    | 248.70 | 0.00  | 0.572      | 0.57              |
|                               | M1                 | 5                    | 250.47 | 1.77  | 0.236      | 0.81              |
|                               | M2                 | 6                    | 251.58 | 2.88  | 0.136      | 0.94              |
|                               | M3                 | 7                    | 253.33 | 4.63  | 0.057      | 1.00              |

<sup>a</sup>Model formulation: M0 =  $\psi(\cdot)\gamma(\cdot)\varepsilon(\cdot)p(\cdot)$ ; M1 =  $\psi(\cdot)\gamma(\cdot)\varepsilon(\cdot)p(\text{season})$ ; M2 =  $\psi(\cdot)\gamma(\text{season})\varepsilon(\text{season})p(\cdot)$  and M3 =  $\psi(\cdot)\gamma(\text{season})\varepsilon(\text{season})p(\text{season})$ ;  $\psi$ =occupancy;  $\gamma$ =colonization;  $\varepsilon$ =extinction;  $p$ =detection probability.



**Fig 2** Plots of the results of dynamic occupancy models showing estimated occupancy and detection probability (with SE bars) for the six species of forest mammals camera trapped with >10 trapping events in Mwanihana Forest, Udzungwa Mountains, Tanzania.

concordant with the results from the comparison of raw data (i.e. RAI, an event rate index) for the fifteen species that were detected in both seasons, whereby no significant differences emerged except for one species, the bushy-tailed mongoose. While for a number of other species the differences in event counts is remarkable, there does not appear to be any pattern of directionality in these differences, as also indicated by the occupancy modelling results. There are, however, interesting indications that would deserve further investigation, such as the marked drop in event count for the tree hyrax in the wet season (two events versus 29 in dry season). Tree hyrax is a predominantly arboreal species, which is, however, commonly camera trapped on the ground in dry season (e.g. Rovero *et al.*, 2014b); hence, this result may reflect a decrease in terrestrial activity by this species in the wet season, possibly mirroring a general pattern of compressed mobility by this species in the wet season. Milner & Harris (1999) found decreased activity in territorial calling by the

closely related *D. arboreous* in Rwanda, a finding that may support a pattern of decreased mobility, but also in contrast with an apparent lack of differences for *D. validus* reported in southern Udzungwa forests by Topp-Jørgensen *et al.* (2008).

This is, to our knowledge, the first study to address the effect of rainfall-driven seasonal variations in occupancy estimation in forest mammals. The main result of a lack of major responses in detectability does not support our hypothesis and indicates the lack of any influential variation with season in factors such as movement patterns and the sensitivity of the camera sensors in relation to wetness. That colonization and extinction (and therefore, occupancy) too did not vary between dry and wet season is perhaps less surprising and indeed in line with our hypothesis. Target species are resident, forest-dependent mammals, and no major movements outside the sampled sites were expected. Elephants and buffalos, the only species that are known to migrate in and out the forest, were



detected too infrequently for any meaningful conclusion, and the differences in events for the 'edge-lover' Harvey's duiker (184 and 215 in wet and dry season, respectively) are not compatible with the marked shift in range outside the sampled area that would determine significant changes in occupancy. Importantly, however, changes in activity and movement patterns *within* the area sampled, which may be associated with seasonality in resource availability, cannot be excluded. These may include the shifting of home ranges along the forest elevation gradient, although as we sampled within a portion of this gradient (i.e. approximately 940 m), this potential factor may not have a strong influence in our results. Still, for example, Mwamende (2009) found that Sanje mangabey in the same forest as our study moved more in dry than wet season possibly in response to sparser food availability, particularly fruits. While such variation would not alter estimated occupancy, it may explain the significant variation in detectability we found for the bush pig. This species had an higher event count in wet season relative to dry season (and an higher, albeit not significant increase in estimated occupancy); however, its detectability decreased significantly, which is compatible with the hypothesis of an altered movement pattern affecting the likelihood with which the animals are detected by the camera traps.

We acknowledge that our study used a limited sample size (twenty camera trap sites deployed), which constrained the number of species on which occupancy modelling could be applied. However, the results for these species are clear and the complementary information from the comparison of event counts are broadly in agreement with the main finding from the modelling. Therefore, we consider our findings a valid first contribution to address the main question of the study, although we do caution against generalizing our results to different habitats and target species. We identify two important implications for the design of monitoring programmes that aim to determine population trends. First, the choice made by the TEAM Network of using a discrete season to sample the population/s of interest over multiple years without need for accounting for the full spectrum of seasonal variations, which would likely imply logistic constraints and greater costs, seems supported, at least at our site. Our findings are mirrored by a study conducted in the same area that found that line transect-based detectability and estimated local abundance of arboreal primates did not change between wet and dry seasons, justifying the choice of sampling in the dry season only (Rovero *et al.*, 2015). Second, our

results support the choice of dry season for easier implementation of camera trapping (TEAM Network, 2011). Indeed, despite using tropicalized and professional camera traps that are among the top quality line on the market, 25% of the camera units failed during the wet season while all worked fine in the dry season, a difference which is likely due to moisture accumulation on the camera trap sensor (Kays *et al.*, 2009) causing malfunctioning or blurred images (which may in turn prevent proper species identification).

In conclusion, we provided a first contribution on the effects of seasonal variation on occupancy and detectability of tropical forest mammals. Further assessments with larger sampling efforts and allowing for a broader range of species to be analysed will help elucidating the consistence of our results. With the increasing use of camera trapping in a wide range of wildlife research applications (e.g. O'Connell, Nichols & Karanth, 2011; Rovero *et al.*, 2013), including standardized monitoring programmes (Ahumada *et al.*, 2011; Ahumada, Hurtado & Lizcano, 2013), consideration of the potential sources of variations in the results will become of concomitantly increasing relevance.

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## PAPER FOUR

### **The effect of human disturbance on the spatial and temporal patterns of relative abundance of medium to large bodied forest mammals in the Udzungwa Mountains National Park of Tanzania**

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## **Abstract**

Medium to large forest mammals are threatened by a range of anthropogenic factors including poaching and habitat degradation. However, there is a lack of systematic data to assess the effects of anthropogenic activities on temporal and spatial patterns of abundance for forest mammals. In this study, we conducted systematic camera trapping surveys for six consecutive years (2009 – 2014) in Mwanihana forest within the Udzungwa Mountains National Park deploying 60 cameras for 30 days yearly during the dry season. The forest was once open to firewood collection by local people on its eastern border before it was stopped in 2011, and also faces varying poaching pressures. We compared the effects on species relative abundance of (1) poaching between the northern and southern sides, where contrasting incidence was found, and of (2) firewood collection before and after it was banned. Also we ran correlation tests between species' relative abundance and total number of snares removed per each year. We found significantly higher relative abundances on the southern side for all species pooled together and selected species susceptible to poaching than on the northern side. Some species moreover, e.g. Harvey's duiker (*Cephalophus harveyi*), showed significant differences in relative abundance on the eastern side of the forest after firewood collection ban, indicating recolonization of the area. Overall we showed that firewood collection impacted negatively on certain species' relative abundance. Similarly, species' relative abundance on certain species was low in the northern side where poaching pressures were high. Also a subgroup of poached species' relative abundance increased with decreased poaching activities over time. Efforts to curb poaching activities should be intensified alongside providing environmental education to the locals.

**Keywords:** Poaching, firewood collection, camera trap data, human populations, Mwanihana forest.

## INTRODUCTION

Medium to large mammals are a key component of tropical forest communities in terms of biomass and as indicators of ecosystem health. These mammals provide important ecosystem services such as seed dispersal, food and nutrient cycling (Ahumada *et al.* 2011). Yet, they are threatened by a number of global and local factors including direct human disturbance (Chapman *et al.* 2015). The effects of human activities on wildlife and its habitats originate from different activities such as tourism (Razafimahaimodison 2003), recreation (Batten 1977), industrial development (Meire 1993), logging (Mligo 2011), firewood collection (Mookherjee *et al.* 2010) and hunting (Hegerl *et al.* 2015; Rovero *et al.* 2015). In the tropics, hunting/poaching has been reported as responsible on the declining populations of most forest mammal species (e.g. Laurance *et al.* 2006; Hegerl *et al.* 2015; Rovero *et al.* 2015). For example in Bukit Barisan Selatan National Park in Sumatra-Indonesia, the effects of hunting has led to the decrease of tiger (*Panthera tigris*) population and its preys (e.g. mouse deer (*Tragulus spp.*, pigs (*Sus scrofa*), and Samba deer (*Cervus unicolor*)) (O'Brien *et al.* 2003).

Firewood collection, a practice less investigated in terms of impacts on mammals, can also have detrimental effects (Mligo 2011). Firewood collectors usually target dead trees especially those with hollow trunks and fallen timber as they are capable of burning well and produce less smoke (Driscoll *et al.* 2000). However, the fallen timber and dead wood provides habitat for some invertebrates and fungi which in turn act as essential food sources for some forest mammals such as suni (*Nesotragus moschatus*), bushpig (*Potamochoerus larvatus*), Abbott's duiker (*Cephalophus spadix*) and Sanje mangabey (*Cercocebus sanjei*) (Estes 1992; Kingdon 2008; Rovero *et al.* 2009; Mwamende 2009).

In this context, determining the effects of human disturbance such as poaching and firewood collection on mammal abundance over time and space is therefore critical in

conservation management. However we generally lack systematic and comparable data; exceptions are those from the Tropical Ecological and Assessment Monitoring (TEAM) Network. TEAM's data are long time based data obtained from a global network of 16 stations based on standardized protocols that monitors tropical biodiversity including terrestrial vertebrates. In East Africa, several studies that looked into the effects of human disturbances in the tropical forests are limited to short term studies only (e.g. Nielsen 2006; 2011; 2014; Rovero *et al.* 2014b & Chapman *et al.* 2015) while some focused on comparisons between protected areas (PAs) with effective and ineffective management (Hegerl *et al.* 2015; Chapman *et al.* 2015 & Rovero *et al.* 2015).

In this study, we used camera traps (CTs) data collected for a period of six years (2009 – 2014) to determine the effects of human disturbance on the abundance and spatio-temporal patterns of forest mammals in Mwanihana forest within the Udzungwa Mountains National Park (UMNP), Tanzania. This is the only PA with a national park status found within the Eastern Arc mountains (Harrison 2006). Since its establishment the park has been subjected to a number of human activities including firewood collection which was permitted within Mwanihana forest on its eastern border side (TANAPA 2011). In addition, the target forest is also facing varying poaching pressures due to increasing human populations, especially on its northern side (TANAPA 2016). Our specific objectives were (i) to determine the effects of firewood collection on forest mammals' relative abundance (as proxied by the photographic event rate) and (ii) to determine the effects of poaching activities on spatio-temporal patterns of mammals' relative abundance in relation with human proximity to the forest. We hypothesized that some mammals would tend to recolonize the eastern side of Mwanihana forest after firewood collection ban, and that species' relative abundance would vary with poaching

pressure, while overall mammals species' relative abundance would increase due to decreased poaching activities with time.

## **MATERIALS AND METHODS**

### **Study area**

We conducted the study in Mwanihana forest, located on the eastern side of UMNP (Fig.1). UMNP is centred on 7°46'S, 36°51'E has a size of 1990 km<sup>2</sup> and is also on the eastern part of the Udzungwa Mountains. The Udzungwa Mountains are a part of Eastern Arc Mountains characterized by a mosaic of moist forest blocks interspersed with drier habitats found in south-central Tanzania (Rovero *et al.* 2014a). Mwanihana is one of the largest forest blocks in the range (192 km<sup>2</sup> of closed forest habitat) with continuous vegetation cover from 300 to over 2000 m above sea level (Bowkett *et al.* 2008). The forest habitat broadly ranges east-west from lowland deciduous forest to montane evergreen forest (Lovett *et al.* 2006). The habitats at lower altitudes are mostly comprised of dry forest, followed by semi-deciduous forest of moderate to old-growth (transitional) forest and evergreen old growth montane forest (Lovett *et al.* 2006; Rovero *et al.* 2006; Martin *et al.* 2015). The estimated mammal species richness in Mwanihana forest ranges between 32 to 34 species which include Udzungwa-endemic species such as Sanje mangabey and Udzungwa red colobus (*Procolobus gordonorum*) (Rovero *et al.* 2014b). Temperature in Udzungwa varies according to the pronounced altitudinal gradient while there is also modest seasonal variation, with the maximum in November (mean 24.2°C), and minimum in July (mean 19.4°C; data from [www.worldclim.org](http://www.worldclim.org) in Dubois *et al.* 2015). The total annual rainfall in Mwanihana forest is around 1500 mm, with light and heavy rainy seasons from November to February and March to May, respectively, and the dry season from June to October (TEAM Network unpublished data; Dubois *et al.* 2015).



## Human disturbance data

The history of firewood collection goes back before the area was gazetted a national park status in 1992. Before, the area had a status of forest reserve in which controlled consumptive utilization of natural resources were permitted including firewood collection and logging. Although all the national parks in Tanzania adhere to the strict policy of “Non-consumptive” utilization, still the UMNP management permitted locals living in villages adjacent to the eastern boundary of the Park to collect firewood from the forest, up to 1 km within the boundary (Jones 2013). Firewood collection was also associated with poaching activities mainly through the use of snares (Rovero *et al.* 2014b) and only restricted to the deadwood and fallen logs (Pers. comm. Prisca Lyimo). This practice, which was permitted to women only, was initially conducted twice a week and later on

reduced to once per week before put into halt in the end of June 2011. Apart from firewood collection which was permitted by the Park officials, the area is also facing illegal activities mainly on its north-eastern border due to the presence of dense populated villages. According to the recent national census (National Bureau of Statistics 2013), a total of 107,383 residents are living in the areas stretching from Ruaha Township on the north-east side of the park all the way down to Mang'ula village on the south-eastern side of the forest.

Over 3,800 snares have been found in UMNP from year 2007 - 2013, with over 32% of the snares coming from the northern side of Mwanihana forest (UMNP 2014). To quantify the potential effect of poaching at the camera trap sites, we surveyed the areas around each camera trap site for any possible poaching activities during a period of six years from 2009 – 2014. The survey was done alongside camera trap setup and removal exercises from July to November each year based on three camera trap arrays i.e. array I “South”, II “Centre” & III “North” comprised of 20 camera sites each. During the survey the number of active snares that were found per each camera trap array was recorded (and removed by park rangers) every year. Each survey lasted for 20 days per array. During the period, a total number of snares removed decreased from 290 to 119 in year 2009 - 2014, with a trend of increased snares found in the north (min = 64, max = 142), relative to central (36-88) and southern (19-60) part of the forest.

### **Camera trapping data**

We conducted six consecutive camera-trapping surveys during the dry months of the year (July – November) following TEAM standardized protocol ([www.teamnetwork.org](http://www.teamnetwork.org)) from 2009 to 2014, using 60 fixed camera locations. The surveys also covered a period before (2009 – 2010) and after firewood collection (2011 –

2014) ban was reinforced in the park. Using ArcGIS 10, we placed CTs at random in a regular grid of 60 locations across the forest, at a density of one camera per 2 km<sup>2</sup>. Through ensuing ground survey, we excluded cameras in excessively steep or open canopy/rocky areas. We selected the final camera position as an active wildlife trail located within a maximum of 100 m from the original location (Fig. 1). Due to the number of cameras available and the time needed for the field team to set cameras, we sampled the 60 points by deploying three consecutive arrays of 20 camera traps (south, central and northern Mwanihana respectively). We used automated digital cameras with infrared flash (Reconyx RM 45 and HC 500 models, Reconyx Inc., Holmen, Wisconsin, USA). Cameras were set to take photos without delay between consecutive triggers and tied to a tree about 2-3 m away from the wildlife trail at an average height of 50 cm and left running for 30 days. Because cameras can run over such period in autonomy, we did not check them, to avoid unnecessary disturbance. At the end of sampling, memory cards were recovered and mammal images extracted for identification using specialized software (Desk TEAM, Fagraus *et al.* 2011). A single taxonomic authority (IUCN 2014) was used for species identification. Once validated by the TEAM Network secretariat, we downloaded the data package from the open-access repository at <http://www.teamnetwork.org>.

### **Data analysis**

We processed camera trap data using ad-hoc codes in R (R Development Core Team, 2013; see also Ahumada *et al.* 2011). We derived for each photographed species the number of camera-trapping events as the number of species' images filtered by 1 hour. Hence, in a situation whereby the same species were captured by the same camera more than once within 1 hour we scored one event, to compromise between scoring the same individual multiple times and missing new events of animal passing (e.g. Kinnaird *et al.*

2003). We computed the sampling effort (camera-days) as the number of 24-h periods from deployment of camera until the camera was retrieved and because it was constant across camera sites (i.e. 30 days); our metric of abundance resulted normalized by time across sites. While this metric is an index that does not account for imperfect detection (O'Brien *et al.* 2011), and therefore is of limited inference, our choice is supported by studies that show how this index is correlated with true abundance (Carbone *et al.* 2001; O'Brien *et al.* 2003; Rowcliffe *et al.* 2008), including the study by Rovero & Marshall (2009) on Harvey's duiker (*Cephalocephus harveyi*) in the Udzungwa Mountains. We did not oversight the limited value of such index as especially associated with the failure of accounting for potential differences between species due to factors such as trail use, body size, daily range and behaviour (Trolle and Kéry 2003; Kelly and Holub 2008; Rowcliffe *et al.* 2008 & Sollmann *et al.* 2013), however we did not aim to compare this index among species. We then used this metric to determine both the temporal and spatial variations of target species within the study area.

In order to test our first hypothesis (variations in relative abundance due to poaching), we did three analyses: (1) We divided the area in two equal portions, north and south containing 30 CTs each and compared the cumulative trap rate for all years between portions using an independent two sample t-test, given the evidence that the northern side underwent higher poaching activity. We performed the analysis for all species pooled as well as the individual species that had enough trapping events (> 60) and selected a pool of six species which are likely affected by poaching. (2) To determine if the differences in relative abundance between forest portions changed with time, we also used analysis of covariance (ANCOVA) to compare the slopes of the regression between years and trapping rates for north and southern areas. (3) We assessed the relation between mean trap rates per year and the number of snares removed each year by using a Spearman's

correlation coefficient, applied to all mammal species pooled together and the set of selected individual species assumed to be under poaching pressure and a subset of poached and not poached species.

To test our second hypothesis (variation in relative abundance due to firewood collection banning), we used a paired two sample t-test to compare the differences between pre- and post-firewood collection ban on both the eastern side (treatment) and the western side (control). The eastern side is where firewood collection occurred and covered an area with 24 CTs. While the western side covered an area where firewood collection was not permitted and contained the remaining 36 CTs. We therefore assumed that the differences in relative abundance before and after the firewood collection ban may have been more pronounced in the eastern side where a re-colonization by some species may have occurred.

All the analysis was performed by using R-Statistical software version 3.2.2 ([www.r-project.org](http://www.r-project.org)).

## RESULTS

Of the total 360 CTs set (i.e. 60 x 6) for a period of six years five malfunctioned while one was stolen, and the remaining 354 accumulated 10,993 camera days (24 – hour period), with a mean per year of 1,832 and mean per month 31 (Table 1). A total of 86,187 independent images of mammals were yielded and the observed species richness for the past six years ranged from 25 species in year 2012 to 28 species in years 2012 and 2014 with a mean value of 26.7 (Table 1). The north – south comparison revealed a significant difference in the mean trapping rates for all species pooled together with the southern side having greater relative abundance than northern side (Table 2).

Furthermore, Harvey's duiker, suni and bush pig showed significant differences in their mean trapping rates with greater relative abundance in the southern side than northern side (Table 2). Results from the analysis of variance with time showed that for all the species pooled together there was a marginal significant difference in the slope of the regression between mean trap rate of northern and southern side of the forest with steeper slope on the southern side thus marginal greater relative abundance ( $P = 0.068$ ; Fig. 2, Table 3). For species-specific analysis, suni, red duiker and Sanje mangabey showed no significant differences (i.e. similar slopes of regression), while for bush pig we found a significant interaction between year and area ( $P = 0.029$ ; Fig 2, Table 3). This indicates that the slope of the regression is different between northern and the southern side, with southern side being steeper hence greater relative abundance than northern side. Lastly, we found only a negative significant correlation between the relative abundance and number of snares removed for a subset of poached species, while for a subset of not poached species, all species pooled together and the selected species showed negative correlations which were not statistically significant (Table 4, Appendix 1).

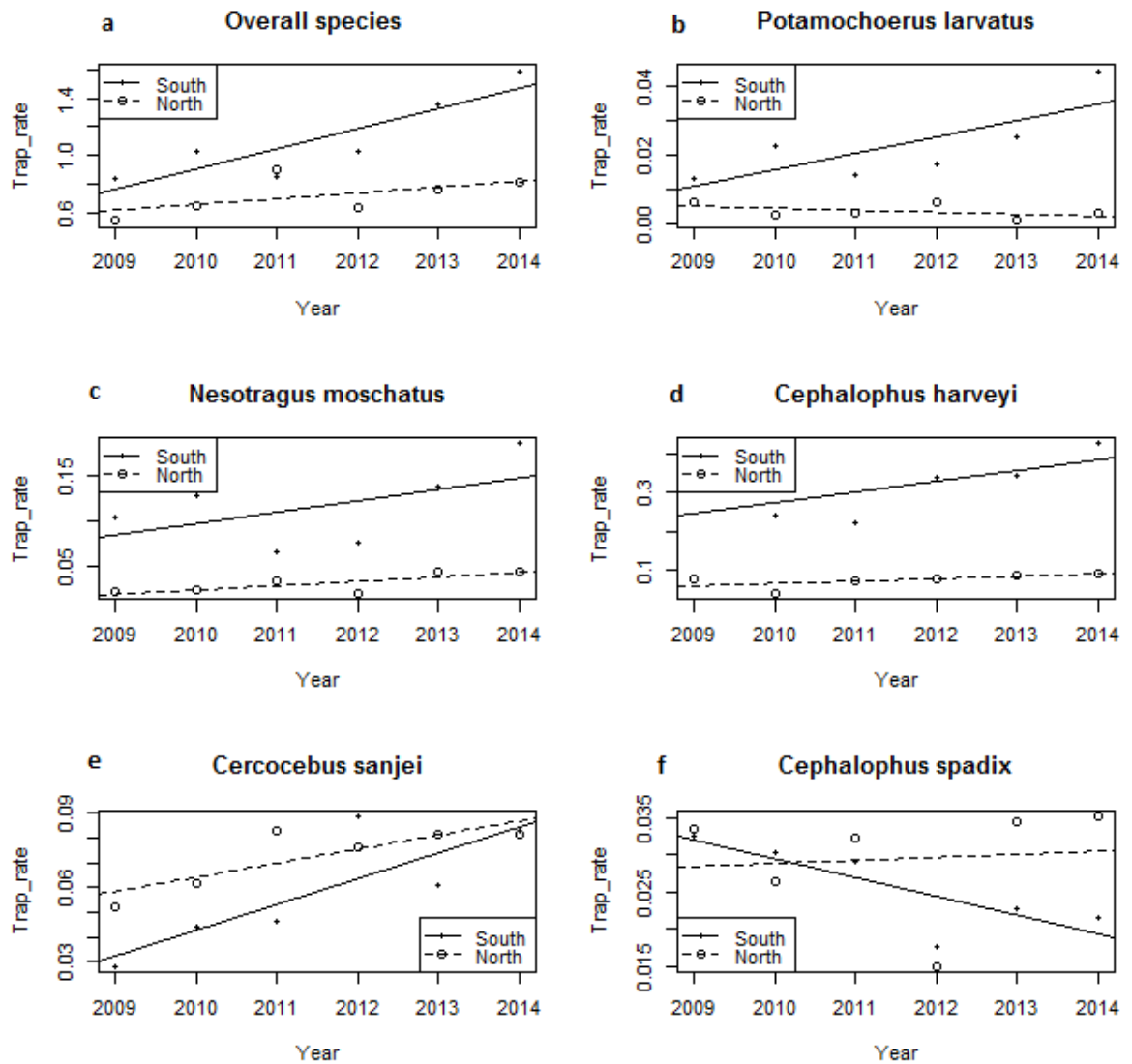
For the effects of firewood collection, we found that for all species pooled together there was a significant difference in relative abundance between pre- and post-firewood collection ban period for both the eastern and western sides (Table 5). For selected species, results showed that for Harvey's duiker there was a significant difference on relative abundance only on the eastern side and no significant difference on the western side after firewood collection ban, while for suni, there was marginal significant difference on relative abundance on the eastern side and no significant difference in the western side after firewood collection ban (Fig 4, Table 5). Sanje mangabey showed significant difference in relative abundance for both the eastern and western sides of the forest (Table 5).

**Table 1.** Summary of camera trapping efforts and results in Mwanihana Forest, Udzungwa Mountains National Park, Tanzania.

| Year                                  | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | Mean values |
|---------------------------------------|------|------|------|------|------|------|-------------|
| Number of camera set                  | 60   | 60   | 60   | 60   | 60   | 60   | 60          |
| Number of functional cameras          | 58   | 59   | 59   | 60   | 59   | 59   | 59          |
| Camera-trap days (24 h periods)       | 1818 | 1874 | 1829 | 1842 | 1818 | 1812 | 1832        |
| Mean camera-trap days per camera      | 31.3 | 31.8 | 31   | 30.7 | 30.8 | 30.8 | 31          |
| Total number of events (1-h interval) | 1259 | 1547 | 1593 | 1615 | 1941 | 2197 | 1692        |
| Number of species recorded            | 27   | 27   | 28   | 25   | 26   | 28   | 26.7        |

**Table 2** Results from an independent two sample t-test comparing species' trapping rates (index of relative abundance) between northern and southern sides of Mwanihana forest (sample size for each area is 30 camera trap sites). Values are mean (SD).

| Species name              | North (SD)   | South (SD)  | t - value | P      |
|---------------------------|--------------|-------------|-----------|--------|
| <b>All species pooled</b> | 1.12 (0.54)  | 1.3 (0.64)  | 2.28      | <0.05* |
| Harvey's duiker           | 0.07 (0.07)  | 0.31 (0.39) | 3.33      | <0.05* |
| Abbott's duiker           | 0.03 (0.03)  | 0.03 (0.03) | -0.51     | 0.6125 |
| Sanje mangabey            | 0.06 (0.07)  | 0.06 (0.05) | -1.13     | 0.2651 |
| Bush pig                  | 0.005 (0.01) | 0.02 (0.03) | 2.94      | <0.05* |
| Suni                      | 0.03 (0.04)  | 0.12 (0.16) | 2.91      | <0.05* |



**Figure 2.** Regression lines for camera trapping rates (index of relative abundance) for all species of mammals pooled together (a) and for the selected mammal species detected (b,c,d,e,f) in the southern and northern part of Mwanihana forest from 2009 to 2014.



**Table 3** Ancova results for slopes comparisons from the two models, one with area: year interaction and a second model without the interaction, for all species pooled together (bolded) and the selected species highly susceptible to poaching on the southern and northern sides of Mwanihana forest - Udzungwa Mountains National Park, Tanzania.

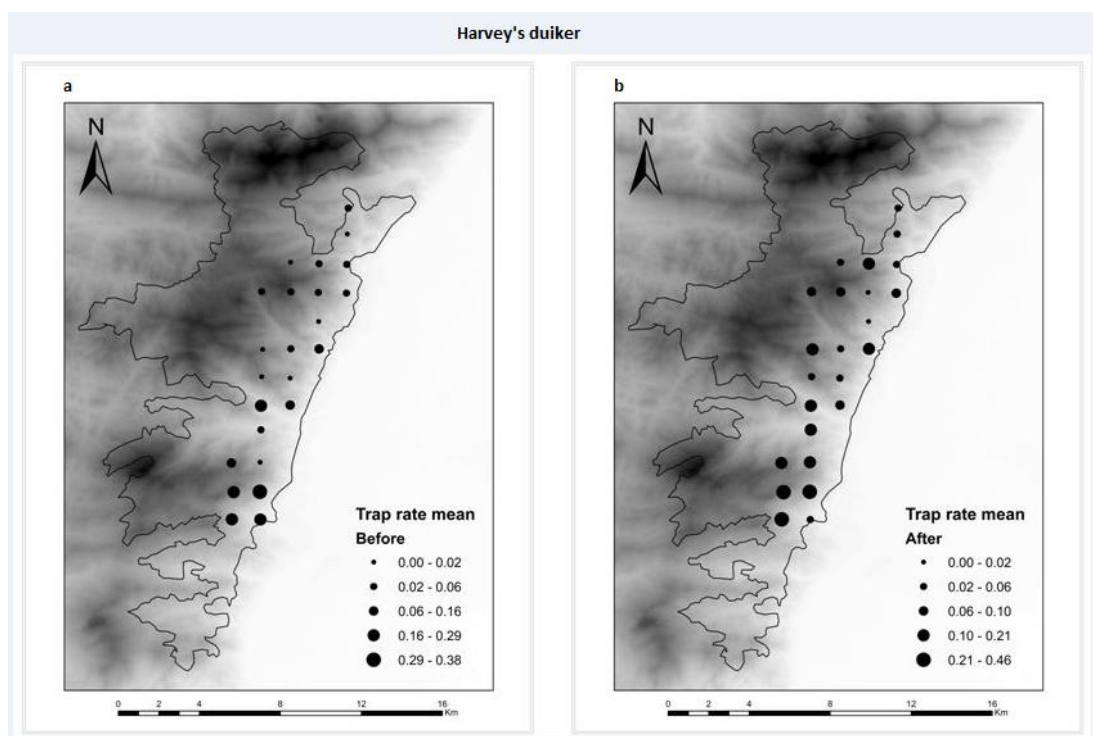
| Species name                       | F <sub>9,1</sub> | P            |
|------------------------------------|------------------|--------------|
| <b>All species pooled together</b> | <b>4.430</b>     | <b>0.068</b> |
| Harvey's duiker                    | 1.925            | 0.203        |
| Sanje mangabey                     | 1.459            | 0.262        |
| Suni                               | 0.659            | 0.440        |
| Bushpig                            | 7.001            | < 0.05*      |
| Abbott's duiker                    | 1.789            | 0.218        |

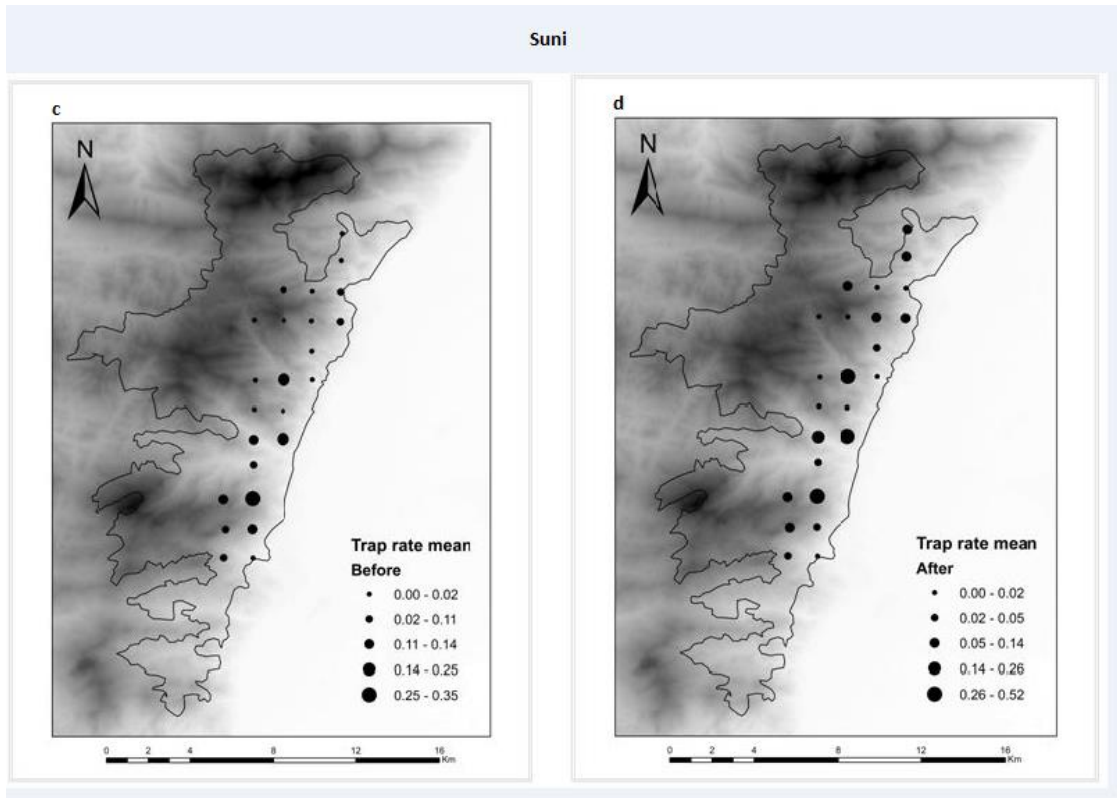
**Table 4** Results from Spearman's rank correlation coefficient test which show relation between mammal species' mean camera trapping rate (index of relative abundance) per year with the number of snares removed in Mwanihana forest.

| Species name      | $r_s$  | P      |
|-------------------|--------|--------|
| Harvey's duiker   | -0.771 | 0.103  |
| Abbott's duiker   | 0.371  | 0.497  |
| Sanje mangabey    | -0.771 | 0.103  |
| Suni              | -0.086 | 0.919  |
| Bush pig          | -0.6   | 0.242  |
| Giant pouched rat | -0.429 | 0.419  |
| Poached group     | -0.829 | 0.054* |
| Not poached group | -0.429 | 0.419  |
| All species       | -0.771 | 0.103  |

**Table 5** Camera trapping rates (SD in parenthesis) for pre (2009 – 2010) and post (2011 – 2014) firewood collection ban and results of a two sample paired t-test for all species pooled together and selected species of mammals susceptible to poaching and human disturbance on the eastern and western sides of Mwanihana Forest - Udzungwa Mountains National Park, Tanzania. Values are mean (SD).

| Species name     | East        |             |       |           | West        |             |       |           |
|------------------|-------------|-------------|-------|-----------|-------------|-------------|-------|-----------|
|                  | Pre (SD)    | Post (SD)   | t     | P         | Pre (SD)    | Post (SD)   | t     | P         |
| Species overall  | 0.67 (0.41) | 0.9 (0.37)  | -3.94 | < .001*** | 0.82 (0.59) | 1.06 (0.60) | -3.51 | < .001*** |
| Harveyi's duiker | 0.09 (0.11) | 0.13 (0.12) | -2.51 | < .05*    | 0.22 (0.38) | 0.25 (0.38) | -1.45 | 0.156     |
| Abbott's duiker  | 0.01 (0.01) | 0.01 (0.01) | -1.2  | 0.241     | 0.04 (0.05) | 0.04 (0.04) | 1.27  | 0.212     |
| Sanje mangabey   | 0.04 (0.06) | 0.08 (0.07) | -3.32 | < .05*    | 0.05 (0.06) | 0.25 (0.07) | -3.13 | < .05*    |
| Bush pig         | 0.02 (0.03) | 0.02 (0.04) | -0.7  | 0.488     | 0.01 (0.03) | 0.01 (0.02) | -0.64 | 0.526     |
| Suni             | 0.08 (0.09) | 0.12 (0.16) | -19.5 | 0.064     | 0.06 (0.16) | 0.05 (0.09) | 0.95  | 0.348     |





**Figure 3** Maps of Mwanihana forest with the 24 camera trap sites with dots proportional to camera trapping rate where firewood collection occurred for Harvey's duiker before (a) and after (b); and suni before (c) and after (d) firewood collection ban on the eastern side of the forest. See methods for details.

## DISCUSSION

Although we used camera trap rate as an index of relative abundance which does not account for imperfect detection (O'Brien *et al.* 2011), and therefore is of limited inference, our choice is supported by studies that show how this index is correlated with true abundance (Carbone *et al.* 2001; O'Brien *et al.* 2003; Rowcliffe *et al.* 2008), including the study by Rovero & Marshall (2009) on Harvey's duiker in the Udzungwa Mountains (see method section for more details). We did not aim to compare this index among species. Instead, we determined how relative abundances were affected by

firewood collection. Also we demonstrated how different poaching pressures in Mwanihana forest affected mammals' relative abundance whereby in areas that had high poaching pressures we recorded low relative abundance compared to areas with low poaching pressures. Our results are similar to Nielsen (2006) in which lower abundance of forest antelope were noticed in the areas where poaching and trapping occurred. Similarly Hegerl *et al.* (2014) found high abundance of forest mammals species in Mwanihana forest which experience less poaching activities due to effective management (found within a national park) compared to Uzungwa Scarp Forest Reserve - USFR (currently known as Uzungwa Scarp Nature Reserve), a PA with less effective management. Moreover, we showed that the relative abundance for all species pooled together was significantly higher on the southern side compared to the northern side suggesting that poaching pressure has been higher on the northern side. Inadequate allocation of resources such as the number of ranger posts and personnel may be one of the main factors causing high poaching pressure on the northern side. The park head quarter is located on the southern side of Mwanihana forest where more resources for anti-poaching activities such as vehicles, anti-poaching wardens and rangers are found and therefore considered more secure than the northern side. Our findings mirror those reported by Kühl *et al.* (2012) in Tai National Park – Ivory Coast whereby the density of animals, particularly primates, were higher in the areas near research centres, eco-tourism or park offices due to low poaching incidences than the remaining part of the park. The study also revealed that a subgroup of species mainly comprised of red duiker, suni and bush pig showed a significant decrease in their relative abundances on the northern side where poaching pressure is very high. These results correspond with the findings by Topp-Jørgensen *et al.* (2009) in USFR on which relative abundance of forest ungulates decreased because of poaching. Furthermore, a study by Rovero *et al.* (2012) in the same area noted that, poachers shifted their targets to forest canopy species such as colobine

monkeys following the decline of antelope population in the area. Among other factors, it has been established that, poachers target prey species based on the body size, preference for game meat and cultural factors (Escamilla *et al.* 2000).

Results from the analysis of covariance that compared the slopes of regression lines between the northern and southern sides have shown that for the selected species only bush pig had significantly higher relative abundance on the southern side than northern side. This is one of the mammal species prone to poaching; hence its increase in relative abundance over time may be linked to the reduced poaching pressure on the southern side. However, Chapman *et al.* (2015) observed that bush pig is among ungulate species that is resilient to human disturbance. In contrast, for the other species targeted by this analysis we found similar slopes between northern and southern sides suggesting that time had no effects on their relative abundance. For the red duiker, previous studies in the area have shown that, this species prefers forest edge (Rovero *et al.* 2014b) and hence a disturbance tolerant species including areas infested with snares. Similarly suni has been described as a lowland forest dweller avoiding montane forest habitat (Rovero *et al.* 2014b) and also preferring dense vegetation (Bowkett *et al.* 2008). The preferences of this species for both the lowland forest and dense vegetation usually found along the eastern park border where more snares would be expected may indicate that this species is less impacted by poaching. On the other hand, Sanje mangabey, which is a semi-arboreal monkey known to spend over 70% of its time on the forest floor (Rovero *et al.* 2009), appeared also to be less impacted by snares. It has been argued that these monkeys may be capable to spot and escape snares (Rovero *et al.* 2012). Conversely, the relative abundance of a subgroup of poached species showed a significant negative correlation with the numbers of snares removed over the years suggesting that snares was an important factor affecting their relative abundances. Our results are concordant with that

of Laurance *et al.* (2006) in the rainforests of southern Gabon in which poaching pressures particularly the use of snares were negatively correlated with the species abundance particularly duikers, forest buffalo (*Syncerus caffer nanus*) and red river hogs (*Potamochoerus porcus*).

We also found that for all species pooled together, there were significant differences on the trapping rates between pre- and post-firewood collection on both the eastern and the western sides suggesting that, other confounding factors apart from firewood collection had some effects on overall forest mammals' relative abundance. However, based on the selected species particularly red duiker and suni, our results showed significant increase in relative abundance on the eastern side after firewood collection ban as compared to the western side. For the red duiker this is an indication that the species is recolonizing the area. Harvey's duiker is a typical forest floor-dwelling species feeding on variety of food items including roots, flowers, rotting wood and fungi on the forest floor (Estes, 1992). The removal of dead wood on the forest floor may therefore impact the feeding habits of the species. Another forest antelope, suni, showed a marginal significant increase on its relative abundance on the eastern side post-firewood collection ban. Being described as "lowland forest dweller" antelope (Rovero *et al.* 2014b), the banning of firewood collection for this species too may have led to recolonization, particularly through the re-accumulation of rotting wood and fungi which constitutes important dietary items for this species (Estes 1992). For the Sanje mangabey, we found significant difference on its relative abundance after firewood collection ban on both the western side where firewood collection did not occur and eastern side where firewood collection occurred. Hence, other confounding factors apart from firewood collection may be affecting its overall increase in relative abundance, a finding which may reflect the preference of this species for forest interiors (Rovero *et al.* 2014b).

## CONCLUSION AND RECOMMENDATIONS

We showed how human disturbance in particular firewood collection activity resulted to low relative abundance on certain species e.g. Harvey's duiker. Similarly, poaching activities also had impacts on species' relative abundance leading to low abundance in the areas where poaching pressure was high. Furthermore, the decrease in poaching activities overtime has led to the overall increase of relative abundance of a subgroup of species highly susceptible to poaching. The effects of poaching affecting species relative abundance has also been documented elsewhere (e.g. Laurence *et al.* 2006; Neilsen *et al.* 2006; Rovero *et al.* 2012; Hergel *et al.* 2014; Chapman *et al.* 2015). We recommend that, efforts to curb poaching activities especially on the northern side of the park should be reinforced with increased patrols in the area. Lastly, environmental education awareness on the importance of conserving wildlife should be given to the communities living adjacent to the park boundary.

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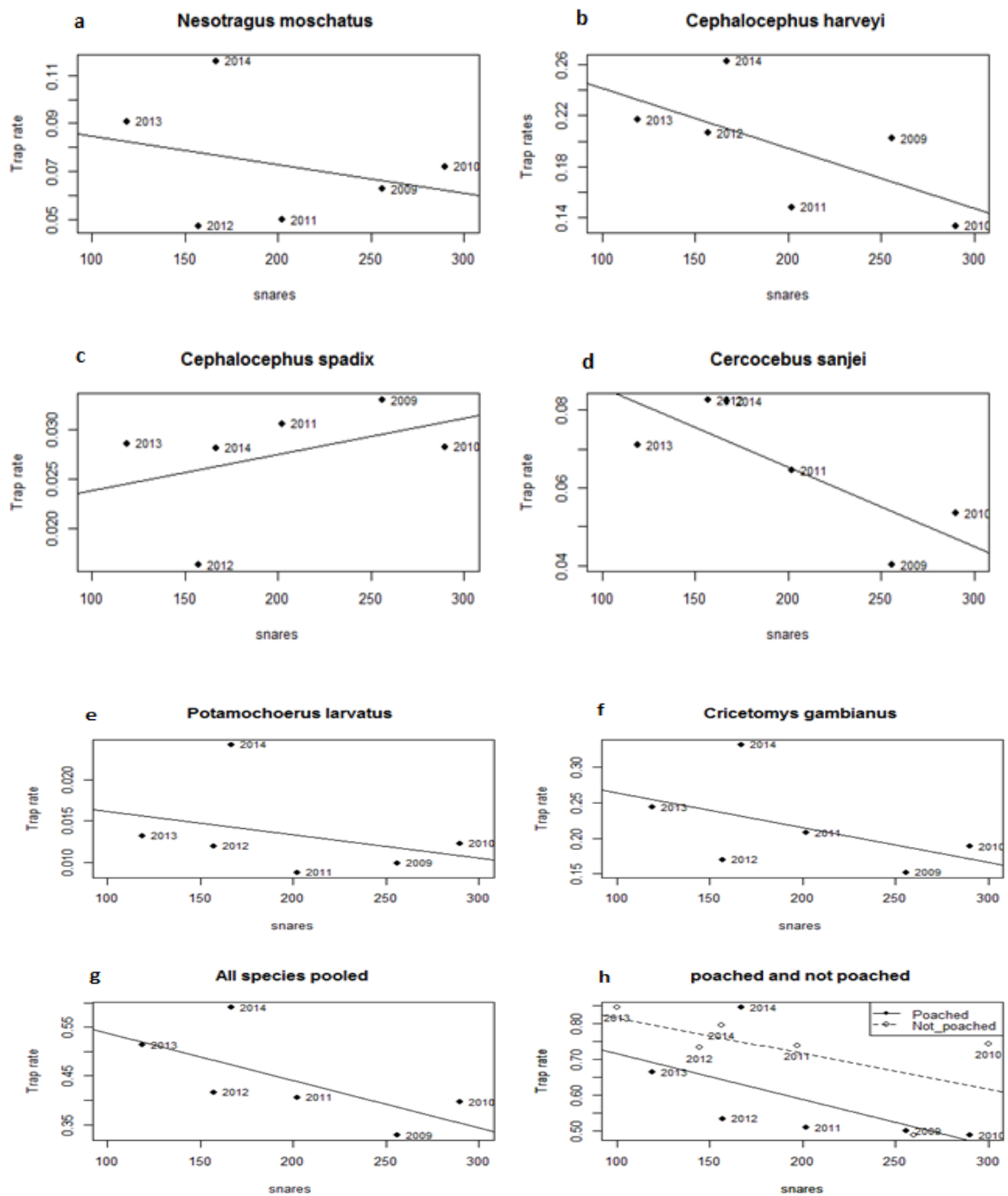
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**Annex 1** Results from Spearman's rank correlation coefficient test which show relation between mean camera trapping rate (index of relative abundance) per year with the number of snares removed for the mammal species in Mwanihana forest



## **CHAPTER THREE**

### **3.0 MAJOR FINDINGS, CONCLUSIONS AND RECOMMENDATIONS**

#### **3.1 Major Findings**

This study aimed to determine patterns of spatial and temporal variations of forest mammal communities in Mwanihana forest within the UMNP. Forest mammal community plays key important roles in the ecosystem services such as seed dispersal, food and nutrient cycling. Yet their spatial and temporal variations are affected by a number of factors including both natural and anthropogenic. However, there is little information on their status and trends across all the tropical forests. Focusing on the Udzungwa Mountains in Tanzania, this study (1) documented the status of forest mammals i.e. species richness and selected species' occupancy (proxy of abundance) and environmental factors deemed relevant to their spatial variation, hence realizing a baseline assessment (*Paper 1*) upon which following analysis were based. (2) It determined vegetation factors at a fine scale level to assess habitat choice of selected species (*Paper 2*). Furthermore, the study documented the effect of seasonality (especially rainfall) on the abundance of mammal community with respect to occupancy and detectability (*Paper 3*), which is relevant for resident forest mammal species. Finally, it assessed the effects of anthropogenic factors mainly poaching and firewood collection on species' temporal and spatial variations (*Paper 4*). Major findings are detailed in sub-sections 2.1.1 to 2.1.4 with respect to the study specific objectives:

##### **3.1.1 Determine species richness and estimate abundance**

The estimated species richness of forest mammals was found to range between 32 (median) to 34.3 (mean) in Mwanihana forest. However, the observed species richness for



the past six years i.e. 2009 – 2014 in the area is averaged at 26.7 species. While for the 11 most recorded mammal species ( $> 20$  events), the estimated occupancy which is a surrogate for abundance ranged between 0.25-0.86 with Harvey's duiker being the most abundant species ( $\psi=0.86$ ). The study also revealed the relative high occurrence of a number of species that are poorly known, and poorly detected using alternative methods. For example, the Abbott's duiker is a IUCN-Endangered 'giant' duiker endemic to and found only in a handful of montane forests in Tanzania including Udzungwa was the third most common species in terms of occupancy ( $\psi=0.72$ ). Similarly, the fourth most common Sanje mangabey ( $\psi =0.62$ ) classified as Endangered and also endemic to only two forests in the Udzungwa mountains was considered rarer than this study reveals. Although ranked at position 11, in the occupancy ranking, the grey-faced sengi (or elephant-shrew) which is also endemic to Udzungwa-endemic and classified by IUCN as Vulnerable was also considered rarer than this study could reveal.

### **3.1.2 Determine seasonal variation on the abundance of the forest mammal community**

The species abundances between wet and dry seasons showed no variations as the model revealed neither recolonization nor extinction occurred. However, only bush pig (*Potamochoerus larvatus*) showed a significant decrease in detectability from dry to wet season. The study indicates that seasonal variation, as especially related to rainfall, may have limited effect on occupancy and detectability of resident mammals in the Udzungwa rainforests and possibly in similar habitats.

### **3.1.3 Assessing factors associated with variations in forest mammal community**

The study revealed a number of potential covariates both as proxies of gross habitat, namely the distance to the Eastern National Park border, and as fine-scale vegetation features, namely the stem density of small trees, appeared to influence habitat associations for most of the selected species. The selected species were those that had trapping events  $\geq 10$  (refers *paper 2*). For example two of the forest ungulates, Abbott's duiker and bush pig, their trapping events were positively correlated with distance to the National Park border, a factor considered as a proxy of anthropogenic disturbance. For the endangered and Tanzania-endemic Abbott's duiker, this is an interesting and conservation-relevant finding as previous study on forest antelope in the area could not determine the drivers of relative abundance for this species due to insufficient data. Conversely, few species like bush pig and Lowe's genet appeared to be influenced by a greater set of covariates such as distance to the forest edge, small trees density, small plant species diversities and mean basal areas for large trees. While a small number of species were only affected by one covariate, such as the Udzungwa-endemic Sanje mangabey (mean basal area for understory forest) and the Eastern Arc-endemic Abbott's duiker (distance to the National Park border). On the other hand, the anthropogenic factors such as firewood collection and poaching also affected forest mammals' distribution. For example, the relative abundance of Harvey's duiker appeared to increase significantly on the eastern side of the forest after firewood collection ban. Also the overall species relative abundance was significantly higher on the southern side of the forest where poaching pressure is low relative to the north.

#### **3.1.4 Mapping species distribution using remote sensing and ground data on relevant habitat features**

The study has shown how spatially explicit maps could be derived through occupancy modelling. These maps have ecological values as they help to show how abundance of certain species is associated with its preferred habitat. This is indeed important for the strategic planning and management of the species and the habitat. For example, Sanje mangabey's  $\psi$  is positively associated with montane forest habitat hence provide a novel idea of where exactly the species is likely to be found within the forest. Likewise, the occupancy for suni is associated with lowland forest habitats, also providing indication of the species' preferred habitat.

### **3.2 Conclusion and Recommendations**

This study shows how camera trap data collected using a robust, standardized field methodology, and analysed with statistical approaches that account for imperfect detection can provide a robust baseline assessment of mammal communities in tropical forests. In particular, the study estimated species richness using a sampling protocol requiring repeated observations at sample locations. The approach that accounted for imperfect detection provided information needed to resolve the ambiguity between species absence and non-detection. Based on occupancy analysis, the study determined how ecological covariates such as gross habitat, distance to forest edge and distance to park border explain the occupancy of most species in the community. Importantly, the study also provided a framework for deriving spatially-explicit, fine resolution models of estimated species occupancy in relation to covariates, which represent a valuable tool for conservation management of threatened and/or poorly known species.

Furthermore, the study confirms the usefulness of camera trapping in studying habitat-species associations for elusive forest mammals. The study also provided the insights of using a habitat sampling approach, i.e. measuring vegetation features at the fine scale,

an approach that for this area was previously only conducted on forest antelope and on the grey-faced sengi. The results are of particular conservation relevance for the range-restricted species, such as the Lowe's servaline genet and Abbott's duiker for which limited ecological data existed before this study. The study also provided a first contribution on the effects of seasonal variation on occupancy and detectability of tropical forest mammals. The study indicated that seasonal variation, as especially related to rainfall, may have limited effect on occupancy and detectability of resident mammals in the Udzungwa rainforests and possibly in similar habitats; however it remains a factor to consider when designing camera trapping studies.

Lastly this study showed how human disturbance particularly firewood collection activity within the wildlife habitats resulted to low relative abundance on certain species e.g. Harvey's duiker. Similarly, poaching activities resulted to low abundance in the areas where poaching pressure was high. Furthermore, the decrease in poaching activities overtime has led to the overall increase of relative abundance of a subgroup of species highly susceptible to poaching.

In line with what has been accomplished in this study, the following recommendations can be drawn:

- i. The study applied a robust analytical framework to profiling tropical mammal communities detected by the standard camera trapping protocol adopted by the TEAM Network (<http://www.teamnetwork.org>), and a number of studies adopting similar designs outside the network, there emerges a growing need for standardized analytical procedures to facilitate and enhance the sound use of the large data-sets being accumulated.

- ii. Since occupancy estimates were limited to certain number of species that had enough events, further assessments with larger sampling efforts and that allows for a broader range of species to be analyzed will help elucidating the consistence of the results.
- iii. With the increasing use of camera trapping in a wide range of wildlife research applications, including standardized monitoring programmes, consideration of the potential sources of variations in the results such as rainfall will become of concomitantly increasing relevance.
- iv. The analytical approach used in fine scale habitat analysis i.e. the use of an event-based index, has the limits described in the methods, and these should be considered in future studies by adopting inferential approaches.
- v. It is acknowledged that greater effort would be required to adequately determine habitat associations for a greater portion of species in the community. However, the TEAM monitoring programme is on-going towards this goal.
- vi. These species-habitat specific relationships may be of particular relevance to the need of protecting the full array of forest habitat, including the interior in which moist montane forest is found but also the forest edge which is preferred by some species and yet is the area more prone to human disturbance. Particular emphasis should indeed be given to the areas along the Park border where human activities resulting in severe habitat degradation are higher.
- vii. Efforts to curb poaching activities especially on the northern side of the Park should be reinforced with more added patrols in the area.

- viii. Lastly, environmental education awareness on the importance of conserving wildlife should be given to the communities living adjacent to the Park boundary.

## APPENDIX

### Appendix 1: Camera-trapping vegetation form

Camera ID: CT-UD-\_\_\_/\_\_\_ Recorder name\_\_\_\_\_

Date\_\_\_\_\_ Canopy cover (%):

1(25)\_\_\_2(50)\_\_\_3(75)\_\_\_4(100)\_\_\_

| Plot (20 nearest >10 DBH) |                      |     | Plot (20 nearest 5-10 DBH) |                      |     |
|---------------------------|----------------------|-----|----------------------------|----------------------|-----|
| Stem #                    | Species (Tree/Liana) | DBH | Stem #                     | Species (Tree/Liana) | DBH |
| 1                         |                      |     | 1                          |                      |     |
| 2                         |                      |     | 2                          |                      |     |
| 3                         |                      |     | 3                          |                      |     |
| 4                         |                      |     | 4                          |                      |     |
| 5                         |                      |     | 5                          |                      |     |
| 6                         |                      |     | 6                          |                      |     |
| 7                         |                      |     | 7                          |                      |     |
| 8                         |                      |     | 8                          |                      |     |
| 9                         |                      |     | 9                          |                      |     |
| 10                        |                      |     | 10                         |                      |     |
| 11                        |                      |     | 11                         |                      |     |
| 12                        |                      |     | 12                         |                      |     |
| 13                        |                      |     | 13                         |                      |     |
| 14                        |                      |     | 14                         |                      |     |
| 15                        |                      |     | 15                         |                      |     |
| 16                        |                      |     | 16                         |                      |     |
| 17                        |                      |     | 17                         |                      |     |
| 18                        |                      |     | 18                         |                      |     |
| 19                        |                      |     | 19                         |                      |     |

|                  |  |  |                  |  |  |
|------------------|--|--|------------------|--|--|
| 20               |  |  | 20               |  |  |
| Max distance (m) |  |  | Max distance (m) |  |  |

4 random plots 3x3 m within 10 m of camera (stem >1m height <5 cm DBH)

| Stem # | Species – PLOT<br>1 | Total No.<br>of<br>individuals | Stem<br># | Species – PLOT 2 | Total No.<br>of<br>individuals |
|--------|---------------------|--------------------------------|-----------|------------------|--------------------------------|
| 1      |                     |                                | 1         |                  |                                |
| 2      |                     |                                | 2         |                  |                                |
| 3      |                     |                                | 3         |                  |                                |
| 4      |                     |                                | 4         |                  |                                |
| 5      |                     |                                | 5         |                  |                                |
| 6      |                     |                                | 6         |                  |                                |
| 7      |                     |                                | 7         |                  |                                |
| 8      |                     |                                | 8         |                  |                                |
| 9      |                     |                                | 9         |                  |                                |
| 10     |                     |                                | 10        |                  |                                |
| 11     |                     |                                | 11        |                  |                                |
| 12     |                     |                                | 12        |                  |                                |
| steep  |                     |                                | steep     |                  |                                |

(add more rows if needed 4 plots 1x1 m within the above 4 plots of 3x3,

| Plot 1x1<br># | Logs and<br>stems (%) | Herbs and<br>grasses<br>(%) | Bare<br>soil<br>(%) | Leaf litter<br>(%) | Rocks<br>(%) | Seedlings<br>(%) | Total | leaf<br>litter<br>depth<br>* |
|---------------|-----------------------|-----------------------------|---------------------|--------------------|--------------|------------------|-------|------------------------------|
| a-1           |                       |                             |                     |                    |              |                  |       |                              |
| a-2           |                       |                             |                     |                    |              |                  |       |                              |
| a-3           |                       |                             |                     |                    |              |                  |       |                              |
| a-4           |                       |                             |                     |                    |              |                  |       |                              |
| b-1           |                       |                             |                     |                    |              |                  |       |                              |
| b-2           |                       |                             |                     |                    |              |                  |       |                              |
| b-3           |                       |                             |                     |                    |              |                  |       |                              |
| b-4           |                       |                             |                     |                    |              |                  |       |                              |
| c-1           |                       |                             |                     |                    |              |                  |       |                              |
| C-2           |                       |                             |                     |                    |              |                  |       |                              |
| c-3           |                       |                             |                     |                    |              |                  |       |                              |
| c-4           |                       |                             |                     |                    |              |                  |       |                              |
| d-1           |                       |                             |                     |                    |              |                  |       |                              |



|     |  |  |  |  |  |  |  |  |
|-----|--|--|--|--|--|--|--|--|
| d-2 |  |  |  |  |  |  |  |  |
| d-3 |  |  |  |  |  |  |  |  |
| d-4 |  |  |  |  |  |  |  |  |

Leaf litter depth (middle of each 1-m plot):

|                                       |              |    |
|---------------------------------------|--------------|----|
| $\leq 2$ cm                           | Very Thin    | VT |
| $2 \text{ cm} < x \leq 5 \text{ cm}$  | Thin         | T  |
| $5 \text{ cm} < x \leq 10 \text{ cm}$ | Deep         | D  |
| $x > 10 \text{ cm}$                   | Very<br>Deep | VD |

Disturbance signs at the site \_\_\_\_\_ distance from  
nearest recorded disturbance (hunting camp, snare, mining area, etc.) \_\_\_\_\_ (km/lat-  
long of disturbance \_\_\_\_\_)