



Nathalie Cavada

Modelling environmental changes in the Udzungwa Mountains of Tanzania through impact assessment on rainforest mammals





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Nathalie Cavada

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rainforest mammals

Supervisors

Dr. Marco Ciolli, DICAM - University of Trento
Dr. Francesco Rovero, MUSE - Museo delle Scienze di Trento

Credits of the cover image
Nathalie Cavada
"Up there in the canopy" - watercolour on paper



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University of Trento
Doctoral School in Civil, Environmental and Mechanical Engineering
<http://web.unitn.it/en/dricam>
Via Mesiano 77, I-38123 Trento
Tel. +39 0461 282670 / 2611 - dicamphd@unitn.it

*A voi,
che avete salutato con entusiasmo ogni mia partenza,
nell'attesa di lontani rientri:
salde guide dei miei decisi passi incerti.*

*A te,
che giocando "al più grande",
illumini per me gli angoli più bui.*

*A te,
che anche distante, eri e sei così vicino.*

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SUMMARY

The management and conservation of threatened animal populations require accurate knowledge on their distribution and abundance. At the same time, knowledge on the factors driving changes and fluctuation in distribution and abundance is also critical. Nevertheless, gaining such insight is especially challenging for species living in patchy and fragmented landscapes, as is the case for most mammals in tropical forests.

This thesis addressed these issues by developing and validating analytical frameworks that allow to make robust spatial inference on population abundance, and ultimately aimed at gaining knowledge on the conservation status of selected mammal species in the rainforest of the Udzungwa Mountains of Tanzania, with emphasis on arboreal primates. This area is an outstanding hotspot for biodiversity and endemism at continental level and it is especially important for primates. Results of the research project were used to provide management recommendations for the conservation of target species and of the environment these inhabit, which is undergoing rapid and critical modifications through habitat depletion and fragmentation.

In Chapter 1, data from camera traps (i.e. remotely-triggered cameras that take images of passing animals) were analysed from 60 locations in the Udzungwa Mountains of Tanzania to determine fine-scale habitat associations for 11 medium-to-large mammal species. Generalized linear models (GLM) were applied to determine the relationship between camera-trapping events and habitat and human disturbance parameters, obtaining good fit for the 9 most recorded species. Results provided novel insights into the ecology of the target species and validated the usefulness of camera trapping to assess communities of forest mammals.

Chapter 2-4 focused on arboreal primates, and distance sampling from line transects was the detection method of choice. The three target species included the endangered and endemic Udzungwa red colobus (*Procolobus gordonorum*). Analysis were performed on data from previous field-based programmes in the area, as well as on a set of data that was sampled during an additional field

campaign by the candidate in the period September-November 2015. The overall dataset available included thus distance sampling data of the three study species, that were collected along transects of 2 km in length (N=186) in the five major forest blocks found in the study area. Such dataset also included environmental and human disturbance parameters that were sampled at vegetation plots (N=512) of 25 × 25 m placed every 500 m along each transect.

In Chapter 2 a hierarchical modelling approach was applied. This recently developed approach incorporates the effect of environmental covariates on both the detection and the state processes of the distance sampling. Such method takes in full account the contrasting habitat and protection level among the different forest blocks in the area, making the inference process more informative. Indeed, results of the study showed that, relative to this novel approach, density was underestimated by the canonical distance sampling, particularly in the less protected forests.

The inference on density is spatially explicit to the scale of the covariates used in the hierarchical modelling. In Chapter 3, an approach that calibrated remote-sensing imagery to ground measurements of tree density to derive basal area, as a significant predictor of primate density, was thus developed. GLM was applied to relate 9.8 ha of ground samples of tree basal area to various metrics extracted from Landsat 8 imagery. The potential of this approach was tested for spatial inference of animal density by comparing the density predictions for the endangered colobus monkey, to the previous estimates from field transect counts. A species distribution model was derived, and this was able to predict primate densities that matched those based on field measurements.

Lastly, in Chapter 4, a further application of hierarchical distance sampling for primates was provided. Such analysis accounted for a comprehensive set of environmental covariates of both detectability and abundance and a novel field routine was proposed to measure the spread of the groups during transect sampling, as this affects distance measurements and hence density estimates.

The general approach proposed in this thesis has important, inherent applications as it magnifies the relevance of abundance models for informing conservation. This is particularly crucial for species whose spatial pattern can be complex in relation to human and habitat disturbance factors and given that, almost universally, management decisions need to be focused on priority areas.

In this perspective a Bayesian modelling approach will be applied in a multi-site framework, comprehensive of all the five forest sampled in the study area, as a further development of the research project. Such analysis will allow for an efficient comparison of animal densities across the forest blocks, while properly accounting for statistical uncertainty in the estimates of those parameters that are found to influence both species detectability and abundance.

INTRODUCTION

Environmental changes and anthropogenic pressures are eroding biodiversity at unprecedented rates, with negative impact on the survival and fecundity of animal species (Millenium Ecosystem Assessment 2005, Ceballos et al. 2015, Urban 2015). Modifications and degradation in the extent and spatial configuration of habitats can in fact reduce population size and growth rates, elevating the chance of extinction of populations and species (Ronald Pulliam 1988, Naeem et al. 1999, Acevedo-Whitehouse & Duffus 2009). Assessing the impact that such natural and human-induced factors have on the distribution and dynamics of selected species is therefore crucial to plan for adequate conservation actions and, in turn, to better predict the effects on species of the current environmental conditions. As the number of species threatened with extinction is way larger than our capacity to effectively protect them with the limited resources available to conservation (Myers et al. 2000), it is widely acknowledged that efforts may be more proficiently focused on species that are known to be intensively subjected to environmental changes, habitat loss and over-exploitation. Such species are indeed highly representative of dysfunctions in the ecosystems (Bridgewater 2016).

Among the vertebrates, the significant role of forest mammals as indicators of ecosystem health (Ahumada et al. 2011) and their susceptibility to habitat loss and degradation and to hunting (Schipper et al. 2008, Visconti et al. 2011) make them a model study subject to develop appropriate and effective management and conservation strategies, in a world that is undergoing rapid changes and alterations of physical and biological systems. Hence, gaining knowledge on forest mammals' occurrence as well as on habitat associations represents an important step for defining appropriate conservation strategies, especially for tropical forests (Tobler et al. 2008). Tropical regions of the Western Hemisphere, Africa and Asia host indeed the larger species richness of mammals (Gaston 2003, Lomolino et al. 2006), as well as the highest diversity, with several species that are highly threatened (Ceballos & Ehrlich 2006). In particular, knowledge on the dynamics that govern relevant environmental parameters is of

primary importance, since it directly affects management success. Even if significant research advances keep raising our capacity to understand the effects of landscape fragmentation and alteration on species survival, still several difficulties arise in the attempt to define general patterns of association between animal abundance and the entangled features of the habitat they occupy. Complex site- and species-specific factors may in fact interplay in masking our capacity to define general patterns of species and habitat associations and to identify the processes that drive populations to extinction (Onderdonk & Chapman 2000, Henle et al. 2004).

In this perspective, primates represent good ecological indicators among mammals, being the taxa with the highest percentage of threatened species (Schipper et al. 2008; Estrada et al. 2017) and carrying out critical ecological functions in their ecosystems (Marshall & Wich 2016). Moreover, they are particularly sensitive to habitat changes (Cowlshaw & Dunbar 2000, Marsh 2003, Struhsaker 2010) and are highly dependent on closed-canopy forest (Mittermeier & Cheney 1987, Chapman et al. 2006, Lovett & Marshall 2006). These are also habitats that are continuously subjected to modifications, both natural and human-driven (Isabirye-Basuta & Lwanga 2008), and where hunting and diseases represent additional critical sources of threat (Cowlshaw & Dunbar 2000, Schwitzer et al. 2015), that affect primate populations negatively. Nevertheless, primates are reported to be resilient in forests that show variable degrees of degradation and disturbance (Johns & Skorupa 1987, Chapman et al. 2000, Cavada et al. 2016), as a result of an interplay of factors that are still not clearly identified and that might be site- and species-dependent.

AIM AND OBJECTIVES

This thesis research aimed at modelling species responses to habitat parameters and threats in the complex landscape of the Udzungwa Mountains of Tanzania, a remarkable biodiversity hotspot (Myers et al. 2000) and an outstanding region for primate endemism and conservation (Rovero et al. 2014b). The first study aimed at determining fine-scale habitat associations of terrestrial mammals detected by camera trapping, as a methodologically novel approach to study the rare and poorly known forest mammals inhabiting the study area. The major focus of this research was then placed on three arboreal primates (see Materials and Methods), as keystone species that are crucial study subjects for ecology and conservation science.

Specific objectives of the thesis were as follows:

1. Apply camera-trapping to assess the community of medium-to-large forest mammals in the study area and derive a proxy of species' relative abundance, providing insights on poorly known species' habitat associations (Chapter 1).
2. Study arboreal primates as important ecological indicators by testing novel approaches to estimate population densities; apply, for this purpose, a hierarchical distance sampling approach; test if such approach could lead to an increase in the accuracy of the density estimates that were previously obtained for the same study area, from a canonical distance-sampling analysis (Chapter 2).
3. Develop an approach for calibrating remote-sensing imagery to ground measurements of primate density predictors; use these modelled habitat predictors to derive spatially explicit models of animal density (Chapter 3).
4. Extend the dataset available from previous field-based programmes in the study area, by collecting data from a previously un-sampled forest; test a novel field routine for measuring the spread of social groups (Chapter 4).
5. Test a Bayesian analysis as a future perspective, that can allow for an efficient comparison of animal densities across all the forest blocks, while simultaneously evaluating the influence of parameters both at a site-level as well as at the level of the entire

study area; apply such approach to properly account for statistical uncertainty in the estimates of those parameters that are found to influence both species detectability and abundance (Perspectives).

6. Use stepwise and general results to gain insight on the conservation status of the target species and on the changes that are undergoing in the environment these inhabit, to provide management recommendations for conservation purposes.

MATERIAL AND METHODS

Study area

The Udzungwa Mountains of Tanzania

The Udzungwa Mountains are located in south-central Tanzania and represent the largest mountain chain in the Eastern Arc Mountains, covering an area of about 19,000 km² (Platts et al. 2011, Figure 1). The area is characterized by the presence of moist forest blocks that are interspersed with drier habitats and that show a variable size, ranging from 12 to over 500 km² (Marshall et al. 2010). The natural habitat, that also include scattered forest fragments, is surrounded by woodland, grassland, cropland and human settlements, with a different degree of anthropogenic pressure that is exerted upon several unprotected forests (Marshall et al. 2007)(Figure 2). The Udzungwas hold the highest amount of closed canopy and intact forest within the Eastern Arc (Burgess et al. 2007). The area was also found to host several rare and endemic species, with a highly restricted range, making it an outstanding hotspot for biodiversity and conservation (Rovero et al. 2014b).

Rainfall is concentrated in two periods (November-December and March-May), ranging from 2,000 to 2,500 mm/year in the east-facing, moister forests (Barelli et al. 2015).

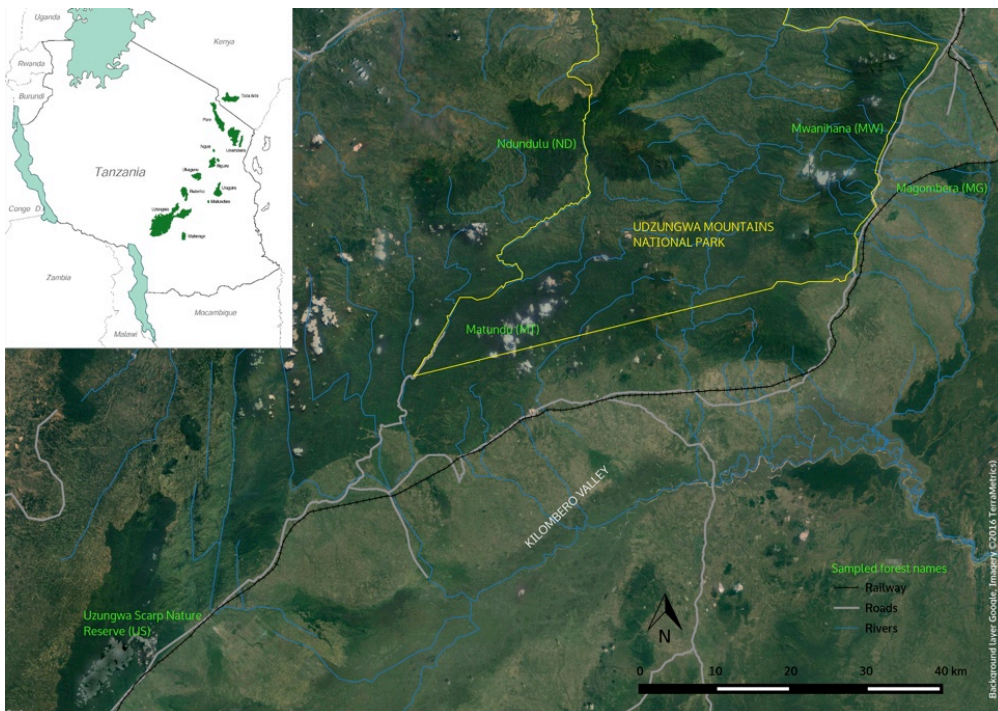


Figure 1. Map of the Udzungwa Mountains of Tanzania as seen from the satellite, showing the location of the sampled forests.



Figure 2. Example of the variety of forest habitats encountered in the Udzungwa Mountains, Tanzania. Photo: Francesco Rovero and NC.

Sampled forest blocks

The five forest blocks selected for the study (Figure 1.1) present wide variation in terms of elevation range (290-2,576 m a.s.l.), habitat type (Figure 2) and level of protection.

1) Magombera (MG) is a small (12 km²), unprotected and highly isolated forest fragment, of low elevation (270-300 m a.s.l.) and with flat surface, covered in evergreen lowland forest and surrounded by crop fields and human settlements (Marshall 2008);

2) Matundu (MT) is the largest forest block (562 km²), intensively logged in the past and now protected under the Udzungwa Mountains National Park (UMNP) jurisdiction. Given the past disturbance the forest is covered with regenerating, secondary vegetation that is mainly lowland deciduous and semi-evergreen (Marshall et al. 2007). The elevation ranges from 280 to 1,000 m a.s.l.;

3) Mwanihana (MW) is a well protected forest as part of the UMNP. The forest escarpment extends for 151 km² (Marshall et al. 2010) and from 350 to almost 2,300 m a.s.l. Along such elevational gradient the forest is covered with deciduous vegetation in the lowland zones, while evergreen forest is found in the montane areas (Lovett et al. 2006);

4) Uzungwa Scarp (US) is a newly gazetted Nature Reserve of 314 km², where high disturbance occurs, given a lack of ranger patrols on the area. The forested habitat is similar to the one found in MW, but both canopy and understorey structures are altered from pole and timber cutting. Hunting has a great impact on several animal species, including primates, with strong negative effects which are especially impacting the colobine monkeys (Rovero et al. 2012).

5) Ndundulu (ND) is a forested area of 231 km² (Marshall et al. 2010), outside the UMNP. Is part of the Kilombero National Reserve and is relatively well protected. The forest ranges from 1300 to 2000 m a.s.l. and is covered in montane forest vegetation. Sporadic logging activities took place until the mid of the 1990s (Dinesen & Lehmborg 1996).

Target species

The main research focused on the following three arboreal primate species that occurs throughout the Udzungwa Mountains range:

1) Peter's Angolan colobus (*Colobus angolensis*) (Figure 3)

Within the Udzungwas the species is reported to be distributed more commonly at higher altitudes, in the upper-montane forest

areas (Marshall et al. 2005). The male/multi-female groups range in size from 2 to 14 individuals (Rovero et al. 2009), that spend most of the time resting and feeding mainly on mature leaves. Angolan colobus is often found in association with Udzungwa red colobus. The main threat for the species is represented by forest degradation (Struhsaker & Rovero 2007, Marshall 2008).



Figure 3. Peter's Angolan colobus (*Colobus angolensis*). Photo: Scott Olson. Drawing: Jonathan Kingdon (2013).

2) Udzungwa red colobus (*Procolobus gordonorum*) (Figure 4)

The species, classified as IUCN-Endangered, is endemic to the Udzungwa Mountains, where it occurs in all forest blocks, exception given for Mufindi, located in the south-west portion of the area (Rovero & Perkin 2008). The multi-male/multi-female groups range in size from 3 to 83 individuals and are often found in association with Angolan colobus. The species is a good ecological indicator of forest integrity, with larger groups that are found in large patches of mature, moist and mixed evergreen and semi-deciduous forest (Struhsaker et al. 2004, Rovero et al. 2009). The species feeds predominantly on young leaves, with a diet that also comprises petioles, buds and less frequently fruits (Rovero 2003, Pucci & Rovero 2004). Threats for the species are represented by habitat loss, due to logging, conversion to agriculture, collection of firewood, and charcoal production, and hunting (Struhsaker et al. 2016).



Figure 4. Udzungwa red colobus (*Procolobus gordonorum*). Photo: Thomas Struhsaker. Drawing: Jonathan Kingdon (2013).

3) Sykes' monkey (*Cercopithecus mitis/monoides*) (Figure 5)

The species is influenced relatively less by habitat degradation than the two colobines, being an opportunistic species, able to exploit all vertical forest strata and feeding predominantly on fruits (Rovero et al. 2009). The monkey lives in mono-male/multi-female groups, which size ranges from 2 to 22 individuals (Rovero et al. 2006). They are found in associations with Sanje mangabeys, Angolan colobus and Udzungwa red colobus.



Figure 5. Sykes' monkey (*Cercopithecus mitis/monoides*). Photo: NC

Species' detection methods and data collection

Camera trapping

Camera traps are automatic cameras taking images of passing animals and were used for data collection in a preliminary study (Chapter 1). The aim was to assess habitat associations for terrestrial mammals on a fine scale to gain insights about the communities of species inhabiting Mwanihana forest in the UMNP. Camera trapping is a tool widely used to study medium-to-large mammals (Rovero et al. 2010, O'Connell et al. 2011, Meek et al. 2012). The use of a systematic array of several camera traps is important for data quality and for the subsequent application of statistical models that allows for robust inference (Trolliet et al. 2014).

In the study reported in Chapter 1, 60 camera traps were displaced on a regular grid in the forest of Mwanihana, covering a total area of 120 km² (i.e. 1 camera trap every 2 km²). The camera-trap models selected for the study were Reconyx RM 45 and HC

500, able to take photos in consecutive intervals of 1 second between each shot, storing captured data in compact flash memory cards of 2 GB. The cameras were left on the site for a minimum of 30 days (O'Brien 2008) and yielded pictures of the captured species together with date and time of the photo.

Distance sampling

For primate abundance and density estimation (Chapter 2 and 4), distance sampling along line transects (Buckland et al. 2001, 2004) was the method of choice, as this is commonly applied to obtain reliable abundance estimates (Buckland et al. 2010a). For this purpose, line transects and linear paths across the forest) were randomly superimposed on the whole survey region, as equally spaced transects of the same length.

Distance sampling data for the present work came from uniformly and equally spaced line transects of 2 km in length (with transects shortened at 1.5 km in MG for space constraints), distributed in the five main forest blocks in the study area. The full dataset comprised N=151 line transects providing 197 repetitions, with 355,66 km walked. While walking along each transect, records of the animal groups detected were taken (N=420), together with their distance from the observer and the angle from the line of the detection. For data analysis such measurements were then converted in perpendicular distances (PD) from the transect, applying trigonometry.

The application of the distance sampling method required also to respect the basic principle of transect randomization, and to satisfy a set of key assumptions :

- 1) Animals/groups on the line were detected with certainty.
- 2) Animals/groups were detected prior to their movement, before any response to the observer.
- 3) Measurements of distance were taken with high accuracy.
- 4) An adequate number of transect repetitions was acquired.
- 5) Group sizes were accurately recorded.

Moreover, for animal occurring in groups, as is the case for many primate species, distance should be measured from the centre of the group. This is most commonly achieved by measuring the

distance to the first individual sighted, which is also the one closest to the line. Such measurements of PD need afterward to be corrected, taking into account the spread of the groups (Whitesides et al. 1988, Marshall et al. 2008). A common way of determine group spread values is to take species- specific measurements during a parallel study and to include the averaged value in the subsequent distance analysis (Buckland et al. 2010a). To further reduce biases, a new method for group spread sampling was applied and validated in Chapter 4, obtaining observation-specific values of group spread while simultaneously sampling the distance measurement from the first individual observed. The perpendicular distance was then corrected, multiplying it by $1 + r/AOD$, with r being half the group spread and AOD being the animal-to observer distance.

Habitat data

Environmental and human disturbance covariates

To model habitat specific density of the primate target species, a set of covariates characterizing the forest habitat and parameters representing anthropogenic sources of disturbance in the area were sampled inside squared vegetation plots, of 25×25 m that were placed every 500 m along each transect walked for primate data collection (N=604). Plot level data habitat covariates were then averaged for each transect, to obtain transect level data for further analysis.

A list of the sampled parameters, together with detailed information on the sampling procedure can be found in Table 4.1 in Chapter 4.

Remote sensing data

The modelling process to be applied for obtaining spatially explicit maps of species density requires to collect information on influential environmental variables over space (i.e. on the whole study area). Such sampling activity can be highly costly (Jones 2011), particularly when operating over large areas and in tropical forests. The implementation of methods that are low in costs, robust and fast to apply is therefore essential, as well as the need

to evaluate the quality and the effectiveness of the information that can be derived (Jones et al. 2008, De Barba et al. 2010, Maniatis & Mollicone 2010). In this perspective the use of remote sensing data shows a considerable potential, as it can allow to derive spatially explicit data over large areas and at moderate costs (Wilkie & Finn 1996, Proisy et al. 2007) to improve the modelling of species distribution (Franklin 2009), especially if these are employed to derive vegetation structural related properties (Zimmermann et al. 2007). High thematic accuracy can be provided by optical data at high resolution, such as the satellite images delivered by IKONOS or QUICKBIRD (Mumby & Edwards 2002). Even if the availability of remote sensed products is continuously increasing (He et al. 2015), the acquisition costs of these images as well as their quality can represent a critical issue in many regions of the world (Ploton et al. 2012), and mainly in the tropics. Broader availability is provided by Landsat data that have been used to investigate several ecological problems in various environments (Foody et al. 2003, Cohen & Goward 2004, Weng 2009). Landsat series offer moreover data for some decades, providing a longer temporal insight that is useful when focusing on the study of environmental changes rate and habitat modifications. These data however are not always able to directly provide sufficiently sensitive and detailed information as well as adequate reliability to investigate many important ecological issues and to derive the desired relevant environmental variables. This is true in particular if the variable of interest is related to the vegetation canopy and to its structure (Falkowski et al. 2004, Duncanson et al. 2010).

Hence further investigation was claimed to develop an analysis tool able to characterize specific features related to the forest structure, also for those areas where Landsat images represent the only feasible and easily accessible information. Details and results of such analysis are reported in Chapter 3.

Data analysis

Hierarchical distance sampling

Management and conservation of wildlife require not only accurate information about the size of the population, but also

knowledge on how the abundance and density are influenced and shaped by habitat parameter and human disturbance factors, as addressed in Chapters 2-4.

The conventional distance sampling approach uses measurements of PD to estimate a detection function, meaning the probability that a group of animals is detected, as a function of its distance from the line, while assuming that animals on the line are detected with certainty (meaning that the probability of detection is 1 at distance 0). After estimating the detection function, it is possible to estimate the proportion of animals that were detected within a strip of distance w from the transect, on either side. These represent a portion of the true density of the animals along each transect. The expected animal density can then be modelled and estimated, adjusting encounter rates and correcting for animals that were missed in the strip. Such approach however does not describe how density varies spatially, as also influenced by habitat covariates.

In this perspective, hierarchical distance sampling (HDS) (Royle et al. 2004) is a framework that has been implemented as an extension of the conventional distance sampling to allow the spatially explicit modelling of abundance and density at multiple survey sites, as a function of site-specific covariates, thus accounting for variation in local density among sample units. Assuming that multiple transects have been surveyed and distance data were recorded, hierarchical models represent a unified framework for analysis. Such framework recognizes that observations are generated by a combination of a state process (i.e. the one that determines abundance at each site) and a detection process (i.e. the one that yields observations conditional on the state process).

The transect-level abundance distribution is assumed to be $N_t \sim \text{Poisson}(\lambda_t)$, with sample unit $t = 1, \dots, M$

The detection process is modeled as $y_{tj} \sim \text{Multinomial}(N_t, \pi_{tj})$, with $t = 1, \dots, M$ and $j = 1, \dots, J$ where π_{tj} is the multinomial cell probability for transect t in distance class j . Over each distance interval these probabilities are computed integrating a detection function, with scale parameter σ for a half-normal detection function. Covariates effects can be computed as affecting parameters λ and σ .

A great potential of such modelling framework is that it allows for accurate evaluation on how changes in covariate values could affect population density and distribution in the study area, as well as their detection probability. This, in turn, allows for the implementation of spatially-explicit models and highly informative maps, where spatially diffused values for the influential covariates are available (Chapters 2,3,4).

CHAPTER 1

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

Based on the paper: Martin EH, **Cavada N**, Ndibalema VG, Rovero F (2015) Modelling fine-scale habitat associations of medium-to-large forest mammals in the Udzungwa Mountains of Tanzania using camera trapping. *Tropical Zoology*: 1–15.

Summary

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. We 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.

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 & Chapman 2003, Tobler et al. 2008, Rovero et al. 2013b). Despite such widely recognized importance, 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).

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 & Nichols 1998, 2002, O'Connell et al. 2011, Fleming et al. 2014). Camera traps are non-invasive, relatively easy to use and cost efficient (Rovero et al. 2013b, Fleming et al. 2014). A number of studies (O'Brien 2008, Ahumada et al. 2011, 2013, Rovero et al. 2014a, b) have proved the efficiency of camera traps in mammal studies. A limited set of studies focused on habitat associations (Linkie et al. 2007, Bowkett et al. 2008, Rovero et al. 2013a) and 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 performed on a community of medium-to-large forest mammals, using camera trapping in a 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 et al. 2014b). The area is particularly rich in mammalian forest fauna (Rovero & De Luca 2007). Forest mammals have been the subject of a number of studies that deployed camera trapping (De Luca & Mpunga 2005, Bowkett et al. 2008, Ahumada et al. 2011, Rovero et al. 2013a, 2014a). Our study objectives were: 1) to assess the community of medium-to-large forest mammals as detected through an extensive

camera-trapping effort; 2) to derive a proxy of species' relative abundance and 3) to 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 Tanzania are a system of moist forest blocks interspersed with drier habitats. We conducted the study in Mwanihana forest, in the eastern Udzungwa Mountains National Park (UMNP; Figure 1.1) that is centred on 7°46'S, 36°51'E and has a size of 1,990 km². Mwanihana is one of the largest forest blocks in the range (151 km² of closed forest habitat) with continuous vegetation cover, from 300 to over 2,000 m above sea level (Rovero et al. 2013a). The forest habitat is characterised 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 1,500 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).

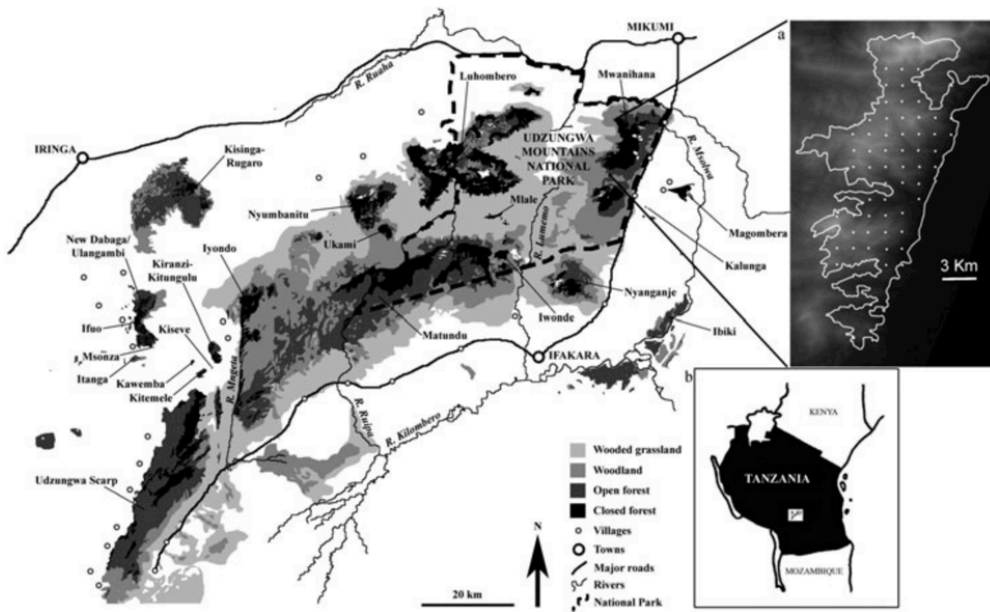


Figure 1.1 Map of the Udzungwa Mountains showing the main forest blocks with closed canopy forest darker in colour. The study forest was Mwanihana (top right inset) (a) where the 60 camera trap sites are shown as white dots on the background representing a Digital Elevation Model; (b) shows the location of Udzungwa Mountains in Tanzania. Source: Rovero, Martin et al. 2014.

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 monitoring programme, the TEAM network, of which Udzungwa has been a part since 2009. For this study, we only used data for year 2013, for which we also conducted habitat analysis. While pooling data for multiple years would have increased the sample size, we preferred not to introduce potential bias in our analysis due to temporal discordance between animal and habitat data, as well as due to habitat differences between years. Using ArcGIS 10 (ESRI 2011), we placed camera traps in a pre-designed, regular grid of 60 locations across the forest, at a density of one camera per 2 km². We selected the final camera position to be on active wildlife trails, located within a maximum of 100 m from the original location using a handheld GPS unit (Figure 1.1). 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). We used automated digital cameras with infrared flash (Reconyx RM 45 and HC 500 models, Reconyx Inc., Holmen, WI, USA). We set cameras to take photos with no delay between consecutive triggers and we tied each camera to a tree about 2–3 m away from the wildlife trail, at an average height of 50 cm and left them running for 30 days. As cameras can operate autonomously over such periods, we did not check them to avoid unnecessary disturbance. At sampling completion, we recovered memory cards and we extracted mammal images for identification, using a specialized software (DeskTEAM, Fegraus et al. 2011). We used a single taxonomic authority (IUCN, 2015) 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 1.1). Thus, we took measurements of vegetation at three spatial scales. At the broadest scale, we measured the 20 nearest trees starting with the tree closest to the camera trap location and moving clockwise until we reached the 20th tree. We split trees into two categories: trees with a diameter at breast height (DBH) of 5–10 cm and trees greater than 10 cm. At mid-scale, we randomly placed four 3 × 3 m plots within 10 m radius of each camera and within each plot we recorded the number of stems >5 cm DBH and taller than 1 m. At the smallest scale, we recorded the percent cover of leaves, seedlings and herbs, bare soil and dead logs, within four, 1 m² plots positioned at the corners of each 3 × 3 m plot, resulting in a total of 16, 1 m² plots around each camera trap. We also recorded the proportion of leaf litter that was at least 5 cm deep in the plots as

measured with a ruler. We calculated a visibility index of the plot around each camera trap location by estimating the percentage of 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 derive a mean value of visibility for each plot. We adopted this method to quantify the density of the vegetation growth for forest floor that was not measured by stem density (SD). In addition, we calculated the shortest linear distances from each camera trap point to National Park border and forest edge, using geoprocessing 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 1.1. 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) ^a
20 small trees (5–10 cm DBH)	Mean basal area (MBA2) Diversity (Simp2) ^b
3 × 3 m plots	Small trees stem density (SD3) Diversity (LogSimp3) ^c
1 × 1 m plot (forest floor cover)	Herbaceous layer and seedlings (Herbs_Seedl) ^d Sum of deep and very deep leaf litters (SumDepthD_VD) Visibility ^e Distance to the National Park

border (DistToNPBorder)^f
Distance to the forest edge
(DistToForestEdge)^f

^aSimp1 correlated with Richness 1 ($r = 0.9$, $p < 0.01$, $n = 59$).

^bSimp2 correlated with Richness 2 ($r = 0.8$, $p < 0.01$, $n = 59$).

^cLogSimp3 correlated with Richness 3 ($r = 0.8$, $p < 0.01$, $n = 59$).

^dHerbs_Seedl correlated with Leaves ($r = -0.7$, $p < 0.01$, $n = 59$).

^eMeasured 20 m from the centre of the plot.

^fCalculated by using ArcGIS version 10.

Data analysis

TEAM data are.csv files that we analysed using ad-hoc codes in R (R Core Team, 2015; 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 et al. 2013a, 2014a). 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 standardised 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 (O'Brien et al. 2003, Rowcliffe et al. 2008, 2011), 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 & Kéry 2003, Kelly & Holub 2008, Rowcliffe & Carbone 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. We randomised 1,000 times the order in which samples were included in the curve and we used the results to get confidence intervals around the mean using the package “*vegan*” in R (Oksanen et al. 2015). 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 m² 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 & 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 version 3.2.1 (R Core Team 2015) using the packages “*lattice*” for graph visualizing and “*nlme*” for running the model (Sarkar 2008, Pinheiro et al. 2016). 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 the presence of outliers in the explanatory variables. In order to obtain a normalized distribution for explanatory variables, we performed a log transformation to correct for the extreme values found for the parameter SD. We used co-plots to highlight collinearity among some of the variables. For the covariates that showed high autocorrelation (correlation coefficient $r > 0.6$), we considered only one variable from each pair

for further analysis. This yielded a final set of 12 variables that we used for the model formulation (Table 1.1).

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 we detected over-dispersion in the model (i.e. over-dispersion >1.5), we corrected standard errors using a quasi-Poisson GLM, adding an over-dispersion parameter ϕ 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 assured that the algorithm employed could not affect the model selection process.

In order to determine which variable to drop, we applied “Chi” and “F” tests when using a Poisson GLM and quasi-Poisson GLM respectively (Zuur et al. 2010). We then validated the final model containing only the variables showing significance at 0.05 level. We looked at the homogeneity of the residuals and we further plotted these against the fitted values and against each explanatory variable in the model, as well as against those covariates that we excluded from the model.

Results

Of the 60 camera traps set, one was stolen, and the remaining cameras accumulated 1,818 camera days (mean 30.8), yielding 12,911 images of mammals. Twenty-six species were recorded from all the 59 sites (Table 1.2). 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 ≤ 20 events, of which seven species scored ≤ 5 events (Table 1.2). The species accumulation curve showed an initial steep shape and flattened out at around 1,000 camera days, when 24 species were recorded, i.e. the 92% of the total number of species detected (Figure 1.2). 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, the deviance explained was $>30\%$ (Table 1.3).

We found the trapping events for the two carnivore species modelled, servaline genet and bushy-tailed mongoose, to be influenced by different variables. For the bushy-tailed mongoose, we found leaf litter depth and SD to be negatively correlated with species' trapping events, with the latter variable being more significant (Table 1.3). For the servaline genet, instead, we found the herbaceous cover and visibility index 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 1.3). For the Afrotheria, the model explained 29.8% of deviance of grey-faced sengi's trapping events and showed significant positive correlation with small tree diversity (Table 1.3). 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 1.3). 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). For suni, the variables retained in the model, i.e. SD of small trees, distance to forest edge and National Park border, had negative correlations with the species trapping event; only visibility index showed a positive correlation. 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 1.3). 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 1.3).

Table 1.2. 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 where 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, 1896)	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)	Abbot's duiker	52	0.458
<i>Genetta servalina</i> (Pucheran, 1855)	Lowe's servaline genet	37	0.356

<i>Potamocheirus 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> (Sparrman, 1779)	African buffalo	7	0.068
<i>Atilax paludinosus</i> (G. [Baron] Cuvier, 1829)	Marsh mongoose	6	0.085
<i>Colobus angolensis palliatu</i> s (Grubb et al., 2003)	Peter's Angolan colobus	3	0.068
<i>Panthera pardus</i> (Linnaeus, 1758)	Leopard	3	0.034
<i>Procolobus gordonorum</i> (Matschie, 1900)	Udzungwa red colobus	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

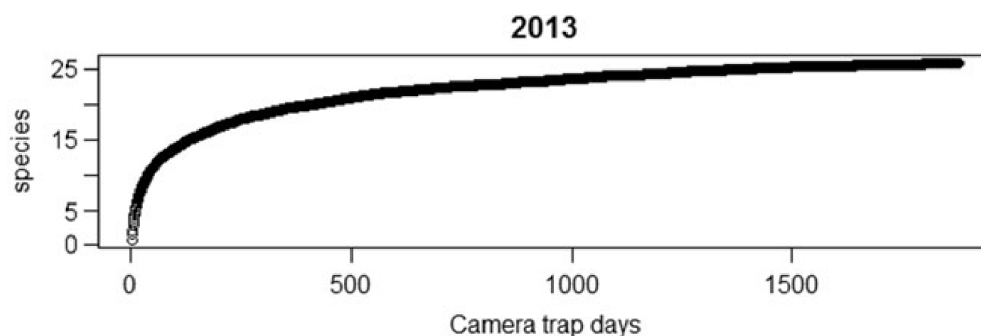


Figure 1.2. Species accumulation curve with sampling effort for the community of medium-to-large mammals detected by camera trapping in the Udzungwa Mountains of Tanzania.

Table 1.3. Results of generalized linear models of habitat predictors of abundance for the 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 1.1 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	
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	-6.414 (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	

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. We thus 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 et al. 2014a) 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 that approximately 30 species may in fact be present in the area (Rovero & De Luca 2007, Rovero et al. 2014a). This in turn confirms the need of a sampling effort longer than 1,000 camera days to describe a complex forest-dwelling community of larger mammals (Tobler et al. 2008, Rovero et al. 2010). Our image event score constitutes an index that does not provide information on differences in abundance among species (see Methods); nevertheless, the fact 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 the Udzungwa red colobus and the 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 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 et al. (2014a) 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 mid-elevation forest (Lovett et al. 2006), where availability of prays may be optimal for these two forest dwelling species (De Luca & Mpunga 2005). In addition, SD of large trees was positively correlated with trapping events of Lowe's genet, indicating their preference for closed canopy and highly sheltered areas (Rovero et al. 2013a). 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 2015). Being diurnal, this species may prefer more dense vegetation to avoid detection from aerial predators (Rovero et al. 2013a). For the Sanje mangabey, another Udzungwa-endemic and IUCN-endangered species (IUCN, International Union for Conservation of Nature 2015), 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.).

The results for the two ungulates Abbott's duiker and bush pig 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 et al. 2014a). 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 indicate a greater re-colonization of the lower elevation forest by this species in Mwanihana. In contrast, for the other forest antelope, the suni, 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 et al. 2014a). 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 for 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, was positively correlated with the trapping events of the giant pouched rat. This may likely indicate the species' preference for highly sheltered areas with complex habitat, which may in turn mean greater 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 that provides food sources and perfect refuges when fleeing from predators and 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 was 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: the interior areas in which moist montane forest is found, but also the forest edge that is 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 that should be considered in future studies by adopting inferential approaches. We have provided insights on the mammal community inhabiting the study area, using a habitat sampling approach, i.e. measuring vegetation features at the fine scale, which was previously done only on the forest antelope and on the grey-faced sengi (Bowkett et al. 2008, Rovero et al. 2014a). 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 larger portion of species in the community.

CHAPTER 2

Primates in human-modified and fragmented landscapes: the conservation relevance of modelling habitat and disturbance factors in density estimation

Based on the paper: **Cavada N**, Barelli C, Ciolli M, Rovero F (2016) Primates in human-modified and fragmented landscapes: the conservation relevance of modelling habitat and disturbance factors in density estimation. PLoS ONE 11(2): e0148289. doi:10.1371/journal.pone.0148289

Summary

Accurate density estimation of threatened animal populations is essential for management and conservation. This is particularly critical for species living in patchy and altered landscapes, as is the case for most tropical forest primates. In this study, we used a hierarchical modelling approach that incorporates the effect of environmental covariates on both the detection (i.e. observation) and the state (i.e. abundance) processes of distance sampling. We applied this method to already published data on three arboreal primates of the Udzungwa Mountains of Tanzania, including the endangered and endemic Udzungwa red colobus (*Procolobus gordonorum*). The area is a primate hotspot at continental level. Compared to previous, 'canonical' density estimates, we found that the inclusion of covariates in the modelling makes the inference process more informative, as it takes in full account the contrasting habitat and protection levels among forest blocks. The correction of density estimates for imperfect detection was especially critical where animal detectability was low. Relative to our approach, density was underestimated by the canonical distance sampling, particularly in the less protected forest. Group size had an effect on detectability, determining how the observation process varies depending on the socio-ecology of the target species. Lastly, as the inference on density is spatially explicit to the scale of the covariates used in the modelling, we could confirm that primate densities are highest in low-to-mid elevations, where human

disturbance tend to be greater, indicating a considerable resilience by target monkeys in disturbed habitats. However, the marked trend of lower densities in unprotected forests urgently calls for effective forest protection.

Introduction

Knowledge on abundance and distribution of animal species is required when planning for conservation actions (Linkie et al. 2006, Rodríguez et al. 2007, Ramos-Fernandez et al. 2013). In this context, primates are excellent study subjects as they represent good ecological indicators in tropical rainforest, being highly sensitive to habitat changes, hunting and other forms of disturbance (Marsh 2003, Struhsaker 2010, Rodríguez-Luna et al. 2013). Indeed they are the mammal order with the highest proportion of species under threat (Chapman & Peres 2001, Schipper et al. 2008), due to the effect of different drivers (Jones 2011, Marsh 2013), that often interplay following complex and site-specific patterns (Rovero et al. 2012). Ideally, therefore, proper estimation of population densities should accurately account for potential covariates, including spatially explicit ones, that can help to understand how ecological processes are involved in the high spatial heterogeneity of population abundance, as well as to understand how these populations will respond to environmental changes (Underhill & Gibbons 2002, Ramos-Fernandez et al. 2013). In this perspective, modelling the spatial patterns of threatened populations at a landscape-level can be very informative, particularly when considering species that occupy highly diverse habitats (Baillie et al. 2000, Levi et al. 2009, Arroyo-Rodríguez & Fahrig 2014). Such approach is also of clear conservation relevance for site prioritization, i.e. to identify the main drivers of change in variation of species density and locate those areas that need urgent intervention (Margules & Pressey 2000).

Meanwhile, it is widely acknowledged that models of animal density and their habitat preferences need to consider imperfect detectability of species at occupied sites (Yoccoz et al. 2001, Martin et al. 2005, Kéry & Schmidt 2008) to avoid incorrect

estimates and predictions (Kellner & Swihart 2014, Lahoz-Monfort et al. 2014). This is particularly relevant for primates for which population assessments are inherently complex because of the habitat characteristics (Yoccoz et al. 2001, Buckland et al. 2010a), and the social structure (Buckland et al. 2010b). Hence, the use of the ‘canonical’ application of distance sampling (Buckland et al. 2001), i.e. the one that does not consider the differential influence of covariates on abundance and detection, may not be the most informative approach when analysing density of primates that occupy heterogeneous landscapes. Here, we address this issue by providing an application of the hierarchical modelling framework by Royle, Dawson and Bates (2004), that allows to include covariates both in the observation (detection) and in the state (abundance) processes.

We applied such method to distance sampling data collected in the Udzungwa Mountains of Tanzania, an outstanding hotspot for primate diversity and endemism in Africa, where relevant background work has been already conducted on primates. We targeted three species of arboreal monkeys, including the endemic and threatened Udzungwa red colobus (*Procolobus gordonorum*). Previous studies by Araldi *et al.* (2014) applied the conventional distance sampling approach and, even though these authors realized a robust survey effort for well-informed density estimates, they did not consider the relationship between densities and environmental covariates. Barelli *et al.* (2015) presented an assessment of primates’ responses to habitat factors and human disturbance using the observed encounter rate of primate social groups as the response variable in a multivariate regression framework. Hence, they did not account for imperfect detection. Both studies provided informative results regarding contrasting density estimates among forest blocks (Araldi et al. 2014) and the consistent influence of elevation and climber coverage on the encounter rate of primates (Barelli et al. 2015). However, further investigation using a spatially explicit, inferential framework is highly relevant to understand how habitat and disturbance covariates affect density and detectability. The objectives of our study were: 1) to obtain species-specific models from distance sampling data, using an approach that has rarely but successfully

been applied to derive the abundance of endangered animal populations (Schmidt et al. 2012, Sillett et al. 2012, Kellner & Swihart 2014); 2) to assess if such selected models could improve the sensitivity of estimates of primate population density; 3) to gain relevant information for conservation purposes by modelling the spatial variation of primate density in a highly heterogeneous and complex human-natural system.

Materials and Methods

Study area and species

The Udzungwa Mountains (7°40' - 8°40' S, 35°10' - 36°50' N; Figure 2.1) extend over >19,000 km² (Platts et al. 2011) and represent the southern block of the Eastern Arc Mountains of Kenya and Tanzania (Lovett & Wasser 1993, Araldi et al. 2014), within the Afromontane biodiversity hotspots (Myers et al. 2000). The mountains are characterized by the presence of several forest blocks that differ in elevation range (290 - 2,576 m a.s.l.), area (from 12 to >500 km²), habitat type and protection level (Marshall et al. 2010, Araldi et al. 2014).

Data were collected by Araldi *et al.* (2014) and Barelli *et al.* (2015) in four different forest blocks, namely Magombera (MG), Matundu (MT), Mwanihana (MW) and Uzungwa Scarp (US), with MG and US showing intense human disturbance due to the absence of legal protection (Struhsaker et al. 2004, Marshall 2008).

The study focused on three species of arboreal primates that show a widespread distribution across the Udzungwa Mountains: the Peters' angolan colobus (*Colobus angolensis palliatus*) (henceforth BW), the endemic and endangered (IUCN, 2015) Udzungwa red colobus (henceforth RC) and the Tanzania Sykes' monkey (*Cercopithecus mitis monoides*) (henceforth SY).

We refer to Barelli et al. (2015) and Araldi et al. (2014) for detailed information about the study area and species.

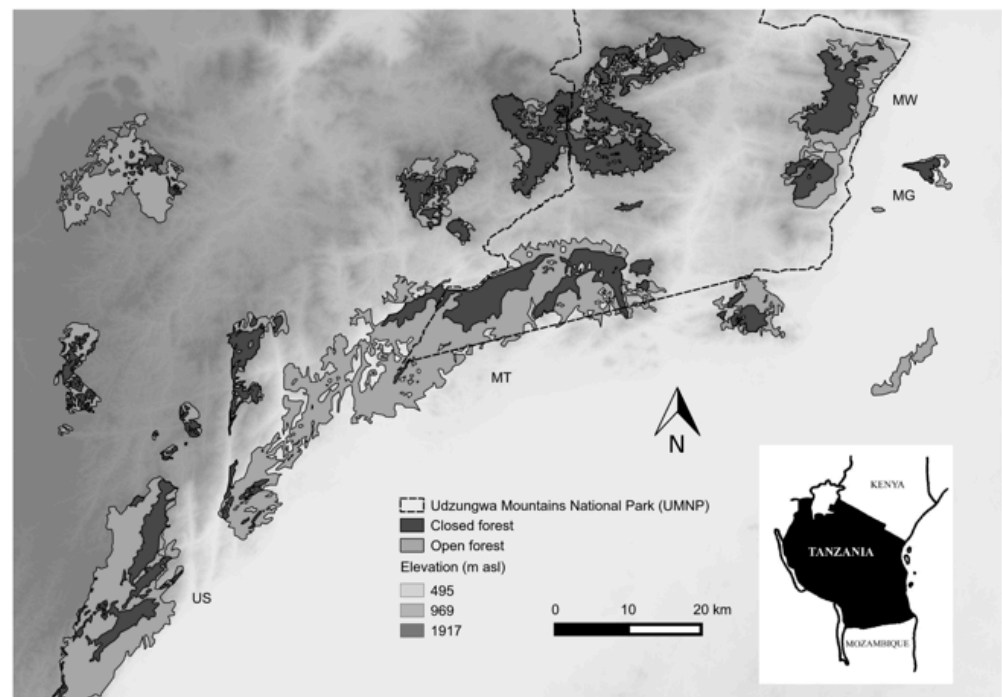


Figure 2.1. Map of the Udzungwa Mountains National Park, Tanzania, showing the four forests surveyed (Magombera, MG; Matundu, MT; Mwanihana, MW and Uzungwa Scarp, US) for primate density data collection.

Data set: primates and habitat covariates

We used data in Araldi et al. (2014) and Barelli et al., (2015) that were collected through systematic line transects following the standardized distance sampling approach (Buckland et al. 2001). Authors achieved a uniform coverage of target forests (Figure 2.2). Arboreal vegetation and disturbance parameters were collected by establishing four squared vegetation plots, 25 × 25 m each, centered on each line transect, with a total of 176 plots sampled (see Barelli et al. 2015).

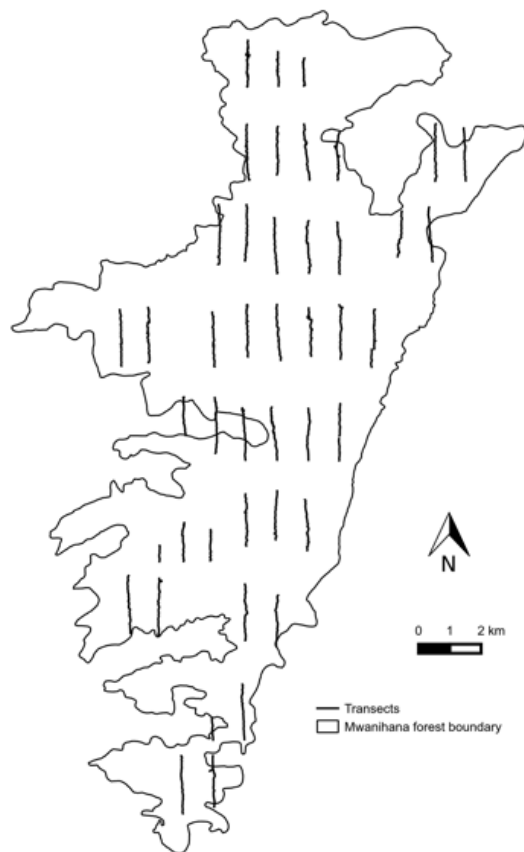


Figure 2.2. Map of Mwanihana forest (MW) with the sampling grid, as an example of diffused grid of transects walked for primate density estimations in Udzungwa Mountains National Park of Tanzania.

Statistical method

We modelled the observed data as a hierarchical coupled logistic regression. One step of the modelling process is related to the partially observed true state (occurrence, the result of a biological process); the other step describes detection, that is the result of both the biological process and the observation process (i.e. how animals are detected). In detail we assumed animals' abundance at transect level to have a Poisson distribution ($X_i \sim \text{Poisson}(\lambda_i)$; $i=1, \dots, n$), with λ being the expected value of X ($\lambda = E(x)$). We modelled the detection process according to a multinomial distribution and we expected the detection probability to monotonically decrease with the increasing distance from the observer, as per conventional distance sampling theory (Buckland

et al. 2001). We verified this process by looking at the histograms of the distance records. We removed outliers from the data set, defining a species-specific right-truncation distance, looking at the right tail of the plotted distance frequency distribution. We set such truncation distance at 100 m for BW and SY and at 90 m for RC. Observations taken at larger distances were scarce and provided little information for the estimation of the detection function (Buckland et al. 2001). In detail, we removed 64 outliers for RC and SY and 67 outliers for BW. We noted heaps mainly in the first distance class, suggesting that rounding errors were mainly close to distance = 0. We therefore grouped in intervals distances that were recorded on a continuous scale, correcting for heaping and to improve estimates of density and model fit (Buckland et al. 2001). Thus, we defined 5 bins of 20 m for the analysis on BW, 6 bins of 15 m for the analysis on RC and 4 bins of 25 m for the analysis on SY.

Using the function *'distsamp'* in R package *'unmarked'* (Fiske & Chandler 2011) we modelled data separately for each of the three primate species. We first checked the performance of different detection functions (uniform, half-normal and hazard-rate) on the simplest model, without considering the covariates effect. Based on the Akaike Information Criterion (AIC), we retained the half-normal function $g(y) = \exp - (y^2 / 2 \sigma^2)$, with y being the distance class and with σ being the scale parameter for the detection function. We then incorporated in the model the influence of transect-specific covariates on both λ and σ , using a log link function. We built models using all the possible combinations of environmental and human-disturbance variables, sampled at the transect level, to determine how they affect both the detection process and the presence of the animals, based on a set of assumptions (Table 2.1); see also Barelli et al. (2015). In addition to distance, which is an inherent covariate of the detection process, we assumed detection to be influenced by the following covariates: (1) group size, assuming that larger groups are more easily detected in the canopy at larger distances (Buckland et al. 2001); (2) forest block, as a nominal covariate representative of the heterogeneity among forests, given that each forest is a discrete area sampled; (3) canopy cover and (4)

percentage of climbers; (5) steepness and (6) distance to anthropic disturbance (i.e. roads and villages). We used these covariates also when modelling the state process, in addition to (7) elevation and (8) diversity of tree communities, calculated as the Simpson's reciprocal diversity index; we also considered, as proxies of disturbance, (9) count of signals of human presence along transects (cutting signs, recent and old paths, and trails made by humans, sites where pit sawing had been carried out or charcoal was produced, as well as signs of recent and old poacher camps, incidence of animal snares) and (10) distance from the forest edge.

We used AIC to rank all the candidate models and we considered as equivalent those models showing $\Delta AIC < 2$ (Anderson & Burnham 2002). This criterion prevent us from unequivocally define a single best model on which to base predictions. We thus determined Akaike weights (w_i) for each of the best models (R package *MuMIN*; Barton 2015) and to further reduce ambiguity, we derived the relative importance of each variable, on a scale from 0 to 100. We decided to favor the model with the lowest number of parameters, selecting only the variables that showed an importance of at least 50%. To verify the goodness of fit of the selected model we performed a parametric bootstrapping, simulating 200 datasets from the fitted model and defining a function that returned the fit-statistic of the Pearson's X^2 . We used non parametric bootstrap to estimate the uncertainty (i.e. SE) of the parameters in the model. We then used the resulting best species-specific models selected, to predict primate group density, as well as their detectability, in each sampled forest block and in each of the plot that were sampled along the transects, for which measurements of the influential habitat variables were available.

We also assessed how the hierarchical structure of our analysis could improve our estimates, by comparing our results with those from Araldi et al. (2014), and assumed these authors' estimates to be comparable with those from our null model, i.e. one that assumes no covariates effect. To test for differences between the two approaches, we used a t-test after assessing normality with Shapiro-Wilk tests (Royston 1982).

Table 2.1. List of the covariates sampled in the four forest blocks of the Udzungwa Mountains, Tanzania. Covariates were examined in the model building step for the three primate species (BW, RC and SY) and their predicted effect on both the detection and the density processes is reported as (+) (= positive) and (-) (= negative).

Habitat variables	Variable effect	Hypothesized relationship with the detection process
<i>Covariates on detection</i>		
Forest block	no interpretation	Highly diverse morphology in each forest block, natural or human driven.
Group size	+	Large groups are more easily detected even at larger distances (Buckland et al. 2010b).
Canopy cover	-	Closed canopy area reduces visibility.
Distance from disturbance	-	Proximity to human disturbance and therefore to disturbed habitats can facilitate animal detection.
Percentage of climbers	+	Climbers are representative of areas that have been logged in the past and are found in lowland regenerating forests (Isaac & Cowlshaw 2004, Marshall 2007); being proxies of open habitats they can allow better detection.
Steepness	+	A steep terrain originates naturally-broken canopy (Barelli et al. 2015) that increases detectability.
<i>Covariates on density</i>		
Forest blocks	no interpretation	High variability among the forest blocks in terrain morphology,

		vegetation structure and formal protection level.
Canopy cover	-	Preference by three target species is shown for disturbed habitats with a patchy canopy cover (Barelli et al. 2015).
Total basal area	-	Mature, old-growth forests that present large total basal area values are less preferred (Lovett et al. 2006, Barelli et al. 2015).
Mean basal area	+	Colobines are found to selectively feed on large tree species (Struhsaker 2010), showing high scores for mean basal area.
Simpson diversity index	+	A higher species diversity can represent a greater variety of food sources, thus allowing primates presence (Medley 1993, Chapman & Chapman 1999, Cowlshaw & Dunbar 2000).
Percentage of climbers	+	Vegetation diversity in the tropics is also related to vines and climber species, on which Udzungwa primates rely for a large portion of their dietary requirements (Rovero & Struhsaker 2007).
Elevation	-	Lower to mid-elevations are characterized by the presence of semi- deciduous forests where colobines can find young and more digestible leaves (Barelli et al. 2015). The frugivorous Sikes' monkeys (Dunn et al. 2012, Arroyo-Rodríguez et al. 2015), are not found at higher elevations, where fruit productivity is low.

Steepness	+	Steep terrains facilitate moderate climbers spread and colonization (i.e more digestible food items; (McGraw 1996)), due to natural occurring brakes in the canopy.
Human impact	-	Noisy and disturbing human activities such as logging, together with hunting may affect animals behaviour and can cause avoidance and fleeing responses (Rovero et al. 2009, Manduell et al. 2012).
Distance from edge	+	
Distance from disturbance	+	

Results

After right truncating the data at 100 m we retained 90 observations for BW and 129 for SY, while we retained 97 observations for RC with a 90 m truncation. Detection functions indicated that all assumptions for the method were met, i.e. they showed a monotonic decrease with increasing distance as well as good fit on the observed data. No spikes were present after binning the data in distance classes.

Model selection for BW resulted in a model containing an effect of group size (+, i.e. a positive effect) on detection and an effect of percentage of climbers (+), human impact (-, i.e. a negative effect) and forest block on density. The best model for RC contained an effect of forest block, climbers percentage (+) and distance from disturbance (-) on detection and an effect of mean basal area (+), percentage of climbers (+), elevation (-) and distance from human disturbance (-) on density. The best model for SY retained an effect of group size (+) on detection and of climber percentage (+) and elevation (-) on abundance (Tables 2.2 and 2.3; Figures 2.3 and 2.4; Figures A and B in Appendix 1).

The bootstrap P value based on the Chi-square statistic showed adequate fit for all the species specific models (P=0.94 for BW; P=0.18 for RC; P=0.37 for SY). Testing for differences between density estimates from our null model and estimates in Araldi et al.

(2014) confirmed the equivalence of the two methods ($P=0.16$). This in turn supports our hypothesis of a better performance (based on delta AIC of models with covariates vs null models) of our best models to estimate primates density (Figure 2.5; Table 2.4) relative to the conventional approach ($\Delta AIC=106.507$ for BW; $\Delta AIC=45.93$ for RC; $\Delta AIC=82.83$ for SY; Table 2.2).

Spatially explicit maps of estimated density at the plot level are shown in Figure 2.6 and Figure C in Appendix 1.

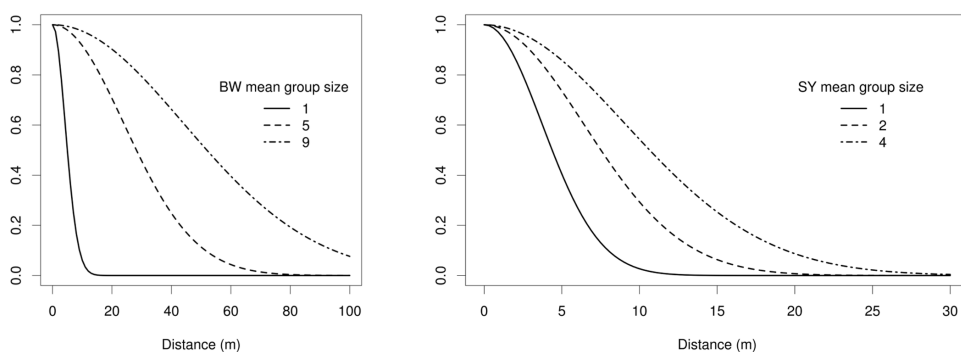


Figure 2.3. Detection functions from the best AIC models, shown for the 0.25, 0.50 and 0.75 quartiles of the covariate group size for Peters' Angola colobus (BW) and Tanzania Sykes' monkey (SY).

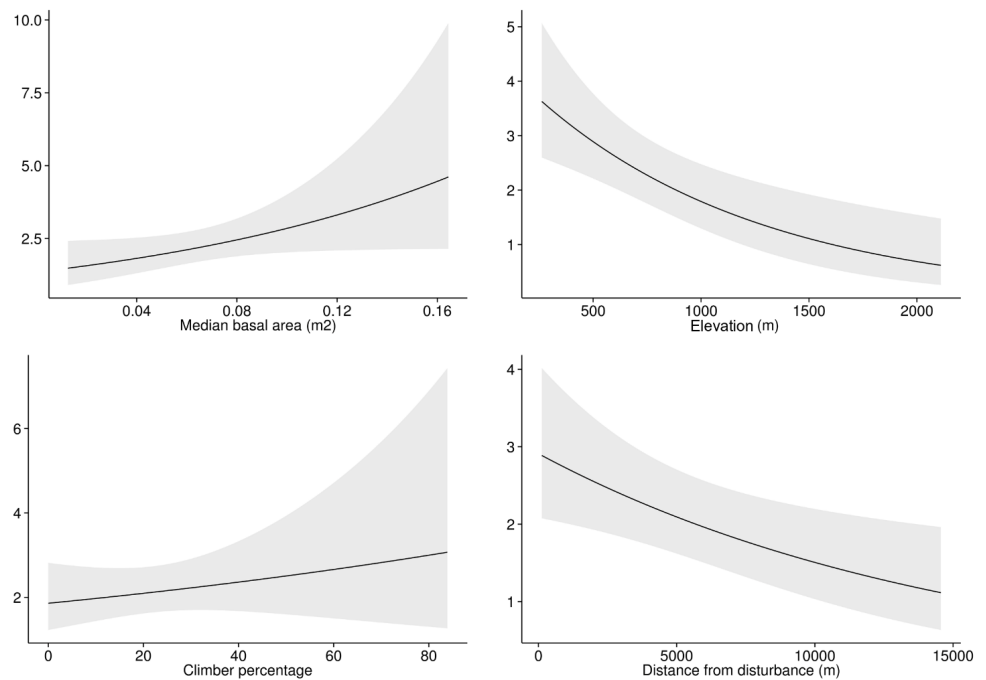


Figure 2.4. Covariates effect on group density estimation, shown for the best model selected for the Udzungwa red colobus (RC).

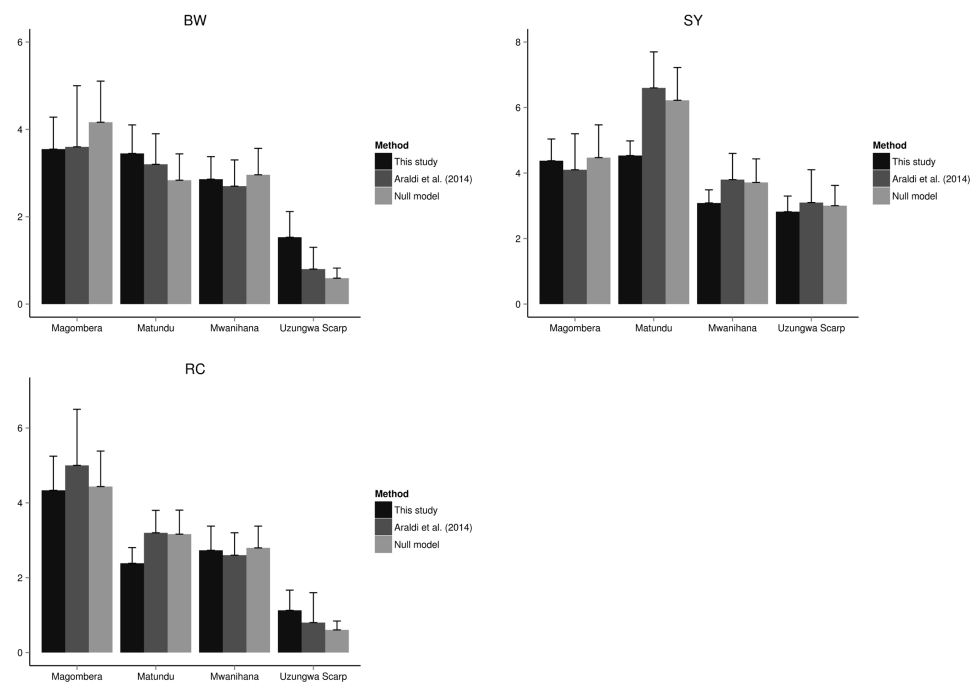


Figure 2.5. Comparison between the estimated density values for the three primate species (Peters' Angola colobus, Udzungwa red colobus, Tanzania Sykes' monkey), obtained applying different methods (i.e. hierarchical modelling with covariates (this study); the study by Araldi et al. (2014); null model without covariates).



Figure 2.6. Predicted density (groups/km²) for the three primate species (Peters' Angola colobus, Udzungwa red colobus, Tanzania Sykes' monkey) from the best selected models (see Table 2.2) in the forest of Mwanihana. Predicted values were obtained for the plots that were sampled along the transects, for which exact values of the influential covariates were available.

Table 2.2. Akaike information criterion (AIC) value for high ranked models of primate density (λ) and the shape parameter (σ) of a half-normal detection function.

Model	AIC	ΔAIC
Peters' Angola colobus (<i>Colobus angolensis</i>)		
σ (Group size) λ (Percentage of climbers + Human impact + Forest block)	425.84	
σ (Group size) λ (Percentage of climbers + Forest block)	426.49	0.65
σ (Group size) λ (Canopy cover + Percentage of climbers + Simpson diversity index + Forest block)	428.47	2.63
$\sigma(\cdot)\lambda(\cdot)$	533.05	106.561
Udzungwa red colobus (<i>Procolobus gordonorum</i>)		
σ (Forest block + Distance from disturbance + Percentage of climbers) λ (Mean basal area + Percentage of climbers + Elevation + Distance from disturbance)	557.41	
σ (Forest block + Distance from disturbance) λ (Mean basal area + Percentage of climbers + Elevation + Distance from disturbance)	558.25	0.84
σ (Forest block + Distance from disturbance + Percentage of climbers) λ (Mean basal area + Percentage of climbers + Steepness + Elevation + Distance from disturbance)	558.59	1.18
$\sigma(\cdot)\lambda(\cdot)$	603.34	45.93
Tanzania Sykes' monkey (<i>Cercopithecus mitis monoides</i>)		
σ (Group size) λ (Percentage of climbers + Elevation)	513.14	
σ (Group size + Human impact + Canopy cover + Percentage of climbers) λ (Percentage of climbers + Elevation)	514.45	1.32
σ (Group size) λ (Percentage of climbers + Steepness + Elevation)	514.55	1.41

$\sigma(\cdot)\lambda(\cdot)$ 595.96 82.83

Table 2.3. Parameter estimates and their standard error for the final models selected for the three primate target species that presented the lowest AIC values.

Model and coefficient		CI (95%)	SE
Peters' Angola colobus			
<i>Detection (σ)</i>			
Intercept	10.2	10.12 – 10.2	2.15
Group size	12	11.98 – 12.06	3.278
<i>Density (λ)</i>			
Intercept	1.42	1.01 – 1.83	0.692
Percentage of climbers	0.2	0.02 – 0.37	0.192
Human impact	-0.14	-0.36 – -0.08	0.228
Forest Matundu	-0.3	-0.87 – 0.27	0.473
Forest Mwanihana	-0.35	-0.91 – 0.2	0.369
Forest Uzungwa Scarp	-0.97	-18.3 – -0.1	0.951
Udzungwa red colobus			
<i>Detection (σ)</i>			
Intercept	2.54	1.22 – 3.87	6.95
Forest Matundu	8.43	-52.13 – 68.99	7.98
Forest Mwanihana	6.14	-24.36 – 36.65	7.11
Forest Uzungwa Scarp	-0.87	-1.86 – 0.12	8.78
Distance from disturbance	-1.78	-3.51 – -0.04	5
Percentage of climbers	0.51	-0.17 – 1.18	4.51
<i>Density (λ)</i>			
Intercept	0.74	0.49 – 1	1.55

Mean basal area	0.21	0 – 0.43	0.41
Percentage of climbers	0.09	-0.11 – 0.3	0.63
Elevation	-0.53	-0.83 – -0.22	0.37
Distance from disturbance	-0.27	-0.47 – -0.07	0.44
Tanzania Sykes' monkey			
<i>Detection (σ)</i>			
Intercept	6.57	6.53 – 6.61	1.385
Group size	7.06	7.03 – 7.08	2.809
<i>Density (λ)</i>			
Intercept	1.28	1.1 – 1.47	0.117
Percentage of climbers	0.16	-0.03 – 0.35	0.078
Elevation	-0.22	-0.45 – 0	0.107

Table 2.4. Forest specific values of detectability and group density for the three primate target species.

Species and forest	Detectability (SE)	Density (groups/km ²) (SE)
Peters' Angola colobus (<i>Colobus angolensis</i>)		
Magombera	0.15 (0.01)	3.49 (0.73)
Matundu	0.11 (0.007)	3.45 (0.66)
Mwanihana	0.13 (0.006)	2.9 (0.53)
Uzungwa Scarp	0.04 (0.007)	1.43 (0.57)
Udzungwa red colobus (<i>Procolobus gordonorum</i>)		
Magombera	0.12 (0.006)	4.88 (0.97)
Matundu	0.17 (0)	2.4 (0.41)

Mwanihana	0.17 (0)	1.83 (0.33)
Uzungwa Scarp	0.06 (0.005)	1.2 (0.34)
Tanzania Sykes' monkey (<i>Cercopithecus mitis monoides</i>)		
Magombera	0.13 (0.01)	4.38 (0.66)
Matundu	0.16 (0.009)	4.53(0.45)
Mwanihana	0.12 (0.01)	3.09 (0.4)
Uzungwa Scarp	0.16 (0.01)	2.82 (0.48)

Discussion

Our study aimed to show the importance of accounting for habitat covariates of primate detectability and abundance in distance sampling studies in complex landscapes. The hierarchical analytical approach allowed us to obtain reliable, informative and spatially-explicit estimates relative to previous studies that did not consider the covariate effect (Araldi et al. 2014) nor abundance estimation with imperfect detection (Barelli et al. 2015). Moreover, the method we used allows for inference on density outside the sampled area. This is of particular relevance when the variables that are retained in the modelling are spatially diffused, as it usually applies to those derived from remote sensing.

A first important result is how the species-specific group size influences detection. By using this approach, group size effect could be explicitly evaluated and therefore modelled. On the contrary, in conventional distance sampling group size is regressed on estimated probability of detection. The positive relationship between group size and detection in BW and SY, but not RC, is likely explained by different grouping patterns. The average group size of BW and SY was indeed similar (3.84 and 3.41 respectively) and was almost five times lower than group size of RC (17.03). Groups of RC could have been consequently more easily detected even far from the transect line. Indeed focal studies have shown that RC can average 40 individuals in undisturbed forests such as Mwanihana, while BW and SY average group size is <10 and much smaller for SY (Rovero et al. 2009). Thus group size

represents a critical parameter that needs to be carefully considered to avoid underestimation of animal densities, with particular relevance for species whose social units are small (i.e. <5-10 individuals) as is the case of SY, for which, indeed, the parameter 'group size' had a higher effect on detection. As predicted, we found detectability for RC to be negatively influenced by distance from disturbance. This variable represents a proxy for forest structures that can hamper visibility, such as tall and dense canopy in interior forest. Climber percentage, on the contrary, had a positive association with RC detectability. Even if producing a small effect on the detection process (for climber coverage <75%), moderate presence of climbers constitutes a structure of the sub-canopy layer that is seemingly preferred by arboreal primates (see below).

As for the effect of covariates on animal density, we found the percentage of climbers to have a positive effect for all the three species we examined. This result is in line with findings from Barelli et al. (2015) and Rovero and Struhsaker (Rovero & Struhsaker 2007); climbers represent a food source (Dunn et al. 2012, Arroyo-Rodríguez et al. 2015), influence canopy connectivity and provide supports for movements in the canopy (McGraw 1996, Manduelli et al. 2012).

We found a negative association between elevation and density of RC and SY. This also matches the findings from previous studies (Marshall 2007, Rovero & Struhsaker 2007, Barelli et al. 2015) that explained this result in terms of different food availability along the elevation gradients of the study area. Human impact was found to have a negative association only with BW. Hunting pressure is indeed reported to be targeted mainly on this species, which skin is highly demanded (Rovero et al. 2012). RC and SY appear less affected by hunting and this differential degree of human impact is reported in several other studies (Isaac & Cowlishaw 2004, Kümpel et al. 2008, Linder & Oates 2011, Rovero et al. 2012). Density of RC was related to the mean basal area of trees, that had a positive effect, and to distance from disturbance, with a negative effect, contrary to what we hypothesized. This is in line with results by Rovero and Struhsaker (2007) and confirms the preferences shown by the species for larger trees that can be

found also at forest edges. Here, even if logging is more intense, productivity of the remaining large trees can still be high (Johns 1983), thanks to an increase in illumination (Davies & Oates 1994).

We found lower values for group density estimates in the US forest block for all the three species and mainly for BW and RC, for which density values were about the 40% lower in US. Nevertheless, variation in density between US and the other forest blocks was particularly substantial for BW (Table 2.4), for which the parameter level US was found to have a high negative effect on density estimation. Importantly, the variation in density estimates among forests was almost two times lower than that reported in Araldi et al. (2014). Such underestimation may have been smoothed by our analysis because of adding the effect of covariates on both the detection probability and the state process (Marques & Buckland 2003, Marques et al. 2007). This is of particular conservation relevance in highly disturbed habitats, like US, where animals are sparse and shy, and therefore tend to hide and go undetected relatively more than in other forests (Table 2.4). In general, our results further confirm that the absence of protection in US highly affects the colobine monkeys, with pressures that mainly derive from targeted hunting and to lesser extent to habitat degradation (Rovero et al. 2012, 2015). These findings in turn support the hypothesis that colobines are more sensitive than Tanzania Sykes' monkeys to highly disturbed habitats and to human impact that deeply affects the structural characteristics of the forest (Chapman & Chapman 1999, Anderson et al. 2007, Rovero et al. 2015).

Conclusions and conservation recommendations

Obtaining reliable and informative estimates of primate density in complex and human-modified landscapes is difficult, yet with habitat degradation and loss being a pan-tropical phenomenon, an increasing proportion of primate species is found in degraded and patchy habitats (Arroyo-Rodríguez & Fahrig 2014). Our study demonstrates how the inference on abundance is improved by accounting for habitat covariates as separately affecting the observation and the state processes. Indeed when compared to the

canonical approach to distance sampling, the method we used refined density estimation differences among forests. This is of particular relevance to populations in highly impacted forests as US, where animals can go easily undetected and are unevenly located within the sampled area; more generally, it represents a valuable tool for the study of threatened and/or low density populations, as failure to model covariates of detectability and abundance will likely produce biased density estimates. We also showed that group size influences the observation process and is of particular importance for species or populations with small social units. Lastly, this approach allows spatially explicit modelling of animal density at the scale of the covariates used in the modelling. Hence, when significant covariates are available across the study area (forest blocks in our case), and even beyond, such as from remote sensing layers (e.g. elevation, slope, distance to disturbances, etc.), inference on density can be extended over such areas (hence even beyond the measurement points), providing a critical tool to predict the status of populations in fragmented or otherwise heterogeneous landscapes.

CHAPTER 3

Integrating field and satellite data for spatially-explicit inference on the density of threatened arboreal primates

Based on the paper: **Cavada N**, Ciolli M, Rocchini D, Barelli C, Marshall AR, Rovero F (2017) Integrating field and satellite data for spatially-explicit inference on the density of threatened arboreal primates. *Ecological Applications* 27(1): 235-243

Summary

Spatially explicit models of animal abundance are a critical tool to inform conservation planning and management. However, they require the availability of spatially diffuse environmental predictors of abundance, which may be challenging especially in complex and heterogeneous habitats. This is particularly the case for tropical mammals, such as non-human primates, that depend on multi-layered and species-rich tree canopy coverage, which is usually measured through a limited sample of ground plots. We developed an approach that calibrates remote-sensing imagery to ground measurements of tree density to derive basal area, in turn used as a predictor of primate density based on published models. We applied generalized linear models (GLM) to relate 9.8 ha ground samples of tree basal area to various metrics extracted from Landsat 8 imagery. We tested the potential of this approach for spatial inference of animal density by comparing the density predictions for an endangered colobus monkey, to previous estimates from field transect counts, measured basal area, and other predictors of abundance. The best GLM had high accuracy and showed no significant difference between predicted and observed values of basal area. Our species distribution model yielded predicted primate densities that matched those based on field measurements. Results show the potential of using open-access and global remote sensing data to derive an important predictor of animal abundance in tropical forests and in turn to make spatially explicit inference on animal density. This

approach has important, inherent applications as it greatly magnifies the relevance of abundance modelling for informing conservation. This is especially true for threatened species living in heterogeneous habitats where spatial patterns of abundance, in relation to habitat and/or human disturbance factors, are often complex and, management decisions - such as improving forest protection - may need to be focused on priority areas.

Introduction

Species abundance estimation and the identification of factors predicting its variation is a pervasive goal in ecology and conservation biology and it is gaining increasing attention through the emergent potential of spatially explicit modeling (Guisan & Zimmermann 2000, Guisan & Thuiller 2005, Wulder & Franklin 2006, Anadón et al. 2010). This is particularly true for threatened species living in heterogeneous landscapes, where habitat structure and human disturbance vary according to complex spatial patterns. In these contexts, inference on abundance becomes truly informative only when it accounts for such heterogeneity (Arroyo-Rodríguez & Fahrig 2014). Human-modified landscapes are also expanding in tropical areas, where forest fragmentation, degradation and defaunation strongly affect species viability (Balmford & Whitten 2003, Arroyo-Rodríguez & Fahrig 2014). However, because of limited and substandard data, spatially explicit models are less exploited in tropical areas compared to temperate ones (Cayuela et al. 2009). Thus, integrating the use of field data with remote sensing data represents an advantageous approach to ensure data quality for spatial modelling in these areas (Wilkie & Finn 1996, Proisy et al. 2007).

Remote sensing data (especially Landsat) have been used to investigate several ecological questions, mainly related to land cover change, carbon storage and habitat mapping (Schroeder et al. 2011, Legaard et al. 2015, Mayes et al. 2015, Twongyirwe et al. 2015). However, the resolution and quality of Landsat data do not always adequately represent environmental components that are

most important for target species, such as vegetation structure, because optical satellite imagery is not three-dimensional (Hall et al. 1995, Duncanson et al. 2010). Therefore, methods are needed to characterize features of the forest structure that are relevant to target species, particularly for inaccessible areas where Landsat images represent the only feasible option.

In this study, we aimed to derive arboreal primate density from remote sensing estimates of 'tree stem basal area'. Basal area is typically related to canopy cover (Alexander 1971, Farr et al. 1989, Smith et al. 1992), but the two measures are not directly interchangeable (Cade 1997). In particular, mean basal area specifically measures the contribution of each tree to biomass and hence identifies forest structure, succession stage and disturbance. Accordingly, it is a common measure of habitat quality for predicting animal abundance (Braithwaite et al. 1989, Medley 1993, Umapathy & Kumar 2000). This is especially true for non-human primates (Mborá & Meikle 2004, Cristóbal-Azkarate et al. 2005, Anderson et al. 2007, Rovero & Struhsaker 2007) which are globally threatened and in urgent need of conservation actions (Schipper et al. 2008, Schwitzer et al. 2015). Our specific objectives were to: 1) model measured basal area against a combination of different metrics and indices derived from Landsat imagery; 2) test the performance of the best-performing model to predict values of basal area outside of the sampled areas; 3) use the results to derive a spatial map of population density of the endangered (IUCN 2015) Udzungwa red colobus monkey (*Procolobus gordonorum*), based on previously published density-basal area model; 4) compare the modelled primate density to previous predictions from field measurements; 5) further refine these estimates using environmental and human predictors.

Materials and Methods

Study area

The Udzungwa Mountains are located in the south-central part of Tanzania and represent the largest mountain block in the Eastern Arc Mountains, covering an area larger than 19,000 km² (Platts et al. 2011). Closed forest blocks, ranging in size from 12 to over 500

km² (Marshall et al. 2010), are interspersed with drier habitats. We focused our study on the forest of Mwanihana, one of the largest forest blocks (151.6 km²) and under the protection of the Udzungwa Mountain National Park (UMNP) since 1992. Highly variable habitat types are distributed along the altitudinal gradient of the forest ranging from 350 to 2,263 m a.s.l. Deciduous forest is found in the lowland, with semi-deciduous and evergreen forests covering the sub-montane and montane areas, while *Hagenia* and bamboo-dominated forest characterize the upper montane level (Lovett et al. 2006). Woody vegetation density increases with elevation, with the largest trees found at mid elevation, probably a result of human disturbance and tree respiration costs (Marshall et al. 2012).

Vegetation data

We derived field data for tree stems ≥ 10 cm DBH (Diameter at Breast Height; 1.3m) from three sources (Figure 3.1): (1) From the Tropical Ecology Assessment and Monitoring Network (TEAM) (<http://www.teamnetwork.org/>, dataset ID 0327011905 4443), comprising six vegetation plots of 100 × 100 m on a horizontal plane (i.e. adjusted for slope), following a standardized protocol (TEAM Network 2011); (2) 153 vegetation plots of 25 × 25 m, sampled along line transects uniformly distributed in the forest (from Barelli et al. 2015); (3) 33 new randomly placed vegetation plots of 25 × 25 m, sampled in June-July 2015, stratified according to the predominant habitat gradient from disturbed lowland deciduous to mature montane evergreen forest. All newly-sampled plots were placed in the centre of Landsat pixels for concordance with our remote-sensing imagery.

We obtained a single, cloud free, L8 OLI/TIRS Landsat image (Landsat scene ID LC81670652014299LGN00, courtesy of the U.S. Geological Survey), acquired October 26, 2014.

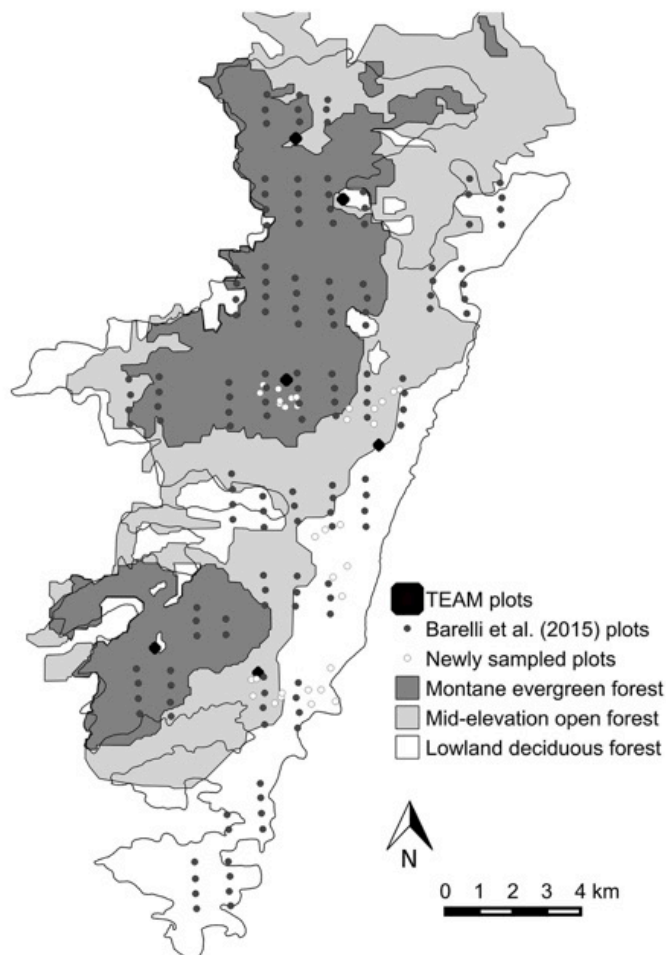


Figure 3.1. Map of Mwanihana forest in the Udzungwa Mountains of Tanzania showing the distribution of three vegetation plot data sets used to derive basal area.

Primate density data

Density data on the Udzungwa red colobus from across the study area were obtained from an earlier study (Cavada et al. 2016). This study used environmental covariates from the 153 plots established by Barelli et al. (2015) and distance sampling along line transects, to estimate colobus density across the study area. Transect data were modelled as a hierarchical coupled logistic regression, assuming a Poisson distribution for the animal abundance at a transect level. The detection process of the

distance sampling was modelled according to a multinomial distribution, assuming a monotonical decrease of the detection probability with the increasing distance of the animal groups from the observer. The influence of a series of environmental and human disturbance covariates was evaluated and incorporated on both the abundance and detection steps in the model. Final density estimates at the plot level were derived from environmental correlates that included mean basal area, elevation and distance from disturbance (i.e. forest edge), that were found to significantly affect the abundance and detectability of the red colobus in the study area.

Analysis

Landsat metrics and vegetation indices

To model basal area we first derived various Landsat metrics (Table 3.1). This began with a Principal Component Analysis (PCA) to extract uncorrelated information from the different spectral bands provided by the Operational Land Imager (OLI) sensor of the Landsat 8 satellite. After applying PCA we further compressed the spectral data applying the Tasseled Cap Transformation (TCT) to represent forest structure (Cohen et al. 1995). We also used a GRASS module (Neteler et al. 2012), modified to derive vegetation-related spectral indices, combining specific bands of the Landsat 8 satellite images (Appendix 2). Such indices enhance the signal related to vegetation, while minimizing background edaphic, solar and atmospheric effects (Jackson & Huete 1991).

Table 3.1. Vegetation indices extracted from a Landsat 8 image for comparison to ground sampled measures of mean basal area (MBA).

Index	Algorithm	Description	References
Simple Ratio (SR)	$SR = \rho_{nir}/\rho_{red}$	Index related to changes in the amount of green vegetation; reduces the	(Jordan 1969)

		effect of atmosphere and topography.	
Corrected Simple Ratio (SRC)	$SRC = SR (1 - ((\rho_{mir} - \rho_{mir\ min}) / (\rho_{mir\ max} - \rho_{mir\ min})))$	Linearizes the relationships with parameters, accounting for MIR band.	(Brown et al. 2000)
Normalized Difference Vegetation Index (NDVI)	$NDVI = (\rho_{nir} - \rho_{red}) / (\rho_{nir} + \rho_{red})$	Estimates the amount of vegetation, it assumes values that are normalized for the amount of incident radiation.	(Rouse et al. 1974)
Corrected Normalized Difference Vegetation Index (NDVIC)	$NDVIC = NDVI (1 - ((\rho_{mir} - \rho_{mir\ min}) / (\rho_{mir\ max} - \rho_{mir\ min})))$	Linearizes the relationships with parameters, accounting for MIR band	(Nemani et al. 1993)
Modified Simple Ratio (MSR)	$MSR = (\rho_{nir} / \rho_{red} - 1) / ((\rho_{nir} / \rho_{red})^{1/2} + 1)$	Linearizes the relationship between the index and biophysical parameters	(Chen 1996)
Reflectance Ratio (RR)	$RR = \rho_{mir} / \rho_{red}$	Substitutes NIR band in SR with MIR band, which is more sensitive in distinguishing complex and stratified forest structures	(Tonolli et al. 2011)

Normalized Difference Water Index (NDWI)	$NDWI = (\rho_{nir} - \rho_{mir}) / (\rho_{nir} + \rho_{mir})$	Sensitive to vegetation water	(Hardinsky et al. 1983)
Specific Leaf Area Vegetation Index (SLAVI)	$SLAVI = \rho_{nir} / (\rho_{red} + \rho_{mir})$	Estimates Specific Leaf Area	(Lymburner et al. 2000)
Red Green Ratio (RGR)	$RGR = \rho_{red} / \rho_{green}$	Sensitive to different foliar pigments	(Gamon & Surfus 1999)
Red Green Index (RGI)	$RGI = (\rho_{green} - \rho_{red}) / (\rho_{green} + \rho_{red})$	Normalization of RGR results	(Coops et al. 2006)
Green Normalized Difference Vegetation Index (GNDVI)	$GNDVI = (\rho_{nir} - \rho_{green}) / (\rho_{nir} + \rho_{green})$	Estimates the amount of green vegetation, exploiting the green channel, sensitive to chlorophyll	(Gitelson et al. 1996)
Normalized Canopy Index (NCI)	$NCI = (\rho_{mir} - \rho_{green}) / (\rho_{mir} + \rho_{green})$	Linearizes the relationships with parameters, accounting for MIR and green bands	(Vescovo & Gianelle 2008)
Tasseled Cap Angle (TCA)	$TCA = \arctan(TCG/TCB)$	Index based on the angle formed by brightness (TCB) and greenness (TCG) in the vegetation plane, calculated from TCT (Tasseled Cap Transformation)	(Powell et al. 2010)

Model building

To relate field sampled values of basal area to the metrics calculated from the Landsat images, we used all newly-sampled plots, plus a subsample of the TEAM and Barelli et al. (2015) plots. The subsample plots were those showing at least 75% overlap with Landsat pixels (N=115). In each plot we calculated the basal area (BA, m²) for each sampled tree (DBH ≥10 cm) as $BA = \pi * (DBH/2)^2$. We then derived the mean basal area (MBA) for each plot, for use as the response variable (following Barelli et al. (2015) and Cavada et al. (2016)).

We used generalized linear modelling (GLM) to investigate the relationship between the MBA- field sampled values and the Landsat metrics and indices. Prior to building the models, we checked for the presence of collinearity among predictor variables to remove those providing identical information. We thus calculated Variance Inflation Factor (VIF), using a cut off value of 10 (Marquardt 1970, Hair et al. 2006, Kennedy 2008) and we retained the uncorrelated predictors P1, P2, RGI, RR, SLAVI. From an Empirical Cumulative Distribution Function (ECDF) of the response variable, we decided to use an inverse Gaussian error distribution for the GLM with an inverse squared link function (Figure 3.2).

We built models using all the possible combinations of the retained Landsat predictors and we used the Akaike Information Criterion (AIC) to rank the candidate models. We considered those models showing $\Delta AIC < 2$ as equivalent (Anderson and Burnham 2002) and defined an average model by determining Akaike weights (w_i) for each of the best models, using the packages 'AICcmodavg' (Mazerolle 2015) and 'MUMin' (Barton 2014) in R version 3.2.1 (R Core Team 2015). For validating the model we randomly split the MBA dataset into two subsets, one for model fitting with 75% of the data (N=109) and one with the remaining 25% of the data (N=37). We then used bootstrapping to verify the goodness of fit of the selected average model: we simulated 1,000 datasets from the subset derived for model fitting (i.e the one considering 75% of the data) and then defined a function that returned the fit-statistic Pearson χ^2 . We validated the model by checking the distribution of

the residuals for the validation subset. We evaluated model bias by comparing both observed and predicted values, to a null model of mean residual prediction equal to zero, using Wilcoxon's signed rank test (for $\alpha=0.05$).

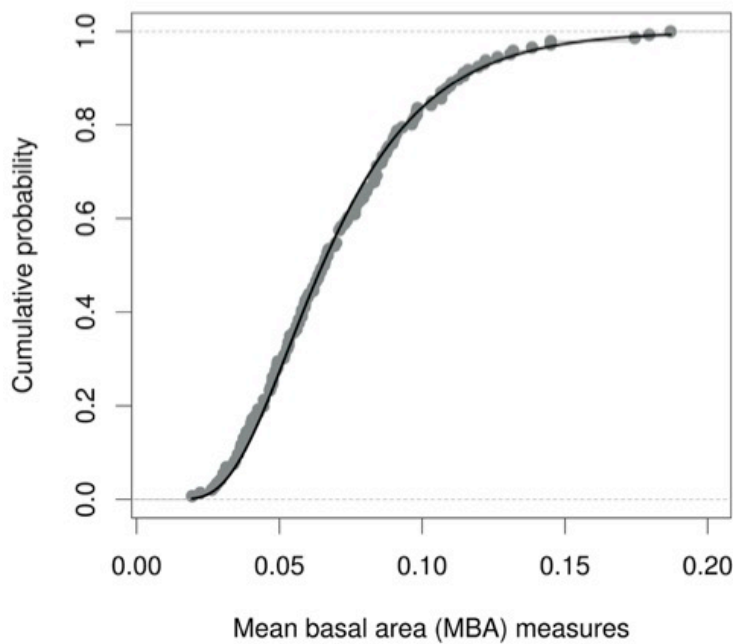


Figure 3.2. Empirical cumulative distribution function of ground sampled measures of mean basal area (MBA, grey dots) collected at tree plots in Mwanihana forest, Udzungwa Mountains, Tanzania. The black line shows the fit of the theoretical inverse Gaussian distribution.

Predictions: MBA values and RC density

To predict density values for groups of red colobus across the entire Mwanihana forest, we first derived spatially diffused values for MBA from our best fitting averaged model, giving an MBA value for each Landsat pixel in the entire study area. We removed those values of MBA that appeared as outliers in the derived dataset (i.e. $>0.5 \text{ m}^2$). We believed these outliers were found for those pixels where our model was not able to derive realistic MBA values, inside those areas close to forest borders as well as in areas located at high elevation (above 1,800 m), where trees are sparse and are replaced by other vegetation (Lovett et al. 2006).

Besides MBA, previous modelling of red colobus group density was most effective using elevation (negative sign) and distance from disturbance/forest edge (negative sign) (Cavada et al. 2016). We therefore calculated spatially diffused values for these variables from a Digital Elevation Model (DEM) and from a shapefile of the forest edge, respectively. We then used a published hierarchical model (Cavada et al. 2016) to predict primate density across the Mwanihana forest using these two variables and spatially diffused values for MBA derived from our model.

Finally, we verified the accuracy of our approach by comparing the predicted primate density to density estimates in Cavada et al. (2016) for those plots in Barelli et al. (2015) (N=65) that were excluded while building the MBA model (see 'Model building' above). These density estimates were plot-specific values derived from the hierarchical analysis described above, and hence were effectively the only field based and site-specific density estimates that could be used for such validation. We compared observed and predicted values using OP regression (Piñeiro et al. 2008) and we compared the slope and the intercept of the fitted model with the 1:1 line.

Results

After selecting the plots suitable for the analysis, we retained 61 plots from Barelli et al. (2015) and 54 TEAM sub-plots. Adding these to the 33 newly sampled plots, we obtained an overall dataset of 148 plots and their corresponding sampled MBA values. We built models using all the possible combinations of the metrics and indices calculated from the Landsat images, including a null model. We retained six competing models of MBA (Table 3.2) that were averaged for predictions. The resulting average model retained the first and the second components of the PCA and the indices RGI, RR and SLAVI (Table 3.3). This model showed adequate fit based on the bootstrap P value based on the Chi-square statistic ($P=0.66$) and no significant difference between observed and predicted MBA values ($W=602$, $P=0.92$). The MBA model failed to derive plausible values in those areas located at high altitudes as well as close to the forest edge (Figure 3.3). We

obtained a spatially-explicit map of estimated density of red colobus groups across the whole study area, as influenced by the covariates MBA (predicted from our model and with a positive effect), elevation and distance from disturbance (i.e from the forest edge), both with a negative effect, according to the hierarchical model defined in Cavada et al. (2016) (Figure 3.4).

The OP regression yielded a R^2 of 0.84 attesting the accuracy of the predicted red colobus group density values as derived by using the spatially diffused values for MBA obtained from the GLM analysis (Figure 3.5).

Table 3.2. Akaike Information Criterion (AIC) value for high ranked models ($\Delta AIC < 2$) of mean basal area (MBA) modelled as a function of predictors derived from a Landsat 8 image.

Model	AIC	ΔAIC
MBA~P1+RGI	-620.70	0
MBA~P1+RGI+RR	-619.89	0.81
MBA~P1+SLAVI	-619.46	1.24
MBA~P1	-619.097	1.607
MBA~P1+P2+RGI	-619.096	1.609
MBA~P1+RR+SLAVI	-618.98	1.72

P1=First component of the Principal Component Analysis; P2= Second component of the Principal Component Analysis; RGI=Red Green Index; RR=Red Ratio; SLAVI=Specific Leaf Area Vegetation Index.

Table 3.3. Estimates and standard errors for the parameters retained in the averaged model for mean basal area (MBA) modelled as a function of metrics and indices extracted from a Landsat 8 image.

Model-averaged coefficients	Estimate	SE	p
P1	-37.92	19.61	0.05
RGI	31.71	15.43	0.04
RR	19.40	16.45	0.2

SLAVI	27.09	16.18	0.09
P2	18.15	24.64	0.4

P1=First component of the Principal Component Analysis; P2= Second component of the Principal Component Analysis; RGI=Red Green Index; RR=Red Ratio; SLAVI=Specific Leaf Area Vegetation Index.

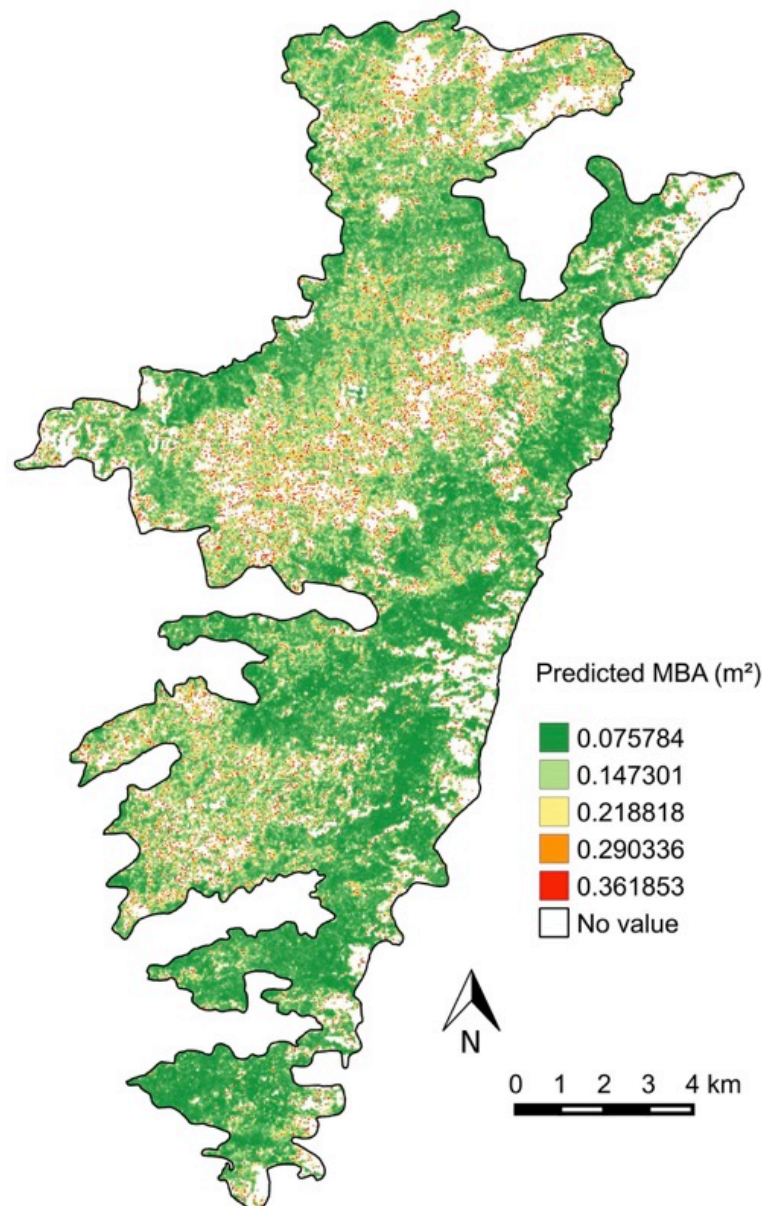


Figure 3.3. Predicted values of mean basal area (MBA) across Mwanihana forest using the average model of ground sampled values versus Landsat 8 metrics. White areas show pixels where the model failed to predict plausible values of MBA (i.e. $<0.5\text{m}^2$).

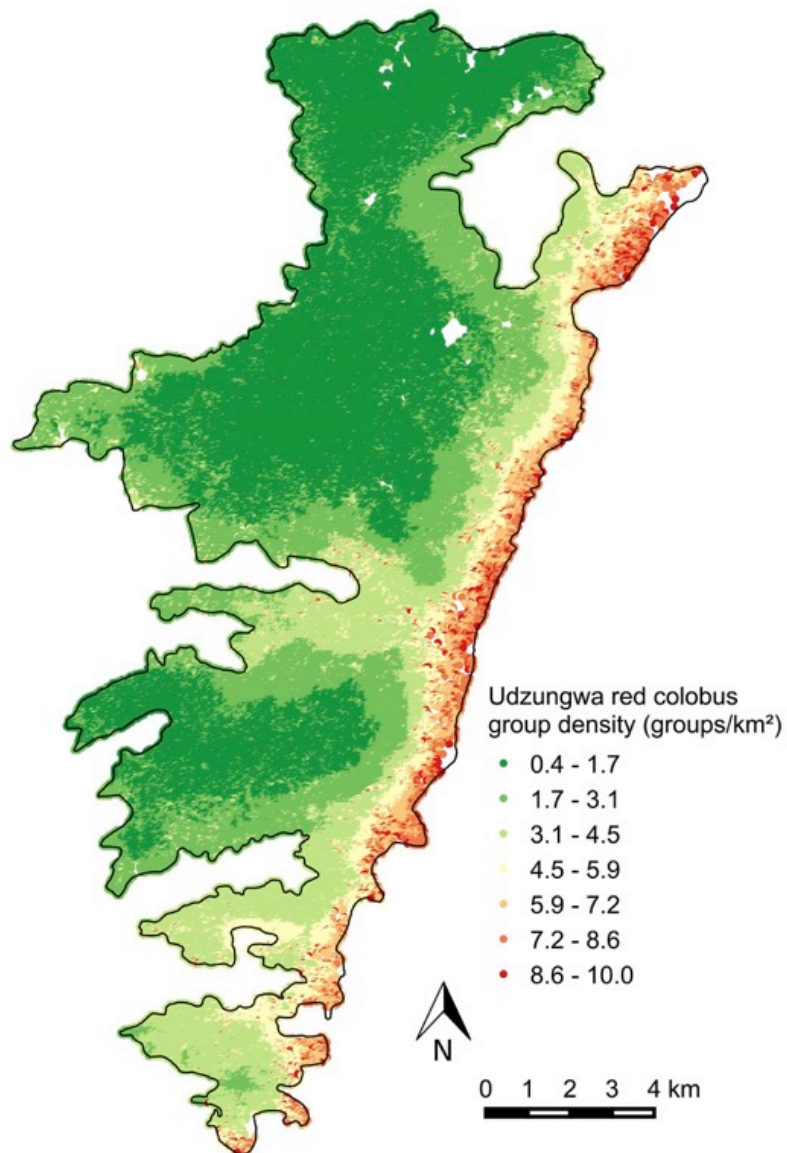


Figure 3.4. Predicted Udzungwa red colobus group density in Mwanihana forest using a species density model (Cavada et al. 2016) derived from remotely sensed mean basal area.

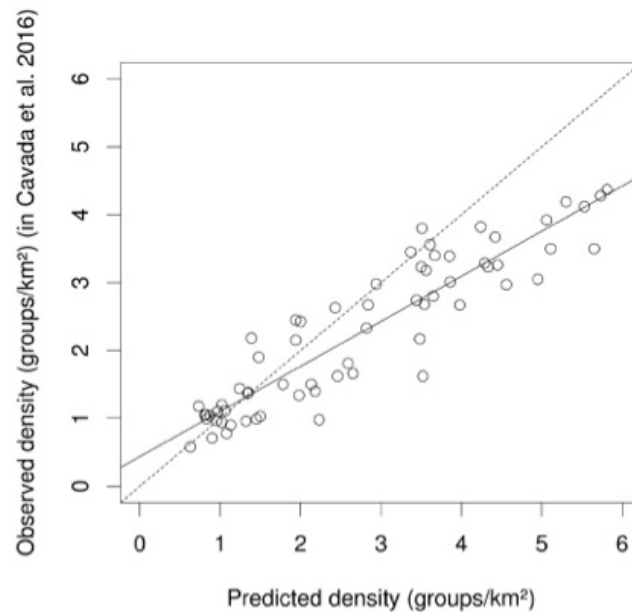


Figure 3.5. Linear regression (dotted line) of observed versus predicted values of Udzungwa red colobus density (groups/km²) among test vegetation plots (N=66). A 1:1 relationship is indicated by the solid line.

Discussion

We have successfully predicted and mapped the spatial density of an endangered primate, hence showing how modelling ecologically-relevant predictors of abundance can improve predictions on species distribution (Franklin 1995), across a broad spatial extent. The species' density pattern highlighted in our map is consistent with results in previous studies that were based solely on ground data and hence with limited spatial inference (Rovero & Struhsaker 2007, Barelli et al. 2015, Cavada et al. 2016).

Our best supported models showed high accuracy in predicting MBA values, making it a reliable tool for inference beyond the ground measurement sites, with a good level of confidence and precision. MBA is a highly relevant descriptor of the canopy structure as well as a significant covariate that has emerged in different studies as influential for predominantly arboreal primates (Rovero & Struhsaker 2007, Cavada et al. 2016). As a parameter quantifying forest cover, MBA is also a recognized proxy for habitat degradation and fragmentation (Urquiza-Haas et al. 2007). The best fit model we derived from GLM retained the

first two components of the PCA. This fitted the acknowledged evidence that Landsat products are able to discriminate forested habitats, through the information provided by specific spectral channels (Blair & Baumgardner 1977, Jakubauskas 1996, Eklundh et al. 2001, Cohen & Goward 2004), in terms of the differential reflectance emitted by the higher strata of the canopy. The information provided by the Landsat sensors can highlight specific vegetation components (Thenkabail et al. 2000, Almeida & De Souza Filo 2004); in fact, the bands of the visible spectrum and of the Short-wave Infrared (SWIR) can be correlated with several forest structures, including basal area (Muukkonen & Heiskanen 2005, 2007, Hall et al. 2006). The relationship with MBA shown by the first PCA component of our model might be due to a large presence of trees with great basal area and tall canopy, causing pronounced shadowing which translates in a lower reflectance.

Among the vegetation indices retained by the models, RGI can be interpreted as a proxy of the forest phenology by the time when the Landsat image was acquired. Since such an index provides information on the ratio of red to green reflectance, the positive effect we found on MBA could be due to the contribution the index generally gives in evaluating the size of the tree crowns, which is related to the basal area extent. During that period, a high amount of trees shows indeed a breakdown of green pigments and leaves fade from green to yellow and red (Motohka et al. 2010). The positive effect we found for RR was also confirmed by other studies that found a correlation between the visible and the SWIR band of the Landsat with several physical structures of the forest canopy, including basal area (Muukkonen & Heiskanen 2005, Hall et al. 2006, Tonolli et al. 2011). In addition, the positive relationship we found between MBA and SLAVI index is not surprising given that the index accounts for the sensitivity of the mid-infrared wavelength to the structure of the canopy, especially for heterogeneous forest compositions (Lymburner et al. 2000).

As the main goal of our study, we used the predicted and spatially diffused values of MBA to derive a map of the Udzungwa red colobus density. This matched, at a wider and spatially diffuse scale, the density estimates found in prior studies (Barelli et al. 2015; Cavada et al. 2016). In particular, it confirmed the red

colobus's preference for lower-elevation forest close to its edge, variably disturbed and covered with regenerating vegetation that is recognized as an important food source for the species (Barelli et al. 2015). Densities decreased where MBA values increased, i.e. in the interior and old growth forest parts and at higher elevation. This in turn indicates resilience of the animal to anthropogenic disturbance and again the preference shown by the species for forest edges. Such a counter intuitive density trend is clearly visualized in the spatially explicit map we obtained. This provides novel indications for the protection of forest areas that are located at the interface with intense anthropogenic activity.

We have confirmed that the use of remote sensing represents a robust tool to improve model performance and to reduce the costs of data collection (He et al. 2015), which implies bypassing the sample size limits associated with field measurements. We stress the importance of carefully evaluating the process regarding the selection of adequate satellite images, given the sensitivity for seasonality shown by some vegetation indices. High resolution images should certainly be preferred when deriving remote-sensing based predictor variables that can be essential to improve predictive species modelling. Nonetheless, the quality of such images can often be poor, due to cloud coverage that hides the underlying canopy, i.e. the carried amount of information is lower than the spectral noise (Woodcock & Strahler 1987, Ricotta et al. 1999). This phenomenon consistently arises in images of tropical mountain forests, since clouds accumulate relatively more in dense forest cover areas due to evapotranspiration (Nagendra & Rocchini 2008). Still, we demonstrated that since high resolution products in some cases cannot be used, medium resolution images like Landsat proved to be an excellent source of data for applications both in the study of tropical forest structure and to develop reliable species distribution models. However, caution is recommended regarding the generalization of our approach, which is mainly relevant to comparable study systems in terms of both habitat and target species characteristics.

Conclusions

Spatially explicit, predictive models of animal abundance can offer a powerful insight on the species status and distribution, helping to identify those sites where urgent intervention is needed in terms of protection and conservation. Overcoming the lack of high resolution and high quality remote sensing products as well as of spatially diffused covariates of abundance is essential, as it can firmly boost the usefulness of species distribution models. By focusing on the endangered Udzungwa red colobus, we showed the potential of this approach to derive accurate spatially diffused estimates of animal density and distribution. This approach is particularly suitable for species for which data availability is incomplete and spatial coverage is heterogeneous, affecting the capacity of developing site-specific conservation and restoration programs where urgent forest and species protection is needed.

CHAPTER 4

Optimizing field and analytical procedures for estimating densities of arboreal and threatened primates in tropical rainforest

Based on the paper: **Cavada N**, Ciolli M, Barelli C, Rovero F (in press) Optimizing field and analytical procedures for estimating densities of arboreal and threatened primates in tropical rainforest. *American Journal of Primatology*

Summary

The application of distance sampling to primate density estimation is challenging and susceptible to estimation biases, mainly due to the difficulties of properly accounting for variation in species' detectability and of accurately sampling the spread of the social groups. We apply a hierarchical distance sampling approach to primate data, to account for a comprehensive set of environmental covariates of both detectability and abundance, and we propose a novel field routine to measure the spread of groups during transect sampling. We confirm the good potential of this approach, given we obtained refined estimates of primate density (as measured by the Akaike Information Criterion) in comparison to estimates from models without covariates.

Introduction

Accurate estimation of abundance and distribution of threatened animal populations is required to inform conservation. In the case of primates, which are among the most threatened mammals (Schipper et al., 2008), distance sampling from line transects is the method of choice, especially for arboreal species (Buckland et al. 2001). The key advantage of this method is that it accounts for imperfect detection of animals; however, it does not adequately consider the effect of habitat factors on both the detection and the abundance of target species, especially when they live in heterogeneous forests (Cavada et al. 2016).

Hierarchical analytical frameworks that include habitat covariates in distance sampling have been developed by Royle

et al. (2004) and applied to birds. The first application to arboreal primates (Cavada et al. 2016) has already shown its improvement for density estimates in comparison to the canonical approach. This judgment was based on a comparison of the Akaike Information Criterion (AIC) scores of competing models, i.e. the quality of the models in terms of goodness of fit and its complexity. However, although it included several habitat covariates, it did not consider 'tree height' as a feature of forest structure of potential critical influence for both abundance and detectability. Most critically, moreover, a number of earlier studies (e.g. Plumptre & Cox 2006; Buckland et al. 2010b) have stressed the need to consider the spread of primates' social group, as this affects distance measurement and hence density estimates. However, this has been usually addressed by using a post-hoc correction of group spread derived from parallel studies (Araldi et al. 2014) instead of a direct estimation of groups spread during counts. Here, we use a novel dataset from a primate hotspot in Tanzania to propose an application of hierarchical distance sampling to arboreal primates that comprehensively considers habitat covariates, including the measurement of group spread during census.

Materials and Methods

Study area and primate data collection

Between September and November 2015 we counted primates along 26 line transects of 2 km in length, throughout the forest of Ndundulu (231 km², Marshall et al., 2010) in the Udzungwa Mountains of Tanzania (Figure 4.1). The area is of exceptional biological diversity and endemism (Rovero et al. 2014b) and is characterized by the presence of distinct forest blocks in a mosaic of drier habitats (Cavada et al. 2016). Following Buckland et al. (2001) we designed the sampling to achieve a complete coverage of the study area (Figure 4.2) and an adequate number of repetitions (N=35). We walked the transects placed in the northern part of the forest, which were spaced by 1 km, two times each, and we walked the transects placed in the southern part, which were spaced by 500 m, one time each. This design stratified the transects according to elevation gradients and size of the two

main areas of the forest: the northern, higher elevation forest habitat, and the southern, lower elevation habitat. Along these transects we counted each group encountered of three monkey species inhabiting the area: Udzungwa red colobus (*Procolobus gordonorum*, hereafter RC), Peters' Angola colobus (*Colobus angolensis palliatus*, hereafter BW), and Tanzania Sykes' monkey (*Cercopithecus mitis monoides*, hereafter SY), and, simultaneously, we estimated the group spread. To achieve this, we measured the distance from the observer to the first individual seen (animal-observer distance, or AOD; Animal 1 in Figure 4.3), as for standard distance sampling. We then calculated the perpendicular distance of the animal to the transect (PD1) using trigonometry. We also recorded the position of the two individuals located at the two extremes of an imaginary line crossing the group (Animals 2 and 3 in Figure 4.3) and we calculated each of their PD to transect (PD2 and PD3 in Figure 4.3). We then derived the length of the distance (D) between the two, representing one axis of group spread, as the leg of a rectangular trapezoid (Figure 4.3). We finally corrected PD1 using the standard formula proposed by Whitesides et al. (1988), i.e. multiplying it by $1+(r/AOD)$, with r being half of the group spread. This procedure assumes that AOD is the one from the observer to the first individual sighted, that is also the one closest to the transect (Buckland et al. 2010). We applied this approach to RC only, as they have the larger social groups (Cavada et al. 2016), making particularly challenging the measurement of group spread.

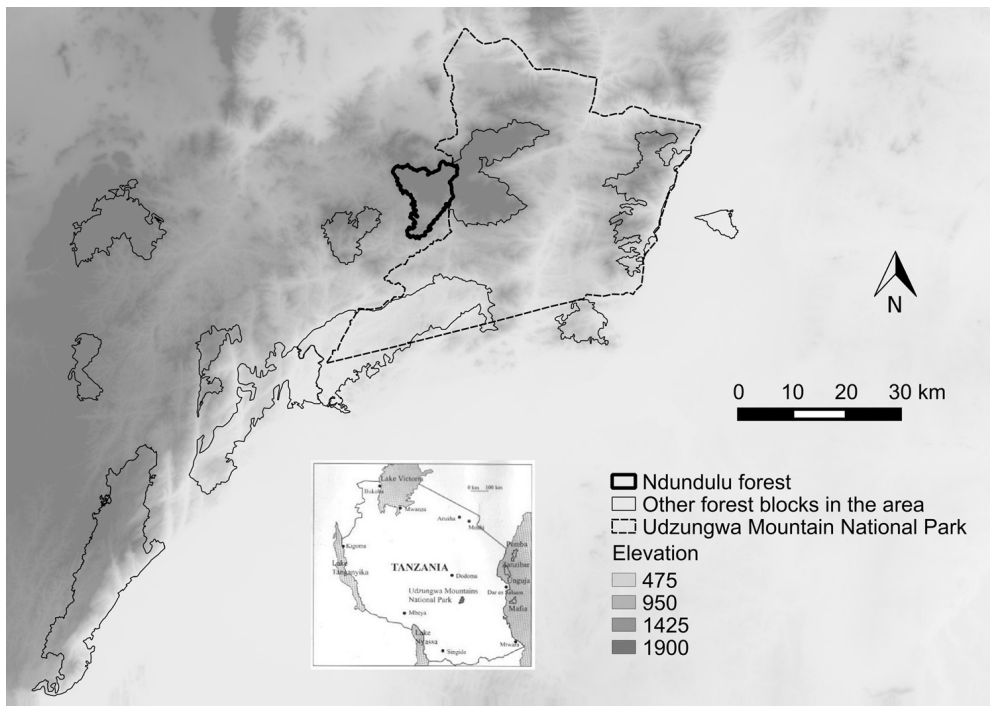


Figure 4.1. Map of the Udzungwa Mountains National Park, Tanzania, showing the surveyed forest of Ndundulu and other surrounding forest blocks.

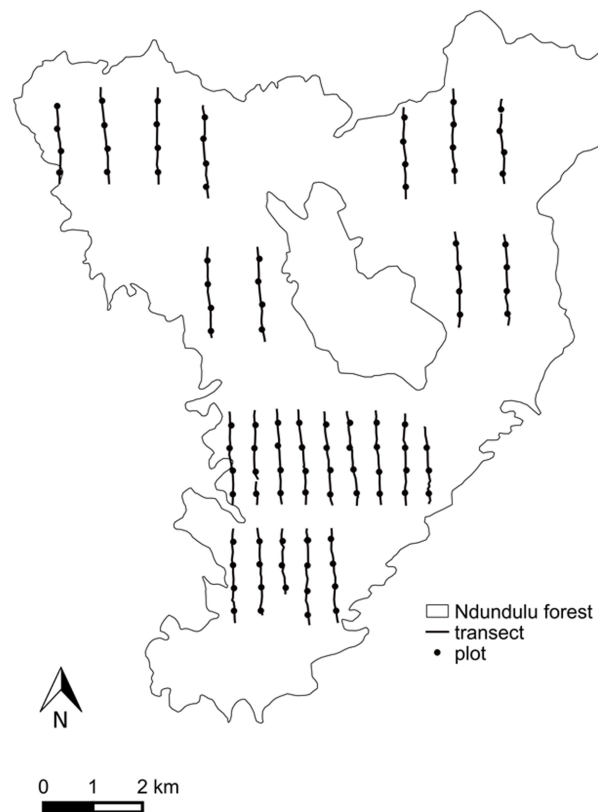


Figure 4.2. Map of Ndundulu forest, Tanzania, showing the location of 26 transects walked for primate surveys, yielding 35 sampling repetitions, as well as the 104 vegetation plots sampled in the survey period (September – November 2015)

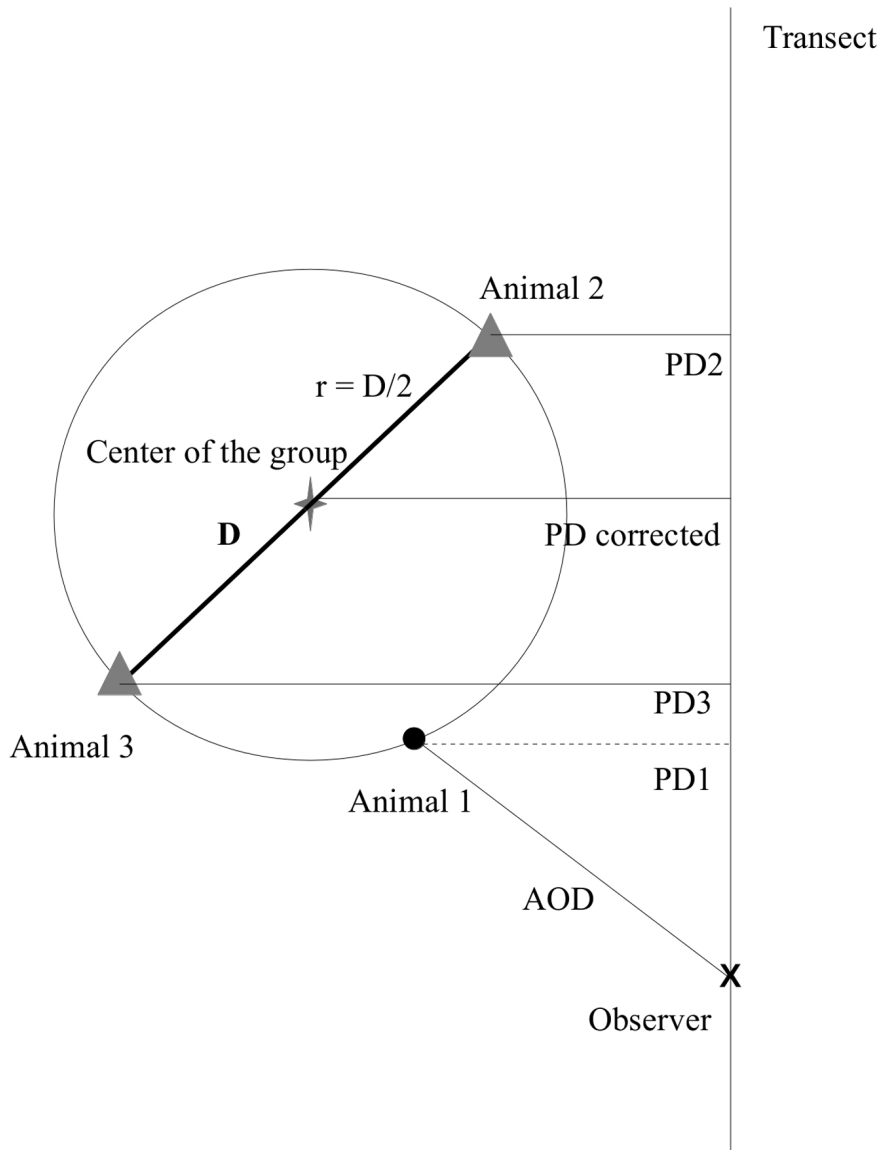


Figure 4.3. Scheme of sampling procedure for measuring group spread. Animals 2 and 3 represent the two individuals of the group placed at the two extremes of an imaginary line crossing the centre of the group, as seen during sampling. Their projected perpendicular distances (PD2 and PD3) to the transect, form the bases of a rectangular trapezoid. D is the leg of the geometric figure, as well as the group spread value. The correction for group spread is then applied to PD1, the perpendicular distance from Animal 1 (i.e. the first individual sighted) to the transect.

Vegetation data collection

We collected vegetation covariates at plots of 25 × 25 m, placed every 500 m along each transect (N=104). We also measured for each plot the dominant tree height, which we defined as the average height of the seven trees with the largest diameter at breast height (DBH; Günter et al. 2011; Table 4.1), a feature not recorded in previous studies (Barelli et al. 2015; Cavada et al., 2016). As the modelling procedure requires transect level covariates (and not observation level covariates), plot level data were then converted in transect level data by taking, for each covariate, the average value from the set of four plots established along each transect.

Table 4.1. List of covariates sampled in Ndundulu forest, Tanzania, used to estimate density of primates detected from line transects.

Covariate	Sampling description
Group size ^a	Number of individuals in social groups counted at each observation.
Canopy cover ^{a,b}	Visually estimated extent of canopy cover above each plot, defined using five classes, from completely open to completely closed (0%, 25%, 50%, 75%, 100%).
Distance from disturbance ^{a,b}	Distance measured from the forest border.
Percentage of climbers ^{a,b}	Proportion of climbers covering tree crowns, defined using five classes, from no climbers to completely covered crown (0%, 25%, 50%, 75%, 100%).
Steepness ^{a,b}	Slope of the plot.
Total basal area ^b	Sum of single trees basal area (BA, m ²). BA was calculated from tree measured DBH ≥ 10 cm as $BA = \pi * (DBH/2)^2$.
Mean basal area ^b	Average BA for each plot.
Height ^{a,b}	Average height of the seven larger trees, in terms of DBH, within each plot. Single trees height was measured using a Suunto hypsometer.

Elevation ^b	Measured with a Garmin 64s GPS in the centre of each plot.
Simpson diversity index (D) ^b	$D = 1 / \sum_{i=1}^S p_i^2$, with i being the number of a certain species and p_i the total number of species inside each plot.

^a fitted on detection

^b fitted on abundance

Analysis

For each species, we modelled group encounters ($N = 100$ total), along each transect ($N=26$), in a hierarchical framework, i.e. following Royle et al. (2004) that applied a coupled logistic regression whereby the regression modelling the observation (detection) process is conditional on the regression modelling the state (abundance) process. Thus, we first grouped continuous values of distance that were measured in the field, in distance classes (h) of width 20 m. We then assigned each primate observation (y_{sh}) along each transect (t) to its specific distance class (h). Using the function *distsamp* (Chandler 2014) in the package *unmarked* (Fiske & Chandler 2011) in R (R Core Team 2015) we modelled local abundance (X_t) at each transect, assuming for it a Poisson distribution: $(X_t \sim \text{Poisson}(\lambda_t); t = 1, \dots, n)$ with λ representing the expected value of $X(\lambda = E(x))$. We also modelled detection frequencies (i.e. the observed count of individuals in each distance class h), assuming for these a multinomial distribution, conditional on the population size X_t : $(y_{t1}, \dots, y_{tH}) \sim \text{Multinomial}(X_t, \pi_t)$, where $\pi_{t h}$ is the multinomial probability for distance class h and transect t , that depend on the parameter σ of the detection function, for which we assumed a half-normal distribution, as $g(y) = \exp(-y^2/2\sigma^2)$. We then evaluated the effect of all combinations of transect-level habitat covariates, as influencing both the detection-function parameter σ as well as the expected abundance λ_t . We ranked the candidate models according to the AIC, retaining models with $\Delta\text{AIC} < 2$ (Anderson & Burnham 2002). We assessed best model fit through parametric bootstrapping. Thus, we used the

function *parboot* in 'unmarked' that generated 10,000 datasets from our best performing model and refitted the model to these simulated data; this defined a function that returned a distribution of Pearson's X^2 . The procedure then computed the P value by comparing fitted versus simulated values. Non-significant P indicates adequate model fit, i.e. no difference between fitted versus simulated data. We then averaged candidate models ($\Delta AIC < 2$) using the package MUMin (Barton 2015) in R. This procedure determines the Akaike weights and averages the estimates of the parameters of interest among the set of candidate models. These were in turn used to derive species-specific primate density estimations (groups/km²). We note that density is the primary outcome of this modelling approach, while abundance in terms of total number of groups can be later derived when the total extent of the study area is known (Araldi et al. 2014). We also derived density predictions at plot level. This was done by feeding the species-specific averaged model with covariate values as sampled at each vegetation plot, hence allowing the model to predict plot specific values of density. For RC, using Wilcoxon signed-rank, we compared our group spread measurements with those in Araldi et al. (2014), who measured them in a single and different forest block in Udzungwa through a separate study and then applied the average value for each species across all targeted forests.

Results

We walked 68.5 of the planned 70 km of transects. We right-truncated the distance data at 100 m for BW and SY and at 90 m for RC, because the few detections at larger distances provided little information for the estimation of species-specific detection functions and could possibly complicate model fitting (Buckland et al. 2001). We thus retained 26, 32 and 42 observations for BW, SY and RC groups respectively.

The best performing models revealed that 'group size' had a positive effect on the detectability of all species (Figure 4.4), while 'tree height' had a significant, positive effect on the density of BW and RC (Table 4.2, Table 4.3). The bootstrap P

value based on the Chi-square statistic was non-significant, hence indicating good fit for all the species-specific best models ($P=0.6$ for BW; $P=0.37$ for SY; $P=0.49$ for RC). Encounter rate, detection probability and group density estimates for each species are reported in Table 4.4, while the spatial distributions of density estimates are mapped in Figure 4.5. Our group-specific measurements of group spread of RC were significantly different from those in Araldi et al. (2014; Wilcoxon signed rank test: $W=2012$, $P=0.04$).

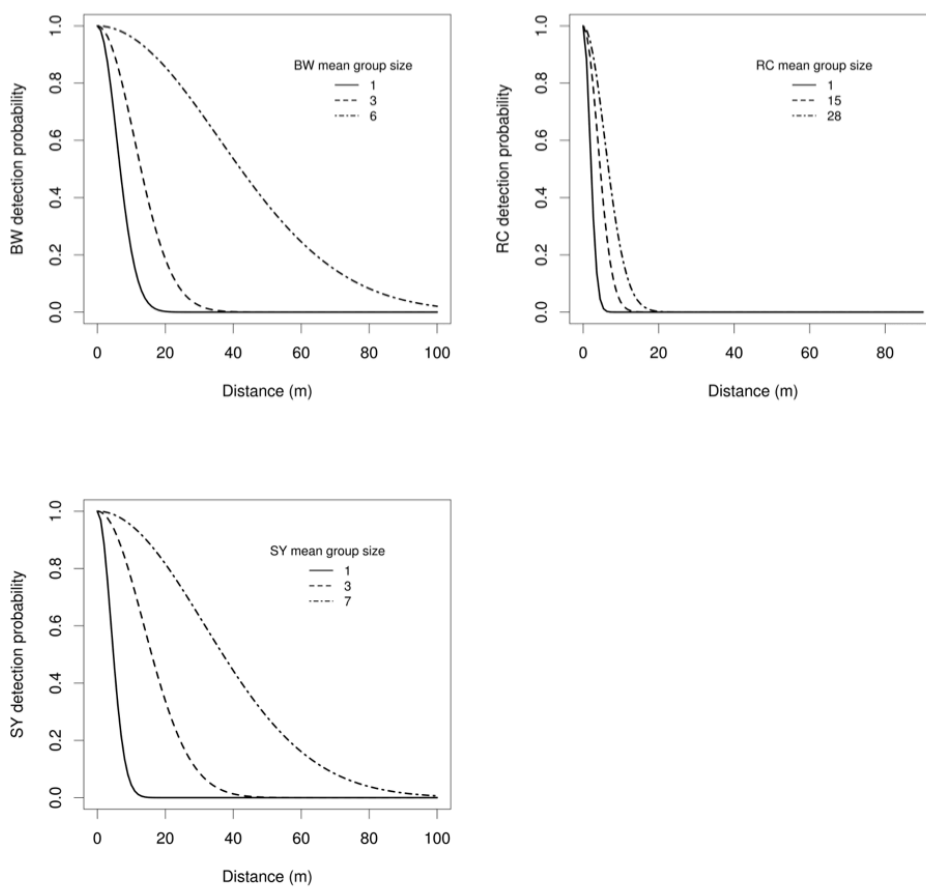


Figure 4.4. Detection function from the best AIC models, shown for the 0.25, 0.50 and 0.75 quartiles of the covariate 'group size', for three primate species in Ndundulu forest, Tanzania.

Table 4.2. Summary of model selection for the hierarchical distance sampling analysis performed on primates in Udzungwas, Tanzania. The Akaike information criterion (AIC) value is shown for high ranked models ($\Delta\text{AIC} < 2$) of primates' density (λ) and the shape parameter (σ) of a half-normal detection function. The null model ($\sigma(\cdot) \lambda(\cdot)$) is shown for comparison.

Model	AIC	ΔAIC
Peters' Angola colobus		
$\sigma(\text{Group size}) \lambda(\text{Height} + \text{Simpson diversity index})$	104.30	
$\sigma(\text{Group size} + \text{Canopy cover}) \lambda(\text{Tree height} + \text{Simpson diversity index})$	105.54	1.24
$\sigma(\text{Group size}) \lambda(\text{Tree height} + \text{Mean basal area})$	105.76	1.46
$\sigma(\text{Group size} + \text{Canopy cover} + \text{Distance from disturbance}) \lambda(\text{Tree height} + \text{Simpson diversity index})$	105.93	1.62
$\sigma(\cdot) \lambda(\cdot)$	120.31	16.01
Udzungwa red colobus		
$\sigma(\text{Group size} + \text{Percentage of climbers}) \lambda(\text{Tree height} + \text{Elevation})$	127.84	
$\sigma(\text{Group size}) \lambda(\text{Tree height} + \text{Elevation})$	128.39	0.56
$\sigma(\text{Group size} + \text{Percentage of climbers}) \lambda(\text{Tree height} + \text{Elevation} + \text{Steepness})$	129.27	1.43
$\sigma(\text{Group size} + \text{Percentage of climbers} + \text{Tree height}) \lambda(\text{Tree height} + \text{Elevation})$	129.31	1.48
$\sigma(\text{Group size} + \text{Percentage of climbers}) \lambda(\text{Tree height} + \text{Distance from disturbance} + \text{Elevation})$	129.54	1.70
$\sigma(\text{Group size} + \text{Percentage of climbers}) \lambda(\text{Canopy cover} + \text{Tree height} + \text{Elevation})$	129.58	1.74
$\sigma(\cdot) \lambda(\cdot)$	148.77	20.93
Tanzania Sykes' monkey		
$\sigma(\text{Group size}) \lambda(\text{Steepness})$	86.58	
$\sigma(\text{Group size}) \lambda(\text{Canopy cover} + \text{Percentage of climbers} + \text{Steepness})$	87.34	0.76
$\sigma(\text{Group size} + \text{Canopy cover}) \lambda(\text{Steepness})$	87.51	0.94

$\sigma(\text{Group size} + \text{Percentage of climbers}) \lambda(\text{Steepness})$	87.72	1.14
$\sigma(\text{Group size} + \text{Distance from disturbance}) \lambda(\text{Steepness})$	87.87	1.30
$\sigma(\text{Group size} + \text{Tree height}) \lambda(\text{Steepness})$	87.93	1.36
$\sigma(\text{Group size}) \lambda(\text{Percentage of climbers} + \text{Steepness})$	88.16	1.58
$\sigma(\text{Group size}) \lambda(\text{Percentage of climbers} + \text{elevation} + \text{Steepness})$	88.21	1.63
$\sigma(\text{Group size}) \lambda(\text{Canopy cover} + \text{Percentage of climbers} + \text{Total basal area} + \text{Steepness})$	88.22	1.64
$\sigma(\text{Group size}) \lambda(\text{Percentage of climbers} + \text{Distance from disturbance} + \text{Steepness})$	88.39	1.81
$\sigma(\text{Group size} + \text{Canopy cover} + \text{Steepness}) \lambda(\text{Percentage of climbers} + \text{Mean basal area} + \text{Steepness})$	88.53	1.95
$\sigma(\cdot) \lambda(\cdot)$	105.37	18.79

Table 4.3. Results of model averaging, showing model averaged parameter estimates and their standard error for the three primate target species detected from line transects in Ndundulu forest, Tanzania.

Model and coefficients	Estimate	SE	CI (95%)
Peters' Angola colobus			
<i>Detection (σ)</i>			
Intercept	3.34	0.51	2.32 - 4.37
Group size	3.59	4.40	-5.05 - 12.21
Canopy cover	1.29	1.92	-2.46 - 5.04
Distance from disturbance	-0.83	0.96	-2.72 - 1.05
Tree height	-1.81	2.07	-5.86 - 2.25
Climber percentage	0.16	0.28	-0.39 - 0.71

Density (λ)

Intercept	1.21	0.33	0.56 - 1.85
Tree height	0.52	0.50	-0.46 - 1.51
Simpson diversity index	-0.58	0.29	-1.16 - -0.01
Distance from disturbance	0.08	0.26	-0.43 - 0.59

Udzungwa red colobus*Detection (σ)*

Intercept	3.56	0.24	3.08 - 4.03
Group size	1.30	0.73	-0.14 - 0.59
Climber percentage	0.39	0.29	-0.18 - 0.95
Tree height	-0.38	0.56	-1.47 - 0.72

Density (λ)

Intercept	1.35	0.24	0.88 - 1.82
Tree height	0.63	0.25	0.14 - 1.11
Elevation	0.22	0.19	-0.14 - 0.59
Steepness	-0.15	0.20	-0.54 - 0.24
Distance from disturbance	-0.11	0.21	-0.52 - 0.29
Canopy cover	0.11	0.22	-0.32 - 0.54

Tanzania Sykes' monkey*Detection (σ)*

Intercept	6.52	0.66	5.22 - 7.81
Group size	11.09	0.99	9.16 - 13.02
Canopy cover	1.14	0.25	0.66 - 1.63
Climber percentage	-1.76	0.15	-2.06 - -1.46
Distance from disturbance	-0.86	0.16	-1.16 - -0.55

Tree height	-0.07	0.04	-0.15 - 0.01
Steepness	-1.67	0.08	-1.83 - -1.51
<i>Density (λ)</i>			
Intercept	1.09	0.29	0.51 - 1.66
Steepness	-0.35	0.29	-0.91 - 0.22
Climber percentage	-0.11	0.40	-0.89 - 0.66
Canopy cover	0.45	0.30	-0.13 - 1.04
Elevation	-0.35	0.25	-0.85 - 0.15
Distance from disturbance	-0.10	0.29	-0.67 - 0.48
Total basal area	-0.37	0.41	-1.19 - 0.46
Mean basal area	-0.46	0.23	-0.91 - -0.01

Table 4.4. Encounter rate, detectability (\pm SE) and group density (\pm SE (CI) for three primate species detected from line transects in Ndundulu forest, Tanzania.

Species	Encounter rate (groups/km)	Detectability (SE)	Density (groups/km²) (SE) (CI)
Peters' Angola colobus	0.38	0.14 (0.01)	3.5 (1.05) (1.94 - 6.30)
Udzungwa red colobus	0.61	0.11 (0.01)	3.86 (0.92) (2.42 - 6.15)
Tanzania Sykes' monkey	0.47	0.12 (0.01)	2.97 (0.86) (1.67 - 5.26)

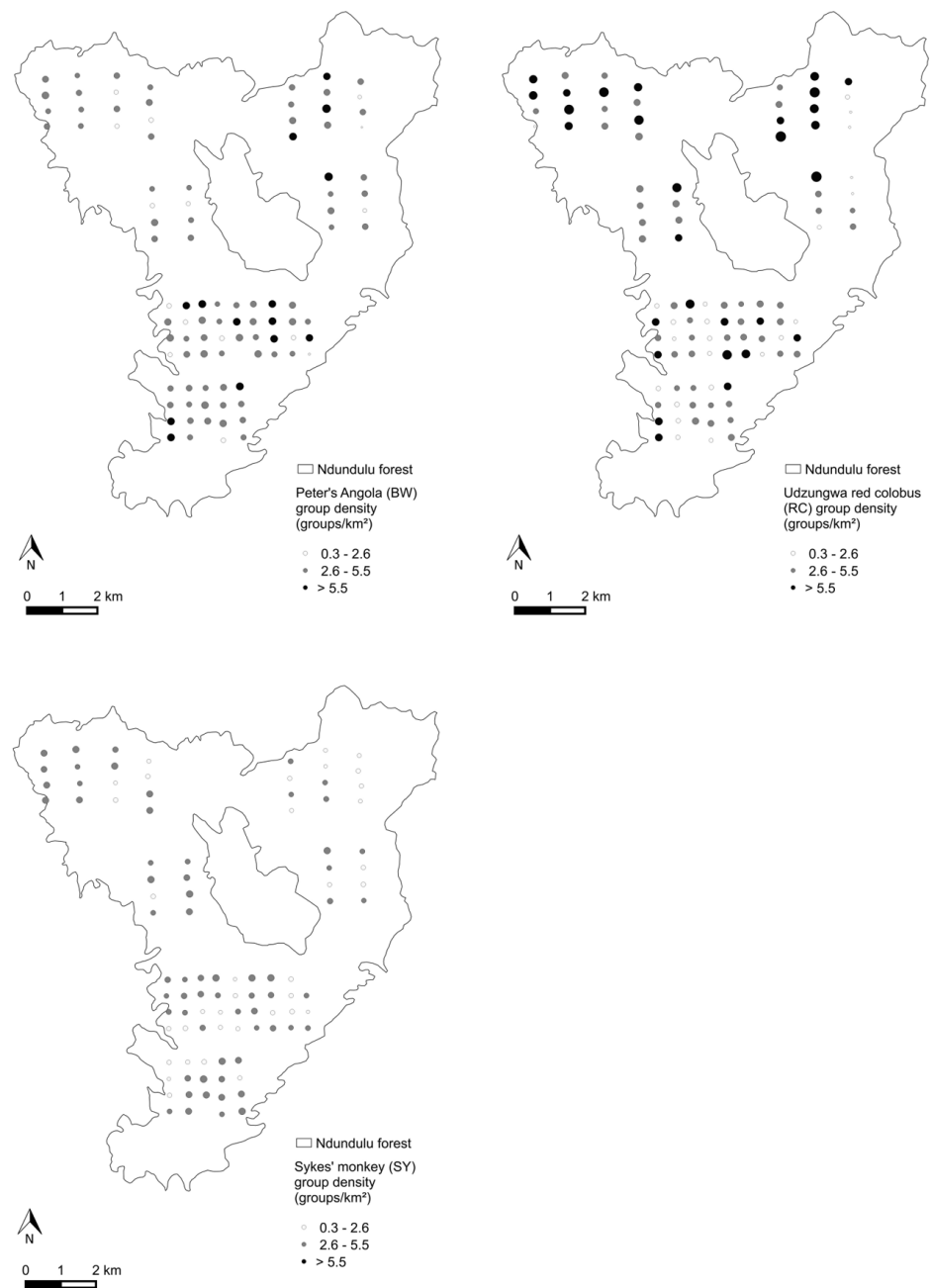


Figure 4.5. Maps of spatially explicit density (groups/km²) of three primate species, predicted from the species-specific averaged model, in Ndundulu forest, Tanzania. Values are shown for each plot sampled along transects, for which covariate measures were available.

Discussion

We provide a novel test of hierarchical modelling that integrates

habitat covariates for primate density estimation, confirming its importance as supported by earlier evidence (Cavada et al. 2016). Indeed inclusion of 'tree height' as a predictor variable in the analysis proved to enhance the accuracy of our final models, as shown by the AIC scores in Table 4.2. It is plausible that arboreal primates prefer taller trees for easier locomotion (Anderson et al. 2007) and predator avoidance. We also suggest a field procedure to measure primate group spread while conducting line transects to obtain observation-specific measurements. This, too, improved the precision of density estimates, as we found that measurements taken at different locations and/or in different seasons introduce biases. Such biases could be the result of averaging measurements obtained from one site (and season) and applied to different ones, making the PD correction highly imprecise. We acknowledge that in areas where animals are poached and flee rapidly our method may be less useful.

In conclusion, we show how accounting for forest and species-specific covariates can lead to improved estimates of primate detectability and density.

Conclusions

The analytical approach we applied, with its hierarchical structure, allowed us to derive species-specific models that performed better than the null models, i.e. those that did not consider the covariate effects. For animals inhabiting fragmented forest patches, which is increasingly the case, population density is, in fact, likely to be influenced by patch-specific factors, and therefore estimations need to account for patch-specific covariates. Future studies may include the sampling and the evaluation of additional covariates, to further increase the precision of the results. These could include for example parameters related to the phenology and distribution of fruiting trees, which would be especially relevant to more frugivorous species. The hierarchical approach we followed also provides an opportunity for deriving spatially explicit density estimates (Figure 4.5), and, when diffused covariate values are available (most typically from remote sensing), it allows to make fine-resolution maps of predicted density (Cavada et al. 2017)

CONCLUSIONS AND PERSPECTIVES

The history of mammal evolution in the Udzungwa Mountains is thought to be exceptionally long (Kingdon & Howell 1993), given the ancient origin of the crystalline mountains. This has important implications in terms of capability of the animals to cope with the rapid, human-driven changes occurring in the region. In this perspective, we developed a research framework that could help to model and assess the impact that such changes has on selected animal species.

A general insight was first gained on forest mammal habitat associations (Chapter 1), with results from camera trapping that, on a fine-scale, are of particular conservation relevance, especially for elusive and range restricted species, for which ecological data were still limited.

An assessment of population density and abundance was obtained for the main arboreal primate species inhabiting the Udzungwa Mountains (Chapter 2), through distance sampling and its hierarchical modelling applications. The estimates on animal occurrence that were derived were useful to delineate the ecological status of the study species. At the same time, the models allowed to establish a spatially explicit relationship between species specific detectability and densities and a suite of environmental and human disturbance variables.

Part of the research outputs were synthesized in a geo-referenced model, describing distribution and density for the endangered and endemic Udzungwa red colobus (Chapter 3). The spatial analysis approach that was applied allowed to fine tune field sampled data on primate occurrence, together with their correlation with habitat parameters. To derive spatially explicit data for influential habitat covariates, a remote sensing data-base was used. In detail it was demonstrated how Landsat images, when properly selected and processed, can be useful to provide missing information on significant environmental parameters. It was this way possible to develop an analytical and modelling framework that is of high utility when high resolution satellite images are not available for the study area. This new analytical method allowed to infer abundance of the species across the study area, meaning

outside the transects and in those regions that were not actively sampled during the field surveys. For the first time it was possible to model at a landscape level those factors that were found to be influential in determining the presence and density of the species. At the same time such approach helped to predict the species distribution range in the study area.

During the research period, a fifth forest was added to the database already available on the four other major forest blocks in the area. This helped to better understand and depict the ecological scenario for the arboreal primate populations in the area of the Udzungwa Mountains. At the same time the new field sampling campaign allowed to develop and test a novel sampling procedure for primate group spread. This was a crucial step, since group spread is recognized as a critical and challenging factor to sample and analyse, when applying the distance sampling approach to species living in social units (Chapter 4).

The overall methodology developed for the project represents, as a whole, a strong tool that can help to rapidly evaluate the state of target mammal species in complex and disturbed landscapes. The results obtained can indeed help to create and provide specific management recommendations for conservation purposes. The outputs of this research are relevant to identify those sites on which to concentrate conservation efforts and to take into evidence the need to improve protection measures in unprotected environments, as well as in those forest sites at the direct interface with anthropic activities. As remarked throughout all the chapters of this thesis, the development of efficient and rapid research methods is a contingent requirement, in order to obtain outputs that are useful to primate conservation (Estrada et al. 2017). Both environmental and anthropogenic pressures that threaten the majority of world's primate species might indeed still be reversed with an immediate implementation of management decisions, supported by effective scientific evidences. The further development of the findings reported in this research will thus be helpful for primate conservation that is in turn essential to maintain intact ecosystems and the multitude of services these provide, which range from stable water supplies and pollination, to the buffering of global warming (Wich et al. 2011, Estrada et al.

2017).

The overall data set collected during the study period include information, in terms of primate sightings and vegetation plots, from five forest blocks in the Udzungwa Mountains. These are altogether a representative sample of the wide variation of forest size, elevation range, habitat type and disturbance in the whole area. For future analysis, to fully evaluate such highly differentiated landscape and thus gaining an exhaustive and spatially-explicit insight on primate populations in the whole area, an integrated multiregion Bayesian approach (Royle & Kéry 2007, Sutherland et al. 2016) will be applied. Such novel approach to data analysis will result in accurate species specific as well as site-specific estimates of density and detectability, thus allowing for more efficient comparisons between the different forest blocks. At the same time, the effect of site-specific covariates will remain a central component of the analysis, as uncertainty in the estimation of significant parameter will be derived too, thus increasing the accuracy in the results. Moreover, the application of such analytical framework will help to improve the general knowledge on how forest specific habitat parameters and human disturbance factors are interplaying in shaping animal occurrence and distribution in a fragmented environment.

REFERENCES

- Acevedo-Whitehouse K, Duffus ALJ (2009) Effects of environmental change on wildlife health. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 364: 3429–3438.
- Ahumada JA, Hurtado J, Lizcano D (2013) Monitoring the status and trends of tropical forest terrestrial vertebrate communities from camera trap data: A tool for conservation. *PLoS ONE* 8: 6–9.
- Ahumada JA, Silva CEF, Gajapersad K, Hallam C, Hurtado J, Martin E et al. (2011) Community structure and diversity of tropical forest mammals: Data from a global camera trap network. *Philosophical Transactions: Biological Sciences* 366: 2703–2711.
- Alexander RR (1971) *Crown competition factor (CCF) for Engelmann spruce in the central Rocky Mountains.*
- Almeida TIR, De Souza Filho CR (2004) Principal component analysis applied to feature-oriented band ratios of hyperspectral data: A tool for vegetation studies. *International Journal of Remote Sensing* 25: 5005–5023.
- Anadón JD, Giménez A, Ballestar R (2010) Linking local ecological knowledge and habitat modelling to predict absolute species abundance on large scales. *Biodiversity and Conservation* 19: 1443–1454.
- Anderson DR, Burnham KP (2002) Avoiding Pitfalls When Using Information-Theoretic Methods. *The Journal of Wildlife Management* 66: 912–918.
- Anderson J, Cowlishaw G, Rowcliffe JM (2007) Effects of forest fragmentation on the abundance of *Colobus angolensis palliatus* in Kenya's coastal forests. *International Journal of Primatology* 28: 637–655.
- Araldi A, Barelli C, Hodges K, Rovero F (2014) Density estimation of the endangered Udzungwa red colobus (*Procolobus gordonorum*) and other arboreal primates in the Udzungwa

Mountains using systematic distance sampling. *International Journal of Primatology* 35: 941–956.

Arroyo-Rodríguez V, Asensio N, Dunn JC, Cristòbal-Azkarate J, Gonzalez-Zamora A (2015) Use of lianas by primates: More than a food source. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (eds) *Ecology of lianas*, 407–426. John Wiley & Sons.

Arroyo-Rodríguez V, Fahrig L (2014) Why is a landscape perspective important in studies of primates? *American Journal of Primatology* 909: 901–909.

Baillie SR, Sutherland WJ, Freeman SN, Gregory RD, Paradis E (2000) Consequences of large-scale processes for the conservation of bird populations. *Journal of Applied Ecology* 37: 88–102.

Balmford A, Whitten T (2003) Who should pay for tropical conservation, and how could the costs be met? *Oryx* 37: 238–250.

Barelli C, Mundry R, Araldi A, Hodges K, Rocchini D, Rovero F (2015) Modeling primate abundance in complex landscapes: A case study from the Udzungwa Mountains of Tanzania. *International Journal of Primatology* 36: 209–226.

Barton K (2015) Multi-model inference. R package version 1.13.4. <https://CRAN.R-project.org/package=MuMIn>. Barton K. 2015. MuMIn: Multi-model inference.

Blair BO, Baumgardner MF (1977) Detection of the green and brown wave in hardwood canopy covers using multirate, multispectral data from LANDSAT-1. *Agronomy Journal* 69: 808–811.

Bowkett AE, Rovero F, Marshall AR (2008) The use of camera-trap data to model habitat use by antelope species in the Udzungwa Mountain forests, Tanzania. *African Journal of Ecology* 46: 479–487.

Braithwaite LW, Austin MP, Clayton M, Turner J, Nicholls AO (1989) On predicting the presence of birds in Eucalyptus forest types. *Biological Conservation* 50: 33–50.

- Bridgewater P (2016) The Anthropocene biosphere: Do threatened species, Red Lists, and protected areas have a future role in nature conservation? *Biodiversity and Conservation* 25: 603–607.
- Brown L, Chen JM, Leblanc SG, Cihlar J (2000) A shortwave infrared modification to the simple ratio for LAI retrieval in boreal forests: An image and model analysis. *Remote Sensing of Environment* 71: 16–25.
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) *Introduction to distance sampling. Estimating abundance of biological populations*. Oxford university press, USA.
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2004) *Advanced distance sampling*. Oxford University Press, Oxford.
- Buckland ST, Plumptre AJ, Thomas L, Rexstad EA (2010a) Design and analysis of line transect surveys for primates. *International Journal of Primatology* 31: 833–847.
- Buckland ST, Plumptre AJ, Thomas L, Rexstad EA (2010b) Line transect sampling of primates: Can animal-to-observer distance methods work? *International Journal of Primatology* 31: 485–499.
- Burgess ND, Butynski TM, Cordeiro NJ, Doggart NH, Fjeldså J, Howell KM et al. (2007) The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation* 134: 209–231.
- Cade BS (1997) Comparison of tree basal area and canopy cover in habitat models: Subalpine forest. *Journal of Wildlife Management* 61: 326–335.
- Cavada N, Barelli C, Ciolli M, Rovero F (2016) Primates in human-modified and fragmented landscapes: the conservation relevance of modelling habitat and disturbance factors in density estimation. *Plos One* 11: e0148289.
- Cavada N, Ciolli M, Rocchini D, Barelli C, Marshall AR, Rovero F.

(2017). Integrating field and satellite data for spatially-explicit inference on the density of threatened arboreal primates. *Ecological Applications* 27:235-243 DOI: 10.1002/eap.1438.

Cayuela L, Golicher D, Newton A, Kolb H, de Albuquerque FS, Arets EJMM, Alkemade JRM, Pérez AM (2009) Species distribution modeling in the tropics: Problems, potentialities, and the role of biological data for effective species conservation. *Tropical Conservation Science* 2: 319–352.

Ceballos G, Ehrlich PR (2006) Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences of the United States of America* 103: 19374–19379.

Chandler R. 2014. Distance sampling analysis in unmarked. USGS Patuxent Wildlife Research Center.

Chapman CA, Balcomb SR, Gillespie TR, Skorupa JP, Struhsaker TT (2000) Long-term effects of logging on African primate communities: A 28-year comparison from Kibale National Park, Uganda. *Conservation Biology* 14: 207–217.

Chapman CA, Chapman LJ (1999) Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates* 40: 215–231.

Chapman CA, Lawes MJ, Eeley HAC (2006) What hope for African primate diversity? *African Journal of Ecology* 44: 116–133.

Chapman CA, Peres CA (2001) Primate conservation in the new millennium: The role of scientists. *Evolutionary Anthropology* 10: 16–33.

Chen JM (1996) Evaluation of vegetation indices and modified simple ratio for boreal applications. *Canadian Journal of Remote Sensing* 22: 1–21.

Cohen WB, Goward SN (2004) Landsat's role in ecological applications of remote sensing. *BioScience* 54: 535–545.

Cohen WB, Spies TA, Fiorella M (1995) Estimating the age and structure of forests in a multi-ownership landscape of

- western Oregon, U.S.A. *International Journal of Remote Sensing* 16: 721–746.
- Coops NC, Johnson M, Wulder MA, White JC (2006) Assessment of QuickBird high spatial resolution imagery to detect red attack damage due to mountain pine beetle infestation. *Remote Sensing of Environment* 103: 67–80.
- Cowlshaw G, Dunbar RIM (2000) *Primate conservation biology*. University of Chicago Press.
- Cowlshaw G, Dunbar RIM (2000) *Primate conservation biology*. University of Chicago Press.
- Cristóbal-Azkarate J, Veà JJ, Asensio N, Rodríguez-Luna E (2005) Biogeographical and floristic predictors of the presence and abundance of mantled howlers (*Alouatta palliata mexicana*) in rainforest fragments at Los Tuxtlas, Mexico. *American Journal of Primatology* 67: 209–222.
- Davies AG, Oates JF (1994) *Colobine monkeys: Their ecology, behaviour and evolution*. Cambridge University Press, Cambridge.
- De Barba M, Waits LP, Genovesi P, Randi E, Chirichella R, Cetto E (2010) Comparing opportunistic and systematic sampling methods for non-invasive genetic monitoring of a small translocated brown bear population. *Journal of Applied Ecology* 47: 172–181.
- De Luca DW, Mpunga NE (2005) Carnivores of the Udzungwa Mountains: Presence, distributions and threats. *Small Carnivore Conservation* 32: 1–7.
- Dinesen L, Lehmberg T (1996) Problem identification in the village of Udekwa (Iringa district, Tanzania) in relation to conservation of forest and biodiversity. *Birdlife Denmark and Zoological Museum, Copenhagen, Denmark*. pp. 38.
- Duncanson LI, Niemann KO, Wulder MA (2010) Integration of GLAS and Landsat TM data for aboveground biomass estimation. *Canadian Journal of Remote Sensing* 36: 129–141.
- Dunn JC, Asensio N, Arroyo-Rodríguez V, Schnitzer S, Cristóbal-

- Azkarate J (2012) The ranging costs of a fallback food: Liana consumption supplements diet but increases foraging effort in howler monkeys. *Biotropica* 44: 705–714.
- Eklundh L, Harrie L, Kuusk A (2001) Investigating relationships between Landsat ETM+ sensor data and leaf area index in a boreal conifer forest. *Remote Sensing of Environment* 78: 239–251.
- ESRI (2011) ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.
- Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-duque E, Fiore A Di et al. (2017) Impending extinction crisis of the world ' s primates : Why primates matter. *Science Advances* 3.
- Falkowski MJ, Gessler P, Morgan P, Smith AMS, Hudak AT (2004) Evaluating Aster satellite imagery and gradient modeling for mapping and characterizing wildland fire fuels. *USDA Forest Service / UNL Faculty Publications: Paper 177*.
- Farr WA, DeMars DJ, Dealy JE (1989) Height and crown width related to diameter for open-grown western hemlock and Sitka spruce. *Canadian Journal of Forest Research* 19: 1203–1207.
- Fegraus EH, Lin K, Ahumada JA, Baru C, Chandra S, Youn C (2011) Data acquisition and management software for camera trap data: A case study from the TEAM Network. *Ecological Informatics* 6: 345–353.
- Fiske IJ, Chandler RB (2011) unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43: 1–23.
- Fleming P, Meek P, Ballrad G, Banks P, Claridge A, Sanderson J, Swann D (2014) *Camera trapping: Wildlife management and research*. CSIRO, Melbourne, Australia.
- Foody GM, Boyd DS, Cutler MEJ (2003) Predictive relations of tropical forest biomass from Landsat TM data and their transferability between regions. *Remote Sensing of Environment* 85: 463–474.

- Franklin J (1995) Predictive vegetation mapping: Geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography* 19: 474–499.
- Franklin J (2009) Mapping species distributions: Spatial inference and prediction. *Journal of Tropical Ecology* 1: 320.
- Gamon JA, Surfus JS (1999) Assessing leaf pigment content and activity with a reflectometer. *New Phytologist* 143: 105–117.
- Gaston KJ (2003) *The structure and dynamics of geographic ranges*. Oxford university press, USA, New York.
- Gitelson AA, Kaufman YJ, Merzlyak MN (1996) Use of a green channel in remote sensing of global vegetation from EOS-MODIS. *Remote Sensing of Environment* 58: 289–298.
- Guisan A, Thuiller W (2005) Predicting species distribution: Offering more than simple habitat models. *Ecology Letters* 8: 993–1009.
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186.
- Günter S, Michael W, Stimm B, Mosandl R, editors. 2011. *Silviculture in the Tropics*. Berlin Heidelberg: Springer. 560 p.
- Hair JF, Black B, Babin B, Anderson, Rolph E, Tatham, Ronald L (2006) *Multivariate data analysis*, 6th ed. Prentice Hall.
- Hall FG, Shimabukuro YE, Huemmrich KF (1995) Remote sensing of forest biophysical structure using mixture decomposition and geometric reflectance models. *Ecological Applications* 5: 993–1013.
- Hall RJ, Skakun RS, Arsenault EJ, Case BS (2006) Modeling forest stand structure attributes using Landsat ETM+ data: Application to mapping of aboveground biomass and stand volume. *Forest Ecology and Management* 225: 378–390.
- Hardinsky MA, Klemas V, Smart RM (1983) The influence of soil salinity, growth form, and leaf moisture on the spectral radiance of *Spartina alterniflora* canopies. *Photogrammetric*

Engineering and Remote Sensing 48: 77–84.

He KS, Bradley BA, Cord AF, Rocchini D, Tuanmu M-N, Schmidtlein S, Turner W, Wegmann M, Pettorelli N (2015) Will remote sensing shape the next generation of species distribution models? *Remote Sensing in Ecology and Conservation* 1: 4–18.

Henle K, Lindemayer DB, Margules CB, Saunders DA, Wissel C (2004) Species survival in fragmented landscapes: Where are we now? *Biodiversity and Conservation* 13: 1–8.

Isaac NJB, Cowlshaw G (2004) How species respond to multiple extinction threats. *Proceedings. Biological sciences / The Royal Society* 271: 1135–1141.

Isabirye-Basuta GM, Lwanga JS (2008) Primate populations and their interactions with changing habitats. *International Journal of Primatology* 29: 35–48.

IUCN (2015) The IUCN red list of threatened species. Version 2015-4. www.iucnredlist.org.

Jackson RD, Huete AR (1991) Interpreting vegetation indices. *Preventive Veterinary Medicine* 11: 185–200.

Jakubauskas ME (1996) Thematic mapper characterization of lodgepole pine seral stages in Yellowstone National Park, USA. *Remote Sensing of Environment* 56: 118–132.

Johns AD (1983) Ecological effects of selective logging in a West Malaysian rain-forest. PhD thesis, University of Cambridge, Cambridge, UK.

Johns AD, Skorupa JP (1987) Responses of rain-forest primates to habitat disturbance: A review. *International Journal of Primatology* 8: 157–191.

Jones JPG (2011) Monitoring species abundance and distribution at the landscape scale. *Journal of Applied Ecology* 48: 9–13.

Jones JPG, Andriamarivololona MM, Hockley N, Gibbons JM, Milner-Gulland EJ (2008) Testing the use of interviews as a tool for monitoring trends in the harvesting of wild species. *Journal of Applied Ecology* 45: 1205–1212.

- Jordan CF (1969) Derivation of leaf-area index from quality of light on the forest floor. *Ecology* 50: 663–666.
- Karanth K, Nichols J (2002) *Monitoring tigers and their prey: A manual for researchers, managers, and conservationists in tropical Asia*. Centre for wildlife studies, Bangalore, India.
- Karanth KU, Nichols JD (1998) Estimation of tiger densities in India using photographic captures and Recaptures. *Ecology* 79: 2852–2862.
- Kellner KF, Swihart RK (2014) Accounting for imperfect detection in ecology: A quantitative review. *PLoS ONE* 9: e111436.
- Kelly MJ, Holub EL (2008) Camera trapping of carnivores: Trap success among camera types and across species, and habitat selection by species, on Salt Pond Mountain, Giles County, Virginia. *Northeastern Naturalist* 15: 249–262.
- Kennedy P (2008) *A guide to econometrics*, 6th ed. Wiley-Blackwell.
- Kéry M, Schmidt BR (2008) Imperfect detection and its consequences for monitoring for conservation. *Community Ecology* 9: 207–216.
- Kingdon J (2008) *The Kingdon field guide to African mammals*. A&C Black, London.
- Kingdon J, Howell K (1993) Mammals in the forests of eastern Africa. In: Lovett J, Wasser S (eds) *Biogeography and ecology of the rain forests of eastern Africa*, 229–242. Cambridge University Press, Cambridge.
- Kümpel NF, Milner-Gulland EJ, Rowcliffe JM, Cowlishaw G (2008) Impact of gun-hunting on diurnal primates in continental Equatorial Guinea. *International Journal of Primatology*, 1065–1082.
- Lahoz-Monfort JJ, Guillera-Arroita G, Wintle BA (2014) Imperfect detection impacts the performance of species distribution models. *Global Ecology and Biogeography* 23: 504–515.
- Legaard KR, Sader SA, Simons-Legaard EM (2015) Evaluating the

impact of abrupt changes in forest policy and management practices on landscape dynamics: Analysis of a Landsat image time series in the Atlantic northern forest. *Plos One* 10: e0130428.

Levi T, Shepard GH, Ohl-Schacherer J, Peres CA, Yu DW (2009) Modelling the long-term sustainability of indigenous hunting in Manu National Park, Peru: Landscape-scale management implications for Amazonia. *Journal of Applied Ecology* 46: 804–814.

Linder JM, Oates JF (2011) Differential impact of bushmeat hunting on monkey species and implications for primate conservation in Korup National Park, Cameroon. *Biological Conservation* 144: 738–745.

Linkie M, Chapron G, Martyr DJ, Holden J, Leader-Williams N (2006) Assessing the viability of tiger subpopulations in a fragmented landscape. *Journal of Applied Ecology* 43: 576–586.

Linkie M, Dinata Y, Nugroho A, Haidir IA (2007) Estimating occupancy of a data deficient mammalian species living in tropical rainforests: Sun bears in the Kerinci Seblat region, Sumatra. *Biological Conservation* 137: 20–27.

Lomolino MV, Riddle BR, Brown JH (2006) *Biogeography*, 3rd ed. Sinauer, Sunderland, MA.

Lovett JC, Marshall AR (2006) Why should we conserve primates. *African Journal of Ecology* 44: 113–115.

Lovett JC, Marshall AR, Carr J (2006) Changes in tropical forest vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. *African Journal of Ecology* 44: 478–490.

Lovett JC, Marshall AR, Carr J (2006) Changes in tropical forest vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. *African Journal of Ecology* 44: 478–490.

Lovett JC, Marshall AR, Carr J (2006) Changes in tropical forest

- vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. *African Journal of Ecology* 44: 478–490.
- Lovett JC, Wasser SK (1993) *Biogeography and Ecology of the Rain Forests of Eastern Africa*. Cambridge university press, Cambridge.
- Lymburner L, Beggs P, Jacobson C (2000) Estimation of canopy-average surface-specific leaf area using Landsat TM data. *Photogrammetric Engineering & Remote Sensing* 66: 183–191.
- Maberly CTA (1967) African bushpigs. *Animals* 9: 556–561.
- Manduell KL, Harrison ME, Thorpe SKS (2012) Forest structure and support availability influence orangutan locomotion in Sumatra and Borneo. 15: 1–15.
- Maniatis D, Mollicone D (2010) Options for sampling and stratification for national forest inventories to implement REDD+ under the UNFCCC. *Carbon balance and management* 5: 9.
- Margules CR, Pressey RL (2000) Systematic conservation planning. *Nature* 405: 243–253.
- Marquardt DW (1970) Generalized inverses, Ridge regression, biased linear estimation, and nonlinear estimation. *Technometrics* 12: 591–612.
- Marques FFC, Buckland ST (2003) Incorporating covariates into standard line transect analyses. *Biometrics* 59: 924–935.
- Marques TA, Thomas L, Fancy SG, Buckland ST (2007) Improving estimates of bird density using multiple- covariate distance sampling. *The Auk* 124: 1229.
- Marsh LK (2003) *Primates in fragments: ecology and conservation*. Springer US.
- Marsh LK (2013) Because conservation counts: Primates and fragmentation. In: Marsh LK, Chapman CA (eds) *Primates in Fragments: Complexity and resilience. Developments in primatology: progress and prospects*, 3–11. Springer Science+

Business Media New York.

Marshall A (2008) Ecological Report on Magombera Forest. Unpublished report to WWF- TPO.

Marshall AJ, Wich SA (2016) Why conserve primates? In: Wich SA, Marshall AJ (eds) *An introduction to primate conservation*, 368. Oxford University Press, Oxford, United Kingdom.

Marshall AR (2007) Disturbance in the Udzungwas: Responses of monkeys and trees to forest degradation. PhD thesis, University of York, York, UK.

Marshall AR, Jørgensbye HIO, Rovero F, Platts PJ, White PCL, Lovett JC (2010) The species-area relationship and confounding variables in a threatened monkey community. *American Journal of Primatology* 72: 325–336.

Marshall AR, Lovett JC, White P (2007) Disturbance in the Udzungwas: Responses of monkeys and trees to forest degradation. PhD thesis.

Marshall AR, Lovett JC, White PCL (2008) Selection of line-transect methods for estimating the density of group-living animals: Lessons from the primates. *American Journal of Primatology* 70: 452–462.

Marshall AR, Topp JE, Brink H, Fanning E (2005) Monkey abundance and social structure in two high-elevation forest reserves in the Udzungwa Mountains of Tanzania. *International Journal of Primatology* 26: 127–145.

Marshall AR, Willcock S, Platts PJ, Lovett JC, Balmford A, Burgess ND et al. (2012) Measuring and modelling above-ground carbon and tree allometry along a tropical elevation gradient. *Biological Conservation* 154: 20–33.

Martin TG, Wintle BA, Rhodes JR, Kuhnert PM, Field SA, Low-Choy SJ, Tyre AJ, Possingham HP (2005) Zero tolerance ecology: Improving ecological inference by modelling the source of zero observations. *Ecology Letters* 8: 1235–1246.

Mayes MT, Mustard JF, Melillo JM (2015) Forest cover change in Miombo woodlands: Modeling land cover of African dry

- tropical forests with linear spectral mixture analysis. *Remote Sensing of Environment* 165: 203–215.
- Mbora DNM, Meikle DB (2004) Forest fragmentation and the distribution, abundance and conservation of the Tana river red colobus (*Procolobus rufomitratu*s). *Biological Conservation* 118: 67–77.
- McCullagh P, Nelder JA (1989) *Generalized linear models*. Chapman & Hall, London.
- McGraw WS (1996) Cercopithecoid locomotion, support use, and support availability in the Tai forest, Ivory Coast. *American Journal of Physical Anthropology* 100: 507–522.
- Medley KE (1993) Primate conservation along the Tana River, Kenya: An examination of the forest habitat. *Conservation biology* 7: 109–121.
- Meek PD, Ballard G, Fleming P (2012) *An introduction to camera trapping for wildlife surveys in Australia*. PestSmart Toolkit publication, Invasive Animals Cooperative Research Centre, Canberra, Australia.
- Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: biodiversity synthesis*. Washington, DC.
- Mittermeier RA, Cheney DL (1987) Conservation of primates and their habitats. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW (eds) *Primate societies*, 475–490. University of Chicago Press, Chicago.
- Motohka T, Nasahara KN, Oguma H, Tsuchida S (2010) Applicability of green-red vegetation index for remote sensing of vegetation phenology. *Remote Sensing* 2: 2369–2387.
- Mugerwa B, Sheil D, Ssekiranda P, Van Heist M, Ezuma P (2012) A camera trap assessment of terrestrial vertebrates in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology* 51: 21–31.
- Mumby PJ, Edwards AJ (2002) Mapping marine environments with IKONOS imagery: Enhanced spatial resolution can deliver

greater thematic accuracy. *Remote Sensing of Environment* 82: 248–257.

Muukkonen P, Heiskanen J (2005) Estimating biomass for boreal forests using ASTER satellite data combined with standwise forest inventory data. *Remote Sensing of Environment* 99: 434–447.

Muukkonen P, Heiskanen J (2007) Biomass estimation over a large area based on standwise forest inventory data and ASTER and MODIS satellite data: A possibility to verify carbon inventories. *Remote Sensing of Environment* 107: 617–624.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–8.

Naeem S, Chair FSCIII, Costanza R, Ehrlich PR, Golley FB et al. (1999) Biodiversity and ecosystem functioning: Maintaining natural life support processes. *Issues in Ecology*: 1–11.

Nagendra H, Rocchini D (2008) High resolution satellite imagery for tropical biodiversity studies: The devil is in the detail. *Biodiversity and Conservation* 17: 3431–3442.

Nemani R, Pierce L, Running S, Band L (1993) Forest ecosystem processes at the watershed scale: Sensitivity to remotely-sensed leaf area index estimates. *International Journal of Remote Sensing* 14: 2519–2534.

Neteler M, Bowman MH, Landa M, Metz M (2012) GRASS GIS: A multi-purpose open source GIS. *Environmental Modelling and Software* 31: 124–130.

O'Brien TG (2008) On the use of automated cameras to estimate species richness for large- and medium-sized rainforest mammals. *Animal Conservation* 11: 179–181.

O'Brien TG, Kinnaird MF, Wibisono HT (2003) Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation* 6: 131–139.

O'Connell AF, Nichols JD, Karanth KU (2011) *Camera Traps in Animal Ecology*. Springer, New York.

- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB et al. (2015) vegan: Community ecology package. R package version 2.2-1.
- Onderdonk DA, Chapman CA (2000) Coping with forest fragmentation: The primates of Kibale National Park, Uganda. *International Journal of Primatology* 21: 587–611.
- Piñeiro G, Perelman S, Guerschman JP, Paruelo JM (2008) How to evaluate models: Observed vs. predicted or predicted vs. observed? *Ecological Modelling* 216: 316–322.
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2016) nlme: Linear and nonlinear mixed effects models.
- Platts PJ, Burgess ND, Gereau RE, Lovett JC, Marshall AR, McClean CJ, Pellikka PKE, Swetnam RD, Marchant R (2011) Delimiting tropical mountain ecoregions for conservation. *Environmental Conservation* 38: 312–324.
- Ploton P, Pélissier R, Proisy C, Flavenot T, Barbier N, Rai SN, Coutron P (2012) Assessing aboveground tropical forest biomass using Google Earth canopy images. *Ecological applications : a publication of the Ecological Society of America* 22: 993–1003.
- Plumptre AJ, Cox D. 2006. Counting primates for conservation: Primate surveys in Uganda. *Primates* 47:65–73.
- Powell SL, Cohen WB, Healey SP, Kennedy RE, Moisen GG, Pierce KB, Ohmann JL (2010) Quantification of live aboveground forest biomass dynamics with Landsat time-series and field inventory data: A comparison of empirical modeling approaches. *Remote Sensing of Environment* 114: 1053–1068.
- Proisy C, Coutron P, Fromard F (2007) Predicting and mapping mangrove biomass from canopy grain analysis using Fourier-based textural ordination of IKONOS images. *Remote Sensing of Environment* 109: 379–392.
- Pucci A, Rovero F (2004) Observations on the food habits of the endemic Udzungwa red colobus (*Piliocolobus gordonorum*) from different forest sites in the Udzungwa Mountains,

Tanzania. Proceedings of the 16th meeting of the Italian Primatological Society. Radicondoli, (October 200). *Folia primatologica* 75: 406.

R Core Team. (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

Ramos-Fernandez G, Espadas-Manrique C, Serio-Silva JC (2013) Potential distribution of primates in the Yucatan peninsula, Mexico under current and climate change scenarios. In: Marsh LK, Chapman CA (eds) *Primates in Fragments: Complexity and Resilience. Developments in primatology: progress and prospects*, 475–491. Springer Science+Business Media New York.

Ricotta C, Avena GC, Volpe F (1999) The influence of principal component analysis on the spatial structure of a multispectral dataset. *International Journal of Remote Sensing* 20: 3367–3376.

Rodríguez JP, Brotons L, Bustamante J, Seoane J (2007) The application of predictive modelling of species distribution to biodiversity conservation. *Diversity and Distributions* 13: 243–251.

Rodríguez-Luna E, Shedden A, Solórzano-García B (2013) A region-wide review of Mesoamerican primates: prioritizing for conservation. In: Marsh LK, Chapman CA (eds) *Primates in fragments: complexity and resilience. Developments in primatology: progress and prospects*, 47–55. Springer science+Business Media New York.

Ronald Pulliam H (1988) Sources, sinks, and population regulation. *The American Naturalist* 135: 652–661.

Rouse JW, Haas RH, Schell JA, Deering, WD, Harlan JC (1974) *Monitoring the vernal advancement and retrogradation (greenwave effect) of natural vegetation*. Greenbelt, MD, USA.

Rovero F (2003) *Conservation biology of the Udzungwa red colobus and the Sanje mangabey in the Udzungwa Mountains, Tanzania: the effect of habitat quality and human activities on*

population density and demography.

- Rovero F, Collett L, Ricci S, Martin E, Spitale D (2013a) Distribution, occupancy, and habitat associations of the gray-faced sengi (*Rhynchocyon udzungwensis*) as revealed by camera traps. *Journal of Mammalogy* 94: 792–800.
- Rovero F, De Luca DW (2007) Checklist of mammals of the Udzungwa Mountains of Tanzania. *Mammalia* 71: 47–55.
- Rovero F, Marshall AR (2009) Camera trapping photographic rate as an index of density in forest ungulates. *Journal of Applied Ecology* 46: 1011–1017.
- Rovero F, Marshall AR, Jones T, Perkin A (2009) The primates of the Udzungwa Mountains: Diversity, ecology and conservation. *Journal of Anthropological Sciences* 87: 93–126.
- Rovero F, Marshall AR, Jones T, Perkin A (2009) The primates of the Udzungwa Mountains: Diversity, ecology and conservation. *Journal of Anthropological Sciences* 87: 93–126.
- Rovero F, Marshall AR, Jones T, Perkin A (2009) The primates of the Udzungwa Mountains: Diversity, ecology and conservation. *Journal of Anthropological Sciences* 87: 93–126.
- Rovero F, Martin E, Rosa M, Ahumada JA, Spitale D (2014a) Estimating species richness and modelling habitat preferences of tropical forest mammals from camera trap data. *PloS one* 9: e103300.
- Rovero F, Menegon M, Fjeldså J, Collett L, Doggart N, Leonard C et al. (2014b) Targeted vertebrate surveys enhance the faunal importance and improve explanatory models within the Eastern Arc Mountains of Kenya and Tanzania. *Diversity and Distributions* 20: 1438–1449.
- Rovero F, Mtui A, Kitegile A, Jacob P, Araldi A, Tenan S (2015) Primates decline rapidly in unprotected forests: Evidence from a monitoring program with data constraints. *PLoS ONE*: 1–13.
- Rovero F, Mtui AS, Kitegile AS, Nielsen MR (2012) Hunting or habitat degradation? Decline of primate populations in

Udzungwa Mountains, Tanzania: An analysis of threats. *Biological Conservation* 146: 89–96.

Rovero F, Perkin A (2008) Medium and large mammals. In: Doggart N, Leonard C, Perkin A, Menegon M, Rovero F (eds) *The Biodiversity And Forest Condition Of Udzungwa Mountain Forests In Mufindi District*, 40–47. TFCG Technical paper No 18, Dar es Salaam.

Rovero F, Rathbun GB, Perkin A, Jones T, Ribble DO, Leonard C, Mwakisoma RR, Doggart N (2008) A new species of giant sengi or elephant-shrew (genus *Rhynchocyon*) highlights the exceptional biodiversity of the Udzungwa Mountains of Tanzania. *Journal of Zoology* 274: 126–133.

Rovero F, Struhsaker TT (2007) Vegetative predictors of primate abundance: Utility and limitations of a fine-scale analysis. *American Journal of Primatology* 69: 1242–1256.

Rovero F, Struhsaker TT, Marshall AR, Rinne TA, Pedersen UB, Butynski TM, Ehardt CL, Mtui AS (2006) Abundance of diurnal primates in Mwanihana Forest, Udzungwa Mountains, Tanzania. *International Journal of Primatology* 27: 675–697.

Rovero F, Tobler M, Sanderson J (2010) Camera trapping for inventorying terrestrial vertebrates. In: Eymann J, Degreef J, Häuser C, Monje JC, Samyn Y, VandenSpiegel D (eds) *Manual on field recording techniques and protocols for all taxa biodiversity inventories and monitoring.*, 100–128. ABC Taxa.

Rovero F, Zimmermann F, Berzi D, Meek P (2013b) “Which camera trap type and how many do I need?” A review of camera features and study designs for a range of wildlife research applications. *Hystrix* 24: 148–156.

Rowcliffe JM, Carbone C (2008) Surveys using camera traps: Are we looking to a brighter future? *Animal Conservation* 11: 185–186.

Rowcliffe JM, Carbone C, Jansen PA, Kays R, Kranstauber B (2011) Quantifying the sensitivity of camera traps: An adapted distance sampling approach. *Methods in Ecology and Evolution* 2: 464–476.

- Rowcliffe JM, Field J, Turvey ST, Carbone C (2008) Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology* 45: 1228–1236.
- Royle JA, Dawson DK, Bates S (2004) Modeling abundance effects in distance sampling. *Ecology* 85: 1591–1597.
- Royle JA, Kéry M (2007) A Bayesian state-space formulation of dynamic occupancy models. *Ecology* 88: 1813–1823.
- Royston JP (1982) An extension of Shapiro and Wilk's *W* test for normality to large samples. *Journal Of The Royal Statistical Society Series C-Applied Statistics* 31: 115–124.
- Sarkar D (2008) *Lattice: Multivariate Data Visualization with R*. Springer, New York.
- Schipper J, Chanson JS, Chiozza F, Cox NA, Hoffmann M, Katariya V et al. (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322: 225–230.
- Schmidt JH, Rattenbury KL, Lawler JP, MacCluskie MC (2012) Using distance sampling and hierarchical models to improve estimates of Dall's sheep abundance. *Journal of Wildlife Management* 76: 317–327.
- Schroeder TA, Wulder MA, Healey SP, Moisen GG (2011) Mapping wildfire and clearcut harvest disturbances in boreal forests with Landsat time series data. *Remote Sensing of Environment* 115: 1421–1433.
- Schwitzer C, Mittermeier RA, Rylands AB, Chiozza F, Williamson EA, Wallis J, Cotton A (2015) *Primates in Peril: The World's 25 Most Endangered Primates 2014-2016*. Arlington, VA.
- Sillett TS, Chandler RB, Royle JA, Kéry M, Morrison SA (2012) Hierarchical distance-sampling models to estimate population size and habitat-specific abundance of an island endemic. *Ecological Applications* 22: 1997–2006.
- Silveira L, Jácomo ATA, Diniz-Filho JAF (2003) Camera trap, line transect census and track surveys: A comparative evaluation.

Biological Conservation 114: 351–355.

Simoons F (1953) Notes on the bush-pig (*Potamochoerus*). *Uganda journal* 17: 80–81.

Smith WR, Farrar Jr. RM, Murphy PA, Yeiser JL, Meldahl RS, Kush JS (1992) Crown and basal area relationships of open-grown southern pines for modeling competition and growth. *Canadian Journal of Forest Research* 22: 341–347.

Smithers R (1983) *The mammals of the Southern Africa subregion*. University of Pretoria Press, Pretoria.

Sollmann R, Mohamed A, Samejima H, Wilting A (2013) Risky business or simple solution - Relative abundance indices from camera-trapping. *Biological Conservation* 159: 405–412.

Struhsaker T, Butynski TM, Ehardt C (2016) *Piliocolobus gordonorum*. *The IUCN Red List of Threatened Species 2016*.

Struhsaker TT (2010) *The red colobus monkeys: Variation in demography, behavior, and ecology of endangered species*. Oxford, Oxford University Press.

Struhsaker TT, Marshall AR, Detwiler K, Siex K, Ehardt C, Lisbjerg DD, Butynski TM (2004) Demographic variation among Udzungwa red colobus in relation to gross ecological and sociological parameters. *International Journal of Primatology* 25: 615–658.

Sutherland C, Brambilla M, Pedrini P, Tenan S, Isaac N (2016) A multiregion community model for inference about geographic variation in species richness. *Methods in Ecology and Evolution* 7: 783–791.

TEAM Network (2011) Tropical Ecology Assessment and Monitoring Network Terrestrial vertebrate (camera trap) monitoring protocol.

Thenkabail PS, Smith RB, De Pauw E (2000) Hyperspectral vegetation indices and their relationships with agricultural crop characteristics. *Remote Sensing of Environment* 71: 158–182.

- Tobler MW, Carrillo-Percastegui SE, Leite Pitman R, Mares R, Powell G (2008) An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation*: 1–10.
- Tobler MW, Pitman RL, Mares R, Powell G (2008) An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. 1–10.
- Tonolli S, Dalponte M, Neteler M, Rodeghiero M, Vescovo L, Gianelle D (2011) Fusion of airborne LiDAR and satellite multispectral data for the estimation of timber volume in the Southern Alps. *Remote Sensing of Environment* 115: 2486–2498.
- Trolle M, Kéry M (2003) Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. *Journal of Mammalogy* 84: 607–614.
- Trolliet F, Huynen M-C, Vermeulen C, Hambuckers A (2014) Use of camera traps for wildlife studies. A review. *Biotechnology, Agronomy, Society and Environment* 18: 466–454.
- Twongyirwe R, Bithell M, Richards KS, Rees WG (2015) Three decades of forest cover change in Uganda’s Northern Albertine Rift Landscape. *Land Use Policy* 49: 236–251.
- Umapathy G, Kumar A (2000) The occurrence of arboreal mammals in the rain forest fragments in the Anamalai Hills, South India. *Biological Conservation* 92: 311–319.
- Underhill L, Gibbons D (2002) Mapping and monitoring bird populations: Their conservation uses. In: Norris K, Pain DJ (eds) *Conserving bird biodiversity: General principles and their application*, 34–60. Cambridge University Press.
- Urquiza-Haas T, Dolman PM, Peres CA (2007) Regional scale variation in forest structure and biomass in the Yucatan Peninsula, Mexico: Effects of forest disturbance. *Forest Ecology and Management* 247: 80–90.
- Vescovo L, Gianelle D (2008) Using the MIR bands in vegetation indices for the estimation of grassland biophysical

parameters from satellite remote sensing in the Alps region of Trentino (Italy). *Advances in Space Research* 41: 1764–1772.

Visconti P, Pressey RL, Giorgini D, Maiorano L, Bakkenes M, Boitani L et al. (2011) Future hotspots of terrestrial mammal loss. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 366: 2693–2702.

Wasserman MD, Chapman CA (2003) Determinants of colobine monkey abundance: The importance of food energy, protein and fibre content. *Journal of Animal Ecology* 72: 650–659.

Weng Q (2009) Thermal infrared remote sensing for urban climate and environmental studies: Methods, applications, and trends. *ISPRS Journal of Photogrammetry and Remote Sensing* 64: 335–344.

Whitesides GH, Oates JF, Green SM, Kluberanz RP (1988) Estimating primate densities from transects in a West African rain forest: A comparison of techniques. *Journal of animal ecology* 57: 345–367.

Wilkie DS, Finn JT (1996) *Remote sensing imagery for natural resources monitoring: A guide for first-time users*. Columbia University Press.

Woodcock CE, Strahler AH (1987) The factor of scale in remote sensing. *Remote Sensing of Environment* 21: 311–332.

Wulder MA, Franklin SE (2006) *Understanding forest disturbance and spatial pattern: Remote sensing and GIS approaches*. CRC Press.

Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution* 16: 446–453.

Zimmermann NE, Edwards TC, Moisen GG, Frescino TS, Blackard JA. (2007) Remote sensing-based predictors improve distribution models of rare, early successional and broadleaf tree species in Utah. *Journal of Applied Ecology* 44: 1057–1067.

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data

exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 1–12.

Zuur AF, Ieno EN, Smith GM (2007) *Analysing ecological data*. Springer, New York.

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York.

APPENDICES

Appendix 1. Best selected model detection functions for RC (Figure A), covariates effect on density estimation shown for BW and SY (Figure B) and spatially explicit modelling of animal density in MG, MT and US (Figure C).

Appendix 2. Code for the GRASS 7.0 module that was implemented to derive a series of vegetation indices, combining specific bands of a Landsat 8 image.

Appendix 1.

Figure A. Detection functions from the best AIC models, shown for the 0.25, 0.50 and 0.75 quartiles of the covariates “distance from disturbance” and “climber percentage” for the Udzungwa red colobus (RC).

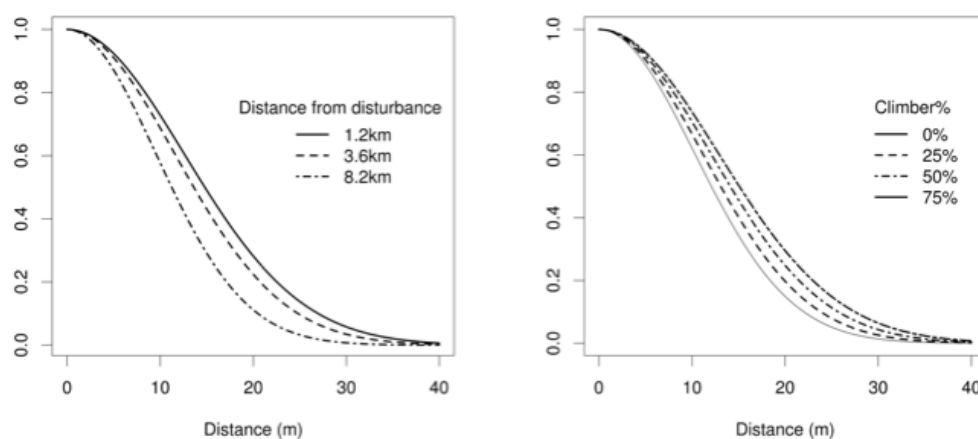


Figure B. Covariates effect on group density estimation, shown for the best model selected for (a) Peters' Angola colobus (BW) and (b) Tanzania Sykes' monkey (SY)

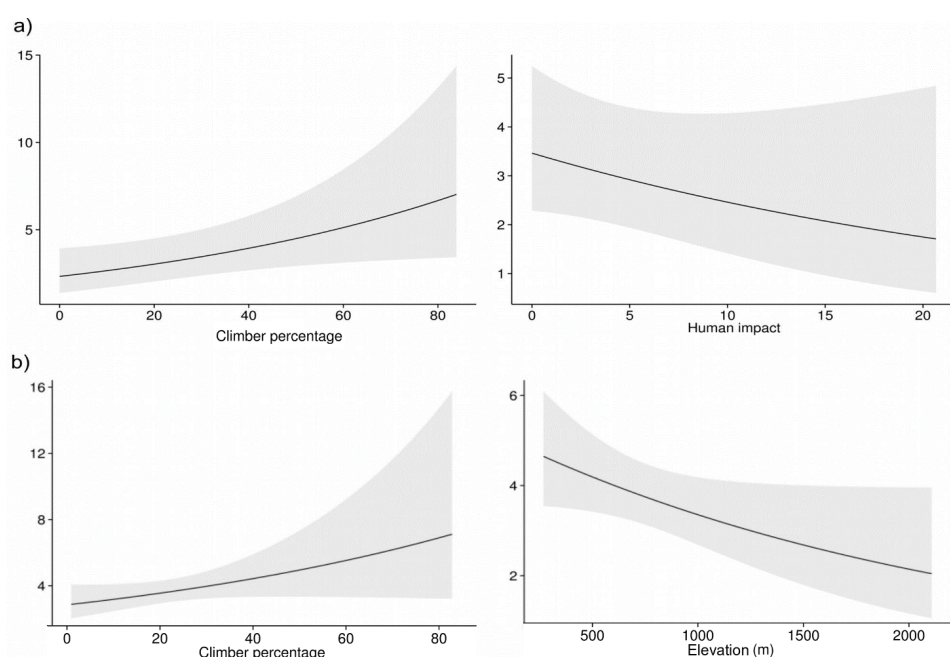
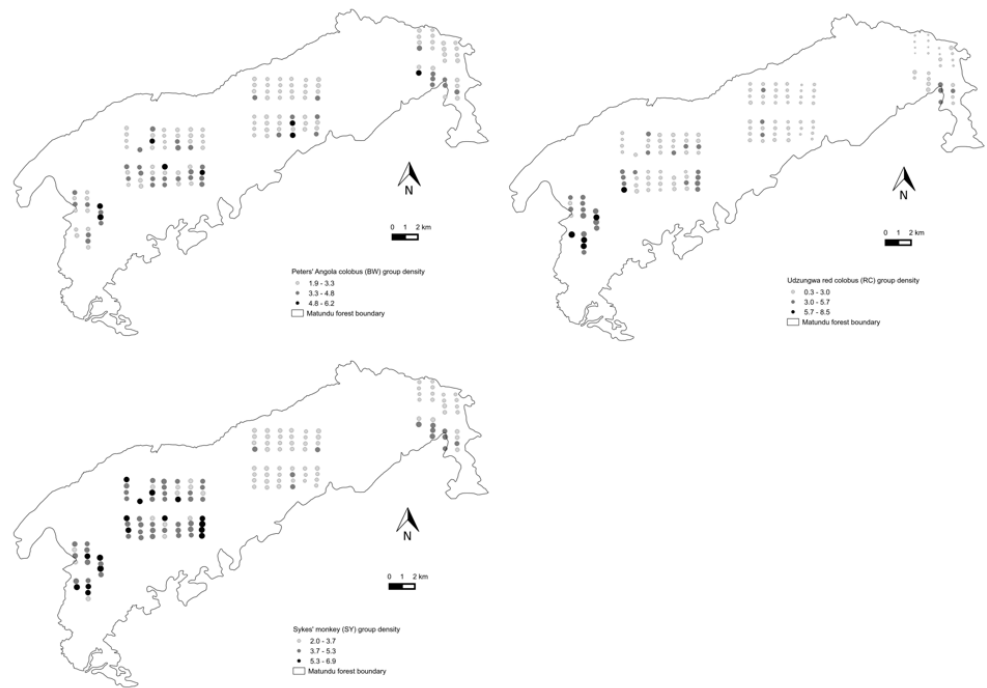


Figure C. Predicted density (groups/km²) for the three primate species (Peters' Angola colobus, Udzungwa red colobus, Tanzania Sykes' monkey) from the best selected models (see Table 3) in the forest of (a) Magombera, (b) Matundu and (c) Uzungwa Scarp.

a)



b)



c)



Appendix 2.

```
#!/usr/bin/env python
%module
% description: Calculates vegetation indices
for Landsat TM/ETM+/OLI spectral bands
% keywords: landsat, vegetation, indices,
spectral, bands
%end

%option
% key: band_prefix
% type: string
% gisprompt: old,cell,raster
% description: Base name of input raster bands
or a raster band map
% required: yes
%end
%option
% key: indices_prefix
% type: string
% description: Prefix for output raster
indices maps
% answer: spectral
% required : yes
%end
%flag
% key: t
% description: Use bands for LANDSAT-4,5,7
(TM/ETM+)
%END
%flag
% key: o
% description: Use bands for LANDSAT-8 (OLI)
%END
%flag
% key: c
% description: Calculates also Cap
Tassellation Indices
%END
%option
% key: tc_prefix
% type: string
% gisprompt: old,cell,raster
```



```

#% description: If c flac: base name of input
Tasselled Cap or a Tasselled Cap map
#% required: no
#%end
#%Option
#% key: sensor
#% type: string
#% required: yes
#% multiple: no
#% options: LANDSAT-4;5;7 (TM/ETM+),LANDSAT-8
(OLI)
#% description: Use bands for sensor
#% answer: LANDSAT-8 (OLI)
#%End

import os, sys, shutil
import os.path, re
import grass.script as g

def main():

    #r.mapcalc float coercing with integer
input
    # (dn_B6-dn_B4)/(dn_B6+dn_B4)
    # 1.0*(dn_B6-dn_B4)/(dn_B6+dn_B4)
    # (1.0*dn_B6-
1.0*dn_B4)/(1.0*dn_B6+1.0*dn_B4)
    # (float(dn_B6)-
float(dn_B4))/(float(dn_B6)+float(dn_B4))

    # define indices formulas

    # RR: SWIR/Red reflectance ratio
    rr_expr = '%(outpref)s_rr =1.0* %(mir)s
/ %(r)s'

    # SR: Simple ratio NIR/Red reflectance
ratio (Jordan, 1969)
    sr_expr = '%(outpref)s_sr =1.0* %(nir)s
/ %(r)s'

    # SRC: Corrected Simple Ratio (Brown et al.
2000)
```

```

src_expr = '%(outpref)s_src =1.0* $sr *(1-
((%(mir)s - %(minmir)s)/(%(maxmir)s -
%(minmir)s))'

# MSR: Modified Simple Ratio (Chen, 1996)
msr_expr = '%(outpref)s_msr =1.0* (%(nir)s
/ %(r)s -1)/(sqrt(%(nir)s / %(r)s)+1)'

# RGR: Red Green Ratio (Gamon and Surfus)
rgr_expr = '%(outpref)s_rgr =1.0* %(r)s
/ %(g)s'

# RGI: Red Green Index (Coops et al.)
rgi_expr = '%(outpref)s_rgi =1.0* (%(g)s -
%(r)s)/(%(g)s + %(r)s)'

# NDVI: Normalized Difference Vegetation
Index (Rouse et al., 1974)
ndvi_expr = '%(outpref)s_ndvi =1.0*
(%(nir)s - %(r)s)/(%(nir)s + %(r)s)'

# NDVIc: Corrected NDVI (Nemani et al.,
1993)
ndvic_expr = '%(outpref)s_ndvic =1.0* $ndvi
*(1-((%(mir)s - %(minmir)s)/(%(maxmir)s -
%(minmir)s))'

# GNDVIgreen: NGreen Normalized Difference
Vegetation Index (Gitelson et al., 1996)
gndvi_expr = '%(outpref)s_gndvi =1.0*
(%(nir)s - %(g)s)/(%(nir)s + %(g)s)'

# NDWI: Normalized Difference Water Index
(Gao, 1996)
ndwi_expr = '%(outpref)s_ndwi =1.0*
(%(nir)s - %(mir)s)/(%(nir)s + %(mir)s)'

# SLAVI: Specific Leaf Area Vegetation
Index (Lymburner et al., 2000)
slavi_expr = '%(outpref)s_slavi
=1.0* %(nir)s /(%(r)s + %(mir)s)'

# NCI: Normalized Canopy Index (Vescovo &
Gianelle, 2008)

```

```
nci_expr = '%(outpref)s_nci =1.0* (%(mir)s
- %(g)s)/(%(mir)s + %(g)s) '

# NBR: Normalized Burn Ratio -> NOT
IMPLEMENTED
# fire/burn index, use TM7/OLI_SWIR2

# TCA: Tasselled Cap Angle (Powell et al.,
2010; Gomez et al., 2011)
tca_expr = '%(outpref)s_tca =1.0*
atan(%(gr)s / %(br)s)' #deg angle

# ln(-We)
lnmwe_expr = '%(outpref)s_lnmwe =1.0* log(-
%(we)s) '

# MAIN
landname= options['band_prefix'] #'toare_B'
indicespref= options['indices_prefix']
#'spectral'

#remove path before names and anything
aftre the last point (ext)

#landpref=os.path.splitext(os.path.basename(land
name))[0]

#remove ending numer from basename (purge
path and @mapset)
#BASH: echo $(basename $landname) | sed
's/[0-9]*$//'
landpref=re.sub('[0-9]*$',
'',os.path.basename(landname.split('@')[0]))

# define bands maps
if flags['o']:
    #landsat8
    g.message("OLI sensor")
    blue=landpref+'2'
    green=landpref+'3'
    red=landpref+'4'
    ninfrar=landpref+'5'
    minfrar=landpref+'7' #SWIR1
elif flags['t']:
```

```
#landsat7
g.message("TM/ETM+ sensor")
blue=landpref+'1'
green=landpref+'2'
red=landpref+'3'
nir=landpref+'4'
minir=landpref+'5'
else:
#landsat8
g.message("Warning: no sensor
specified, default OLI used")
blue=landpref+'2'
green=landpref+'3'
red=landpref+'4'
nir=landpref+'5'
minir=landpref+'7' #SWIR1

#set region on a band map (are all equal)
g.run_command('g.region', rast = minir)

# mir max and min
min_mir = g.raster_info(minir)['min']
max_mir = g.raster_info(minir)['max']

bands= {
    "outpref" : indicespref,
    "b" : blue,
    "g" : green,
    "r" : red,
    "nir" : nir,
    "mir" : minir,
    "minmir" : min_mir,
    "maxmir" : max_mir,
}

# compute indices with GRASS mapcalc
g.message("Calculating vegetation indices")
g.mapcalc(rr_expr % bands, overwrite =
True)
g.mapcalc(sr_expr % bands, overwrite =
True)
g.mapcalc(src_expr % bands,
sr=indicespref+'_sr', overwrite = True)
g.mapcalc(msr_expr % bands, overwrite =
True)
```

```
    g.mapcalc(rgr_expr % bands, overwrite =
True)
    g.mapcalc(rgi_expr % bands, overwrite =
True)
    g.mapcalc(ndvi_expr % bands, overwrite =
True)
    g.mapcalc(ndvic_expr % bands,
ndvi=indicespref+'_ndvi', overwrite = True)
    g.mapcalc(gndvi_expr % bands, overwrite =
True)
    g.mapcalc(ndwi_expr % bands, overwrite =
True)
    g.mapcalc(slavi_expr % bands, overwrite =
True)
    g.mapcalc(nci_expr % bands, overwrite =
True)

    if flags['c']:
        tcname= options['tc_prefix']
        if tcname=="":
            g.message("Warning: no TC prefix,
defaout 'tct8_C.' used")
            tcpref='tct8_C.'
        else:
            tcpref=re.sub('[0-9]*$',
'',os.path.basename(tcname.split('@')[0]))

        comp= {
            "outpref" : indicespref,
            "br" : tcpref+'1',
            "gr" : tcpref+'2',
            "we" : tcpref+'3',
        }

        g.message("Calculating Cap Tassellation
indices")
        g.mapcalc(tca_expr % comp, overwrite =
True)
        #g.mapcalc(lnmwe_expr % comp, overwrite
= True) #null() 4 We>0

    return 0
#End main
```

```
if __name__ == "__main__":  
    options, flags = g.parser()  
    sys.exit(main())
```


The management and conservation of threatened animal populations require accurate knowledge on their distribution and abundance. At the same time, knowledge on the factors driving changes and fluctuation in distribution and abundance is also critical. Nevertheless, gaining such insight is especially challenging for species living in patchy and fragmented landscapes, as is the case for most mammals in tropical forests.

This thesis addressed these issues by developing and validating analytical frameworks that allow to make robust spatial inference on population abundance, and ultimately aimed at gaining knowledge on the conservation status of selected mammal species in the rainforest of the Udzungwa Mountains of Tanzania, with emphasis on arboreal primates. This area is an outstanding hotspot for biodiversity and endemism at continental level and it is especially important for primates. Results of the research project were used to provide management recommendations for the conservation of target species and of the environment these inhabit, which is undergoing rapid and critical modifications through habitat depletion and fragmentation.

Nathalie Cavada - Born in Bolzano (BZ) in 1986, she holds a degree in Biological sciences (2008) from the University of Bologna and a Master degree in Biology of animal behaviour (2013) from Florence University. She's been focusing on the ecology of primates since year 2010, when she got involved in a rehabilitation and post-release monitoring programme of howler monkeys (*Alouatta pigra*), in the forests of Belize. In 2014 she started a PhD at the University of Trento and in collaboration with the Tropical Biodiversity section at MUSE. Her research interests focus on the ecology and conservation of three primate arboreal species of the Udzungwa Mountains in Tanzania, integrating the analysis on ground collected data with remote sensing and GIS techniques.