

RESEARCH ARTICLE

A Multi-Species Occupancy Modelling Approach to Access the Impacts of Ecological Covariates on Terrestrial Vertebrates in a Tropical Hotspot in Central, Cameroon

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Received: 20 January 2025 | **Revised:** 7 April 2025 | **Accepted:** 8 April 2025

Funding: This work was supported by Aspire Grant Program, Idea Wild Foundation, Primate Action Fund, Primate Conservation Incorporated Grant (PCI), Society for Conservation Biology.

Keywords: camera trapping | covariates | detection probability | generalised linear model | mammal community | multi-species occupancy | species richness | transitional zone

ABSTRACT

Mammalian communities living in tropical forests, particularly those in ecological transition zones, are under constant threat from human activities. In many regions, baseline data on mammal richness, occupancy, detection probability and the environmental factors that influence these metrics are lacking. As a key metric for guiding conservation decisions, species richness can be underestimated due to varying detection probabilities, leading to species being overlooked. Advances in technology and methodology have revolutionised wildlife monitoring, fostering the increase of multi-species occupancy models (MSOMs) for efficient studies of community, shifting focus from single species to entire communities. MSOMs, hierarchical models that share information across species via random effects, address imperfect detection to provide accurate and unbiased species richness estimates. To fill this information gap, we used camera trap data from Mpem and Djim National Park, Central Cameroon. We used generalised linear models and a model selection approach to evaluate factors affecting species detection events. Similarly, we used MSOMs within a Bayesian hierarchical framework to evaluate our initial species richness estimate at each camera trap location and to understand the influence of environmental covariates on the occupancy and detection probability of 19 vertebrates recorded in the area to inform management decisions for these species. From 915 independent photographic events obtained over 1700 days of capture, the study results highlight the importance of habitat, distance to river, normalised difference vegetation index and topographic position index (TPI) in explaining patterns of detection events. We found that forest (GLM: B 0.31, IRR 1.36, CI 0.14–0.48, $p < 0.001$), NDVI (GLM: B 0.31, IRR 1.36, CI 0.21–0.41, $p < 0.001$) and TPI (GLM: B 0.17, IRR 1.19, CI 0.08–0.26, $p < 0.001$) were positively associated with species detection events, whereas distance to river (GLM: B –0.19, IRR 0.83, CI 0.027 to (–0.11), $p < 0.001$) was negatively associated with species detection events. However, the mean probability of community occupancy was 0.33 ± 0.10 [2.5%–97.5% CI: 0.17, 0.54], while the mean probability of community detection was 0.07 ± 0.02 [2.5%–95% CI: 0.04, 0.12], indicating that, on average, approximately 33% of the sites are likely to be occupied by the community of interest, with a 7% probability of detection at occupied sites. After accounting for imperfect detection, the maximum occupancy and detection probability estimated from the MSOMs were 0.88 ± 0.07 (2.5%–97.5% CI: 0.71–0.98) and 0.22 ± 0.2 (2.5%–97.5% CI: 0.18–0.27) for *Philantomba monticola*, respectively. Globally, the community responses were close to zero and relatively weak, probably due to mixed responses at the species level. Despite their weak effect, distance to road (β : -1.53 ± 1.97 [2.5%–97.5% CI: -1.72 – 5.62])

and NDVI ($\beta: -0.09 \pm 0.22$ [2.5%–97.5% CI: -0.50 – 0.38]) had a negative significant effect on occupancy. However, there were significant responses at the species level with *Cephalophus nigrifrons*, for example, exhibiting a strong response to NDVI. This study contributes to baseline information on the ecology of mammal communities in Central Cameroon and supports the need for future multi-season surveys to understand the influence of temporal factors on community occupancy and richness in the area.

1 | Introduction

Assessments of future global change predict that biodiversity will continue to decline (Pereira et al. 2010). In face of this rapid loss of global biodiversity, efficient monitoring will be essential for reliable population estimates and trend assessments (Bessone et al. 2020), in order to improve conservation management and reduce biodiversity loss, thus ensuring the future well-being of our planet and humanity (Ahumada et al. 2013). Monitoring is an essential task for conservation strategies as it provides comprehensive information on the spatial distribution of species, their abundance and their relationship with environmental factors (Clément et al. 2014). However, the distribution of mammals species in many African sites specially in transitional landscape such as Forest-Savannah Mosaic (hereafter, FSM) is spatially and temporally heterogeneous (Graham and Duda 2011). Wildlife monitoring in FSM, is crucial not only for assessing species distribution, but also as a critical conservation tool (Hedwig et al. 2018). Mosaic habitats, comprising patches of varying land cover types such as savannah and open or closed canopy forests (Pletcher et al. 2022), are vital for biodiversity conservation. Their diverse structure creates a hotspot that supports species by offering a range of resources and conditions essential for survival and reproduction (Araújo 2002; Hitchman et al. 2018). Unfortunately, environmental changes caused by a growing human population and their heavy reliance on forest resources for subsistence and protein needs, expansion of agricultural land, destruction of wildlife habitats (Fa et al. 2003), as well as poaching, deforestation and urbanisation (Bakala and Mekonen 2021), have seriously affected biodiversity. Among the species affected are terrestrial vertebrates. They are a very diverse group, including ungulates, pholidotes, rodents, primates and carnivores. They play an important role in ecosystem regulation. Some are seed dispersers or primary producers (e.g., herbivores), while others are predators or can be the prey of others (Jansen et al. 2010; Suárez-Tangil and Rodríguez 2021). Their local extirpation can cause severe disturbances in the overall ecosystem functioning and equilibrium (Diplock et al. 2018). Face of these threats, McNamara et al. (2011) state that an organism's adaptive plasticity, or ability to adapt to new environments, is essential for the long-term survival and success of wildlife populations. To inform conservation decisions, such a population needs to be monitored (Nichols and Williams 2006) and its abundance or richness inferred with a good precision and low bias. This is particularly useful for populations living in the FSM, as such areas show high vulnerability to human disturbance, including climate change (Parmesan 2006). Therefore, monitoring should be useful for an adaptive conservation goal (Caravaggi et al. 2017). Various methods have been used by researchers and conservationists to monitor wildlife, including opportunistic surveys, line transects, standing crop nest counts, etc. (see Buckland 2001 and Fotsing et al. 2025). However, due to their automated, non-intrusive monitoring capabilities, low cost and efficiency, camera traps, acoustic recorders and similar devices have been widely used in wildlife monitoring.

They are particularly valuable for studying the occupancy, detection probability, distribution, abundance (species richness) and behaviour of mobile species (Caravaggi et al. 2017; Fotsing, Kamkeng, and Zinner 2024; Fotsing et al. 2025; Sollmann 2018). Furthermore, camera trap data provide an opportunity to model the ecological state variable of interest (e.g., abundance or probability of species occurrence) while accounting for the detection process (e.g., the probability of detecting a species given that it occurs at the site; Ahumada et al. 2013).

In practice, inferring these biological characteristics is challenging due to detection biases that vary across recording locations (Azzou et al. 2021), species, observers and survey methods (Iknyan et al. 2014). For example, animals are more likely to trigger camera traps in open savannah than in dense rainforest (Azzou et al. 2021). As a result, differences in recording rates (i.e., photographic rates) may indicate variations in local abundance and/or detection probabilities (reviewed by Burton et al. 2015; Sollmann 2018). It is therefore critical to account for the variability in detection rates between sites when comparing, for example, species densities (Azzou et al. 2021). Another important question behind such inferences is whether or not a particular site is occupied by a focal species. However, while the detection of a species implies its presence, the absence of a record does not necessarily mean that the species is absent. This raises the problem of imperfect detection, which must also be taken into account during inference (MacKenzie et al. 2004). Variants of occupancy models commonly used in the literature to make these inferences include detection probabilities explicitly (MacKenzie et al. 2002), while others assume that detection probabilities are constant across sites or, more commonly, that they are a function of environmental covariates governed by hierarchical parameters (MacKenzie et al. 2002). The influence of environmental and/or ecological factors must also be taken into account when making such inferences. These factors are known to influence species richness, abundance and distribution (MacKenzie 2018; Sollmann 2018). For example, terrain influences the distribution of water and therefore the distribution of species. Similarly, higher elevation with lower temperature has been acknowledged to be a suitable area for species during the dry season (Mugerwa et al. 2012). As an ecological transition zone located in Central Cameroon, the Mpem and Djim National Park (hereafter MDNP) is mainly characterised by FSM, which hosts important biodiversity hotspots, including several flagship species (Fotsing, Kamkeng, Marcel Senge, et al. 2024; Fotsing, Kamkeng, and Zinner 2024; Fotsing et al. 2025). After the publication of some preliminary studies (see Fotsing, Kamkeng, Marcel Senge, et al. 2024; Fotsing, Kamkeng, and Zinner 2024; Fotsing et al. 2025), there is still a gap in our knowledge regarding the influence of environmental covariates on detection events and community occupancy of vertebrates occurring in the area. This knowledge gap at the local level limits the ability of local conservationists to accurately implement conservation actions in the area.

Over the past decade, most monitoring efforts have focused on single species and sometimes on flagship species of conservation interest, likely due to the resource-intensive nature of wildlife monitoring and limited advancements in statistical and computational tools for handling ecological data (Devarajan et al. 2020). As concern grows about the impact of global change on community composition, information at the community level is becoming increasingly important. Consequently, filling the above gap may be an essential step in advancing ecological understanding and effective conservation management at the local level. At the same time, advances in statistics and the increasing availability of cross-taxon data now facilitate community-scale analyses (Devarajan et al. 2020). In recent years, statistical methods exploring key aspects of community ecology have advanced rapidly (Iknayan et al. 2014; Jarzyna and Jetz 2016; Ovaskainen et al. 2017). Among these methods, several models have incorporated imperfect detection and spatial variation in detectability and occurrence patterns (Dorazio and Royle 2005; Zipkin et al. 2010). For example, hierarchical models, such as multi-species occupancy models (hereafter, MSOMs), are useful for examining the effects of explanatory variables at multiple levels of organisation (Bajaru et al. 2020). MSOMs (e.g., Royle and Dorazio 2008) are based on detection and nondetection data of multiple species across different sites (Bajaru et al. 2020) and provide a practical framework for ecological decision making. It also incorporates habitat covariates to predict occupancy under different scenarios, account for uncertainty in predictions, and enable the estimation of total occupancy across species for conservation planning. MSOMs are particularly useful for inferring the occupancy of rare species, which have very few observations and whose occupancy cannot be inferred separately. Providing wildlife managers with occupancy inferences for these rare species will help them evaluate responses to different management practices, as we have seen in the United States National Park (Zipkin et al. 2010). Many studies have therefore highlighted the robustness, explicit parametric framework, high accuracy, low uncertainty in parameter estimation and easy inclusion of multiple scales in MSOMs (Alexiou et al. 2024; Bajaru et al. 2020; Dorazio and Royle 2005; Ghimirey et al. 2024; Gorczynski et al. 2023). Application of MSOMs analysis would provide an important picture of the status of the mammalian community in MDNP. This would also help to facilitate future research and conservation initiatives in the area as well as encourage replication in other regions of the country.

Considering the above, no other studies to date have used CTs to (1) understand factors affecting species detection events of the vertebrate community in MDNP and (2) apply MSOMs to measure detectability and occupancy, as well as to assess environmental determinants of the vertebrate community in MDNP. This study aims to fill this knowledge gap by using CTs data from MDNP to address the following key research questions: (i) What environmental covariates correlate with vertebrate detection events, occupancy, and detection probability in MDNP? (ii) How do MSOMs (within a Bayesian hierarchical modelling framework) improve estimates of species-specific occupancy and detection probability? (iii) How do environmental and anthropogenic factors influence species richness at CTs locations? (iv) How do environmental covariates, specifically habitat characteristics (e.g., forest cover and NDVI) affect detection probability and occupancy? (vi) What is the effect of distance to water,

effort and distance to human infrastructure (village, road) on vertebrate occupancy and detection probability? Based on previous studies (e.g., Ghimirey et al. 2024; Mackenzie et al. 2017; Teixeira-Santos, Ribeiro, et al. 2020; Teixeira-Santos, Graipel, et al. 2020), we predict that species richness will vary across CTs locations due to imperfect detection. Additionally, we expect that occupancy estimates will be underestimated if imperfect detection is not accounted for. Given the transitional nature of the landscape, we predict that habitat characteristics, specifically forest cover and Normalised Difference Vegetation Index (NDVI) will be positively correlated with vertebrate detection events, detection probability and occupancy. Furthermore, as the site hosts elusive mesocarnivores (see Fotsing, Kamkeng, and Zinner 2024), we anticipate that survey effort will be positively correlated with occupancy and detection probability. Finally, we hypothesise that distance to the nearest water source, effort and proximity to villages will positively correlate with vertebrate detection events and occupancy, while proximity to roads will have a negative effect.

2 | Methods

2.1 | Study Area

The study was conducted in the Mpem and Djim National Park (MDNP, 5°00'–5°20' N, 11°30'–12°00' E) in the Central Region of Cameroon (Ntui Division; Figure 1). MDNP was established in 2004 (Law No. 2004/0886/PM). The park covers 974.8 km², with an average altitude of 640 m above sea level (Fotsing, Kamkeng, Marcel Senge, et al. 2024). The park lies in the northern Congolian FSM, which is home to both forest and savannah species (Fotsing, Kamkeng, and Zinner 2024). The annual minimum and maximum temperatures in the park are 22.9°C and 29.1°C, respectively. The average annual rainfall is 1500 mm (Fotsing, Kamkeng, Marcel Senge, et al. 2024). The climate is a classic Guinean type with four seasons: a long dry season (from mid-November to mid-March); a long rainy season (from mid-March to the end of June); a short dry season (from July to August) and a short rainy season (from September to mid-November (Santoir and Bodba 1995)).

2.2 | Classification of Habitats

MDNP supports a diverse range of vegetation types (Donfack 2021) including open savannah, woodland savannah (WS), grassland savannah (GS), old secondary forest (SF), permanently inundated swamp forest (PISF), young mixed secondary forest (YMSF), savannah forest transition zone and gallery forest. Following the approach of Fotsing, Kamkeng, Marcel Senge, et al. (2024), these habitats were classified into two broad categories of habitat class as follows: (1) forest that includes Near Primary Forest (NPF), Secondary Forest (SF), old secondary forest (OSF), permanently inundated swamp forest (PISF), and young mixed secondary forest (YMSF) and (2) Savannah (SAV) that includes Gallery Forest, woodland savannah (WS) and grassland savannah (GS); see Fotsing, Kamkeng, Marcel Senge, et al. (2024) for more details. A detailed description of each type of habitat, along with their dominant plant species, can be found in Donfack (2021), which provides a comprehensive botanical

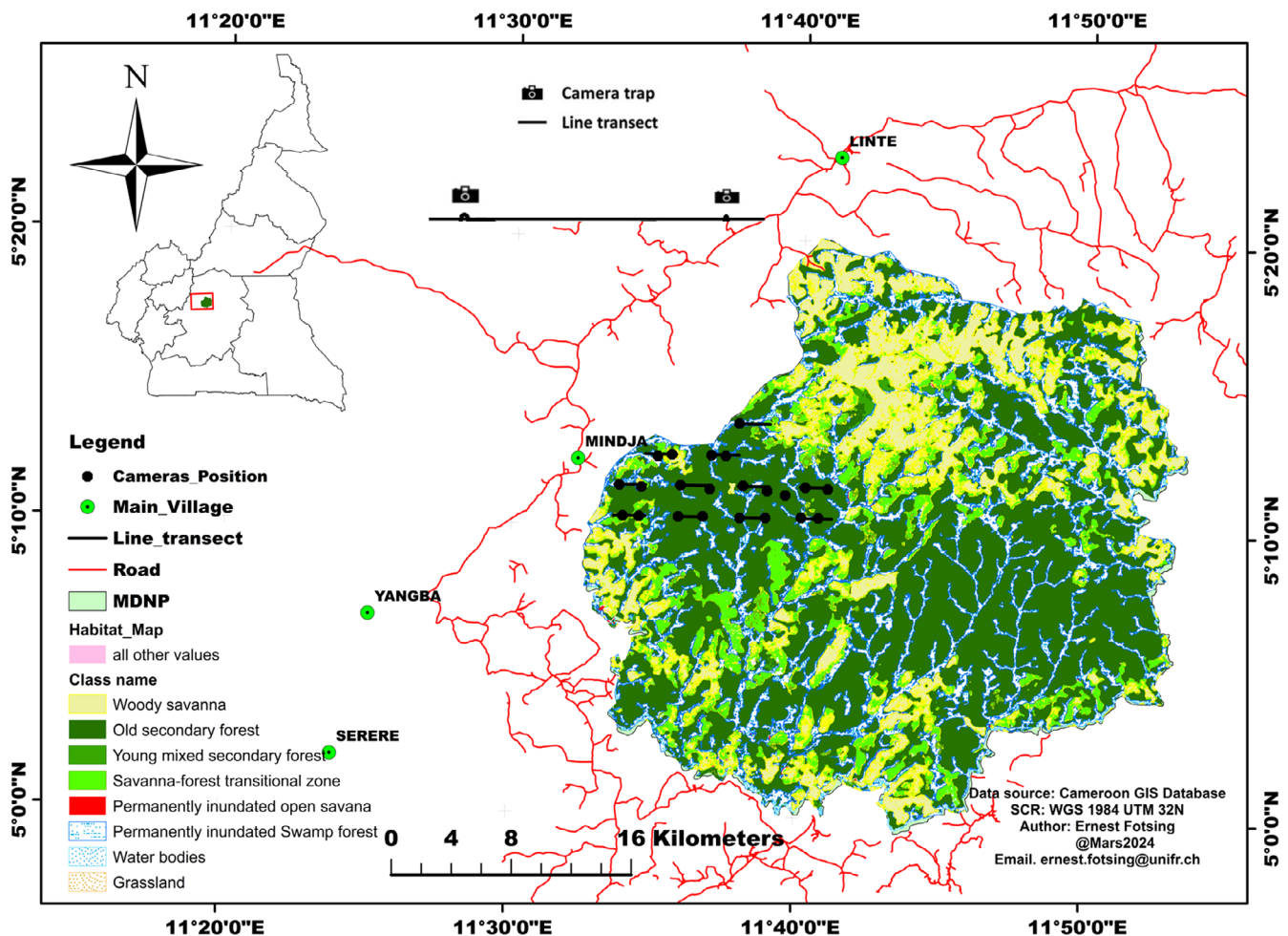


FIGURE 1 | Map of the Mpem and Djim National Park in central Cameroon with the position of 11 line transects (black lines) and the positions of the camera traps (black dots) along the lines. Top left inset map of the Republic of Cameroon with the park in the red frame.

inventory of MDNP. For more details on the classification system, see also Fotsing, Kamkeng, Marcel Senge, et al. (2024).

2.3 | Data Collection

2.3.1 | Camera Trapping

The study was conducted during the dry season between 16.09.2021 and 11.12.2021. We deployed 22 camera traps (CTs; Bushnell Trophy Trail Camera 20MP, infrared, Model 119717CW) along 11 line transects of a 2-km length each in the western part of the MDNP. The transects ran in the east–west direction and were evenly spaced by a 2-km distance, partly in parallel or in a row (Figure 1). Two CTs with an angle of view $\theta = 45^\circ$ were set at 250 and 1750 m from the western start point of each transect. CTs spent approximately 3 months (81 ± 7 days) at each of the 22 locations. To avoid any disturbance caused during data collection along the transects, cameras were systematically positioned 50 m to the north or south of the transect line, oriented north between 40 and 50 cm above the ground (Bessone et al. 2020). The cameras were set with motion sensors on high sensitivity (to increase detection), continuous triggering, that is, 60-s interval between consecutive videos, and the picture quality was set at high resolution (20 mega pixels). The date, habitat

and time for each camera were recorded during the installation (Figure 1).

2.3.2 | Environmental Covariates

To model detection events of species within the study area, we used 13 covariates which include biotic and abiotic variables (see Table 1 for covariates description), including habitat and effort, obtained during data collection and slope, elevation, TPI, terrain ruggedness index (TRI), distance to river (nearest water source), distance to road and distance to village, derived from a variety of sources using remote sensing. First, we obtained topographic data in GeoTIFF format by calculating TPI, TRI and slope in R (V.4.4.2) using digital elevation model (DEM) data from the Shuttle Radar Topography Mission 30-m resolution Digital Elevation Model (Jarvis 2008). Similarly, from the Bioclim website (Fick and Hijmans 2017), we obtained GeoTIFF files of solar radiation (Srad), annual mean temperature (BIO1), Temperature Annual Range (BIO7) and Annual Precipitation (BIO12). We then projected the Coordinate Reference System (CRS) of each raster image to the CRS of our CTs location and extracted the corresponding pixel value for each location using the extract function provided by the terra package in R. Secondly, we used Google Earth images to digitise roads, rivers and villages, and

TABLE 1 | Covariates, definitions and measurements used for modelling detection events, occupancy (ψ) and detection probability (p) in MDNP.

Covariates	Acronyms	Definition	Type
Elevation	dem	Distance above sea level (m)	Continuous
Slope	Slope	Terrain slope (degree)	Continuous
TPI	TPI	Terrain position index	Continuous
Distance to village	DistVillage	Distance of camera positions to nearest village (m)	Continuous
TRI	TRI	Terrain Ruggedness index	Continuous
Distance to river	NeaDistRiv	Distance of camera positions to nearest water sources (m)	Continuous
Distance to road	DistRoad	Distance of camera positions to nearest road (m)	Continuous
Habitat	Habitat	Type of habitat at each location of cameras	Factor
NodifvegI	NDVI	Normalised difference vegetation index (NDVI)	Continuous
Temperature	Bio1	Annual Mean Temperature (°C)	Continuous
Temperature	Bio7	Temperature Annual Range (BIO5-BIO6) (°C)	Continuous
Temperature	Bio12	Annual Precipitation (mm)	Continuous
Srad	Srad	Solar radiation ($\text{kJ m}^{-2} \text{day}^{-1}$)	Continuous
Effort	Effort	Camera trap days	Continuous

then measured the distance to each feature as Euclidean distance using google engine code after we georectified the Google Earth images using GPS points collected from recognisable locations in the field, ensuring better alignment with ground data. Normalised Difference Vegetation Index (NDVI), a widely used vegetation index in ecological studies due to its correlation with biodiversity (Gould 2000; Pettorelli et al. 2011) was computed to measure vegetation greenness. To achieve this, GeoTIFF Landsat Collection 2 Surface Reflectance satellite images for the dry season (22.12.2023) were obtained from the United States Geological Survey (USGS), ensuring no cloud contamination (Vermote et al. 2016). The NDVI calculation was therefore performed in Python v3.11.0 using the formula available in (Borowik et al. 2013).

2.4 | Data Analysis

We first selected all images (videos) that contained animals and identified the species in these images. Identification was done at the species level according to morphological descriptions (e.g., body size, presence or absence of horns, colour of coat, etc.) using the second edition of the African mammals field guide (Kingdom 2016). Videos and/or images that did not contain animals or species that could not be identified were excluded from the analysis. Videos containing one or more individuals of the same species were considered as a single camera event, i.e., a single capture (Grassman et al. 2006). To correct for non-independence of observations, a threshold of 1 h was introduced in the sequence of observations of a given species where no further image was captured to avoid double counting of individual animals that remained in front of the camera (Bahaa-el-din et al. 2016; Tobler et al. 2008). After identification, we generated a detection record of all species using the camtrapR package v4.3.2 (Niedballa et al. 2016) in R V4.3.2 (Core Team 2022).

2.4.1 | Modelling Detection Event

We fitted a Generalised Linear Models (McCullagh and Nelder 1989) to model detection event (response variable) obtained for each species (species counts) as a function of covariates as described above (Table 1). Prior to the analysis, habitat type was converted into categorical factors with savannah set as a reference level to facilitate its inclusion in the modelling process. We also applied the log transformation on effort and the square root on Srad, Bio1, Bio7, Bio12, slope, TRI, TPI, dem, distance to river, distance to village, distance to road and NDVI to achieve an approximately symmetrical distribution and to avoid potentially influential cases. Similarly, we z-transformed to a mean of zero and a standard deviation of one all the continuous predictors to facilitate model convergence and achieve easier interpretable coefficients (Schielzeth and Forstmeier 2009). To avoid multicollinearity in fitting the models, we check for collinearity between predictors using the package usdm in R (Naimi et al. 2014). We also used the 'corr' function to assess the Pearson correlations setting a correlation threshold of 0.7 (Schober et al. 2018) and removed all correlated predictors with a goal to avoid fitting correlated predictors in the model.

Once model assumptions were met, we fitted a Poisson regression model with all the predictors but found evidence of overdispersion ($\hat{c} > 1$) after an overdispersion test performed using the function AER from the package AER (V.1.2.9 (Kleiber and Zeileis 2008)). To address this, we modelled the detection event using a Negative Binomial regression model using the function glm.nb from the package MASS (v. 7.3-60.2 (Venables and Ripley 2022)). We first fitted two models: (1) a full model that included all predictors along with the interaction term between habitat and NDVI and (2) a reduced model that included all predictors except the interaction term. Using a likelihood ratio test (LRT), we compared the fit of the two models (full vs. reduced). The result showed that the inclusion of the interaction

term in the full model did not significantly ($p=0.319$) improve the model fit, indicating the non-significance of the interaction term. We then applied model selection using the dredge function from the MuMin Package (Burnham et al. 2011) on the reduced model that included nine predictors and selected the top-ranking model based on Akaike's Information Criterion (AIC) (Akaike 1973) using the AIC function of the package AICcmodavg (Mazerolle 2017). After calculating the delta AIC (ΔAIC) and AIC weights (AIC_w) from the calculated AIC values, we considered the models with the lowest ΔAIC as the top-ranking model (Burnham and Anderson 2002). The top five ranking model summary is presented in Table 1 (see also the top 10 ranking model structure in Appendix S1). Following that, we assessed model performance by applying the goodness-of-fit (Gof) Chi-squared test to compare the top-ranking model with the null model which assumes no predictors but only intercept.

Once this was done, we exponentiated its coefficients to obtain incidence rate ratios (IRRs) (Kirkwood and Sterne 2003; Zou 2004), which represent the multiplicative change in the expected count of the response variable for a one-unit increase in the predictor variable. We calculated 95% confidence intervals (CIs) for the IRRs using the standard errors of the coefficients (see Table 4). Similarly, we obtained 95% CIs of model estimates and fitted values by means of a parametric bootstrap ($N=1000$ bootstraps). For model diagnostic, we checked model stability using DFBetas, which revealed the model to be of good stability. Also, we assessed the Generalised Variance Inflation Factors (Fox and Monette 1992) with a threshold set at 7 (O'Brien 2007) using the function vif of the package car (version 3.0-13; (Fox and Weisberg 2019)) and this revealed no collinearity issues ($\max(GVIF^{1/(2 \cdot Df)}=2.80)$). Residual plots, including Q-Q plots and residual vs. fitted values plots, confirmed that the model fit assumptions were reasonably met.

2.4.2 | Single Season Multi-Species Occupancy Modelling

2.4.2.1 | Covariates. Environmental covariates for the occupancy and detection component of the MSOMs were the same covariates used to model detection events as described above. To facilitate model convergence, we only included mammal species detected more than one time in the MSOM.

2.4.2.2 | Creation of Detection History Matrix. Occupancy can be determined by the presence/absence of a species at camera trap sites during a sampling session. For each camera location, we used the camtrapR package v.2.2.0 (Niedballa et al. 2016) to create a detection history (1100100), with '1' indicating species detection during the sampling event and '0' indicating nondetection (Ahmad and Gopi 2024). Detection/nondetection records for each camera station were divided into sampling occasions of 10 consecutive days to (i) minimise the risk of temporal interdependence among occasions and reduce the probability of changes in occupancy, (ii) increase the overall detection probability and (iii) prevent model convergence (Holzner et al. 2021). Following that, we use the detection matrix generated to obtain Naïve occupancy values for each species.

2.4.2.3 | Mean of Occupancy and Detection Probability Estimation. The principal advantage to fit occupancy models is that we can explicitly account for imperfect detection (Sollmann et al. 2013). Accounting for imperfect detection allowed us to calculate the probability of a species being present at a location even if it was not observed (Gorzynski et al. 2023). To estimate the mean of occupancy and detection probability for each confirmed species in the region, the MSOMs were run using Bayesian formulation in R version 4.4.2 (Core Team, 2022) using Just Another Gibbs Sampler (JAGS) via the jagsUI package (Kellner 2024). We ran three chains for 30,000 iterations of the model with a 50% iteration burn-in and retained every 2000 samples. Model results provided means of individual species occupancies and detection probabilities with their corresponding CI. We visually assessed trace plots and the Brooks–Gelman–Rubin (Rhat) convergence diagnostic (<1.05) to ensure model convergence.

Basically, we build a simple MSOM where we assume variation between species in occupancy and detection probability is normally distributed among species. This approach is conceptually similar to having a random effects term for species in a generalised linear mixed-effects model.

More specifically, we follow the ideas developed by several authors (e.g., Dorazio et al. 2010; Dorazio and Royle 2005; Kéry and Royle 2021; MacKenzie et al. 2002; Royle and Kéry 2007) to build a model where:

- Our detection history (y_i, k) is binomially distributed (0 and 1) based on the product of detection probability (p_i, k) and occupancy state (z_i, k)
- Occupancy status (0 or 1) is a Bernoulli draw from the occupancy probability (ψ_k)
- The logit of occupancy probability ($\text{logit}(\psi_k)$) is normally distributed among species with a community mean (μ_{psi}) and standard deviation (σ_{psi}).
- The logit of detection probability ($\text{logit}(p_k)$) is normally distributed among species with a community mean (μ_{lp}) and standard deviation (σ_{lp}).
- We use priors based on Beta distributions ($\alpha=1, \beta=1$) for the community means of detection and occupancy probability, which bound the estimates between 0 and 1.
- We use priors based on uniform distributions between 0 and 5 for the standard deviation of species detection and occupancy probability.

Mathematically, we follow the idea developed by James Paterson as follows:

1. $\text{logit}(\psi_k) \sim \text{Normal}\left(\mu_{\text{psi}}, \frac{1}{\sigma_{\text{psi}}^2}\right)$
2. $\mu_{\text{psi}} \sim \text{logit}(\bar{\psi})$
3. $\bar{\psi} \sim \text{Beta}(\alpha=1, \beta=1)$
4. $\sigma_{\text{psi}} \sim \text{Uniform}(\min=0, \max=5)$
5. $\text{logit}(p_k) \sim \text{Normal}\left(\mu_{\text{lp}}, \frac{1}{\sigma_{\text{lp}}^2}\right)$

6. $\mu_{lp} \sim \text{logit}(\bar{p})$
7. $\bar{p} \sim \text{Beta}(\alpha = 1, \beta = 1)$
8. $\sigma_{lp} \sim \text{Uniform}(\min = 0, \max = 5)$

2.4.2.4 | Effect Sizes on Mean of Occupancy and Detection Probability Estimation. We used a single season MSOM of Royle and Nichols (2003) to estimate occupancy probability (ψ), detection probability (p) and species richness at each recorded station (Dorazio et al. 2006; Dorazio and Royle 2005) using the detection matrix generated above while accounting for imperfect detection (MacKenzie et al. 2002). Occupancy models assume that sampling sites are independent (i.e., detection at one site does not influence detection at other sites) and that species occupancy is constant over the survey period (i.e., no colonisation or extinction; Alexiou et al. 2024). Model results also provided CI of the estimated ψ , p and species richness (at each station) as well as the effect size for both environmental variables on ψ and p . Usually, occupancy results should be interpreted as ‘site used’ rather than ‘site occupied’ (Alexiou et al. 2024). To account for uneven sampling effort in the occasions, we a priori included random effects of camera effort (total number of camera trap days) as covariates on detection probability (p). Based on the preliminary results from the detection event model above, we first ran single covariate models on occupancy to identify the meaningful covariates to include in the final model. Covariates were selected by evaluating effect sizes for each species, with 95% Bayesian confidence intervals (BCI) not overlapping zero showing strong support and 75% BCI not overlapping zero showing moderate support. Our final model included distance to nearest water source (DistRiver); distance to road (Disroad); distance to nearest village (DistVillage); camera trap days (Effort); normalised difference vegetation index (NDVI); Habitat (Forest vs. Savannah) and TPI.

2.4.3 | Statistical Modelling

We considered two processes in our workflow analysis as follows: (1) the ecological process and (2) the observation process, which were governed by Bernoulli and Binomial distributions, respectively.

The ecological process is mathematically defined by

$$z_{ik} \sim \text{Bernoulli}(\psi_{ik} \cdot w_k) \quad (1)$$

where z_{ik} indicates if site i is occupied by species k ($z_{ik} = 1$ when occupied, 0 otherwise). The occupancy probability ψ_{ik} denotes probability species k will occupy site i (dependent on-site conditions), and w_k accounts for undetected species (Ghimirey et al. 2024).

The observation process is mathematically defined by

$$y_{ik} \sim \text{Binomial}(p_k \cdot z_{ik}, n_i) \quad (2)$$

where y_{ik} is the number of times species k was observed at site i during n_i attempts to observe the species at that site. The

probability to detect species k on each attempt is given by p_k . We assumed that the probability of detection for individual species was constant across sites and occasions (Kéry and Royle 2021).

We included covariates in our model to estimate species occupancy and detection probability at each site using the logit link function.

We modelled the species occupancy using

$$\text{Logit}(\psi_{ik}) = \beta_{0k} + \beta_{1k} \cdot X_{1i} + \beta_{2k} \cdot X_{2i} + \dots + \beta_{mk} \cdot X_{mi} \quad (3)$$

Similarly, we modelled species detection probability using:

$$\text{logit}(p_{ik}) = \alpha_{0k} + \alpha_{1k} \cdot \text{Effort}_i \quad (4)$$

where β_{0k} is the intercept of the equation, defined by $\beta_{0k} \sim \text{Normal}(\mu_{0k}, \sigma_{0k}^2)$, β_{mk} is the slope associated with the site covariate m , defined by $\beta_{mk} \sim \text{Normal}(\mu_{mk}, \sigma_{mk}^2)$.

X_{mi} is the value of covariate m at site i .

p_{ik} : Detection probability of species k at site i .

α_{0k} : Intercept for species k , representing the baseline detection probability when Effort = 0.

α_{1k} : Coefficient for the effect of effort on detection probability for species k .

Effort _{i} : Covariate representing survey effort at site i .

logit (p_{ik}): Logit-transformed detection probability, where $\text{logit}(p) = \text{logit}(p_{ik}) = \log\left(\frac{p_{ik}}{1-p_{ik}}\right)$.

Priors (as typically specified in JAGS):

$\alpha_{0k} \sim \text{Normal}(\mu_{\alpha_0}, \sigma_{\alpha_0}^2)$ are hyperparameters shared across species

$\alpha_{1k} \sim \text{Normal}(\mu_{\alpha_1}, \sigma_{\alpha_1}^2)$, where μ_{α_1} and σ_{α_1} are hyperparameters for the effect of effort.

As we are also modelling the possible presence of any undetected species, we follow the ideas of Ghimirey et al. (2024) by including w_k in the equation (1) which is governed by the Bernoulli distribution:

$$w_k \sim \text{Bernoulli}(\Omega)$$

where Ω is the augmentation parameter. Indicator w_k will take the value 1 if species k is detectable, and 0 if not (Ghimirey et al. 2024). Augmentation was applied with a maximum of $n = 19$ possible undetected species, equal to the total number of species already detected. We considered this to be small enough to be biologically plausible to our study area but large enough also to not constrain the resulting species richness estimate for the area (Yamaura et al. 2011).

Species richness was obtained by: $N = \sum_{i=1}^n * w_i$

We fit the above Bayesian hierarchical model using JAGS (Plummer 2003) using the package ‘camtrapR’. As we did above, we ran three parallel Markov chains with 30,000 iterations, using a 50% iteration burn-in and thinning by 10. The convergence of the MCMC chains was assessed through visual inspection of chain mixing plots and using the Gelman-Rubin statistic (<1.1 ; Gelman et al. 2021) and Rhat (all estimates <1.01 ; Bajarú et al. 2020). We calculated the Bayesian p -value as $\Pr(\chi^2_{\text{obs}} > \chi^2_{\text{sim}})$ to measure model goodness of fit and values larger than 0.95 or smaller than 0.05 indicates a lack of fit (Bajarú et al. 2020; Gelman et al. 2021). We considered coefficients to have strong support if the 95% BCI did not overlap zero, and moderate support if the 75% BCI did not overlap zero (Bajarú et al. 2020). The effect sizes plots were created using the plotcoef function from R package camtrapR’ using ‘state’ and ‘det’ as an argument for ψ and p . The strength of the covariate effect was determined based on the credible intervals (CI; strong effect = CI without zero, moderate effect = CI contained zero but not centred on zero, weak effect = CI centred on zero) (Bajarú et al. 2020). To assess the normality of the data, we performed the Shapiro–Wilk test on the mean values of species richness at each station. Due to the non-normality ($p < 0.05$), we used the Kruskal–Wallis test to compare the mean of species richness across stations.

3 | Results

We exclude data from one CT’s site due to malfunction out of the 22 trap sites. We defined sampling effort as the total number of trapping days across all monitored habitat classes. We then used data from 21 trap sites for a total of 1700 trapping nights (81 ± 7 days; see table 1 in Fotsing, Kamkeng, Marcel Senge, et al. 2024). For more information about camera trap stations, effort, species diversity, species accumulation curve and other metrics/information, please see our previous publication Fotsing, Kamkeng, Marcel Senge, et al. (2024) and Fotsing et al. (2025).

3.1 | Average Detection Event per Habitat Class

Across habitats, the detection event varied between 1 and 283, with a mean of 180.39 ± 113.43 . However, the mean of detection events in the forest (208.48) was higher than the mean of detection events in the savannah (147.42) and the difference was statistically significant ($W = 64,731$, $p < 0.001$, Figure 2).

3.2 | Assessment of Overdispersion and Model Fit

We fitted a Poisson regression model to assess the effects of environmental variables on species detection events and evaluate overdispersion through a dispersion parameter ($\hat{\epsilon}$) using the ratio of deviance to residual degrees of freedom. This yields a value of $\hat{\epsilon} = 85$, and the formal overdispersion test confirmed significant overdispersion ($z = 30.23$, $p < 2.2e-16$) with an estimated dispersion value of 67.53, far exceeding 1, indicating substantial overdispersion in the data justifying the use of the negative binomial to account for variability in the response variable.

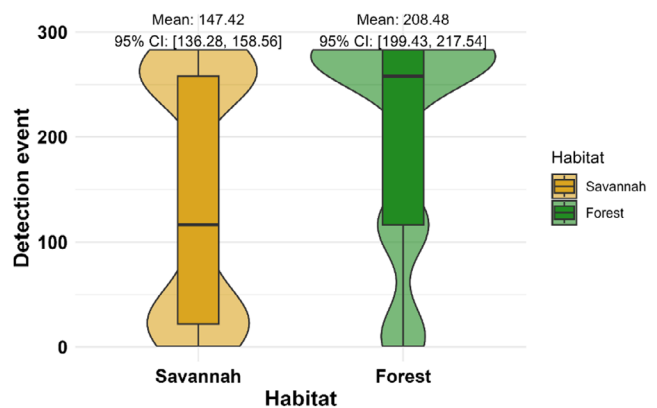


FIGURE 2 | Variation of means of detection event according to habitat. For each species, boxes show the median, upper value, lower value, 25th and 75th percentiles.

3.3 | Effect of Environmental Covariates on Detection Event

Overall, the analysis of deviance performed to compare the fit of the two negative binomial models (full vs. reduced model) predicting detection event suggests that the difference in deviance between the two models was not statistically significant (full-reduced model comparison, $LRT = 0.98$, $p = 0.32$; i.e., $p > 0.05$), indicating that adding the interaction term (Hab * NDVI) does not significantly improve the model’s ability to explain variation in species detection event.

3.3.1 | Goodness-of-Fit Test

The goodness of fit test performed to evaluate the fit of the best model (i.e., reduced model) compared to the null model yielded a highly significant result (LR statistic = 74.58, $df = 4$, $p < 2.44 \times 10^{-15}$; i.e. $p < 0.001$), indicating that the inclusion of environmental predictors significantly improved the model’s fit. This supports the importance of these variables in explaining variation in species detection events. The best model was also found to be good in stability (max $DF_{\text{beta}} = 5$) with no collinearity (max $vif = 2.94$).

3.4 | Relationship Between Species Detection Events and Covariates

Model selection was performed to evaluate the relative support for various candidate models predicting species detection events. The analysis identified model numbers 326 and 334 (see Table 2 for their structure) as the two top-ranked models having a ΔAIC_c value of zero, indicating the best fit to the data (Table 2). These top two models shared the same AIC_c value and included the predictors habitat, distance to river, normalised difference vegetation index, TPI and distance to road models and had the same AIC_w of 0.1496, reflecting their equal likelihood as the best fit. Since model 326 includes fewer predictors ($K = 6$) and ecologically meaningful predictors (habitat, distance to river, NDVI, TPI) compared to model 334, and following the principle of parsimony (Burnham et al. 2011; Forstmeier and Schielzeth 2011), which stated that simpler

TABLE 2 | Model selection using Akaike's Information Criterion (AIC).

Model number	Model structure	<i>K</i>	logLik	AICc	Δ AICc	AIC ω
326	Event ~ Hab + z.s.DistRiver + z.s.NDVI + z.s.TPI + 1	6	5630.705	11,273.50	0	0.149630
334	Event ~ Hab + z.s.DistRiver + z.s.DistRoad + z.s.NDVI + z.s.TPI + 1	6	−5630.705	11,273.50	0	0.149630
330	Event ~ Hab + z.s.DistRoad + z.s.NDVI + z.s.TPI + 1	6	−5630.705	11,273.50	5.46E-11	0.149630
346	Event ~ Hab + z.s.DistRoad + z.s.Distvillage + z.s.NDVI + z.s.TPI + 1	7	−5630.182	11,274.48	0.986087	0.091388
342	Event ~ Hab + z.s.DistRiver + z.s.Distvillage + z.s.NDVI + z.s.TPI + 1	7	−5630.182	11,274.48	0.986087	0.091388

Note: The best-performing models (326) having the delta AICc value of zero. Columns indicate the number of parameters in the model (*K*), negative log-likelihood (logLik), the difference between the AICc values and the top-ranked model (Δ AICc), and the AICc model weights (AIC ω). The best models are in bold.

TABLE 3 | Summary of all significant predictor variables.

GLM output							DFBeta	
Fixed effect	<i>B</i>	SE	<i>t</i> -value	<i>p</i>	conf.low	conf.high	Min	Max
(Intercept)	4.99	0.06	85.99	0***	4.88	5.10	4.984	5
HabForest	0.31	0.09	3.39	$p < 0.001$	0.14	0.48	0.29	0.32
DistRiver	−0.19	0.04	−4.57	$p < 0.001$	−0.27	−0.11	−0.20	−0.18
NDVI	0.31	0.05	6.10	$p < 0.001$	0.21	0.41	0.306	0.319
TPI	0.17	0.05	3.51	$p < 0.001$	0.08	0.26	0.168	0.18

Abbreviations: *B*, estimate; Distriver, distance to nearest water source; HabForest, habitat (Forest vs. Savannah (Savannah was used as reference level)); NDVI, normalised difference vegetation index; TPI, topography position index. ***mean that the intercept is statistically significantly different from zero.

TABLE 4 | Summary of incidence rate ratios (IRR).

Fixed effect	<i>B</i>	IRR	Lower_95_CI	Upper_95_CI	<i>p</i>
(Intercept)	4.99	147.19	131.36	164.93	0
HabForest	0.31	1.36	1.14	1.63	0.00069032
DistRiver	−0.19	0.83	0.77	0.90	4.9645E-06
NDVI	0.31	1.36	1.23	1.51	1.0694E-09
TPI	0.17	1.19	1.08	1.31	0.00044604

Abbreviations: *B*, estimate; IRR, incidence rate ratio.

models are preferred if they explain the data adequately, we choose as our best model 326 even if we acknowledge the fact that models 1–10, as you can see in Appendix S1, can also be considered as competing models and therefore can provide reasonable fit to the data due to the fact that their Δ AICc values are ≤ 2 (Burnham et al. 2011). For a detailed breakdown of model structure, parameter count (*K*), log-likelihood (logLik) and AIC metrics, see Appendix S1.

Overall, the best model results highlight the importance of habitat, distance to river, normalised difference vegetation index and TPI in explaining patterns of detection events (Table 3). In fact, compared to the savannah, forest (GLM: *B* 0.31, IRR 1.36, CI 0.14–0.48, $p < 0.001$, Tables 2 and 3) was positively associated with species detection events, suggesting

that a one-unit increase in forest habitat is associated with a 36% increase in species detection events. Similarly, distance to river (GLM: *B* −0.19, IRR 0.83, CI 0.0.27 to (−0.11), $p < 0.001$, Tables 3 and 4) exhibited a negative correlation with species detection events while NDVI (GLM: *B* 0.31, IRR 1.36, CI 0.21–0.41, $p < 0.001$, Tables 2 and 3) and TPI (GLM: *B* 0.17, IRR 1.19, CI 0.08–0.26, $p < 0.001$, Tables 3 and 4) were positively associated with species detection events. These results suggest that (1) a one-unit increase (e.g., one meters) in distance from the river is associated with a 17% decrease in species detection events (Since the coefficient is negative detection event decreases as the distance from the river increases), (2) a one-unit increase in NDVI (vegetation index) is associated with a 36% increase in species detection events and, (3) one-unit increase in TPI is associated with a 19% increase in species

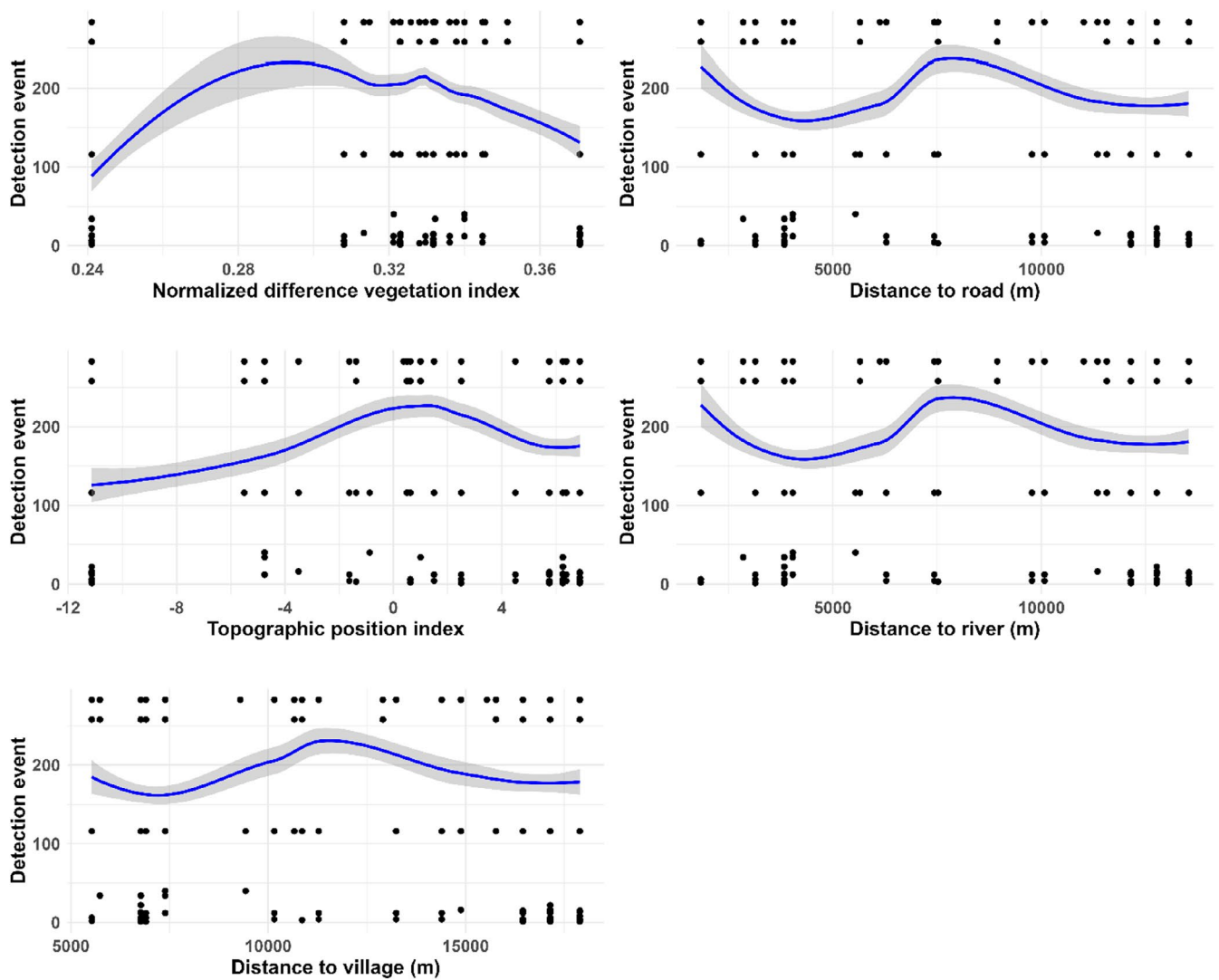


FIGURE 3 | Relationship between species detection events and environmental covariates.

detection events. The relationship between all the predictors and the species detection events was plotted and is displayed in Figure 3.

3.5 | Mean of Species Richness

We observed a great variability in the species richness according to station (Figure 4). However, the mean species richness estimated by the model was 6.9 ± 2.27 . The Shapiro–Wilk test indicated a significant deviation from normality in the data (i.e., mean species richness; $W=0.884$, $p=0.021$). Consequently, the Kruskal–Wallis test was applied, which showed no significant differences in the mean of species richness among the stations ($\chi^2=19$, $df=19$, $p=0.457$).

3.6 | Community and Species-Specific Occupancy and Detection Probability

The mean community occupancy probability was 0.33 ± 0.10 [2.5%–97.5% CI: 0.17, 0.54] (Table 5) which indicates that, on average, approximately 33% of the sites are likely to be occupied

by the community of interest. However, the 2.5%–97.5% credible interval (CI) for this estimate [0.17, 0.54] suggests that the true mean occupancy probability is likely between 17% and 54%. This range reflects the uncertainty in the estimate, where a narrower interval would imply higher confidence in the estimated mean. The mean community detection probability was 0.07 ± 0.02 [2.5%–95% CI: 0.04, 0.12] indicating that the likelihood of detecting the community of interest at a site, given it is occupied, is 7% on average (Table 5). The 2.5%–95% CI for this estimate [0.04, 0.12] means that the true mean detection probability is likely between 4% and 12%. This low detection probability might therefore imply challenges in observing or recording the presence of the community, even in occupied sites.

The naïve occupancy, the detection and occupancy probability obtained differed greatly between species. However, the naïve occupancy ranked between 0.05 for *Potamochoerus porcus* to 0.95 for *Philantomba monticola*. After considering the imperfect detection, the maximum probability of occupancy as estimated via the MSOMs was 0.88 ± 0.07 (2.5%–97.5% CI: 0.71–0.98) for *Philantomba monticola*, and the lowest was 0.13 ± 0.07 (2.5%–97.5% CI: 0.03–0.30) for *Cephalophus nigrifrons* (Table 5, Figure 5). Similarly, the maximum estimated detection probability via the

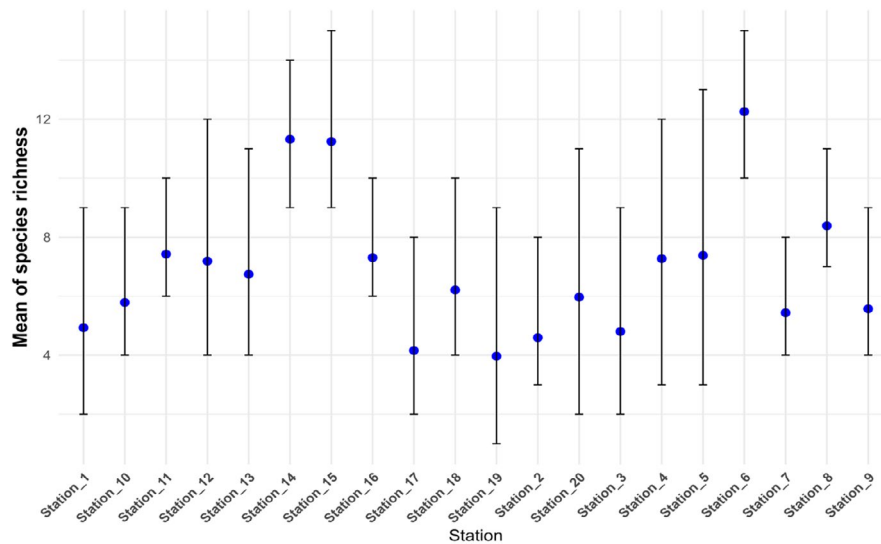


FIGURE 4 | Mean estimate of species richness at each station in the region along with 97.5% CI.

MSOM was 0.22 ± 0.2 (2.5%–97.5% CI: 0.18–0.27) for *Philantomba monticola* and the lowest was 0.03 ± 0.2 (2.5%–97.5% CI: 0.01–0.09) for *Potamochoerus porcus* (Table 4, Figure 5). In fact, it is worth noting that the occupancy and detection estimates for the endangered chimpanzees were 0.31 ± 0.21 (97.5% CRI: 0.05–0.84) and 0.04 ± 0.03 (2.5%–97.5% CI: 0.01–0.10), respectively (Table 5, Figure 5). More details about all species occupancy, detection probability associated with their 2.5%, 25%, 50%, 75% and 97.5% CI can also be found in Appendix S2.

3.7 | Covariates' Influence on Occupancy and Detection Probability

Overall, responses varied with each covariate (Figure 6). In general, community responses were close to zero, probably due to mixed responses at the species level (Figure 6). Overall, the community influence of covariates on detection and occupancy was relatively weak (Figure 6). In fact, despite their weak effect, distance to road (β : -1.53 ± 1.97 [2.5%–97.5% CI: -1.72 to 5.62]) and NDVI (β : -0.09 ± 0.22 [2.5%–97.5% CI: -0.50 to 0.38]) had a negative significant effect on the probability of species community occupancy, with occupancy probability decreasing with increasing vegetation and distance to road, while the effect of other covariates on occupancy and detection was positive (Table 6). However, there were significant responses at the species level (Figure 6). *Cephalophus nigrifrons*, for example, exhibited a strong response to NDVI (Figure 6), with a tendency of its occupancy probabilities to be lowest in areas with greener vegetation (Figure S1). Similarly, we found a moderate response of the distance to nearest water source for several species including *Atherurus africanus*, *Bdeogale nigripes*, *Civettictis civetta*, *Genetta servalina*, *pan troglodytes ellioti*, *Phatginus tricuspis* and *Potamochoerus porcus*, with a tendency of occupancy probabilities to be higher with increasing distance to nearest water source for these species (Figure S2). However, effort had a moderate effect on *Cephalophus callipygus* and *Papio Anubis* detection and occupancy probability (Figure 7A,B) with a tendency of occupancy and detection probability to be higher with increasing effort (Figure 7A,B). In contrast, the occupancy of species

like *Xenogale naso* and *Guttera plumifera* decreased with increasing effort (Figure 7A). Globally, effort had a positive effect on detection probability as it increased with increasing effort for all species (Figure 7B). Similarly, the TPI exhibited a negative significant effect on *Atherurus africanus* and *Cephalophus dorsalis* occupancy probability, with a tendency for occupancy probabilities to be lowest with increasing TPI for these species (Figure S3). Figures S4–S7 show the effect of other covariates on species occupancy.

4 | Discussion

Species richness, defined as the total number of species in an area (or the number of detection event) at a given time for a particular species, is a key indicator of biodiversity (Chaudhary et al. 2022). Its importance as a conservation metric has made it a focus of many ecological studies, which often estimate richness using methods like species accumulation curves, distributions, or nonparametric estimators (Weber et al. 2004). However, due to imperfect detection, fully documenting all species during surveys is nearly impossible, leaving many species undetected (Iknayan et al. 2014; Nichols et al. 1998). MSOMs incorporate imperfect detection within their statistical framework, making them an ideal tool to estimate species richness (Doser et al. 2022; Kéry and Royle 2008; Meyer et al. 2011) and occupancy while taking into account the effect of environmental factors (Alexiou et al. 2024; Bajarú et al. 2020; Kéry and Royle 2008; MacKenzie et al. 2002; Ovaskainen et al. 2017). However, despite the well-established impact of environmental factors on mammalian species abundance, no studies using MSOMs have been made to understand these influences on species occurrence in the MDNP region, which is an important repository of mammalian assemblage (Fotsing, Kamkeng, Marcel Senge, et al. 2024; Fotsing, Kamkeng, and Zinner 2024; Fotsing et al. 2025). To help fill this gap in the literature, we undertook the current studies, and the main objectives were to (1) assess factors that shape vertebrates' detection events and (2) apply MSOMs with a Bayesian framework to evaluate community responses and environmental variables.

TABLE 5 | Estimated occupancy and detection probability for each recorded species in the region along with CI and Rhat estimate.

	Ψ (mean)	Occupancy (Ψ)					p (mean)	Detection probability (p)				
		0.33	SD	2.5%	97.5%	Rhat		0.07	SD	2.5%	97.5%	Rhat
			0.10	0.17	0.54	1.000			0.02	0.04	0.12	1.00
			Ψ						p			
Naive occupancy												
<i>Potamochoerus porcus</i>	0.05	0.22	0.19	0.02	0.75	1.006		0.04	0.03	0.00	0.13	1.00
<i>Papio anubis</i>	0.1	0.15	0.09	0.03	0.36	1.000		0.12	0.05	0.04	0.24	1.00
<i>Atherurus africanus</i>	0.1	0.15	0.08	0.03	0.35	1.001		0.13	0.05	0.04	0.24	1.00
<i>Civettictis civetta</i>	0.1	0.20	0.13	0.04	0.56	1.003		0.08	0.04	0.02	0.17	1.00
<i>Cercopithecus nictitans</i>	0.1	0.30	0.21	0.05	0.85	1.016		0.04	0.03	0.01	0.11	1.00
<i>Phataginus tricuspis</i>	0.1	0.25	0.17	0.05	0.72	1.005		0.05	0.03	0.01	0.14	1.00
<i>Cephalophus nigrifrons</i>	0.1	0.13	0.07	0.03	0.30	1.000		0.22	0.07	0.11	0.37	1.00
<i>Pan troglodytes ellioti</i>	0.1	0.31	0.21	0.05	0.84	1.012		0.04	0.03	0.01	0.10	1.01
<i>Smutsia gigantea</i>	0.1	0.24	0.18	0.05	0.77	1.006		0.05	0.04	0.01	0.14	1.00
<i>Genetta servalina</i>	0.15	0.19	0.09	0.06	0.39	1.001		0.13	0.05	0.06	0.23	1.00
<i>Bdeogale nigripes</i>	0.15	0.28	0.16	0.07	0.73	1.001		0.06	0.03	0.02	0.13	1.00
<i>Orycteropus afer</i>	0.15	0.27	0.15	0.07	0.68	1.001		0.06	0.03	0.02	0.14	1.00
<i>Genetta maculata</i>	0.15	0.40	0.22	0.09	0.92	1.005		0.03	0.02	0.01	0.09	1.00
<i>Cephalophus callipygus</i>	0.15	0.24	0.13	0.06	0.59	1.006		0.08	0.04	0.02	0.16	1.00
<i>Caracal aurata</i>	0.2	0.48	0.21	0.15	0.93	1.005		0.03	0.02	0.01	0.08	1.01
<i>Xenogale naso</i>	0.25	0.40	0.17	0.15	0.83	1.006		0.06	0.03	0.02	0.12	1.00
<i>Guttera plumifera</i>	0.6	0.66	0.13	0.41	0.91	1.002		0.10	0.02	0.06	0.15	1.00
<i>Cephalophus dorsalis</i>	0.8	0.76	0.09	0.57	0.92	1.000		0.19	0.02	0.15	0.24	1.00
<i>Philantomba monticola</i>	0.95	0.88	0.07	0.71	0.98	1.000		0.22	0.02	0.18	0.27	1.00

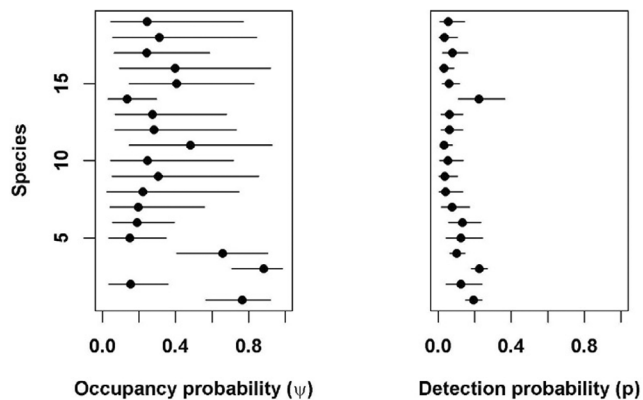


FIGURE 5 | Species-specific occupancy and detection probabilities with confidence intervals.

As predicted, we were able to identify important environmental covariates that influence vertebrate detection events, occupancy and detection probability in MDNP. Our study showed that habitat, NDVI and TPI were positively correlated with species detection events, while distance to rivers was negatively correlated. The competing models show a positive correlation between distance to roads and species detection events in line with the results of Vanthomme et al. (2013) in Gabon, who argued that the construction of roads facilitates access to the park for hunters, and hunting tends to decrease with increasing distance to settlements. However, Koerner et al. (2018) showed that the effect of human-related factors varied significantly between species. Consistent with the study of Diriba et al. (2020) and Derebe et al. (2022), forest habitat exhibits a positive correlation with species detection events compared to savannah, suggesting high richness in the forest. The forest's high

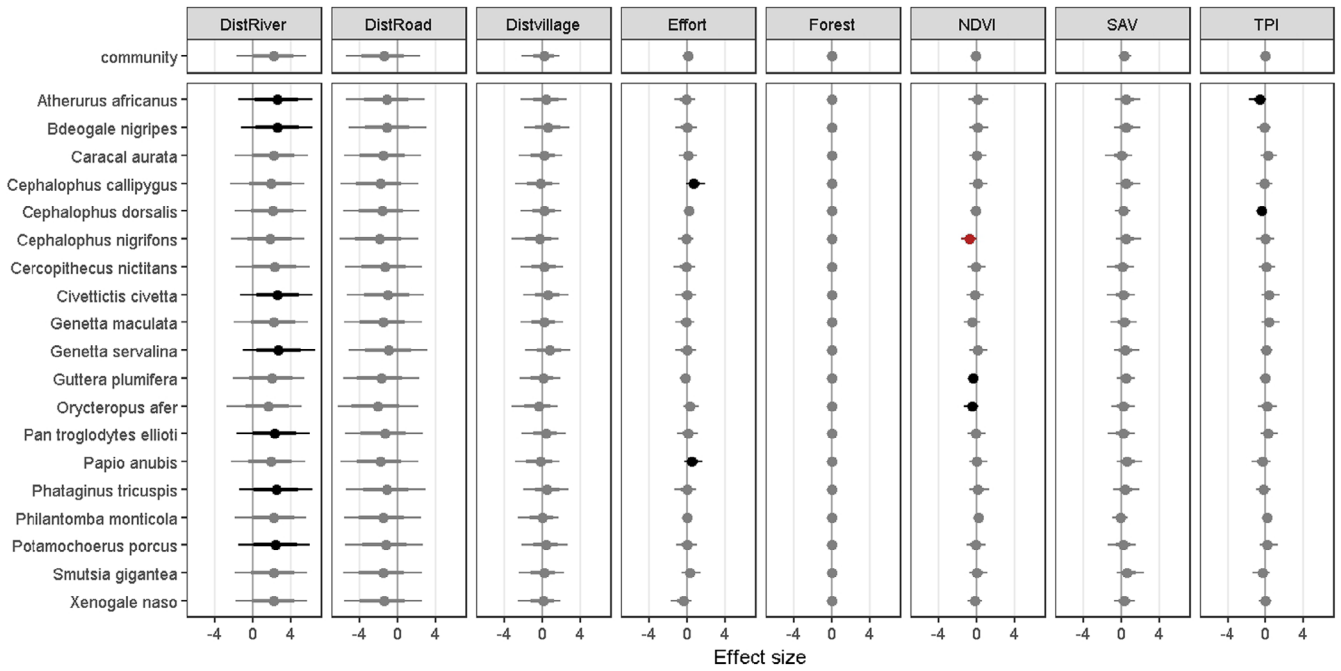


FIGURE 6 | Median, 95% Bayesian confidence interval (BCI) and 75% BCI beta coefficients showing covariate effects on species occupancy probability. Grey bars indicate no support (75% BCI overlaps zero), black bars indicate moderate support (75% BCI not overlapping zero but 95% BCI overlapping zero) and red bars indicate strong support (95% BCI not overlapping zero). Points indicate mean values. Inner and outer bars represent 75 and 95% BCI, respectively. Disroad, distance to road; DistRiver, distance to nearest water source; DistVillage, distance to nearest village; Effort, Cameras traps days; NDVI, normalised difference vegetation index; SAV, Savannah; TPI, topographic position index.

TABLE 6 | Community-level summaries (mean and 97.5% BCI) of hyperparameters for occupancy and detection variables for various groups.

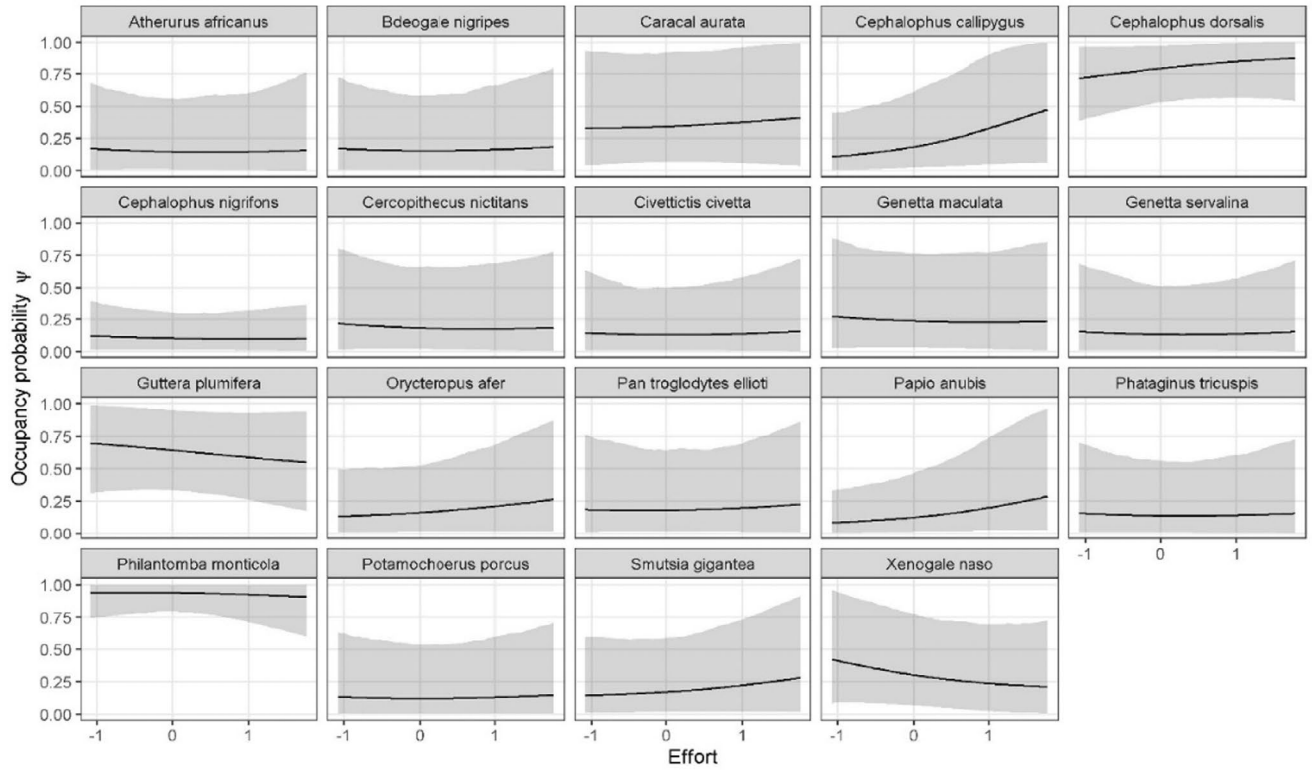
Hyperparameters		Definition	Mean	SD	2.5%	75%	97.5%
$\alpha 0(\text{mean})$		Community mean of the detection probability intercept	-2.64	0.54	-3.87	-2.25	-1.79
$\beta 0(\text{mean})$		Community mean of the occupancy probability intercept	-1.63	0.54	-2.71	-1.28	-0.57
α (Effort effect)		Fixed effect of the continuous observation-level covariate 'effort' on detection probability	0.20	0.10	0.00	0.00	0.02 ^a
β (Habitat effect)		Fixed effect of the continuous observation-level covariate 'Forest' on occupancy probability	0.34	0.34	-0.31	0.56	1.02 ^a
β (DistRiver effect)		Fixed effect of the continuous observation-level covariate 'River' on occupancy probability	2.17	1.88	-1.72	3.58	5.62 ^a
β (DistRoad effect)		Fixed effect of the continuous observation-level covariate 'Road' on occupancy probability	-1.53	1.97	-5.41	-0.16	2.41 ^a
β (Distvillage effect)		Fixed effect of the continuous observation-level covariate 'Village' on occupancy probability	0.12	0.98	-2.16	0.78	1.82 ^a
β (Effort effect)		Fixed effect of the continuous observation-level covariate 'effort' on occupancy probability	0.05	0.23	-0.43	0.20	0.49 ^a
β (NDVI effect)		Fixed effect of the continuous observation-level covariate 'NDVI' on occupancy probability	-0.09	0.22	-0.50	0.06	0.38 ^a
β (TPI effect)		Fixed effect of the continuous observation-level covariate 'TPI' on occupancy probability	0.03	0.20	-0.34	0.16	0.44 ^a

Abbreviations: Distriver, distance to nearest water source; DistRoad, distance to the nearest road; Distvillage, distance to the nearest village; Habitat, habitat (Forest vs. Savannah); NDVI, normalised difference vegetation index; TPI, topography position index.
^aWeak effect.

diversity may be attributed to its heterogeneity, high-quality food and understory cover, which offer shelter for many mammals (Agebo and Tekalign 2022; Geleta and Bekele 2016) while GS support lower species richness (Agebo and Tekalign 2022) with their homogeneous plant species, sparse vegetation, open understory from livestock grazing and limited foraging options

(A) Site covariate: Effort

Random effect



(B) Observation covariate: effort

Fixed effect

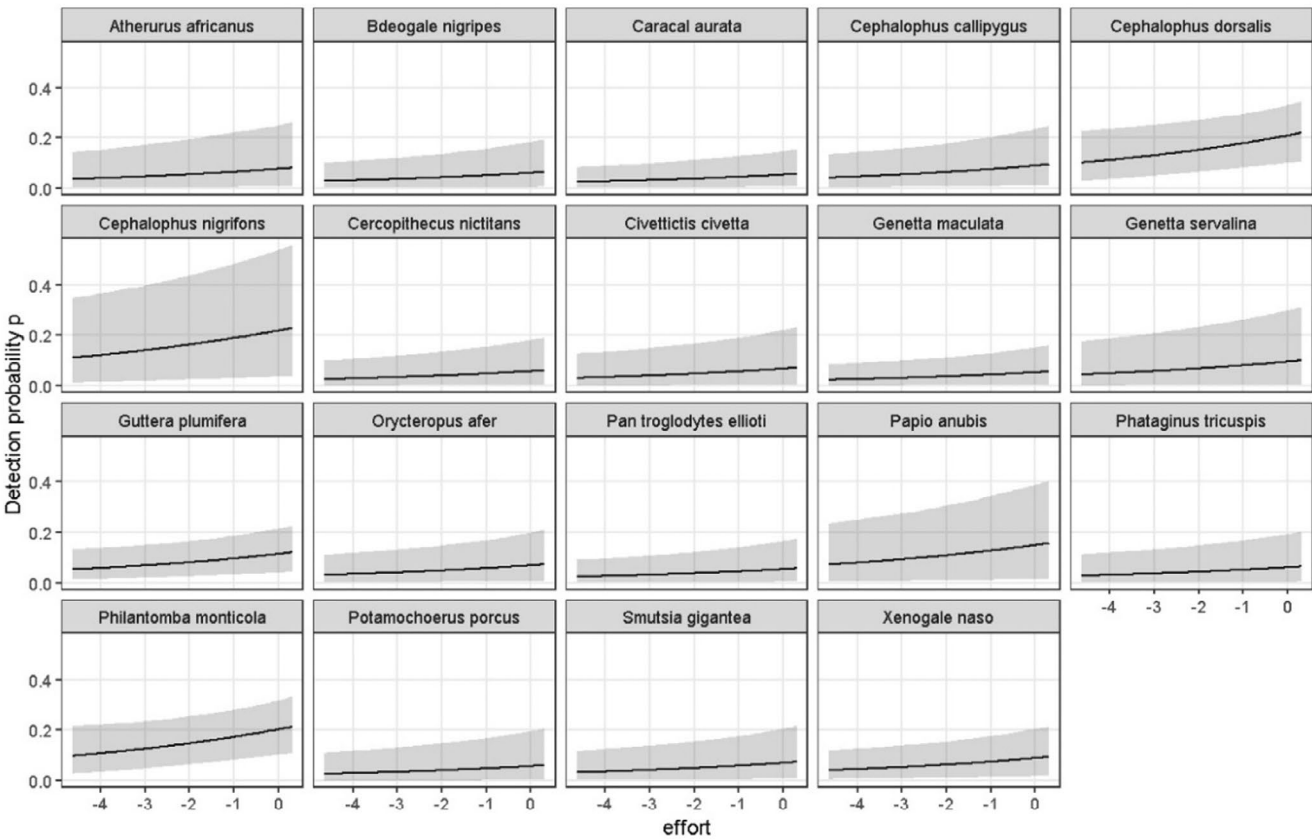


FIGURE 7 | (A) Effect of effort on occupancy probability. (B) Effect of effort on detection probability.

(Geleta and Bekele 2016). However, as this study was conducted during the dry season, lower species richness in savannahs may result from bushfires, hunting (Girma et al. 2012) or food scarcity (Mohammed and Mohd Sah 2024), emphasising the need to consider seasonality in MDNP conservation planning.

Forest cover (%) is a key covariate influencing occupancy for many species and appeared in most top models (e.g., Downs et al. 2016; Zungu et al. 2020). Consistent with studies in Nigeria (Fasona et al. 2024) and Rwanda (Madsen and Broekhuis 2020), our findings highlight the importance of forest habitat (due to its shelter for many species) in shaping community occupancy in MDNP. For example, blue duikers, forest and thicket specialists, rely on dense forests for cover, particularly at midday, when they hide in thick vegetation to ruminate (Skinner and Chimimba 2005).

Consistent with previous studies (Ahumada et al. 2011; Bruce 2017; Hedwig et al. 2018), herbivores were more abundant than all other guilds recorded (see; Fotsing et al. 2025). This may be due to the abundance of food at the site, supporting the explanation of Ofstad et al. (2016) that food abundance shapes the ecology of herbivores. Remote sensing is a cost-effective tool for estimating environmental factors (Hernández-Stefanoni et al. 2011). Obtained from remote sensing, NDVI serves as a reliable indicator of vegetation biomass, assessment of food availability and net primary productivity in habitats (Das and Singh 2016; Sjöström et al. 2009). Its effectiveness has made it widely used by ecologists to estimate forage abundance and habitat quality (e.g., Leyequien et al. 2007; Oindo 2008; Pettorelli et al. 2005, 2011). NDVI reflects vegetation greenness and is linked to species richness (Oindo and Skidmore 2002; Xiyao 2015). Detection events were positively correlated with NDVI, suggesting a preference for greener habitats, likely due to higher food availability. In contrast, Gautam et al. (2019) found NDVI to be an unreliable indicator of food abundance in Nagarhole National Park, India. Aarrestad et al. (2011) suggested that higher primary productivity may reduce species richness and diversity due to competitive exclusion, and Oindo and Skidmore (2002) study in Kenya found that higher average NDVI reduces species richness. Vegetation composition shapes species occupancy and diversity based on feeding strategies, with greening rates linked to food quality (Oindo 2002). Seasonal species occupancy is influenced by factors like food availability, disturbances, movement patterns and habitat use (O'Connell Jr. et al. 2006). The negative mean effect of NDVI on occupancy may reflect seasonal vegetation variability, which reduces herbivore abundance and diversity (Oindo and Skidmore 2002). In tropical and subtropical rainforests, rainfall-driven resource fluctuations impact the activity and movements of forest mammals (Djagoun et al. 2014; Gould 2000).

Occupancy and detection probabilities varied widely among species, reflecting their differing behaviours and resource needs (Madsen and Broekhuis 2020). Species with few detections, like *Potamochoerus porcus*, *Pan troglodytes ellioti*, *Caracal aurata* and *Smutsia gigantea*, showed high variability in occupancy estimates. Overall, medium-sized species also had low detection probabilities, unlike findings by Uzabaho et al. (2022) and Zungu et al. (2020), who reported higher detection probabilities during the dry season. During the dry season, species expand their

ranges to meet resource needs (Gould and Gabriel, 2014) leading to higher occupancy. Blue duikers and mesocarnivores like *Caracal aurata*, *Genetta maculata* and *Xenogale naso* showed greater occupancy, unlike Zungu et al. (2020), who reported higher duiker occupancy in the wet season. This may reflect restricted foraging areas due to restricted movements to key resource areas during the dry season (e.g., Cid et al. 2013) for duikers and widespread prey for mesocarnivores. For some species, occupancy probability increased significantly after accounting for imperfect detection, such as *Guttera plumifera* (naïve occupancy=0.60, $\Psi=0.66$), *Pan troglodytes ellioti* (naïve occupancy=0.1, $\Psi=0.31$), *Caracal aurata* (naïve occupancy=0.2, $\Psi=0.48$) and *Genetta maculata* (naïve occupancy=0.15, $\Psi=0.40$). However, these estimates had high uncertainty due to very few detections, a pattern also noted by Ghimirey et al. (2024) in Nepal, despite differences in species composition. Overall, detection probability was low for all species, with the highest recorded for *Pan troglodytes ellioti* ($p=0.22$). Similar low detection probabilities have been observed in the Dhorpatan Hunting Reserve and Dadeldhura districts (Regmi et al. 2023; Thapa et al. 2022). In contrast, our estimate differs from those of Chaudhary et al. (2022) and Penjor et al. (2021), whose lowest occupancy estimates in Bhutan and India were 0.09 and 0.12, respectively. The difference in habitats and species composition may explain differences in detection probability, making comparisons less relevant. As Ghimirey et al. (2024) noted, low detection probability seems to be the norm rather than the exception. In this study, we used a distance sampling approach, which assumes equal detection probability for all species rather than preferential camera placement. In contrast, targeting felid habitats with camera placement has been shown to impact the detectability of other mammals (Boron et al. 2019; Kolowski et al. 2021). The variation in detection probability in our study may also be attributed to species body size, as Tobler et al. (2008); Tobler et al. (2008) found that detection probability decreases with smaller species size. Globally, observed differences in species responses highlight the need to consider both edge and interior species (Fasona et al. 2024) and account for the specific ecological needs of each group (Arimoro, 2014; Luiselli et al. 2015). Similar varying responses to landscape and habitat variables were found in EThekweni Municipality, Durban, South Africa (Zungu et al. 2020).

Consistent with Hawkins et al. (2003) where distance to rivers influenced the presence of lions, leopards, wild dogs and elephants, and another study in Africa (e.g., Pettorelli et al. 2010; Schuette et al. 2013), our study also shows the effect of distance to river on detection events and occupancy. Water accessibility during the dry season shapes mammal distribution (Sitters et al. 2009). Hawkins et al. (2003) argue that this could be related to the dense vegetation found beside rivers, as they provide a cool environment during the day, denning opportunities for females with offspring, and increased hunting opportunities (Spong 2002). Limited water may increase competition between wildlife and pastoralists, who bring cattle into parks for water (Fotsing, Kamkeng, Marcel Senge, et al. 2024). While rainfall variation may minimally affect occupancy in some areas (Martin et al. 2017), competition at water sources can reduce wildlife detection and richness in savannah ecosystems (Sitters et al. 2009). During the dry season, herbivores return to water, with travel costs limiting their grazing distance (Xiyao 2015).

De Leeuw et al. (2001) found grazers can stay far from water sources where forage quality is often higher. Ogutu et al. (2010) noted that declining vegetation near rivers forces animals to forage farther from water. We may also consider in this study the impact of human disturbances like livestock and poaching (Fotsing et al. 2025), which affect herbivore and carnivore abundances (Xiyao 2015). Interspecific competition, as shown in previous studies (Fotsing, Kamkeng, and Zinner 2024), should also be considered. Consistent with Easter et al. (2019), we found no effect of distance to roads on community occupancy. Elsewhere, duiker abundance has also been shown to be negatively affected by proximity to roads (Laurance et al. 2006; Uzabaho et al. 2022, 2024). However, Madsen and Broekhuis (2020) point out in their studies that species take human disturbance into account on a wider scale and not just in their vicinity, while Loveridge et al. (2017) argue that the avoidance of humans by several large carnivore species may be a result of negative interactions with humans. Similar trends have been observed in other tropical forests, such as the Amazon (Silveira et al. 2021) and Southeast Asia (Wearn et al. 2017), where camera trap studies have demonstrated the influence of habitat fragmentation and human activity on species richness.

We must acknowledge that due to our sampling designs the presence of arboreal mammals is likely underestimated. Our study is the first robust baseline survey highlighting the usefulness of MSOMs to assess community-wide occurrence in an Afrotropical hotspot area in Cameroon and reaffirms the significance of incorporating imperfect detection through MSOMs within the study design and analysis. While this approach is increasingly used in global camera trapping studies (Baker et al. 2011; Fasona et al. 2024; Gaynor et al. 2021; Uzabaho et al. 2024; Zungu et al. 2020), it remains uncommon in Cameroon, where conservation efforts often prioritise a few flagship species. Herbivores like *Cephalophus dorsalis* and *Philantomba monticola* have higher occupancy than mesocarnivores. Without predators' regulation, resource depletion and competition could impact other plant consumer species like *Cercopithecus nictitans* and *Pan troglodytes ellioti* (Anderson et al. 2016; Grueter et al. 2013). Therefore, continued monitoring of both herbivore and mesocarnivore densities (e.g., African golden cat) is crucial in this region.

Our results confirm that habitat structure and environmental gradients strongly influence species occupancy and detectability, a pattern widely observed in tropical ecosystems (e.g., Mackenzie et al. 2017; Teixeira-Santos, Ribeiro, et al. 2020; Teixeira-Santos, Graipel, et al. 2020). The application of MSOMs within a Bayesian framework enhances detectability corrections, making this approach valuable for biodiversity assessments across tropical and subtropical regions. The patterns observed in MDNP suggest that similar ecological and anthropogenic factors shape species occupancy across tropical protected areas, reinforcing the need for habitat conservation strategies that integrate local and regional environmental variables. Our study provides a framework for applying occupancy models to assess biodiversity in other tropical regions, offering insights for conservationists working in data-deficient landscapes. While additional effort could further improve occupancy estimates, our model already accounts for detection probability differences, reducing bias. We acknowledge that our findings are based on a subset of MDNP,

and direct inference should be limited to the western portion of the park. However, since similar habitat types exist across the park, our results may offer preliminary insights into broader occupancy and detection patterns. Future research will expand this study to the entire park, ensuring a more comprehensive understanding of species distributions across MDNP. Our findings can also help evaluate conservation monitoring programmes. Future research should identify species or poaching hotspots (e.g., de Matos Dias et al. 2020), extend analyses to rainy seasons (to assess change in occupancy between season and confirm the impact of environmental covariates), and explore factors like woody cover, species guilds, human disturbance (e.g., livestock and poaching), species body size and rarity in occupancy models. We recommend conducting a new survey across the park, followed by repeat surveys every 3–5 years. Multi-year surveys will track changes in species status and occupancy, community composition and richness, supporting research and future conservation efforts in the region.

Author Contributions

Ernest D. B. Fotsing: conceptualisation; data curation; methodology; data collection; data analysis; writing grant proposal; preparing the original and final draft and supervision. **Meigang M. F. Kamkeng:** conceptualisation, methodology, data curation, data collection, data analysis, project administration, writing and editing the draft. All authors gave their final approval for publication.

Acknowledgements

This research was implemented with the generous support of the Aspire Grant Program, the Global Wildlife Conservation Fund (Primate Action Fund. Re:wild), the Society for Conservation Biology (SCB), the Primate Conservation Incorporated Grant (PCI) and the Idea Wild foundation. We thank the Ministry of Forestry and Wildlife and the Ministry of Scientific Research of the Cameroon Republic for providing the research permit (No. 02048) and research authorisation (No. 0000043) for this study. We are also grateful for the assistance of MDNP conservator Bisseck Jean Pierre for delivering the authorisation to get regular access to the park and for his active participation in the planning of this study with rangers. We also express our gratitude to the local guides involved in fieldwork, especially Ngomane Pierre and Tangri Sylvestre.

Ethics Statement

This research was also conducted following the principles of the American Society of Primatologists and the International Society of Ethnobiology (ISE) Code of Ethics (ISE 2006) for the ethical treatment of nonhuman and human primates.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data are archived in the first author's Github repository account and can be found at <https://github.com/Fotsing2023/Mesocarnivores-ecology-in-MDNP-Cameroon.git>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.