

## Determining Community-level Carnivore Response to Landscape Factors in Bukit Barisan Selatan National Park, Sumatra, Indonesia

Eve T Bohnett<sup>1\*</sup>, Kossi Fandjinou<sup>2</sup>, Bilal Ahmad<sup>3</sup>, Siraj Mammo<sup>4</sup>, Dave Hulse<sup>5</sup>, Thomas Hcctor<sup>6</sup>

<sup>1</sup>Florida Institute for Built Environment Resilience, Department of Landscape Architecture, University of Florida, Gainesville, USA

<sup>2</sup>School of Soil and Water Conservation, Beijing Forestry University, Beijing, China.

<sup>3</sup>Institute of Agriculture Sciences and Forestry, University of Swat, Swat, Pakistan.

<sup>4</sup>Biology Department, Ambo University, Ambo, Ethiopia.

<sup>5</sup>Florida Institute of Built Environment Resilience, Department of Landscape Architecture, University of Florida, Gainesville, USA

<sup>6</sup>Department of Landscape Architecture, University of Florida, Gainesville, USA

\*Email: [evebohnnett@yahoo.com](mailto:evebohnnett@yahoo.com)

Received: 10 November 2020 / Revised: 13 March 2021 / Accepted: 13 March 2021 / Published online: 27 September 2021. Ministry of Sciences, Research, and Technology, Arak University, Iran.

**How to cite:** Bohnett, E.T., Fandjinou, K., Ahmad, B., Mammo, S., Hulse, D., Hcctor, T. (2021). Determining Community-level Carnivore Response to Landscape Factors in Bukit Barisan Selatan National Park, Sumatra, Indonesia, 5 (3), 68-88. [doi: 10.22120/jwb.2021.139653.1198](https://doi.org/10.22120/jwb.2021.139653.1198)

### Abstract

Researchers are challenged to understand the distribution of biodiversity on the landscape or determine if community-level assemblages respond to landscape variability. Canonical ordinations and multispecies occupancy modeling are often utilized and differ in their analytical scale and technique. Community-level data for carnivores (n=18) from camera trapping data (n=60) were tested for their collective response to covariates (distance to villages, roads, plantations, streams, and also topographic variables for elevation and slope) in Bukit Barsan Selatan National Park. Redundancy analysis (RDA) results confirmed that the carnivore community responded to the anthropogenic covariates, with carnivore detections being higher in areas at a high distance from roads and plantations medium distance villages. Then, multispecies occupancy models (MSOM), a comparatively finer temporal scale analysis that incorporated imperfect detections, were compared to RDA. We fit four models (full, anthropogenic, natural, and null) that were mainly inconclusive. In some MSOM models, the carnivore community did respond to environmental covariates, although the coefficients did not show a consistent response between seasons or years. These results indicate that RDA was able to detect broad-scale covariate effects that were not able to be

modeled by MSOM and that these scaling and imperfect detection issues should be considered when attempting to understand landscape community diversity.

**Keywords:** Biodiversity, carnivores, community ecology, multi-species occupancy, redundancy analysis

### **Introduction**

Land-use change and anthropogenic disturbances have been shown to have severe effects on biodiversity, for example, losses of alpha diversity (species richness) through forest conversion (Gibson et al., 2011) or agricultural expansion (Laurance et al., 2014). The urgency of protecting the world's megafauna has become apparent from global analyses, showing Indonesia to be within the top 10 countries globally for megafauna decline (Ripple et al., 2016, 2017). Due to the conversion of natural forests to agriculture, logging, hunting, and trapping, significant alpha diversity losses have occurred in Indonesia (Rodrigues et al., 2014). However, there is an insufficient capacity to predict alpha and beta biodiversity components on the landscape undergoing anthropogenic conversions and then enact interventions that deal with local-scale biodiversity conservation (Wearn et al., 2019). Researchers and conservation planners are challenged to prioritize areas on the landscape to benefit the conservation of the ecosystem components, as it is challenging to gauge community-level richness within a matrix of landscape variability (Zipkin et al., 2009).

Various guilds react to gradients of land use land cover (Goijman et al., 2015; Wearn et al., 2019) or a landscape matrix of human disturbances (Easter et al., 2019; Rezaei et al., 2021). Other studies have classified species into guilds based on relatedness in terms of habitat preferences or diet, where inferences were more specific to a subset of species (Pacifi et al., 2014). Previous camera trapping studies have classified mammal communities into various functional effects groups like trophic guilds or conservation status to look at habitat responses. For example, camera trapping data were used to show dramatic declines of community richness for many guilds in oil palm plantations, compared to logged forests or old-growth areas (Wearn et al., 2017).

Species occurrence and abundance data, along with corresponding environmental covariates, are the basis from which inferences on community-level modeling efforts are built, seeking to answer fundamental questions central to community ecology (Ovaskainen et al., 2016). Species occurrence data are usually analyzed separately and pooled in community-level analysis to understand how environmental factors affect species richness across landscape gradients (Zipkin et al., 2009).

Understanding community-level biodiversity through multivariate methods has been the most widely applied methodology in understanding the structure of ecological community composition related to environmental factors (Borcard et al., 2011). Ordinations have long been a central exploratory methodology in using dimensionality reduction to produce factors or principal components used for identifying the most significant variables within the covariate hyperspace. For example, principal components analysis can reduce an n-matrix of sites within an environmental covariate space to identify one or two principal components composed of a proportion of each variable and more heavily composed of more significant variables

differentiating the sites from one another (Rao, 1964). Other methods, like redundancy analyses (RDA), can examine the multispecies community table along environmental gradients, perform multiple regression on the multivariate response, and reduce dimensions using eigenanalysis approaches to determine significant community-level responses to landscape variability (Dray et al., 2012; Rao, 1964). Researchers have suggested combining classical statistical models for community compositional data, like constrained ordinations or other multivariate analyses with emerging methods for spatial pattern analyses (Dray et al., 2012), or with hierarchical community models (Yamaura et al., 2019), for comprehensive approaches in understanding covariate effects on a community.

Another inferential methodology for understanding community structure within a heterogeneous landscape is the multispecies occupancy model (MSOM) (Dorazio & Royle, 2005). These hierarchical models combine presence-absence data tables for each species, use community-level parameters, and include a detectability model to account for imperfect detection (MacKenzie et al., 2002). Furthermore, MSOM provides a robust inference for multiple species' occupancy, including rarer species, resulting in estimates for species richness estimates and any community-level co-variability.

MSOM has informed appropriate multispecies conservation management actions from site-level species richness estimates. The conservation implications of multispecies occupancy models have assisted in designing management programs (Zipkin et al., 2010), such as assessing patrol enforcement management regimes (Farr et al., 2019) and other anthropogenic disturbances like poaching (Moore et al., 2018). Inferences from MSOM for mammals have been able to show a response to anthropogenic disturbances like habitat fragmentation and land conversion (Boron et al., 2019; Cavada et al., 2019; Dechner et al., 2018; Rovero et al., 2014), or other natural features like distance to water (Cavada et al., 2019).

This study discusses the analytical scale implications in the modeling workflow, as RDA and MSOM are analyzing different temporal scales. RDA methods are referred to as a "global-scale" analytical structure because they seek to understand the broad structure of the community-level data, utilizing data tables of species observations collated across years of survey effort, where there are no assumptions there are finite windows of time to restrict the analysis. MSOM is referred to here as a "local-scale" analysis because they are collected throughout a finite window of time to meet the assumptions of population closure, which indicates there is no species immigration or emigration from the site, resulting in repeated surveys within this time window data, and also scaled into hours, days, weeks, or months depending on the survey or analysis schema. This study seeks to investigate exploratory data analysis and the RDA as a broader temporal scale analysis to understand covariate effects and assess MSOM response to the same covariates at more localized temporal scales. These methods are compared and contrasted for their ability to detect a response in the carnivore community, as we discuss this inherent temporal scaling difference between the analytical methods and their ability and inability to incorporate imperfect detection.

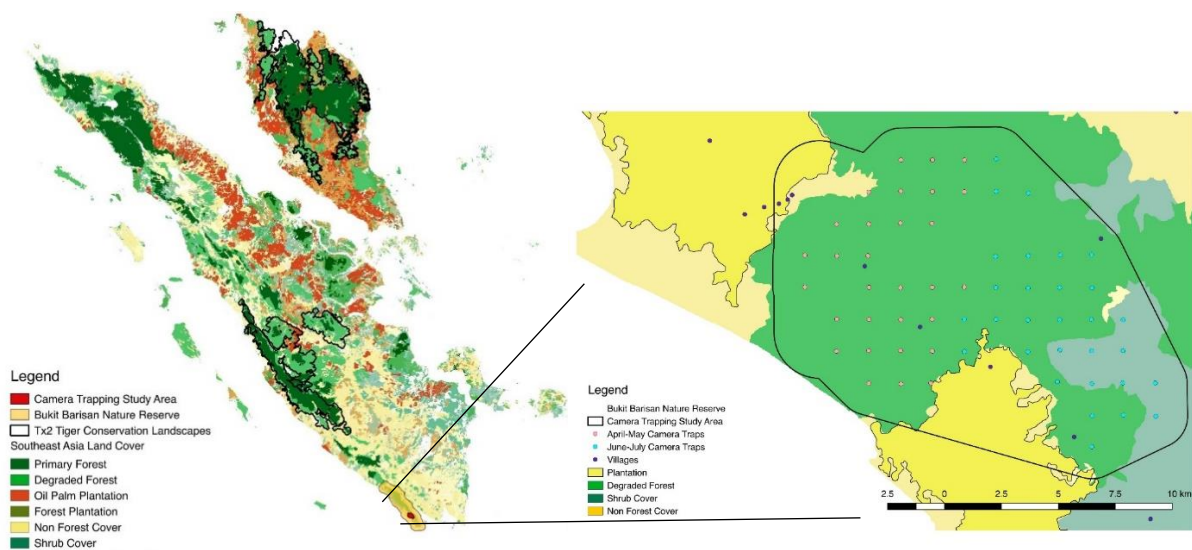
This research asked principal questions at the intersection of landscape ecology and community ecology. What were the primary landscape responses that can be modeled for carnivore communities, utilizing available environmental and anthropogenic covariate data in BBSNP and comparing these multispecies analysis methodologies? Carnivore communities in BBSNP,

Sumatra, Indonesia, have a diverse species pool with the presence of many rare and elusive species of wild felids that are a part of a wider carnivore community, continually being threatened by anthropogenic factors, and we seek to further qualify that threat through these discussed modeling approaches.

## Material and methods

### Study area

To further understand terrestrial mammal distributions in general, Tropical Ecology Assessment and Monitoring (TEAM) Network implemented assessments over seven years (2010-2016), in Bukit Barisan Selatan National Park (BBSNP), Lampung province, Sumatra, Indonesia ( $-5^{\circ}49' S$   $104^{\circ}31' E$ ) (Fig 1).



**Figure 1.** Map of land uses and tiger conservation zones around Sumatra, with a subset of the study area within Bukit Barisan Selatan National Park (yellow polygon) with camera stations' locations (red circle).

Camera stations were colored to designate blocks: block 1 (pink) and block 2 (blue)

BBSNP is a 3568 km<sup>2</sup> with coastal forest, mangrove forest, and lowland rainforest with a mountain range reaching a 1964m elevation (Pusparini et al., 2018). The monsoon season occurs seasonally between November to May. The park is known for the many unique and endangered species, like the Sumatran elephant, Sumatran rhinoceros, and Sumatran tiger. Aside from this study, several research studies have analyzed the carnivores in BBSNP in Sumatra, assessing the distribution and habitat use of felid species (McCarthy et al., 2015), or specifically Sumatran tigers (Allen et al., 2020; Jaya et al., n.d.; O'Brien et al., 2003; Pusparini et al., 2018). Threats to the park's rainforest's integrity include agricultural encroachment and the development of enclaves where squatters have claimed the forest for their uses (O'Brien & Kinnaird, 1996).

### Camera Trapping Design

These surveys used camera traps (n = 60) arranged in a systematic grid with cameras placed at the center of each 2km<sup>2</sup> grid site (Fig 1). During the seven years the study site was operational, there was a rotational design where cameras were moved in April-May and June-July to different sets

of locations according to the yearly data collection protocol. The entire camera trapping grid ran each April - August every year over 544 calendar days, producing 2393 camera trapping nights. The dataset contained 39-59 camera sites with variations year to year, surveyed 85-163 days per year, for an average of 25-32 days per camera (Table 1). All cameras were set for 24 hours, and detections were collated into days, weeks, or months as per the modeling temporal scale.

**Table 1.** Camera station variability in camera number and survey days

Year	Total (April -July)		Block1 (April-May)		Block2 (June-July)	
	#	Survey Days	#	Survey	#Cameras	Survey
2010	59	104	29	36	30	37
2011	55	85	27	34	28	35
2012	50	96	25	36	25	53
2013	39	108	20	35	19	36
2014	43	111	23	73	20	70
2015	39	100	25	36	14	35
2016	51	163	27	60	24	81

### Study fauna

The studied fauna included all mammalian carnivores detected during the seven years of the camera trapping survey. There were 18 carnivores with 135 detection days between 2010-2016 (Table 2).

**Table 2.** Eighteen Carnivores Detected from TEAM Network Cameras 2010-2016

Family	Genus	Species	Common name	IUCN	Detections
Mustelidae	<i>Aonyx</i>	<i>cinerea</i>	Asian small-clawed otter	VU	1
Viverridae	<i>Arctictis</i>	<i>binturong</i>	Binturong	VU	1
Viverridae	<i>Arctogalidia</i>	<i>trivirgata</i>	Small toothed palm civet	LC	1
Canidae	<i>Canis</i>	<i>lupus familiaris</i>	Domestic dog	LC	1
Canidae	<i>Cuon</i>	<i>alpinus</i>	Dhole	EN	4
Viverridae	<i>Cynogale</i>	<i>bennettii</i>	Otter Civet	EN	1
Ursidae	<i>Helarctos</i>	<i>malayanus</i>	Sun bear	VU	25
Viverridae	<i>Hemigalus</i>	<i>derbyanus</i>	Banded palm civet	NT	29
Herpestidae	<i>Herpestes</i>	<i>brachyurus</i>	Short-tailed mongoose	NT	1
Viverridae	<i>Lutra</i>	<i>lutra</i>	Eurasian otter	NT	1
Felidae	<i>Neofelis</i>	<i>diardi</i>	Clouded leopard	VU	5
Viverridae	<i>Paguma</i>	<i>larvata</i>	Masked palm civet	LC	9
Felidae	<i>Panthera</i>	<i>tigris</i>	Tiger	EN	25
Viverridae	<i>Paradoxurus</i>	<i>hermaphroditus</i>	Asian palm civet	LC	1
Felidae	<i>Pardofelis</i>	<i>marmorata</i>	Marbled cat	NT	6
Felidae	<i>Pardofelis</i>	<i>temminckii</i>	Golden Cat	NT	6
Felidae	<i>Prionailurus</i>	<i>bengalensis</i>	Leopard Cat	LC	10
Prionodontidae	<i>Prionodon</i>	<i>linsang</i>	Banded linsang	LC	5

This particular study region has diverse species of special status carnivores. For example, three endangered species were detected: tiger (*Panthera tigris*), dhole (*Cuon alpinus*), and otter civet (*Cynogale bennettii*). The most abundant carnivores in the survey by the number of detections were the banded palm civet (*Hemigalus derbyanus*) ( $n=29$ ), and also IUCN vulnerable sun bear (*Helarctos malayanus*) ( $n=25$ ), and IUCN endangered tiger ( $n=25$ ). Furthermore, many species were only detected one time during all seven years of the survey: binturong (*Arctictis binturong*),

domestic dogs (*Canis familiaris*), short-tailed mongoose (*Herpestes brachyurus*), Asian small-clawed otter (*Aonyx cinerea*), otter civet, Asian palm civet (*Paradoxurus hermaphroditus*), and small-toothed palm civet (*Arctogalidia trivirgata*). There were several species presumed extant by IUCN and not detected during the surveys (Table 3). These undetected species were not included in modeling analysis.

**Table 3.** Eight Carnivore Species Presumed Extant by IUCN and Not Detected by Camera Trap Surveys. These species were not included in any of the modeling efforts

Family	Genus	Species	Common name
Felidae	<i>Catopuma</i>	<i>temminckii</i>	Asiatic Golden Cat
Herpestidae	<i>Herpestes</i>	<i>semitorquatus</i>	Collard Mongoose
Mustelidae	<i>Lutra</i>	<i>sumatrana</i>	Hairy Nosed Otter
Mustelidae	<i>Lutrogale</i>	<i>perspicillata</i>	Smooth-coated otter
Mustelidae	<i>Martes</i>	<i>flavigula</i>	Yellow-throated marten
Mustelidae	<i>Mustela</i>	<i>nudipes</i>	Malayan weasel
Viverridae	<i>Viverra</i>	<i>tangalunga</i>	Malayan civet
Felidae	<i>Prionailurus</i>	<i>planiceps</i>	Flat-headed cat

### Environmental Covariates

Environmental covariates were generated from freely available geospatial data. Elevation and slope were derived from Shuttle Radar Topography Mission (SRTM) raster data. Distance to roads, streams, plantations, and villages was derived from shapefile open street map data and generating a Euclidean distance raster. Any continuous covariates were scaled (-1,1). Program ArcGIS was used for covariate derivations.

### Statistical Analysis and Modeling Framework

#### Exploratory Data Techniques

To understand the distribution of camera traps in the hyperspace of covariate information, first, a PCA was used. Environmental covariates were checked for multivariate normality using the MVN package (Korkmaz et al., 2019). The scree plot identified two significant principal components using an eigenvalue of 1 as the cutoff. Multivariate analysis was checked for spatial autocorrelation using a distance-based Moran's Eigenvector Maps, which found no statistically significant spatial structures in the data, so scaling factors were not included.

For RDA, carnivore community data were Hellinger transformed and modeled in response to environmental covariates (elevation, slope, and distance to villages, roads, streams, and plantations) that were binned into three equal bins and included as factors in the RDA. Additionally, detection days for the camera trap mammal detections were summed across orders (*Cetartiodactyl*, *Eulipotyphla*, *Perissodactyla*, *Pholidota*, *primates*, *Proboscidea*, *Rodentia*, *Scandentia*) and included for additional exploration of the data. A global test of the RDA was run for 1000 permutations to determine model significance ( $\alpha=0.05$ ). Then, forward selection was used to identify the explanatory variables with the highest  $R^2$  for subsequent model refitting. The VEGAN package in program R version 3.6.1 was used to generate PCA and RDA results and plots (Oksanen et al., 2019).

### Multi-Species Occupancy Model (MSOM)

Community-level occupancy models involve predicting species community composition as a function of environmental covariates while accounting for imperfect detection (Dorazio et al., 2006; Dorazio and Royle, 2005; Broms et al., 2016). Models attempting to fit multispecies occupancy have used a multivariate Bernoulli random variable as the latent occupancy state to provide conditions for interspecific independence and account for imperfect detection (Rota et al., 2016). Hierarchical models for communities include a super-community concept with nested levels of single species occurrences.

This model estimates the species-specific occupancy and site-specific species richness by incorporating data augmented from potential species in the species pool. Extending the single species single-season model with an index for each species as the latent variable, then the underlying distribution is a hyperparameter for the entire carnivore community augmented with all 0's (Kery and Royle, 2016). The MSOM was fit for eighteen species in the species pool that were detected in 2010-2016. For example, the smallest scale of MSOM modeled, utilizing the scale of each detection day, for any given year, then there were between four to eight species detected. The remainder from the original 18 species pool was then augmented into the detection array (Table 4).

**Table 4.** Number of carnivores and detections within each year and block out of the species pool of eighteen species

Year	Block 1 (April – May) # Carnivores	Detections	Block 2 (June – July) # Carnivores	Detections	Total Carnivores Per year	Total Detections Per year
2010	4	7	7	12	9	19
2011	4	5	8	22	9	27
2012	5	8	6	13	7	21
2013	4	9	3	3	6	12
2014	5	9	8	14	10	23
2015	7	16	2	3	7	19
2016	5	10	4	4	6	14

For the first set of models, we assumed a closed community for each block subset for every two-month survey period (May-April, June-July) for over seven years resulting in 14 models. For the second set of models, we included a block effect to distinguish block 1 from block 2, and considered every four-month survey period (May-July) as a closed community resulting in a yearly model for 7 models. The scale of the analysis was the 2km<sup>2</sup> grid camera trap survey units within the larger sampling area. We modeled the detection probabilities as a function of the year (Julian date) to account for the detection differences. We also included a third set of models for a broader scale MSOM in the analysis utilizing the block effects and further collating detection days into months with all of the years of data in one model. In models that were run, including all years of data, separate covariates were fit to model each year's effects. These three MSOM

temporals and spatial scales demonstrate whether the models fit better at broader scales in the MSOM framework.

Camera trapping detection records (presence/absence) for all species collected in a combined array of each species from each season were used as the response variable. The analyses were hypothesized to be affected by environmental variables (distance to streams, elevation, and slope) and anthropogenic variables (distance to the villages, plantations, or roads).

In this dataset, the point occurrences were modeled as a Bernoulli distribution, where occupancy ( $\psi$ ) is the probability that a species,  $I$ , occurred at site  $j$  during survey  $k$ .

Superpopulation process

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

State process (occurrence)

$$z_{ik} | w_k \sim \text{Bernoulli}(w_k \psi_k)$$

Observation process (detection)

$$y_{ik} | z_{ik} \sim \text{Bernoulli}(z_{ik} p_{ijk})$$

Model for two-month subset for either block 1 or block 2:

$$\text{logit}(\psi_{ik}) = lpsi_k + betalpsi_1 * covariate1 + betalpsi_2 * covariate2$$

For models with block effects for four-month modeling including both blocks:

$$\text{logit}(\psi_{ik}) = lpsi_k + betalpsi_1 * covariate1 + betalpsi_2 * covariate2 + \text{block effects}$$

Priors and Hyperpriors:

$$lpsi \sim \text{Normal}(\mu_{betalpsi}, \sigma_{betalpsi}^2)$$

$$betalpsi_k \sim \text{Normal}(\mu_{betalpsi}, \sigma_{betalpsi}^2)$$

$$\mu_{betalpsi} \sim \text{Normal}(0, 0.1)$$

$$\sigma_{betalpsi}^2 \sim \text{Normal}(0, 1)$$

### Model for detection

$$\text{logit}(p_{ik}) = lp + betap_1 * date$$

For models that included all years of data:

$$\text{logit}(p_{ik}) = lp + betap_1 * X.2010 + betap_2 * X.2011 + betap_3 * X.2012 + betap_4 * X.2013 + betap_5 * X.2015 + betap_6 * X.2016$$

Priors and Hyperpriors:

$$lp \sim \text{Normal}(\mu_{betalp}, \sigma_{betalp}^2)$$

$$betalp_k \sim \text{Normal}(\mu_{betalp}, \sigma_{betalp}^2)$$

$$\mu_{betalp} \sim \text{Normal}(0, 0.1)$$



$$\sigma_{\beta_{etalp}}^2 \sim Uniform(0,1)$$

Where  $\beta_0$  is the intercept term for occurrence probabilities, and betas are to proximity to plantation or village and elevation. Detection probability ( $p_{i,j}$ ) uses alpha to parameterize the Julian date and effects on species detectability. This study used jagsUI packages in R for a Bayesian approach to MSOM (Kellner, 2019). We used non-informative priors and ran three chains for 6000 iterations, burning 2000 and thinning 10. The convergence of the models was assessed by having an R-hat of <1.1 was acceptable.

### Bayesian Model Selection

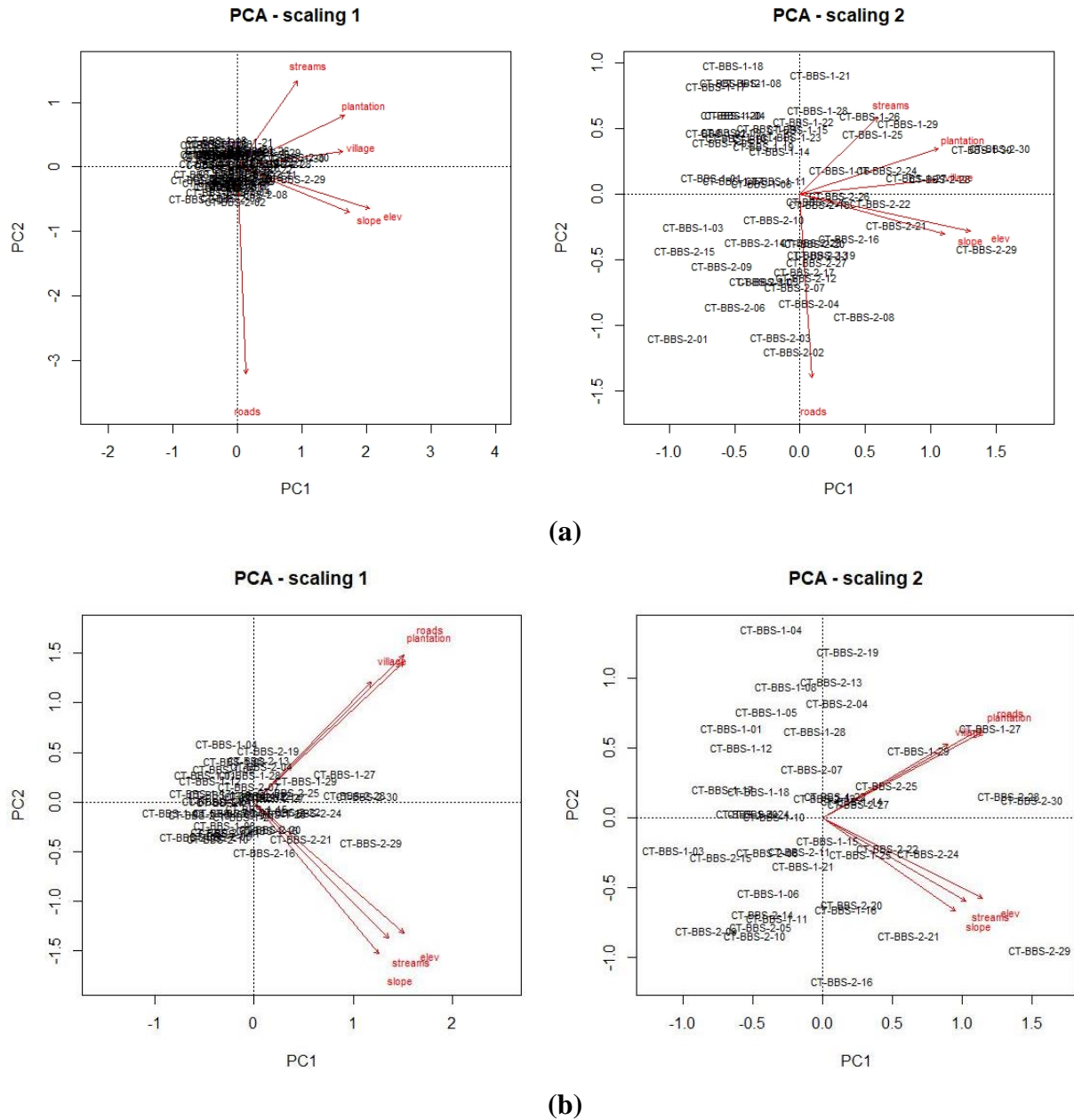
Bayesian model selection methods include techniques of cross-validation, information criteria, or Bayesian model averaging (Hooten & Hobbs, 2015). Model selection and validation have been challenging for Bayesian MSOM for numerous reasons. For example, measures of information criteria, like AIC and BIC, are not suitable for models with latent variables. Broms et al. (2016) designed a series of methods suitable for MSOM, and model selection was developed using the log pointwise predictive density (lppd), Watanabe-Akaike information criterion (WAIC), and Conditional Predictive Ordinate Criterion (CPO) for between model selection. Generating AUC metrics from cross-validation runs has become accepted as an appropriate model evaluation technique (Zipkin et al., 2012). Additional metrics like the Briers log have given additional evaluation ability for MSOM models (Broms et al., 2016). These methods can validate and evaluate MSOM models for camera trapping data and accompanying covariate information. Although few studies employ MSOM for carnivore camera trapping data, these methods are not well employed for the community-level response to environmental covariates. Here we use the methods as outlined above, in Broms (2016), for model selection (lppd, pD, WAIC, CPO) and evaluation (deviance, AUC, Briers log) from k-fold cross validation using 25% testing data to qualify which model fits the best using multiple metrics.

## Results

### Principal Components Analysis

The PCA revealed the distribution of the 60 camera trap sites within the six environmental covariates' hyperspace. Camera traps that had detected at least one carnivore were a subset (n=44) for comparison after comparing the PCA for the 60 total stations (Fig 2a) vs. 44 carnivore stations (Fig 2b).

The covariate space appears polarized and distinct between areas of heavier anthropogenic disturbance and areas with a natural environment (Fig. 3). The principal components 1 and 2 were able to explain 74% of the covariates' variation (Table 5).

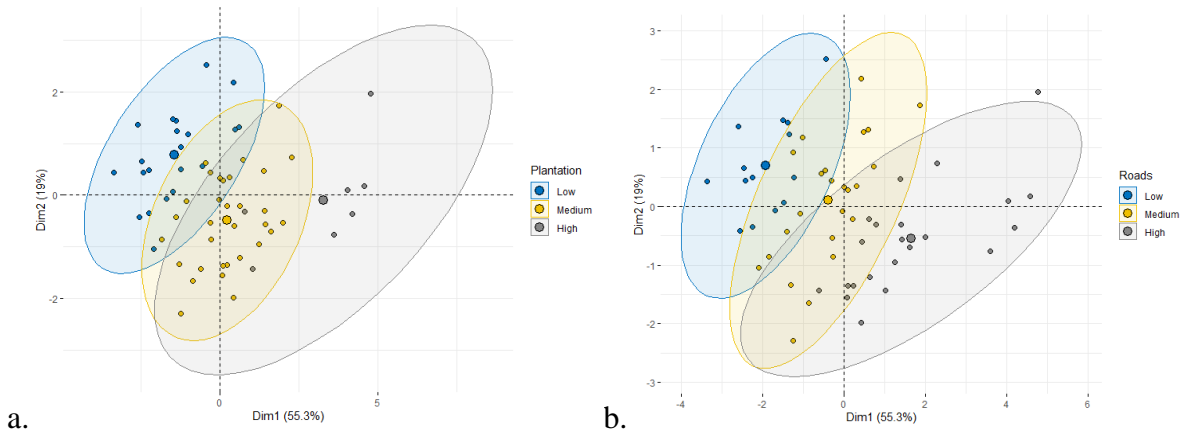


**Figure 2.** PCA biplot of TEAM network camera trap data (n=60) in Bukit Barisan Selatan NP with six environmental covariates (a), PCA biplot of camera trap data (n=44) detected at least one carnivore in Bukit Barisan Selatan NP with six environmental covariates (b)

**Table 5.** Two significant principal components were determined by scree plots, accounting for a cumulative proportion of 74% of the environmental covariate dataset variance.

	PC1	PC2
Standard deviation	1.8219	1.0667
Proportion of Variance	0.5532	0.1896
Cumulative Proportion	0.5532	0.7428

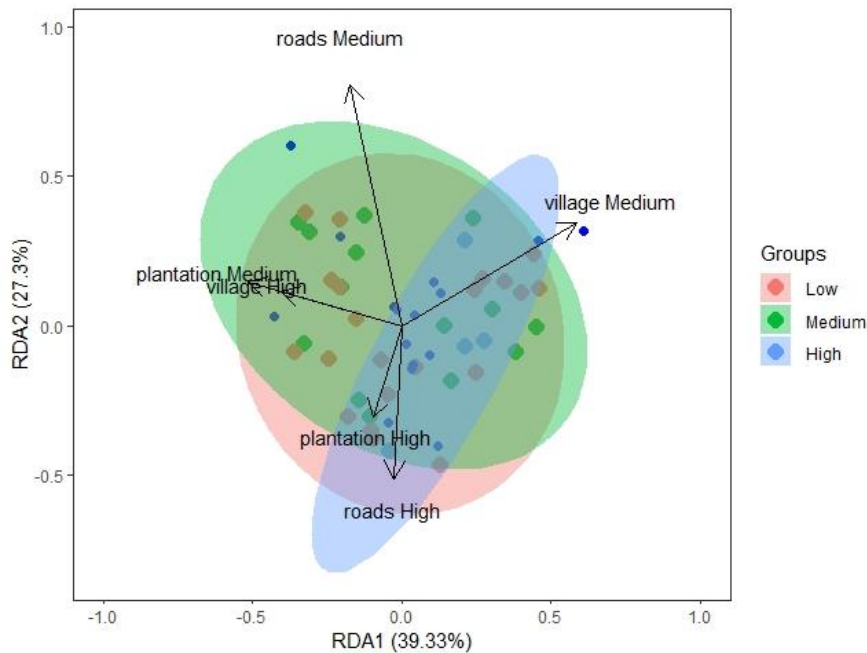
PCA results indicate that within the subspace of environmental variability, distances to roads and plantations were particularly pronounced among the camera trap sites (Fig. 4).



**Figure 4.** PCA plots for the six feature environmental covariate feature space results, revealing differentiation among areas of low medium and high distance to a. plantations and b. roads.

**Redundancy Analysis**

Forward selection of the RDA indicated three significant variables (distance to roads, villages, and plantations). These results were confirmed using a permutation test on the RDA (Table 6), which found the distance to roads, villages, and plantations model significant (p-value 0.028). Permutation results indicated 6 RDA axes with one significant as determined by ANOVA and 16 PCA axes. Variance inflation factors (VIF) were checked to determine collinearity using a threshold of 7, and none of the model variables were found to be strongly correlated. These RDA results confirm that proximity to human disturbances such as roads, villages, and plantations affects the number of detections of carnivores (Fig. 5).



**Figure 5.** Statistically significant RDA results indicated that Hellinger transformed species richness of carnivore detections in response to distance to roads, villages, and plantations model. Areas are shaded to denote low, medium, and high numbers of detections of carnivores

Further results showed that the environmental variables accounted for roughly 15% of the constrained variation, leaving approx 85% of the variation unexplained (Table 7). The first RDA coefficients indicate that the carnivore community preferred areas of high distance to roads and plantations and medium distance from villages.

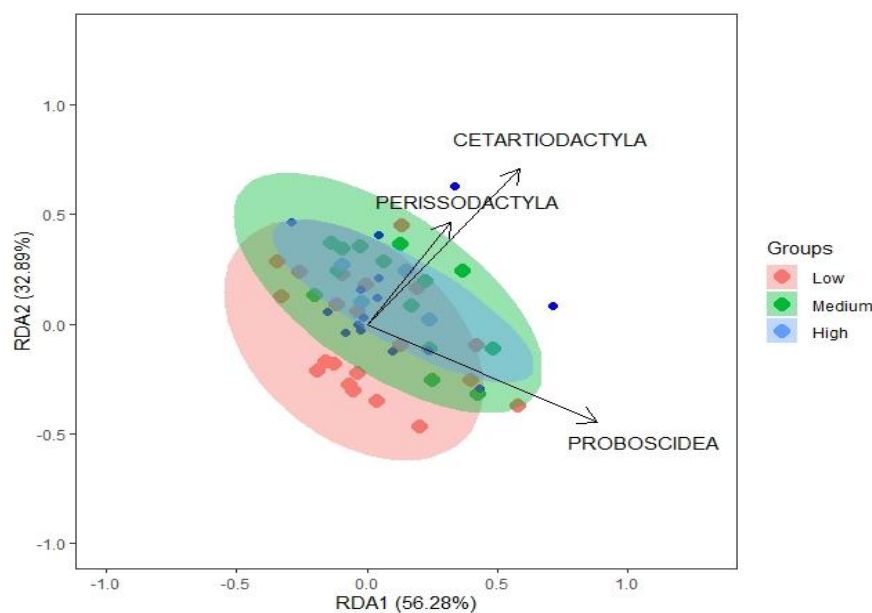
**Table 6.** Results from the RDA of carnivore community data and anthropogenic covariates (distance to roads, plantations, and villages)

Model	Covariates	Df	Variance	F	Pr(>F)
Full	Elevation, slope, distance to roads, villages, streams and plantations	6	0.09116	0.8436	0.744
Anthropogenic	Distance to roads, villages, and plantations	6	0.14772	1.4939	0.028 *
Natural	Elevation, slope, distance to streams	6	0.09116	0.8436	0.736

**Table 7.** Significance of RDA and the proportion of constrained and unconstrained variation in the data.

	Inertia	Proportion
Total	0.65084	1.0000
Constrained	0.09789	0.1504
Unconstrained	0.55295	0.8496

Further RDA results for the sum of detection days across orders indicate a niche space within the wider mammal community that the carnivores inhabit. Notably, the species richness of carnivores was significantly correlated with higher detections of the species in orders Cetartiodactyl (even-toed ungulate), Perissodactyla (odd-toed ungulate), and fewer detections of Proboscidea (elephants), as confirmed by ANOVA with a model significance ( $p=0.028$ ) (Fig 6).



**Figure 6.** Statistically significant RDA results indicated that Hellinger transformed species richness with detection day counts of mammal species in various orders (Proboscidea, Perissodactyla, Cetartiodactyla). With areas shaded for low, medium, and high numbers of carnivore detections.

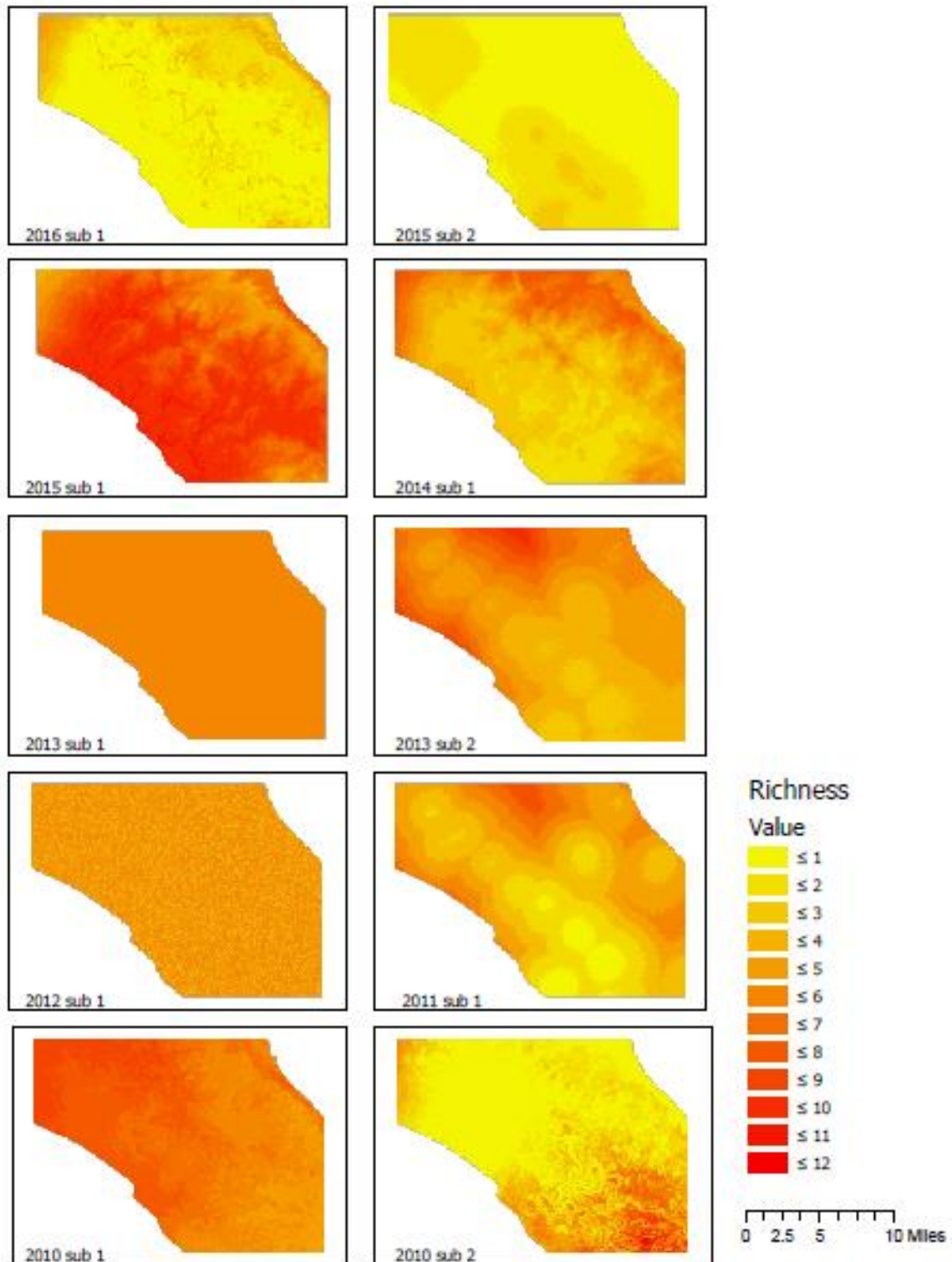
Results from the exploratory analysis indicate from PCA that camera trap sites that detected carnivores show a distinct difference between anthropogenic covariates and natural covariates. Furthermore, the anthropogenic covariates for distance to roads, villages, and plantations are significant to this carnivore community (p-value 0.028), explaining 15% of the data are constrained variation.

### **Single Subset Occupancy Modeling**

Results from the first set of models run for each subset (Block 1 (April-May), Block 2 (June-July)) indicate that the models utilizing covariate information performed better than the null model (Supp. Table 7a and 7b). Overall, 14 seasons were used in this analysis. Model selection using deviance, lppd, pD, WAIC, CPO confirmed the best model among the total, anthropogenic, natural, and null models. In four of the seasons (28%), the full covariate model was the best fit, four of the seasons (28%), the anthropogenic model was the best fit, four of the seasons (28%), the natural model was the best fit, and two of the seasons (14%) the null model was the best fit. This indicates that covariate information helped predict the carnivore community more than the null model. Model evaluation using Deviance, AUC, and Brier was used to confirm whether the models fit the data. Sparse camera trapping datasets were shown to perform adequately with enough carnivore detections. Several models fit the data with AUC scores lower than 0.5, meaning the model can be considered complete random noise. Ten models had AUC scores higher than 0.5, indicating these models fit the model better than non-random during the cross-validation runs (Full (3), Anthro(3), Natural (2), Null (2)) (Supp. Table 8). However, the model results for those that fit marginally well showed different mean covariate responses for each year and season (Supp. Table 9). Our hypothesis that there will be covariate effects on the community as a whole was confirmed. However, the estimates of covariates between years were not consistent. Furthermore, none of the models had an AUC > 0.7, indicating the models overall did not fit very well. Species richness distribution maps were generated from the outputs (Fig 7), which show the projected species richness outputs onto the landscape, further illustrating the models' inconsistency to find a niche subspace within the study area carnivore species richness may be higher or lower between years.

### **Block Design Occupancy Modeling**

The block-design models that included a block effect within the model (May-July) were run for each year of the study. The model selection procedures showed that the full model outperformed all other models, with five out of the seven years (71%) having better selection metrics for the full model (Supp. Table 10). However, the models were shown through model evaluation metrics and k-fold cross-validation not to perform better than random with AUC ~ 0.5 (Supp. Table 11). These results indicate the block-effects while allowing for a more extensive inclusion of surveys between May and July, did not improve the ability of MSOM to estimate covariate effects.



**Figure 7.** Carnivore species richness outputs and projection onto the landscape for the years that had an AUC > 0.5.

### Broad Scale Occupancy Modeling

The block design models that had collated monthly data across years were assessed as the anthropogenic model performing best (Supp. Table 12). However, the AUC ~ 0.5 revealed these results to be no better than random (Supp. Table 13).

## Discussion

The results from the RDA were conclusive for anthropogenic effects on the carnivore community. The RDA produced significant results with the broad-scale exploratory techniques not confirmed by local scale MSOM with imperfect detection. The hierarchical Bayesian MSOM was only marginally able to detect any covariability for species richness and the environmental variables at the smallest scale modeled, which used every survey day, no block effects, and each year separately. The MSOM was inconclusive at larger temporal scales when block effects were added and when data were collated to each month within every year in one model. Of the MSOM models for the smallest scale of data, results were not consistent across years, showing a mix of full, anthropogenic, natural, and null models. Furthermore, even models with the best model selection and evaluation did not have model estimates that were similar for covariates, indicating that MSOM techniques at the local scale did not best represent these data. To illustrate these inconsistencies, the models were plotted to show potential landscape-scale species richness hotspots.

Additional analyses indicated that small variation in the RDA was significant for carnivore species richness described by a niche space of taxonomic orders. Higher numbers of Cetartiodactyla and Perissodactyla indicated higher numbers of carnivores and a marginal distance from Proboscidea. These results indicate that a small amount of variation in the data is likely to co-occurring ungulate species in areas where there is a higher number of carnivores.

The scale of analysis between RDA and MSOM was a topic of concern for this study, as the RDA collates all data across years, producing one column of species counts at each site across the seven years of the study, whereas the MSOM was modeled at different temporal scales using the entire survey of detection days or month and also accounting for imperfect detection. Furthermore, the RDA used factored variables for distance to roads, plantation, and village as significant, revealing that factoring variables into broader categories helped detect significant variables correlated with carnivore species richness.

Previous carnivore studies have performed occupancy modeling, either single season or multi-season single species models on individual carnivores, revealing occupancy patterns and niche partitioning when exposed to anthropogenic pressures (Lantschner et al., 2012; Pettorelli et al., 2010; Rich et al., 2017; Schuette et al., 2013; Van der Weyde et al., 2018). For example, Schuette (2013) showed through individual-species models that distance to human settlements and land uses were shown in Kenya to affect 83% of African carnivores' species in their study area. A unique combination of environmental variables was shown to influence occupancy patterns for each carnivore studied (Schuette et al., 2013). Globally, many mammalian carnivores exist in areas of high spatial overlap or significant spatial avoidance, resulting in carnivore co-occurrences, where resource availability is potentially similar (Davis et al., 2018). Other studies have attempted to estimate the carnivore community's structure, using density estimates derived from spatial capture-recapture models that are spatially-explicit, to understand space use and interspecific interactions (Jiménez et al., 2017). Previous studies on the carnivore community in Bukit Barisan Selatan National Park (BBSNP) have shown that many carnivores have temporal overlap or non-overlap of their busy times of day, indicating felid sympatry (Allen et al., 2020). Through quantitative analysis, these carnivore studies have shown that there are carnivore community organizations and niche overlap in areas of shared resource use.

Other studies have sought to understand community-level covariate effects using MSOM (Boron et al., 2019; Cavada et al., 2019; Dechner et al., 2018; Rovero et al., 2014) using the Bayesian Credible Interval (BCI) or Bayesian p-value to understand whether the model fit. However, methods and metrics for performing model selection (Broms et al., 2016) and evaluation (Zipkin et al., 2012) have developed slowly alongside these multispecies models. Here, we were able to provide several model selection (lppd, pD, waic, CPO) and evaluation metrics (deviance, AUC, briers log) (Broms et al., 2016) for our models to confirm that these MSOM models only marginally fit the data. The models that had AUC better than random included several subsets within the most local scale models, although when projected onto the landscape, it also revealed no distinct patterns between seasons and the model estimates showed no consistency between subsets and seasons.

This study was unable to make definitive conclusions using community-level data and MSOM, which accounts for imperfect detection in a more robust modeling framework to include rare species into the analysis. Using a broad scale of analysis for RDA was more successful, likely because the number of individual carnivore detections was low, so collating the detections across years and further binning the covariates into factors was the best way to analyze carnivore data from this dataset. The comparison between MSOM and RDA has been addressed by Yamaura et al. (2019), who concluded that they are beneficial depending on the application. One significant difference in the modeling techniques presented in this work that RDA does not include imperfect detection and is therefore not making any inferences about occupancy, only detection. We can say that we detected higher numbers of carnivores at sites with greater distances from plantations and roads, and medium distances from villages, although this does not estimate occupancy or species richness that we can project onto the landscape along with covariate estimates. The MSOM did include imperfect detection and was not able to find a consistent correlation between the covariates between years or produce results that are considered genuinely robust ( $AUC > 0.7$ ), only marginally better than random ( $AUC > 0.5$ ). These methods can be more beneficial for larger datasets where the frequency of detection is higher, and the covariate effects are more pronounced, such as a multi-regional study that has shown a much better ability to fit the data (Sutherland et al., 2016). An extension of this study may attempt the same workflow utilizing camera grids from across the state of Sumatra to produce a broader range heterogeneity. In this study, we sought to use sparse carnivore detections that are a product of surveying carnivores that are wide-ranging and difficult to detect. Furthermore, between years the number of cameras was not consistent, with some years having only 30 or 40 cameras and other years having 60 cameras, which means that imputing the data may have been able to help with these inconsistencies.

Large-scale camera trapping data are only now surfacing for public use or in private database repositories that can enable more synergistic research. Large area camera trapping networks have been implemented in order to address questions about mammal distributions at a landscape scale (McShea et al., 2016), and multiple groups such as GBIF, GEO BON, eMammal, TEAM network are working towards global camera trapping coverage for generating biodiversity data for terrestrial mammal assemblages (Steenweg et al., 2017). In combination with environmental data from repositories such as Google Earth Engine, MSOM approaches can help understand how communities use the landscape in response to anthropogenic disturbances. As these data are



generated, then analysis projects like this may be applied to larger projects with more differentiation from which to model, making landscape-scale patterns easier to detect.

The implications of looking at broader scales for patterns using RDA that otherwise would not be detectable using MSOM are significant. The results demonstrate the large-scale detectability patterns for carnivore species that otherwise were not apparent from running MSOM. While there are many implications to not including imperfect detection into the analysis and collating data across years for one response column of data, it appears in this study that any patterns in species richness that was to be detected were only available at larger scales. This also indicates that the data for MSOM may require much larger samples across a larger area to perform adequately at the small temporal scales that it operates and including imperfect detection.

## Conclusions

The analysis presented in this paper utilizes redundancy analysis (RDA) and multispecies occupancy (MSOM) as an exploratory analysis to determine covariate effects on the carnivore community. The exploratory data analysis RDA showed significant results with anthropogenic covariates for high distance to roads and plantations and medium distance to villages with higher carnivore detections. MSOM was intended to model species richness on the landscape given covariates. However, the results were not consistent. Despite the low detection frequency of many species in the study, this camera trapping study enabled us to include these rare carnivores and imperfect detection into our species richness models. The model selection log pointwise predictive density (lppd), Watanabe-Akaike information criterion (WAIC) and Conditional Predictive Ordinate Criterion (CPO), and evaluation metrics (Deviance, Area under Curve (AUC) and Brier's Log) assisted in further understanding the effect of covariate information on the carnivore community as a whole. MSOM was unable to make definitive conclusions about the carnivore community across various spatial and temporal scales, as the models that produced marginal significance had covariate estimates that were not consistently positive or negative between years. The results indicate that species richness patterns were detectable across large spatial and temporal scales using the RDA after collating all detections across seven years and binning covariates, whereas finer temporal scales using the MSOM for survey days and months and including imperfect detection were unable to make meaningful conclusions.

**Acknowledgments:** We are grateful to the TEAM network and William McCarthy to freely download the camera trap data from Bukit Barisan Selatan NP. Thank you to FiBER and the Center for Landscape Conservation Planning to support dissertation research and graduate teaching assistantship. Special thanks to reviewers for taking the time to comment. This work was supported by the Florida Institute for Built Environment Resilience and the University of Florida, Gainesville, FL.

## References

Allen, M. L., Sibarani, M. C., Utoyo, L., & Krofel, M. (2020). Terrestrial mammal community richness and temporal overlap between tigers and other carnivores in Bukit Barisan

- Selatan National Park, Sumatra. *Animal Biodiversity and Conservation*, 97–107. <https://doi.org/10.32800/abc.2020.43.0097>
- Borcard, D., Gillet, F., & Legendre, P. (2011). *Numerical ecology* with R. Springer.
- Boron, V., Deere, N. J., Xofis, P., Link, A., Quiñones-Guerrero, A., Payan, E., & Tzanopoulos, J. (2019). Richness, diversity, and factors influencing occupancy of mammal communities across human-modified landscapes in Colombia. *Biological Conservation*, 232, 108–116. <https://doi.org/10.1016/j.biocon.2019.01.030>
- Broms, K. M., Hooten, M. B., & Fitzpatrick, R. M. (2016). Model selection and assessment for multispecies occupancy models. *Ecology*, 97(7), 1759–1770. <https://doi.org/10.1890/15-1471.1>
- Cavada, N., Worsøe Havmøller, R., Scharff, N., & Rovero, F. (2019). A landscape-scale assessment of tropical mammals reveals the effects of habitat and anthropogenic disturbance on community occupancy. *PLOS ONE*, 14(4), e0215682. <https://doi.org/10.1371/journal.pone.0215682>
- Davis, C. L., Rich, L. N., Farris, Z. J., Kelly, M. J., Di Bitetti, M. S., Blanco, Y. D., Albanesi, S., Farhadinia, M. S., Gholikhani, N., Hamel, S., Harmsen, B. J., Wultsch, C., Kane, M. D., Martins, Q., Murphy, A. J., Steenweg, R., Sunarto, S., Taktehrani, A., Thapa, K., ... Miller, D. A. W. (2018). Ecological correlates of the spatial co-occurrence of sympatric mammalian carnivores worldwide. *Ecology Letters*, 21(9), 1401–1412. <https://doi.org/10.1111/ele.13124>
- Dechner, A., Flesher, K. M., Lindell, C., Vega de Oliveira, T., & Maurer, B. A. (2018). Determining carnivore habitat use in a rubber/forest landscape in Brazil using multispecies occupancy models. *PLOS ONE*, 13(4), e0195311. <https://doi.org/10.1371/journal.pone.0195311>
- Dorazio, R. M., & Royle, J. A. (2005). Estimating Size and Composition of Biological Communities by Modeling the Occurrence of Species. *Journal of the American Statistical Association*, 100(470), 389–398. <https://doi.org/10.1198/016214505000000015>
- Dray, S., Péliissier, R., Couteron, P., Fortin, M.-J., Legendre, P., Peres-Neto, P. R., Bellier, E., Bivand, R., Blanchet, F. G., De Cáceres, M., Dufour, A.-B., Heegaard, E., Jombart, T., Munoz, F., Oksanen, J., Thioulouse, J., & Wagner, H. H. (2012). Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs*, 82(3), 257–275. <https://doi.org/10.1890/11-1183.1>
- Easter, T., Bouley, P., & Carter, N. (2019). Opportunities for biodiversity conservation outside of Gorongosa National Park, Mozambique: A multispecies approach. *Biological Conservation*, 232, 217–227. <https://doi.org/10.1016/j.biocon.2019.02.007>
- Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E., & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478(7369), 378–381. <https://doi.org/10.1038/nature10425>
- Goijman, A. P., Conroy, Michael J., Bernardos, J. N., & Zaccagnini, M. E. (2015). Multi-Season Regional Analysis of Multi-Species Occupancy: Implications for Bird Conservation in

- Agricultural Lands in East-Central Argentina. PLOS ONE, 10(6), e0130874. <https://doi.org/10.1371/journal.pone.0130874>
- Hooten, M. B., & Hobbs, N. T. (2015). A guide to Bayesian model selection for ecologists. *Ecological Monographs*, 85(1), 3–28. <https://doi.org/10.1890/14-0661.1>
- Jaya, I. N. S., Wijanarto, A. B., & Wibisono, H. T. (n.d.). Deforestation and its Implications for Sumatran tigers in Bukit Barisan Selatan National Park, Sumatra (Deforestasi dan Implikasinya terhadap Populasi Harimau Sumatra di Taman Nasional Bukit Barisan Selatan, Sumatra). 9.
- Jiménez, J., Nuñez-Arjona, J. C., Rueda, C., González, L. M., García-Domínguez, F., Muñoz-Igualada, J., & López-Bao, J. V. (2017). Estimating carnivore community structures. *Scientific Reports*, 7(1), 41036. <https://doi.org/10.1038/srep41036>
- Kellner, K. (2019). Package "jagsUI." CRAN Repository.
- Korkmaz, S., Goksulul, D., & Zararsiz, G. (2019). Package 'MVN: Multivariate Normality Tests'. CRAN Repository.
- Lantschner, M. V., Rusch, V., & Hayes, J. P. (2012). Habitat use by carnivores at different spatial scales in a plantation forest landscape in Patagonia, Argentina. *Forest Ecology and Management*, 269, 271–278. <https://doi.org/10.1016/j.foreco.2011.12.045>
- Laurance, W. F., Sayer, J., & Cassman, K. G. (2014). Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*, 29(2), 107–116. <https://doi.org/10.1016/j.tree.2013.12.001>
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8), 2248–2255. [https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)
- McCarthy, J. L., Wibisono, H. T., McCarthy, K. P., Fuller, T. K., & Andayani, N. (2015). Assessing the distribution and habitat use of four felid species in Bukit Barisan Selatan National Park, Sumatra, Indonesia. *Global Ecology and Conservation*, 3, 210–221. <https://doi.org/10.1016/j.gecco.2014.11.009>
- McShea, W. J., Forrester, T., Costello, R., He, Z., & Kays, R. (2016). Volunteer-run cameras as distributed sensors for macrosystem mammal research. *Landscape Ecology*, 31(1), 55–66. <https://doi.org/10.1007/s10980-015-0262-9>
- Moore, J. F., Mulindahabi, F., Masozera, M. K., Nichols, J. D., Hines, J. E., Turikunkiko, E., & Oli, M. K. (2018). Are ranger patrols effective in reducing poaching-related threats within protected areas? *Journal of Applied Ecology*, 55(1), 99–107. <https://doi.org/10.1111/1365-2664.12965>
- O'Brien, T. G., & Kinnaird, M. F. (1996). Birds and mammals of the Bukit Barisan Selatan National Park, Sumatra, Indonesia. *Oryx*, 30(3), 207–217. <https://doi.org/10.1017/S0030605300021657>

- O'Brien, T. G., Kinnaird, M. F., & Wibisono, H. T. (2003). Crouching tigers, hidden prey: Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*, 6(2), 131–139. <https://doi.org/10.1017/S1367943003003172>
- Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P., O'Hara, R. B., Simpson, G., Solymos, P., Stevens, H., Szoecs, E., & Wagner, H. (2019). Package "vegan." CRAN Repository.
- Ovaskainen, O., Abrego, N., Halme, P., & Dunson, D. (2016). Using latent variable models to identify large networks of species-to-species associations at different spatial scales. *Methods in Ecology and Evolution*, 7(5), 549–555. <https://doi.org/10.1111/2041-210X.12501>
- Pacifici, K., Zipkin, E. F., Collazo, J. A., Irizarry, J. I., & DeWan, A. (2014). Guidelines for a priori grouping of species in hierarchical community models. *Ecology and Evolution*, 4(7), 877–888. <https://doi.org/10.1002/ece3.976>
- Pettorelli, N., Lobora, A. L., Msuha, M. J., Foley, C., & Durant, S. M. (2010). Carnivore biodiversity in Tanzania: Revealing the distribution patterns of secretive mammals using camera traps. *Animal Conservation*, 13(2), 131–139. <https://doi.org/10.1111/j.1469-1795.2009.00309.x>
- Pusparini, W., Batubara, T., Surahmat, F., Ardiantiono, Sugiharti, T., Muslich, M., Amama, F., Marthy, W., & Andayani, N. (2018). A pathway to recovery: The Critically Endangered Sumatran tiger *Panthera tigris sumatrae* in an 'in danger' UNESCO World Heritage Site. *Oryx*, 52(1), 25–34. <https://doi.org/10.1017/S0030605317001144>
- Rao, C. R. (1964). *The Use and Interpretation of Principal Component Analysis in Applied Research*. 31.
- Rezaei, S., Mohammadi, A., Cushman, S. A., Bencini, R., Rooney, T., & Naderi, M. (2021). Landscape connectivity for two sympatric carnivores in central Iran [Preprint]. Preprints. <https://doi.org/10.22541/au.161153950.09782632/v1>
- Rich, L. N., Miller, D. A. W., Robinson, H. S., McNutt, J. W., & Kelly, M. J. (2017). Carnivore distributions in Botswana are shaped by resource availability and intraguild species. *Journal of Zoology*, 303(2), 90–98. <https://doi.org/10.1111/jzo.12470>
- Ripple, W. J., Chapron, G., López-Bao, J. V., Durant, S. M., Macdonald, D. W., Lindsey, P. A., Bennett, E. L., Beschta, R. L., Bruskotter, J. T., Campos-Arceiz, A., Corlett, R. T., Darimont, C. T., Dickman, A. J., Dirzo, R., Dublin, H. T., Estes, J. A., Everatt, K. T., Galetti, M., Goswami, V. R., ... Zhang, L. (2016). Saving the World's Terrestrial Megafauna. *BioScience*, 66(10), 807–812. <https://doi.org/10.1093/biosci/biw092>
- Ripple, W. J., Wolf, C., Newsome, T. M., Hoffmann, M., Wirsing, A. J., & McCauley, D. J. (2017). Extinction risk is most acute for the world's largest and smallest vertebrates. *Proceedings of the National Academy of Sciences*, 114(40), 10678–10683. <https://doi.org/10.1073/pnas.1702078114>
- Rodrigues, A. S., Brooks, T. M., Butchart, S. H., Chanson, J., Cox, N., Hoffmann, M., & Stuart, S. N. (2014). Spatially explicit trends in the global conservation status of vertebrates. *PLoS One*, 9(11), e113934.

- Rota, C. T., Wikle, C. K., Kays, R. W., Forrester, T. D., McShea, W. J., Parsons, A. W., & Millsbaugh, J. J. (2016). A two-species occupancy model accommodating simultaneous spatial and interspecific dependence. *Ecology*, 97(1), 48–53.
- Rovero, F., Martin, E., Rosa, M., Ahumada, J. A., & Spitale, D. (2014). Estimating Species Richness and Modelling Habitat Preferences of Tropical Forest Mammals from Camera Trap Data. *PLoS ONE*, 9(7), e103300. <https://doi.org/10.1371/journal.pone.0103300>
- Schuetz, P., Wagner, A. P., Wagner, M. E., & Creel, S. (2013). Occupancy patterns and niche partitioning within a diverse carnivore community exposed to anthropogenic pressures. *Biological Conservation*, 158, 301–312. <https://doi.org/10.1016/j.biocon.2012.08.008>
- Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J. T., Burton, C., Townsend, S. E., Carbone, C., Rowcliffe, J. M., Whittington, J., Brodie, J., Royle, J. A., Switalski, A., Clevenger, A. P., Heim, N., & Rich, L. N. (2017). Scaling-up camera traps: Monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology and the Environment*, 15(1), 26–34. <https://doi.org/10.1002/fee.1448>
- Sutherland, C., Brambilla, M., Pedrini, P., & Tenan, S. (2016). A multi-region community model for inference about geographic variation in species richness. *Methods in Ecology and Evolution*, 7(7), 783–791. <https://doi.org/10.1111/2041-210X.12536>
- Van der Weyde, L. K., Mbisana, C., & Klein, R. (2018). Multispecies occupancy modeling of a carnivore guild in wildlife management areas in the Kalahari. *Biological Conservation*, 220, 21–28. <https://doi.org/10.1016/j.biocon.2018.01.033>
- Wearn, O. R., Carbone, C., Rowcliffe, J. M., Pfeifer, M., Bernard, H., & Ewers, R. M. (2019). Land-use change alters the mechanisms assembling rainforest mammal communities in Borneo. *Journal of Animal Ecology*, 88(1), 125–137. <https://doi.org/10.1111/1365-2656.12903>
- Wearn, O. R., Rowcliffe, J. M., Carbone, C., Pfeifer, M., Bernard, H., & Ewers, R. M. (2017). Mammalian species abundance across a gradient of tropical land-use intensity: A hierarchical multispecies modeling approach. *Biological Conservation*, 212, 162–171. <https://doi.org/10.1016/j.biocon.2017.05.007>
- Yamaura, Y., Blanchet, F. G., & Higa, M. (2019). Analyzing community structure subject to incomplete sampling: Hierarchical community model vs. canonical ordinations. *Ecology*, 100(8). <https://doi.org/10.1002/ecy.2759>
- Zipkin, E. F., Andrew Royle, J., Dawson, D. K., & Bates, S. (2010). Multispecies occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation*, 143(2), 479–484. <https://doi.org/10.1016/j.biocon.2009.11.016>
- Zipkin, E. F., DeWan, A., & Andrew Royle, J. (2009). Impacts of forest fragmentation on species richness: A hierarchical approach to community modelling. *Journal of Applied Ecology*, 46(4), 815–822. <https://doi.org/10.1111/j.1365-2664.2009.01664.x>
- Zipkin, E. F., Grant, E. H. C., & Fagan, W. F. (2012). Evaluating the predictive abilities of community occupancy models using AUC while accounting for imperfect detection. *Ecological Applications*, 22(7), 1962–1972. <https://doi.org/10.1890/11-1936.1>