Comprehensive Single-Season Occupancy Analysis with Covariates

for all Species within Genus Tapirus

by

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Abstract

There are four species within the genus Tapirus: *T. bairdii* (Baird's tapir), *T. indicus* (Malayan tapir), *T. terrestris* (Lowland tapir), and *T. pinchaque* (Mountain tapir). Tapirs perform important ecological roles and are listed as either 'Endangered' or 'Vulnerable' on the IUCN Red List. We utilized camera-trap data to perform a collaborative global study of all tapir species using single-season occupancy analysis. To understand commonalities and differences between tapir habitat selection, we utilized the same analysis techniques and covariates for each species. Covariates were selected based on their potential to influence tapir habitat selection: Human Footprint Index (HFI), distance to road, elevation, and average monthly precipitation. We predicted that different tapir species will have different adaptations and therefore different covariates will be important for the occupancy of each species. Our results indicate empirical support for models incorporating distance to road for Baird's tapir, HFI for lowland tapir, elevation for Malayan tapir, and all covariates for mountain tapir. Our results support our hypothesis but do not align with our model predictions for Baird's or Lowland tapirs. An understanding of the differences and similarities in habitat selection variables for each tapir species is needed to accurately inform policy and land use decisions.

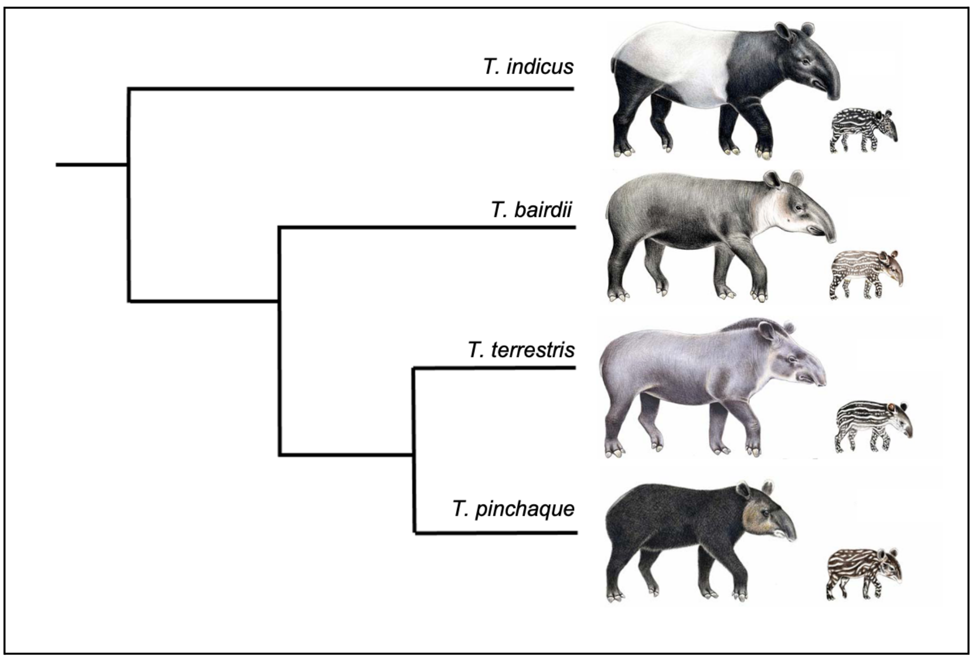
Introduction

Tapir belong to the order Perissodactyla, the family Tapiridae, and the genus *Tapirus*, one of the last remaining megafauna genera, with four extant species: *T. bairdii* (Baird's tapir), *T. indicus* (Malayan tapir), *T. terrestris* (Lowland tapir), and *T. pinchaque* (Mountain tapir). It is commonly known among taxonomists that *T. indicus* is the oldest extant species, followed by *T. bairdii*, then *T. pinchaque* and *T. terrestris* (Figure 1; Ruiz-García *et al*., 2012; Steiner & Ryder, 2011). It has been suggested that the Malayan and American tapirs diverged somewhere from 20 to 30 mya, subsequently traveling through North America around 3 mya, down through Central America, and then finally to South America (Ashley *et al*., 1996). While all the species physically resemble each other, they possess distinct characteristics and adaptations that allow them to inhabit different areas of the world, and therefore tapir species may differ in their ecological needs and susceptibility to anthropogenic factors.

Of the four extant tapir species, three have a New World distribution, and one has an Old World distribution. The Baird's tapir (*T. bairdii*) is native to Mesoamerica, ranging from southern Mexico to northern Columbia and found in a variety of humid habitats from sea level to 3600 m (Naranjo *et al.*, 2000; Schank *et al.*, 2020). The Baird's Tapir can be identified by its short brown coat, distinct black dots on both cheeks, and white markings on their throat, ears, and toes (Figure 1)(Reid, 2009). The Lowland Tapir (*T. terrestris*) has the largest distribution of all extant tapir species and has been found throughout lowland subtropical and tropical regions of northern and central South America including Argentina, Brazil, Bolivia, Ecuador, Peru, Colombia, French Guiana, Guyana, Paraguay, Suriname, and Venezuela (Varela *et al.*, 2019). The Lowland Tapir can be identified by a developed sagittal crest and a short, but prominent, mane along the neck (Figure 1; Hershkovitz, 1954; MacKinnon, 1985). The Mountain Tapir (*T. pinchaque*) has the smallest distribution of all extant tapir species, with a range between 1400m and 4500m in the high Andes

Mountains through Colombia, Ecuador, and Peru (Lizcano *et al*., 2016; Mena *et al.,* 2020). The Mountain Tapir can be identified by its dark thick wooly fur and white wooly fringe around its lips, toes, and tips of its ears (Figure 1; Allen, 1942). The Malayan Tapir (*T. indicus*) is the only Old World representative of this group with a patchy distribution across Indonesia, Myanmar, Malaysia, and Thailand (Traeholt *et al*., 2016). The Malayan Tapir can be easily identified by its coloration, with a white section spanning from the tail to behind the front legs, contrasting the darkly colored head, neck, and legs (Figure 1; Ripley, 1985). This coloration is thought to confuse predators by disrupting body lines and making it difficult for predators to immediately recognize a Malayan Tapir as prey (Sanborn & Watkins, 1950). Of the four extant species, the Malayan tapir is the largest weighing over 300 kg, and the mountain tapir is the smallest, weighing between 150-200 kg (Zimmerman & Hernandez, 2015). The Baird's Tapir and Lowland Tapir fall between, weighing approximately 150-300 kg (Emmons & Feer, 1997; Varela *et al.*, 2019).

Figure 1: Taxonomic tree overviewing the relationship between each species in the genus *Tapirus*. This figure displays the relationship between all extant tapir species and when they diverged in reference to each other. All illustrations are by Stephen Nash of Conservation International and published by the Tapir Specialist Group.



Tapirs are among the largest terrestrial herbivores of tropical forests, performing important ecological roles, such as seed dispersal, nutrient cycling, and other ecosystem functions (O'Farrill *et al.,* 2013). Tapirs also serve an important role as foragers, eating a variety of plant species depending on seasonal changes, species abundance, and habitat occupied (Naranjo, 2009).

Different factors influence the habitat choice of tapirs. The lifestyle of tapir centers around the presence of water due to the importance of water to their life cycle, namely for predator evasion, defecation, and parasite removal (Barongi, 2007; Naranjo, 1995). Another factor that may influence habitat choice is the human influence on a given area. If the area is highly populated, or frequently traversed by hunters, tapirs may be less likely to occupy that region (Linkie *et al*., 2013). Because humans have historically hunted and poached tapirs in the past, specifically with

Baird's tapir, this specific species may have generational caution when humans are around and therefore avoid highly influenced areas (Koster, 2006). Factors such as these are crucial in gaining an accurate picture of where tapirs inhabit and why.

Understanding factors that influence tapir occupancy is especially important given the conservation status of each tapir species. Bairds, Malayan, and Mountain tapir are classified by the IUCN Red list as 'Endangered' and decreasing in population size, and the Lowland tapir is classified as 'Vulnerable' with a decreasing population trend (García *et al.*, 2016; Lizcano *et al.*, 2016; Traeholt *et al.*, 2016; Varela *et al.*, 2019). Across all tapir species, the primary causes of population decline are poaching, fragmentation, and habitat loss (García *et al.*, 2016; Lizcano *et al.*, 2016; Traeholt *et al.*, 2016; Varela *et al.*, 2019). Because of the decline in tapir populations, it is important to realize what factors influence tapir habitat choice in order to accurately inform land use decisions as well as conservation policy.

Due to their elusive nature, tapir can be difficult to observe, requiring alternative study methods. Camera traps can be used to study tapir and estimate occupancy probability (ψ), the proportion of an area where a species is present, in a non-invasive manner (MacKenzie *et al.*, 2017). Occupancy modeling is a widely used hierarchical model which incorporates species occurrence (occupancy), imperfect detection, and predictor covariates to estimate detection (p) and occupancy probability (ψ) for a given species (MacKenzie *et al.*, 2017).

Using this method, we performed a comprehensive single-season occupancy model for all species within genus *Tapirus*, using the same covariates and analysis techniques for each. Several studies have investigated tapir-habitat relationships and the effect of various anthropogenic factors, however, it is difficult to compare ecological aspects between species because each study uses a different methodology and set of variables. To our knowledge, no study has systematically compared how the same set of environmental and anthropogenic factors affect the different tapir species. That information has the potential to reveal commonalities across tapir species, as well as highlight important differences from the ecological and conservation perspective.

For this study, we chose to incorporate average monthly precipitation, human footprint index, distance to road, and elevation as our model covariates (Table 2). Due to differing climates, protection levels, and degrees of human influence across study sites, we hypothesize that tapir species will have different adaptations, and therefore different covariates will be important to the occupancy of each species. Across all species, we predict a positive correlation between occupancy probability and average monthly precipitation, a negative correlation between occupancy probability and human footprint index, and a positive correlation between occupancy probability and distance to road. However, tapir species with broader geographic distribution (Lowland and Baird's tapir) are expected to show greater environmental plasticity and to be less affected by anthropogenic variables than species with restricted distribution (Malayan and Mountain tapir). Additionally, we hypothesize that elevation will be positively correlated with Mountain and Baird's tapir occupancy, given the broader elevational gradient of the survey areas, yet not a significant predictor for Lowland or Malayan tapirs. Based on our hypotheses, we predict average monthly precipitation and elevation will be within the top models for Baird's tapir, average monthly precipitation will be within the top model for Lowland tapir, average monthly precipitation, distance to road, and human footprint index will be within top models for Malayan tapir, and average monthly precipitation, distance to road, elevation, and human footprint index will be within top models for Mountain tapir.

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Through the examination of multiple global datasets, we aim to identify how selected covariates influence the presence of each tapir species for the purpose of standardizing knowledge of tapir occupancy and better informing policy decisions, specifically regarding land use.

Methods

Collaboration

Data for this project were gathered via sources indicated in Table 1. All sources utilized similarly structured camera trapping surveys to collect data.

Table 1: Detailed survey information for each tapir species.

Year	Species	Location	Mean no. of days deployed (SD)[a]	Stations	Effort[b]	Spacing (km)[c]	Records[d]	Source
2011-2019	*T. bairdii*	Costa Rica	89.06 (33.84)	141	12,558	~1-2	293	Mooring *et al.*, 2020
2013-2014, 2016-2020	*T. terrestris*	Brazil	38.70 (11.68)	182	7,043	~3	108	Rocha *et al.*, 2016; Rocha *et al.*, 2020
2009-2011	*T. indicus*	Malaysia	48.08 (36.03)	350	28,792	~1	398	Rayan & Linkie, 2015
2016	*T. pinchaque*	Peru	111.25 (30.9)	85	9,456	~1	85	Mena *et al.*, 2020

[a]Mean no. of days deployed is calculated by totaling the number of days all cameras were active and dividing by camera number. [b]Effort is calculated by totaling the number of days all cameras were active. [c]Spacing indicates the average distance between camera trap locations for each survey. [d]Records indicate the total number of images captured at least 24 hrs apart (independent records).

Data Collection

Tapirus bairdii

The Baird's tapir study was carried out between 2011-2019. The study area was primarily located in the high-elevation tropical montane forest along the western Talamanca Cordillera of Costa Rica, with some study sites located along the Pacific Lowlands of Costa Rica (Figure 2). Data for this survey was collected within Alexander Skutch Biological Corridor, Cabo Blanco National Park, Proyecto Campanario, La Marta National Wildlife Refuge, Carara National Park, La Cangreja National Park, Chirripo National Park, La Amistad International Park, Los Quetzales National Park, Tapantí Macizo de la Muerte National Park, the Savegre Lodge Reserve in the upper Rio Savegre Valley, Bosque de Agua Biological Corridor and El Copal Reserve. Study sites range in elevation from approximately 20-3500m, and are characterized by a distinct wet season (May-November) and dry season (December-April). The study area has an average annual rainfall between 300-800 m and an average temperature between 10-20∘C (tropical montane forest) and 24-32∘C (Pacific lowland) (CCSA, 2019; Herrera *et al.*, 2018).

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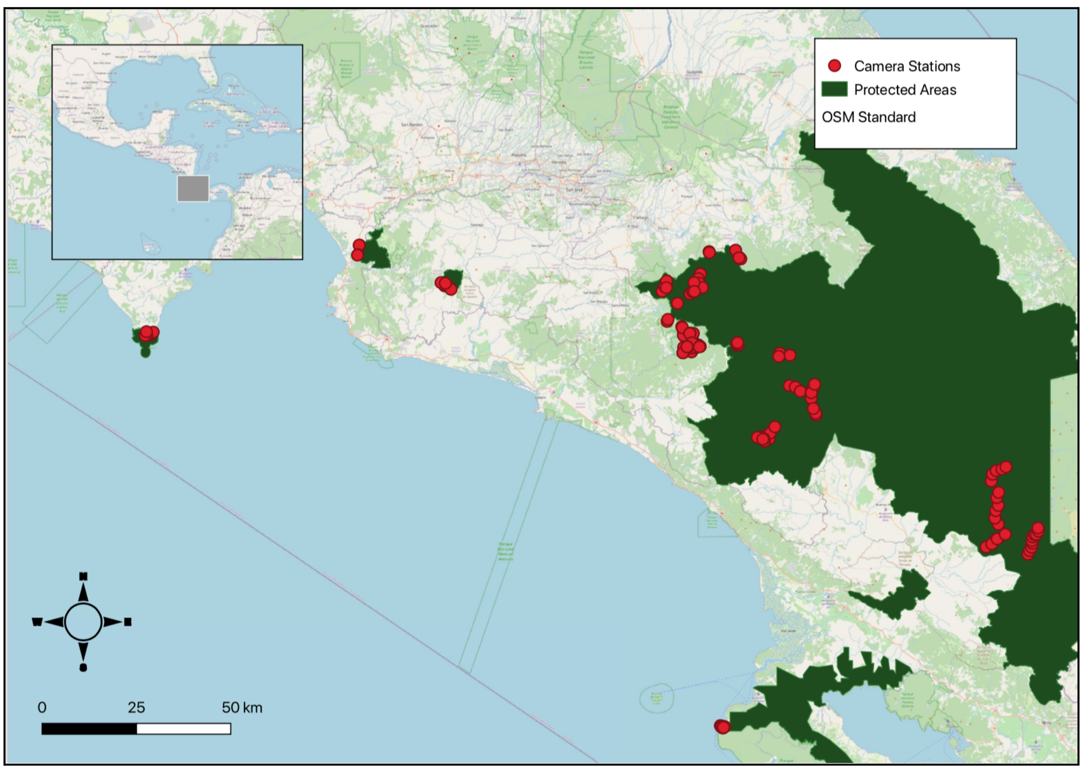
Across the study site, 141 camera stations (Bushnell Trophy Cam) were manually deployed. Cameras were enclosed in a protective case and placed ~1m above the ground along trails. To ensure cameras were functioning correctly, once set, they were tested to ensure photos were taken at the appropriate height and angle. Nearby vegetation was removed to prevent false triggering. Each camera was equipped with a nearby scent station - a PVC pipe holding a piece of sponge soaked in Calvin Klein's *Obsession for Men* (Calvin Klein Inc., New York, NY, USA) – causing tapirs to pause within the camera's field of vision, but not attracting animals that are not already on the trail (Braczkowski *et al.*, 2016). To maintain cameras year-round, researchers worked in collaboration with national park staff, refuge managers, and community volunteers. For full details regarding the study area, trail cameras, and scent stations see Mooring *et al.*, 2020.

Figure 2: Costa Rica camera trap locations for *T. bairdii* survey. Camera station locations are indicated by red dots, and dark green indicates protected area coverage. Inset map contains an overview of the study areas in Costa Rica in Central America, denoted by a gray window. Base map originates from OSM and camera station coordinates are projected in EPSG: 4326. Map was created using the long-term release (LTR) version of qGIS.

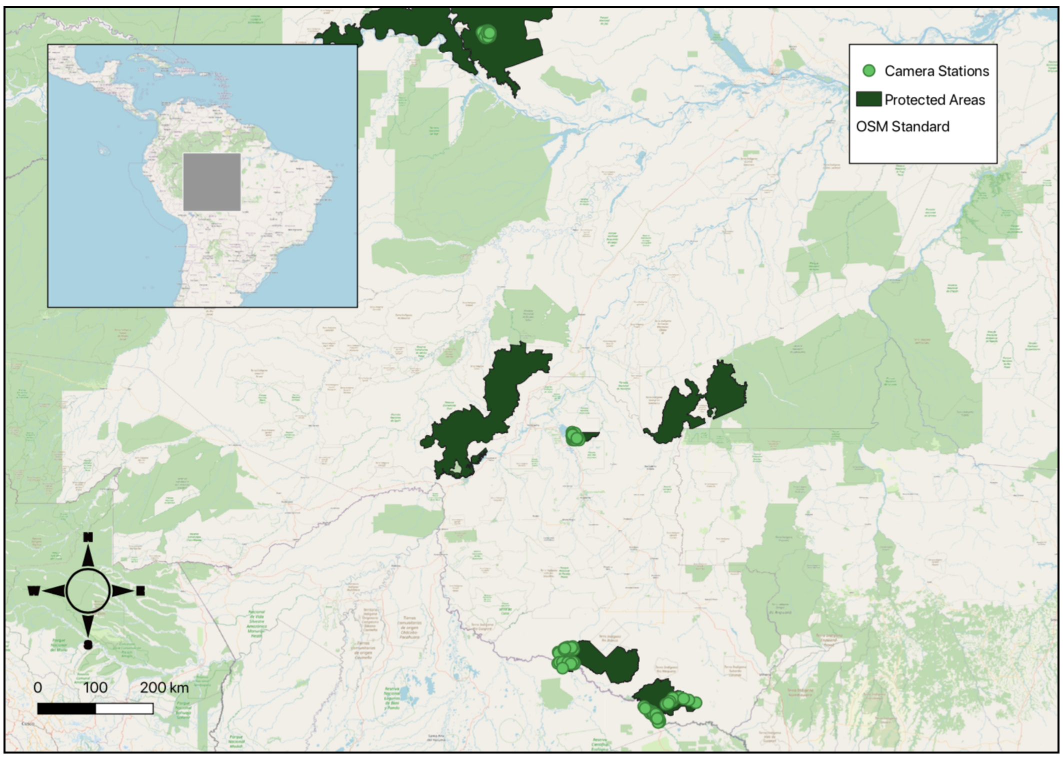


Tapirus terrestris

The Lowland tapir study was carried out during two surveys in the southern Brazilian Amazon rainforest from 2013-2014 and 2016-2020 with one study area in the Central Brazilian Amazon. Data for this survey was collected in the Amaná Sustainable Development Reserve, Campos Amazônicos National Park (CANP), Mapinguari National Park (MNP), Guapore Biological Reserve (GBR), Corumbiara State Park (CSP), and the states of Amazonas, Rondônia, and Mato Grosso (Figure 3). Study sites contained fragmented habitats of remote Amazon rainforest and savannah grassland, ranging in elevation from approximately 50-200m. Study area has an average monthly temperature between 24-28°C and an average annual precipitation between 206-289 cm with a distinct wet season (October/November-March/April) and dry season (April/May-September/October) (Bastos and Diniz, 1982).

Across the study site, 182 camera stations (each site randomly allocated Reconyx PC800 Hyperfire or Bushnell HD Essential/Aggressor) were deployed along trails. Each camera was unbaited and placed ~30cm above the ground and left to run for 24 hours per day. For full details regarding study area and camera trap survey see Rocha *et al.*, 2020 and Rocha & Sollmann, 2023.

Figure 3: Brazilian Amazon camera trap locations for *T. terrestris* survey. Camera station locations are indicated by light green dots, and dark green indicates protected area coverage. Inset map contains an overview of the study areas in the Brazilian Amazon in South America, denoted by a gray window. Base map originates from OSM and camera station coordinates are projected in EPSG: 4326. Map was created using the long-term release (LTR) version of qGIS.

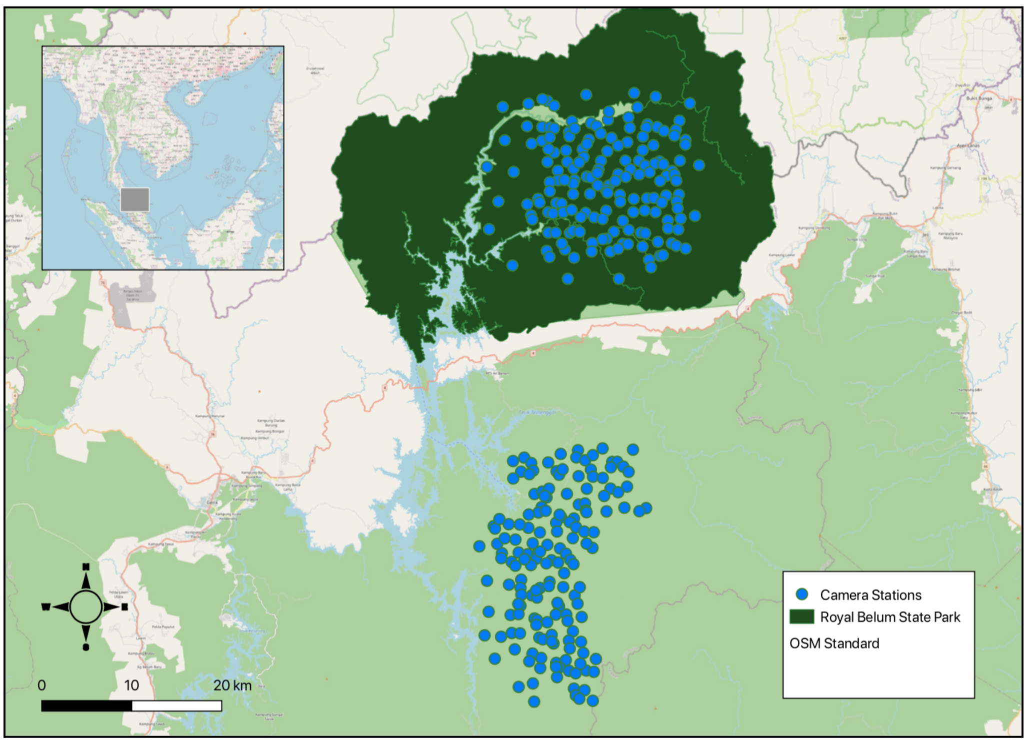


Tapirus indicus

The Malayan tapir study was conducted between 2009-2011. The study area was located in Peninsular Malaysia in the Belum-Temengor Forest Complex (BTFC) in the state of Perak (Figure 4). There are two subsites within the BTFC: the Royal Belum State Park and the Temengor Forest Reserve. The two areas are separated by the Gerik-Jeli Highway and consist of montane, lowland, and dipterocarp forests. While Royal Belum State Park is permanently protected, the Temengor Forest Reserve has a lower level of protection (Abdullah *et al*., 2011). The temperatures in peninsular Malaysia average 27 °C yearly, with an average yearly precipitation of 254 cm. Because of its proximity to the equator, Malaysia has four main seasons: two featuring the presence of a monsoon, and two with the absence of monsoons (Lockard *et al.*, 2023). The southernmost subsite, the Temengor Forest Reserve, went through a period of selective logging in the 1970s, while the Royal Belum State Park has maintained a highly protected status.

The BTFC covers around 3,000 km^2, but the study focused on a 400 km^2 area with an elevation ranging from 289-1763 meters above sea level. The subsites had 70 cameras that were placed in a grid with cells of approximately 2 km^2 and were moved every 3-4 months in order to increase area cover. Therefore, these subsites contained 140 unique locations. To increase detection rates, cameras were placed along trails and inactive logging roads. For full details regarding the study area and camera trap survey see Rayan & Linkie, 2015.

Figure 4: Peninsular Malaysia camera trap locations for *T. indicus* survey. Camera station locations are indicated by blue dots, and dark green indicates protected area coverage. Inset map contains an overview of the study areas in Peninsular Malaysia in Southeast Asia, denoted by a gray window. Base map originates from OSM and camera station coordinates are projected in EPSG: 4326. Map was created using the long-term release (LTR) version of qGIS.

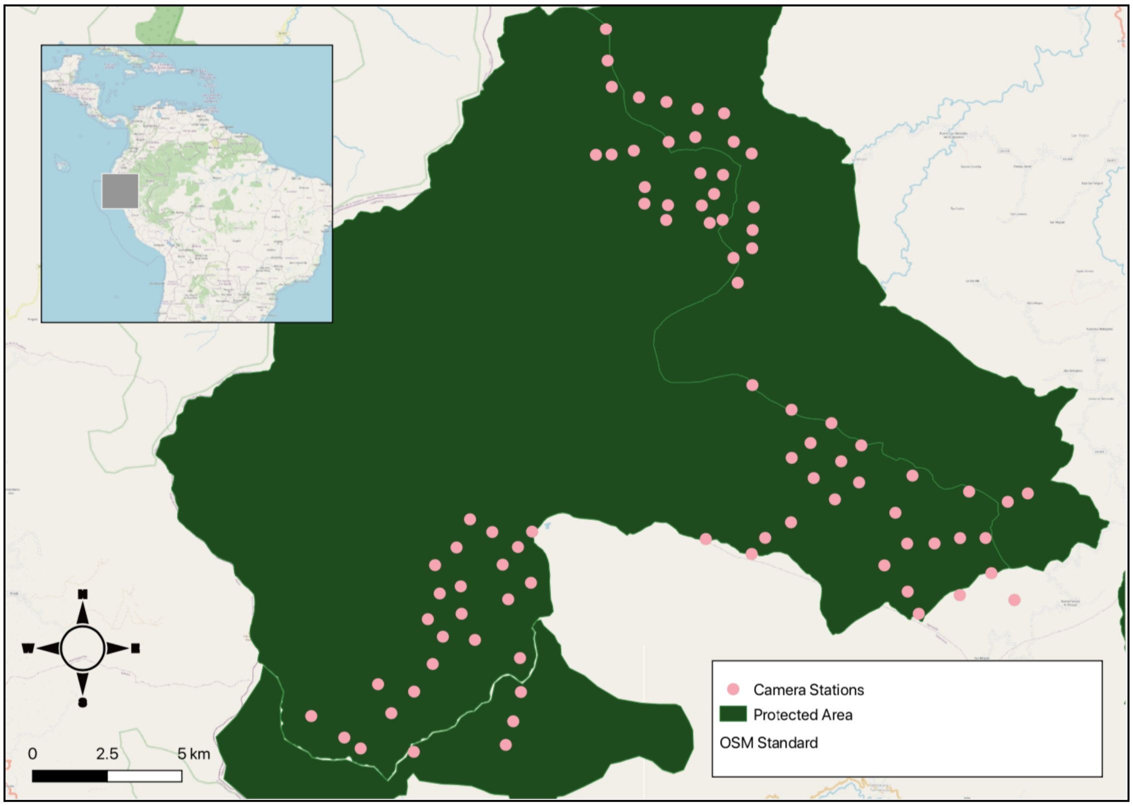


Tapirus pinchaque

The Mountain tapir study was carried out between May-October in 2016. The study area was located in Tabaconas Namballe National Sanctuary (TNNS) in the northern Andes of Peru with study sites along an elevational gradient ranging from montane forests (1600-3000 m elevation) to páramos (>3000m elevation) (Figure 5). The study area has an average annual rainfall between 149-177 cm and an average temperature between 11.2 to 24.6∘C, with a distinct wet season (November-March) and dry season (April-October) (Mena & Yagui, 2019).

Across the study site, 85 camera stations (Bushnell Trophy Cam) were systematically deployed based on a 115-site grid along an elevational gradient with representation of both páramo and montane forest vegetation. To maximize capture probability, cameras deployed along trails where tapir scat had previously been detected. Cameras were attached to a tree or stake ~40 cm above the ground with no attractants and run 24 hrs per day. For full details regarding the study area and camera trap survey see Mena *et al.*, 2020.

Figure 5: Peru camera trap locations for *T. pinchaque* survey. Camera station locations are indicated by light pink dots, and dark green indicates protected area coverage. Inset map contains an overview of the study areas in the Northern Andes of Peru, denoted by a gray window. Base map originates from OSM and camera station coordinates are projected in EPSG: 4326. Map was created using the long-term release (LTR) version of qGIS.



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Covariates

Table 2: Covariate details included in occupancy modeling analysis.

Covariate	Description	Resolution	Source
Human Footprint Index (HFI)	Index for cumulative human presence in the environment, incorporating population density, infrastructure, agriculture, roads, and electric power.	~1km	Venter *et al.*, 2016; Venter *et al.*, 2018
Distance to Road	The distance (in meters) each camera station is from the nearest road.	~6 m	OpenStreetMap
Elevation	The height (in meters) above sea level at each camera station.	30 m	Center, 2018
Average Monthly Precipitation	Average monthly rainfall (mm) calculated from the average of 12 monthly average rainfall readings at each camera station.	30 m	Fick & Hijmans, 2017

Four covariates were selected based on their potential to influence tapir occupancy and their variation between locations (Table 2). The following covariates were used: HFI (human footprint index), distance to road (meters), elevation (meters), and average monthly precipitation (mm) (Center, 2018; Fick & Hijmans, 2017; OpenStreetMap; Venter *et al.*, 2016; Venter *et al.*, 2018). Human footprint index and distance to road were selected based on previous evidence which indicates the influence of anthropogenic factors on tapir occupancy (Ferreguetti *et al.*, 2017; Martinez *et al.*, 2021). Map data to calculate distance to road for each camera trap location is copyrighted by OpenStreetMap contributors and available from https://www.openstreetmap.org. Elevation and precipitation were similarly selected based on previous evidence which suggests their possible importance in determining tapir occupancy (Naranjo, 1995; Mena *et al*., 2020). Historically, the lifestyle of tapir has been known to center around the presence of water (Naranjo, 1995). Due to the variability of environments included in this study, precipitation was selected (as opposed to distance to body of water) as many water sources in the area of study are seasonal and largely dependent on precipitation levels. Once selected, covariates were extracted for each camera trap location using qGIS software (QGIS Development Team, 2023). The ranges of covariate values for each survey are listed in Table 3. It is important to note that human footprint index covariate data is missing for the Mountain tapir due to constant coordinate values across the study site that prevents accurate modeling predictions (Table 3).

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Table 3: Climate and covariate ranges outlined for each study site.

Species	Location	HFI[a]	Distance to Road (m)[a]	Elevation (m)[a]	Average Monthly Precipitation (mm)[a]
T. bairdii	Costa Rica	3 - 18	~100 - 24,000	~20 - 3,400	~150 - 350
T. terrestris	Brazil	0 - 9	~324 - 106,043	~50 - 200	~125 - 300
T. indicus	Malaysia	0 - 7	~10 - 18,000	~300 - 1,750	~180 - 260
T. pinchaque	Peru	4	~750 - 10,000	~1,500 - 3,500	~80 - 120

[a]Data for HFI, distance to road, elevation, and average monthly precipitation were extracted using qGIS from the sources indicated in Table 2.

<u>Occupancy Modeling</u>

All datasets were processed and analyzed separately in R statistical software (R Core Team, 2021). If there was more than one record at the same camera station within less than 24 hrs, the first record was taken and the subsequent records were discarded to increase temporal independence. Cameras did not necessarily run concomitantly. To abide by the closure assumptions of a Single-Season Single-Species occupancy model (Mackenzie *et al.,* 2017), the maximum time period for each camera station survey was four months. These data were used to create a site-by-occasion detection table (0 = non-detection and 1 = detection). Records were collapsed into seven-day time periods to improve model convergence, indicating the number of days within a seven-day period where the species of interest was observed (a value between 0-7). To account for imperfect detection, single-season occupancy models were calculated for each species using the R-package "unmarked" (Fiske & Chandler, 2011). Covariates were added individually and compared using the Akaike Information Criterion (AIC). Models indicating ΔAIC ≤ 2 were determined to have substantial empirical support (Burnham and Anderson, 2002).

Results

Tapirus bairdii

Baird's tapir were detected at 63 of the 141 unique camera stations (naïve ψ = 0.45), with a total of 293 independent records over 11,954 camera days (Table 1). The model incorporating distance to road indicated an ΔAIC ≤ 2, displaying substantial empirical support (Table 4). This model indicates a statistically significant negative correlation between estimated Baird's Tapir occupancy ($\widehat{\psi}$) and distance to road ($P<0.001$) with an estimated occupancy of 0.79 (Table 4) (Figure 6E). All other models indicated lesser levels of empirical support ΔAIC > 2, although models for human footprint index (P = 0.002) and elevation (P = 0.004) were statistically significant to Baird's tapir occupancy probability, indicating a negative correlation between human footprint and occupancy probability ($\widehat{\psi}$ = 0.31)(Figure 6H), and a positive correlation between elevation and occupancy probability ($\widehat{\psi}$ = 0.63) (Figure 6F).

Table 4: Estimated Baird's tapir occupancy ($\widehat{\psi}$) and detection probability ($\widehat{p}$) for all models.

Model[a]	nPars	AIC	ΔAIC	AICwt	CumltvWt	$\widehat{\psi}$	$\widehat{p}$
ψ(Road)p(Effort)	4	1342.33	0.00	1.0	1.00	0.79	0.49
ψ(HFI)p(Effort)	4	1354.00	11.67	1354.00	1.00	0.31	0.49
ψ(Elev)p(Effort)	4	1359.45	17.12	1.9e-04	1.00	0.63	0.49
mod0	2	1365.09	22.76	1.1e-05	1.00	0.47	0.30
ψ(Precip)p(Effort)	4	1367.99	25.66	2.7e-06	1.00	0.52	0.49

[a]Model names incorporate site covariates and survey covariates as follows: ψ(Site Covariates)p(Survey Covariates), and mod0 indicates the null model incorporating no covariates. Models with ΔAIC ≤ 2 are bolded and indicate substantial empirical support (Burnham & Anderson, 2002).

Tapirus terrestris

Lowland tapir were detected at 67 of 182 unique camera stations (naïve ψ = 0.39), with a total of 108 independent records over 7,043 camera days (Table 1). The model incorporating human footprint index displayed substantial empirical support (ΔAIC ≤ 2) indicating a positive correlation between human footprint index and Lowland tapir occupancy ($\widehat{\psi}$ = 0.55), although no significance was found (P=0.068) (Table 5; Figure 6D). All other models displayed lesser levels of empirical support (ΔAIC > 2), and were not statistically significant (Table 5).

Table 5: Estimated Lowland tapir occupancy ($\widehat{\psi}$) and detection probability ($\widehat{p}$) for all models

Model[a]	nPars	AIC	ΔAIC	AICwt	CumltvWt	$\widehat{\psi}$	$\widehat{p}$
ψ(HFI)p(Effort)	4	683.60	0.00	0.7642	0.76	0.68	0.55
ψ(Road)p(Effort)	4	687.00	3.40	0.1396	0.90	0.49	0.55
ψ(Precip)p(Effort)	4	689.17	5.57	0.0471	0.95	0.43	0.55
ψ(Elev)p(Effort)	4	689.32	5.72	0.0437	0.99	0.56	0.55
mod0	2	693.49	9.90	0.0054	1.00	0.53	0.18

[a]Model names incorporate site covariates and survey covariates as follows: ψ(Site Covariates)p(Survey Covariates), and mod0 indicates the null model incorporating no covariates. Models with ΔAIC ≤ 2 are bolded and indicate substantial empirical support (Burnham & Anderson, 2002).

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Tapirus indicus

Malayan tapir were detected at 159 of 329 unique camera stations (naïve ψ = 0.48), with a total of 398 independent records over 28,792 total camera active days (Table 1). The model incorporating elevation displayed substantial empirical support (ΔAIC $\leq$ 2) (Table 6). This model indicates a statistically significant positive correlation between Malayan tapir occupancy probability and elevation (P < 0.001), with an estimated occupancy probability of 0.73 (Table 6) (Figure 6J). All other models indicated lower levels of empirical support ΔAIC > 2, yet models incorporating precipitation (P < 0.001) and distance to road (P = 0.003) were statistically significant, indicating a positive correlation between precipitation and Malayan tapir occupancy ($\widehat{\psi}$ = 0.69) (Figure 6K), and a positive correlation between Malayan tapir occupancy and distance to road ($\widehat{\psi}$ = 0.60) (Figure 6I).

Table 6: Estimated Malayan tapir occupancy ($\widehat{\psi}$) and detection probability ($\widehat{p}$) for all models.

Model[a]	nPars	AIC	ΔAIC	AICwt	CumltvWt	$\widehat{\psi}$	$\widehat{p}$
ψ(Elev)p(Effort)	4	2198.70	0.00	1.0	1.00	0.73	0.58
ψ(Precip)p(Effort)	4	2216.64	17.94	1.3e-04	1.00	0.69	0.58
ψ(Road)p(Effort)	4	2235.43	36.73	1.1e-08	1.00	0.60	0.58
ψ(HFI)p(Effort)	4	2244.69	45.99	1.0e-10	1.00	0.49	0.58
mod0	2	2269.04	70.34	5.3e-16	1.00	0.55	0.14

[a]Model names incorporate site covariates and survey covariates as follows: ψ(Site Covariates)p(Survey Covariates), and mod0 indicates the null model incorporating no covariates. Models with ΔAIC ≤ 2 are bolded and indicate substantial empirical support (Burnham & Anderson, 2002).

Tapirus pinchaque

Mountain tapir were detected at 28 of 85 unique camera stations (naïve ψ = 0.33), with a total of 85 independent records over 9,456 camera days (Table 1). Models incorporating elevation, distance to road, precipitation, and human footprint index displayed substantial empirical support (ΔAIC $\leq$ 2), although no significance was found (Table 7). The top model indicated a positive correlation between elevation and Mountain tapir occupancy ($\widehat{\psi}$ = 0.55) (Figure 6J) even though results were not statistically significant (P=0.23).

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Table 7: Estimated Mountain tapir occupancy ($\widehat{\psi}$) and detection probability ($\widehat{p}$) for all models.

Model[a]	nPars	AIC	ΔAIC	AICwt	CumltvWt	$\widehat{\psi}$	$\widehat{p}$
ψ(Elev)p(Effort)	4	547.01	0.00	0.381	0.38	0.57	0.60
ψ(Road)p(Effort)	4	548.42	1.41	0.189	0.57	0.48	0.60
ψ(Precip)p(Effort)	4	548.47	1.46	0.183	0.75	0.51	0.60
mod0	2	550.56	3.55	0.065	1.00	0.35	0.17

[a]Model names incorporate site covariates and survey covariates as follows: ψ(Site Covariates)p(Survey Covariates), and mod0 indicates the null model incorporating no covariates. Models with ΔAIC ≤ 2 are bolded and indicate substantial empirical support (Burnham & Anderson, 2002).

Figure 6: Tapir occupancy probability (ψ) based on predicted model calculations. The y-axis indicates the probability (0-1) of the specified tapir species occupying that region, while the x-axis indicates the covariate values included in each survey. Based on model predictions, graphs depict the probability of a tapir occupying a region with the indicated covariate value. The line of best fit is indicated by the black line, while the colored band indicates a 95% confidence interval. P-values display the statistical significance of each covariate to tapir occupancy probability.

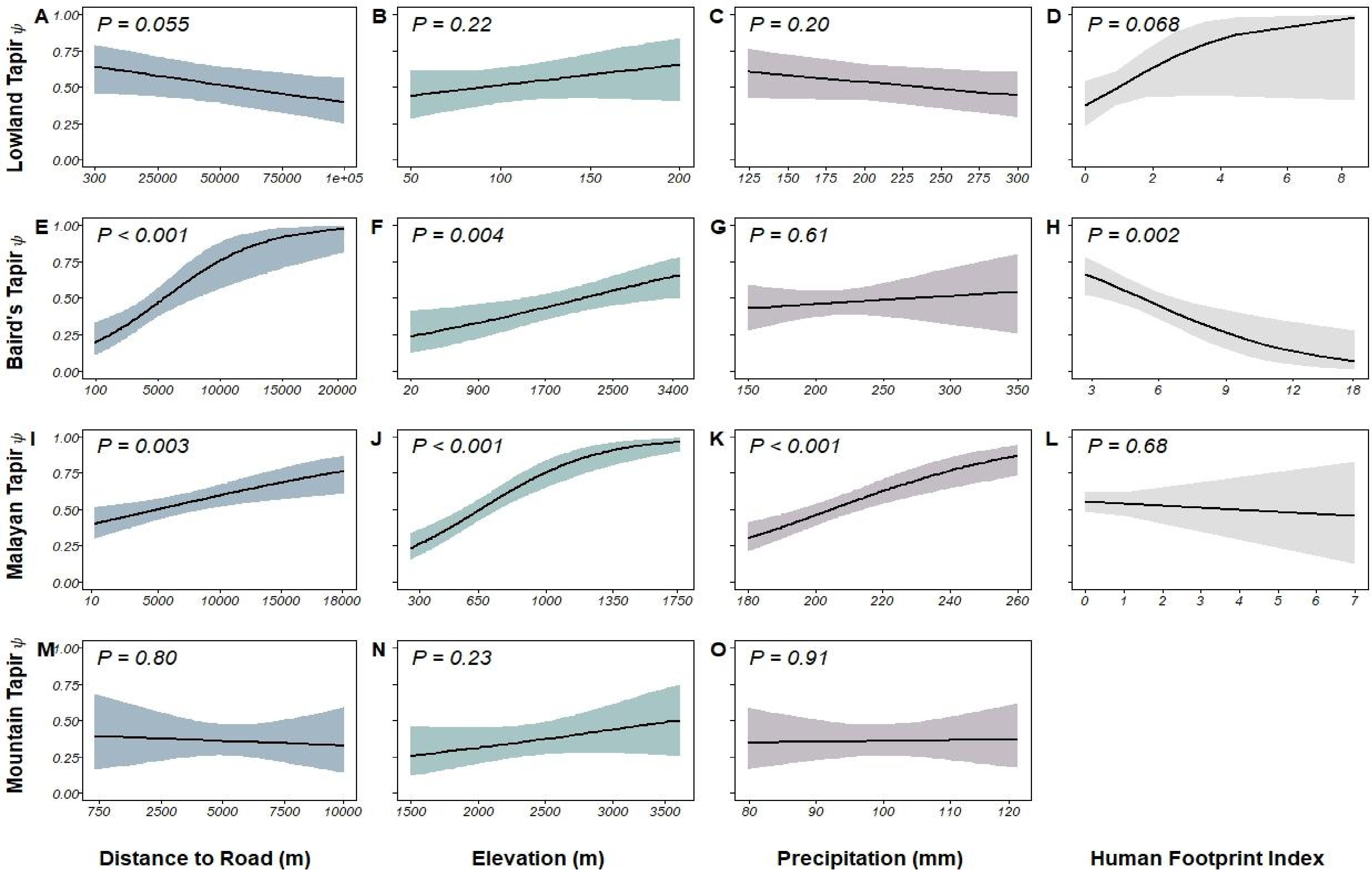
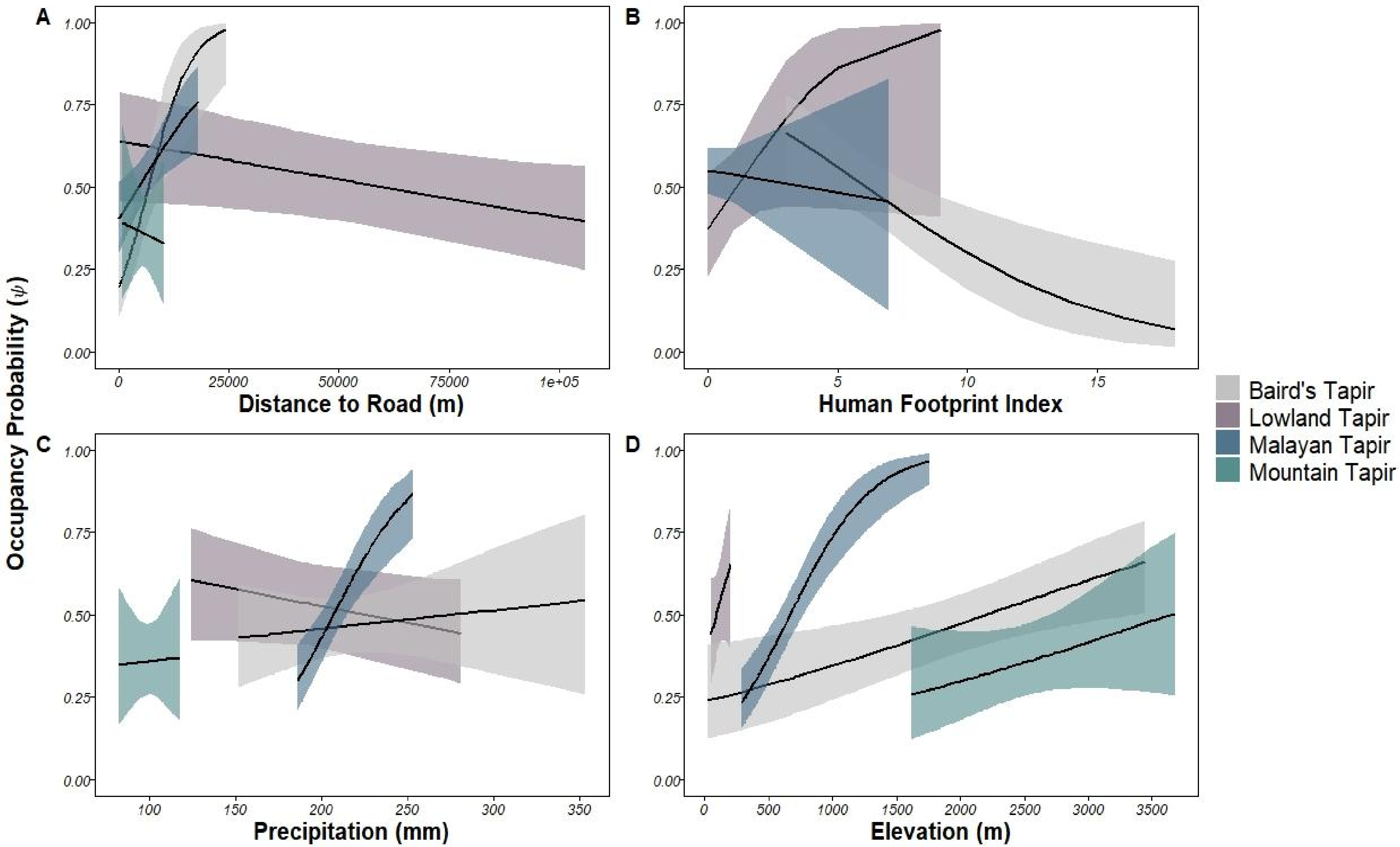


Figure 7: Compared tapir occupancy probability (ψ) for each covariate, incorporating differences between covariate values at each study site. The y-axis indicates the probability (0-1) of the specified tapir species occupying that region, while the x-axis indicates the covariate values included in each survey. Based on model predictions, graphs depict the probability of a tapir occupying a region with the indicated covariate value. The line of best fit is indicated by the black line, while the colored bands indicate a 95% confidence interval.



Discussion

The four extant tapir species are experiencing dramatic population declines as a result of poaching, fragmentation, and loss of suitable habitat. Given this decline in population, it is imperative to understand the factors that influence habitat suitability across the four species. Although tapir have been studied for years, previous studies have focused on a single species, separately analyzing tapir-habitat relationships and the factors that influence habitat suitability. Yet, due to differing habitat variables and analysis techniques, it is difficult to accurately compare results between studies. Given this barrier, the similarities and differences in habitat-suitability between the four extant tapir species are largely unknown. Using the same covariates and analysis techniques across camera-trapping datasets for each species, patterns in habitat suitability can be accurately compared to highlight important commonalities and differences between tapir species to better inform ecological and conservation perspectives.

One of the major results of this study was the difference in predicted species occupancy probability between covariates. While species responded similarly to some covariates, others showed surprising results. Additionally, the major findings of this study highlighted the possibility of covariance which is further discussed with each covariate.

The distance to road model was empirically significant for *T. bairdii* and *T. pinchaque* (Table 4; Table 7). Baird's tapir occupancy was positively correlated with distance to road, indicating a higher probability of occupancy in regions farther from a road, while Mountain tapir occupancy was negatively correlated to road, indicating a higher probability of occupancy nearer to roads (Figure 6M; Figure 7A). The result of the Baird's tapir distance to road model is consistent with our predictions and may be explained by the history of this tapir's relationship with humans. Baird's tapirs have historically been hunted for subsistence and are known to be especially timid and wary of people (Brooks *et al*., 1997). This could explain their decreased likelihood to inhabit areas close to roads. The result of the distance to road model for the Mountain tapir is inconsistent with our prediction and may be explained due to covarying factors. For instance, Mountain tapir may seek out agricultural areas or specific vegetation types that grow nearer roads, therefore causing Mountain tapir occupancy to increase as distance to road decreases. The Human Footprint Index (HFI) was only empirically significant for the *T. terrestris* model, indicating a positive correlation between occupancy probability and HFI (Table 5; Figure 6D; Figure 7B). These results are inconsistent with our predictions, yet may be explained through external covarying factors. Similar to the Mountain tapir distance to road model, Lowland tapir may similarly seek out agricultural areas or vegetation that are closely associated with human presence, therefore causing Lowland tapir occupancy to increase as HFI increases. Elevation was empirically significant for *T. indicus* and *T. pinchaque*, indicating a positive correlation between elevation and occupancy probability for both species (Table 6; Table 7; Figure 6B; Figure 6N; Figure 7D). These results are consistent with our predictions and may be explained as the result of covariance. High-elevation regions tend to be more remote and protected, and previous studies have indicated a more desirable plant composition in areas of higher elevation, which may explain the model results (Downer, 2001). Precipitation was empirically significant only for *T. pinchaque*, indicating a positive correlation between occupancy probability and average monthly precipitation (Table 7; Figure 6O; Figure 7C). This is consistent with our predictions, and lines up with general knowledge of these taxa as a whole, as water is known to be an important factor in the presence of tapir (Naranjo, 1995). Because the study area of *T. pinchaque* contains such a high range in elevation, any precipitation that occurs will be more susceptible to pooling. In addition, the high elevation of the Andes mountains makes this study area exceptionally remote, therefore presumably more suitable for tapirs to inhabit. To fully understand our results, further research and investigation will be required to understand tapir occupancy trends associated with distance to road, human footprint index, elevation, and precipitation.

Differing support between covariates for each species may be a result of research limitations. Data for three of the four species (Mooring et al., 2020; Rayan & Linkie, 2015; Rocha et al., 2016; Rocha et al., 2020) was collected as part of a larger survey targeting a variety of mammal species. This factor had the potential to broaden the range of camera locations, contributing to a wider representation of covariate values. The fourth study (Mena et al., 2020) was a targeted study aimed to collect information for the Mountain tapir. Because the sole subject of this study was to study one species, it had the potential to lessen the range of camera trap locations to regions with anticipated Mountain tapir occurrence, therefore diminishing covariate representation. Additionally, the quantity of camera trap stations and total independent records differed between species (Table 1). The Mountain tapir survey had only 85 cameras and 85 independent records, while the Malayan tapir survey had 329 cameras and 398 independent records. Differences in camera trap number across species also contributed to a difference in effort (camera days) between species, which may influence our results.

These limitations may be further addressed through future collaborative research of tapirs. If researchers continue to work together in planning and data collection, the variance in representation and effort may be resolved. Additionally, collaboration between researchers can allow for the maintenance of homogenous methods in order to provide accurate results. Another possibility for further research is incorporating other covariates that have been thought to affect tapir occupancy. For instance, distance to bodies of water was one covariate we had thought to use, but ultimately decided against due to the variability of such data. However, if this variability could be mitigated and given a distinct definition of what a body of water is, then this would be a plausible option to explore in order to further our understanding of tapir ecology.

Conservation Implications

In conclusion, our results support our hypothesis that due to differing environmental variables across study sites, tapir species will have different adaptations, and therefore different covariates will be important to the occupancy of each species. Through the analysis of camera trap records from four different studies across all species of *Tapirus*, we have successfully gained insight into what environmental covariates affect their occupancy. Within the field of conservation ecology, this study contributes novel information regarding how each species of *Tapirus* compares to one another and how each responds to various environmental covariates. These covariates aid in determining each species' habitat selection. With this in mind, our research has important implications for conservation efforts across the globe. This study emphasizes the positive role comprehensive analyses have within taxa. One notable application of this could be with other members of the Perissodactyla family, such as the rhinoceros. These herbivores are found all across the globe and are highly endangered, with one species extinct in the wild. A study such as this one would be extremely helpful in discovering what the species within this taxa have in common, which will help to place protected areas in the most optimized locations. Overall, a comprehensive occupancy analysis across a taxa enables policymakers, conservationists, and ecologists alike to know what areas are most suitable for a given species, and how different locations and environmental factors play a role in habitat selection. This will aid in extinction prevention and a more scientifically backed approach to environmental policy for not only tapirs, but for other taxa with a broad but fragmented distribution.

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