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Abstract

The Pacific lowlands of Costa Rica have been severely changed by humans over the past several decades and now consist of a patchwork of habitats, much of which is a “human dominated” landscape which has altered the region’s animal community. To improve our understanding of how terrestrial mammals are utilizing human-dominated tropical habitats, we distributed camera traps across the five main different habitat types (old-growth forest, young secondary forest, oil palm plantation, riparian strip forest, and pastures; N =50 camera traps per habitat) of our 80 km² large study area (part of the biological corridor COBIGA) located in the lowlands of the Golfo Dulce Bioregion in southwestern Costa Rica.

Species accumulation curves indicate that young secondary forests had the highest species diversity of ground-dwelling mammals while pastures had the lowest. However, the composition of mammal assemblages recorded at individual sites did not differ significantly between habitat types. But, when pooling sites on the level of habitats and using the species’ incidences, a cluster analysis based on Bray-Curtis similarities, indicate two distinct clusters: one cluster containing the three forest types and a second cluster with the two land-use systems, pastures and oil palm plantations. Additionally, these land-use systems were more heavily utilized at night, while mammal activity proved being relatively higher in forest habitats during the day.

A model selection approach was used to evaluate the importance of different habitat structures for the occurrence of the two most abundant mammal species, Northern Raccoon and Central American Agouti, by considering different spatial scales (50m, 100m, and 200m buffers around camera locations). The presence of roads had the largest negative influence on the presence of Northern Raccoons at the 50m buffer and the 100m buffer. Settlements and gardens had the most positive effect at 50m and at 100m. Further, the Northern Raccoon appeared to avoid old-growth forest. While at all other habitats the species was recorded at 30-43 % of the camera trap sites, it was found only at 10% of the old-growth forest sites. The occurrence of Central American Agouti was positively related to the presence of water bodies (at all buffers) and old growth forests (at 100 and 200m).

Habitat preferences of mammals in our study area proved being very diverse. Some mammals prefer natural forest setting and others do not show an affinity for any specific habitat. Perhaps the relatively high density of riparian forest strips, the protection of remaining secondary forest patches and the implementation of reforestation measures are substantially contributing to improving landscape permeability for forest specialist and generalists and, hence, are facilitating the relatively high mammal diversity within the human-dominated countryside. Future studies should assess spatial movements of animals to identify the true importance of individual habitat structures for mammals, an important precondition for improving the effectiveness of biological corridors.

Keywords: biological corridor, camera traps, tropical countryside habitats, habitat preferences, terrestrial mammals

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Introduction

Like in most tropical regions, also the Pacific lowlands of Costa Rica have been affected by human activities for hundreds of years. However, anthropogenic impacts have been more dramatic over the past decades disrupting ecosystem functioning and jeopardizing biodiversity (Martinez-Ramos et al. 2016). Large lowland areas are now “human dominated” landscapes with severely altered biota. Further, these disturbed areas now serve as a barrier for spatial movements of many forest mammals (Sanchez-Azofeifa et al. 2003). However, certain landscape structures such as strips of gallery forests and patches of secondary forests may enhance landscape permeability, in turn facilitating dispersal movements (Cockle & Richardson 2003).

Biodiversity on a global scale is in decline. There are no areas around the world that still contain their full spectrum of mammals (Morrison et al. 2007). The main reasons for this decline are habitat loss, forest fragmentation, isolation of many of the forest patches as well as the edge effects contributing to the negative impacts (Broadbent et al. 2008). Many studies have been conducted bringing awareness to the importance of edge effects, however it is often difficult to recognize the value of such ecotone structures for conservation. One such study from southwestern Costa Rica shows that years of combining fragmentation with conservation has resulted in medium-sized mammals and several bird species now taking the top spots on the food chain (Gutierrez et al. 2019).

In many rainforests human activities are the main culprit, beside large amounts of deforestation and habitat fragmentation which have reduced tropical rainforests globally (Brinck et al. 2017). Some scientists predict that much of the Earth’s total biodiversity is gone. Species richness of plants, arthropods, and birds sampled in an experiment in mature forest fragments showed a decrease of 20 to 75% after fragmentation (Haddad et al. 2015). This decrease is especially high in tropical rainforests, with some studies suggesting that perhaps an additional 3.5% or more of this already declining biodiversity will occur by 2100 (Newbold et al. 2015). Often overlooked are secondary effects of human interference in near-natural areas such as the increased presence of domestic or free-ranging feral former livestock and pets, such as dogs, cats, pigs and many others. These feral invasive species further increase the negative effects on native wildlife as they act as predators or competitors and therefore are affecting populations of native species (Carvalho et al. 2019).

This study looks at and quantifies the occurrence and habitat utilization of ground mammals in an area of the Pacific lowlands of Costa Rica. One purpose of this study is to help evaluate effects of habitat loss on terrestrial mammal species so that we may better understand how to conserve and better manage remaining habitats, particularly rainforests. This may help in taking appropriate actions to slow down the loss of biodiversity (Turner & Corlett 1996). Unwelcomed results of anthropogenic influences on biodiversity have been studied around the world. Decisions pertaining to where and when the cynical/self-interested activities of humans will occur are often based on socio-economic reasons, though these factors can be region-specific and vary locally also (Pereira et al. 2010).

Our study area consists of remaining rainforest blocks separated by human-dominated areas with patches of secondary forests, strips of riparian forest, small settlements and land-

use systems (predominantly pastures and oil palm plantations; Höbinger et al. 2012). The study area is located within the Biological Corridor La Gamba (COBIGA) which is a part of the larger Osa Biological Corridor. The COBIGA project aims to reconnect the Fila Cal mountains to the north with the lowland forest of the Piedras Blancas National Park to the south. The main focus of the COBIGA is to (1) create a continuous forest as much as possible, and (2) reforest and restore to help increasing landscape permeability for forest species. The ability for species to move between remaining forest areas helps to maintain species diversity (Weissenhofer et al. 2012).

This study also assessed the habitat utilization of the most abundant terrestrial ground mammal species found in this area, such as the Northern Raccoon (*Procyon lotor*) and the Central American Agouti (*Dasyprocta punctata*). The Northern Raccoon is a primarily nocturnal omnivorous species, known to be very adaptable and therefore can be found in a wide variety of habitats (including even settlements) in rural areas (Emmons & Feer 1997, Reid 2009). The Northern Raccoon's natural distribution range consists of all Central America stretching north up to about the middle of Canada (Reid 2009). In contrast, the Central American Agouti is primarily diurnal (Lambert et al. 2009) and prefers forest habitats, although it can additionally utilize second growth and plantations (Reid 2009).

This study addressed the following questions: Does COBIGA help to facilitate spatial movements of ground mammals within this human-dominated countryside? Which mammals are utilizing these human-dominated habitats and which mammals prefer the natural forest settings? Is there a difference in the spatial distribution across our study area between various terrestrial mammal species, which is shaped by different habitat preferences?

We expect that most mammals use strip forests along streams and rivers, and patches of secondary forests for spatial movements, while they may avoid human-dominated areas due to increased human activity and the associated activities of domestic dogs and livestock in these areas (Hughes & Macdonald 2013). This may result in a decreased species richness in land-use systems such as pastures and oil palm plantations and negative effects of settlements and roads. Further, in human-dominated areas a shift of animal activity may be found from diurnal to nocturnal activity perhaps to avoid disturbance caused by human activities as found in other studies (Gaynor et al. 2018).

Methods

Study area and study site selection

The study area is located in the Pacific lowlands of Costa Rica in the surrounding areas of La Gamba Tropical Field Station and the Biological Corridor La Gamba "COBIGA" (Fig. 1). COBIGA connects the lowland rainforests of the Golfo Dulce with the mountain rainforest of the Fila Cal, a mountain range to the north. This area is one of the most diverse places on Earth for ground mammal species (Gutierrez et al. 2019) and is currently being studied in hope that conservation practices may be put in place to help protect this region. The natural forest in this area has the highest carbon density on the planet and is therefore important as a carbon sink (Taylor et al. 2015). Much of this area and the surrounding areas are since

decades protected by national parks, including Corcovado National Park to the Northeast and Piedras Blancas National Park to the Southwest. In addition, there are many smaller privately-owned sections of protected forest and many smaller wildlife refuges.

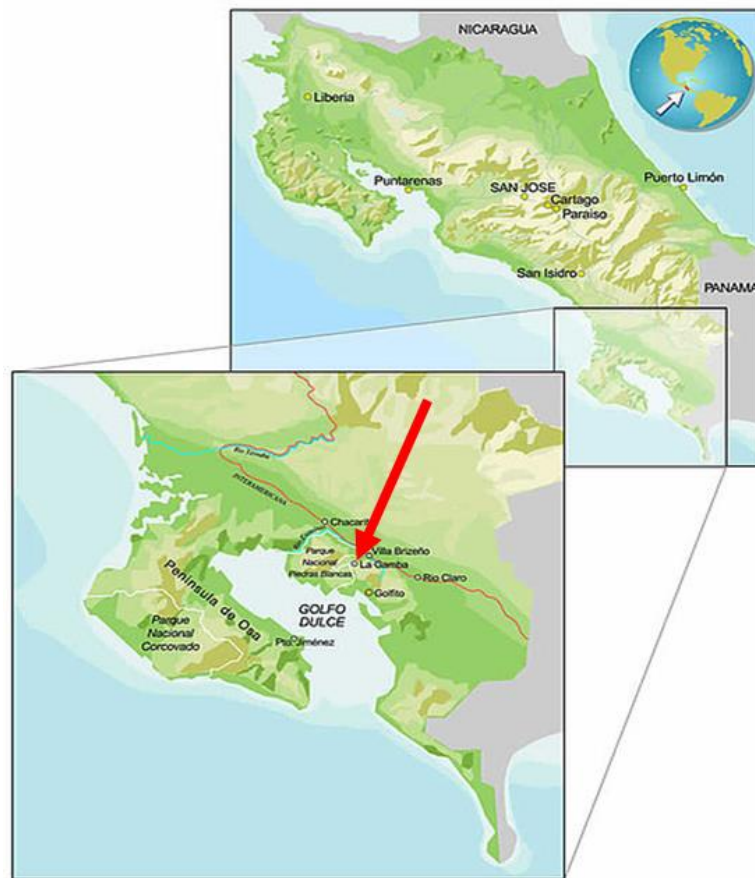


Fig. 1. The study area located in the Pacific lowlands of Costa Rica in the surrounding areas of La Gamba Tropical Field Station (indicated by red arrow). Courtesy: <https://www.lagamba.at/en/tropical-field-station>.

The climate is humid and hot and has annual temperatures averaging approximately 28°C and a relative humidity of 88-98% depending on the season. The “rainy season” is from August to December with the “dry season” next, through to April. The annual rainfall average is approximately 5200 to 6400 mm (Weissenhofer & Huber 2008).

It is estimated that ecotourism in this area contributes to about 60-80% of the economy. Because of this, initiatives to save the rainforests, and in turn biodiversity, have resulted in an increased awareness of the importance of reforestation and conservation. In contrast to many other tropical regions, this areas’ forest cover is increasing (Sanchez-Azofeifa 2003). However, despite the strong push for conservation, there are still many human activities that persist in this area, such as palm oil production, hunting, goldmining and agriculture (Hunt et al. 2015). In many tropical ecosystems commercial hunting has contributed to the decline of many “game” species (Nichols et al. 2009).

Study sites were selected in a variety of habitats (Fig. 2) based on satellite-born images and subsequent ground surveys. These habitats were categorized as pasture, oil palm plantation, strip forest (a narrow zone or “strip” of land, trees or vegetation often bordering streams or rivers), secondary forest (as result of natural regeneration or due to targeted

reforestation measures), and old-growth forest (approximately at least 100 years old). Much of the study area was located on private land; therefore, permission was needed to access selected study sites.



Fig. 2. The five studied main habitat types: (A) palm oil plantation, (B) pasture, (C) old-growth forest, (D) young secondary forest, (E) strip forest. A total of 200 camera trap sites were selected, 40 in each of the 5 habitat types.

Assessment of mammals with camera traps

One powerful tool being used to study the ecology of medium-sized and large mammals is the use of camera traps and their use rapidly became one of the most important tools in the conservation and ecological studies of terrestrial vertebrates (Rowcliffe & Carbone 2008). Camera trapping involves using a remotely activated camera that has a trigger mechanism which can be activated by a motion sensor, an infrared sensor, or a beam of light. Camera trapping is a growing method for capturing wild animals on film (Trolle 2003, Michalski & Peres 2007, Tobler et al. 2008). Research applications include, but are not limited to, studies of a wide variety of mobile organisms, estimations of population size and species richness, research on habitat use and can also help in other areas such as the detection of rare and elusive species (Swan et al. 2010).

Camera traps were exposed at 200 sites (Fig. 3) with two-days exposure each, hence, for a total of 400 camera trap days. Cameras had this two-day exposure time before data was collected; afterwards cameras were relocated. The camera traps were equally distributed across the five different habitat types (N = 40 camera trap sites per habitat), covering an area of approximately 80 square kilometers. Camera trap sites were selected using various current maps and then ultimately chosen after a visit of each site. Cameras were placed and checked for data, then relocated every two days between November 16, 2018 and January 25, 2019. Cameras were placed a minimum of 200 meters away from their earlier site every

two days (Royle 2009). GPS coordinates were used to ensure the distance between camera trap locations.

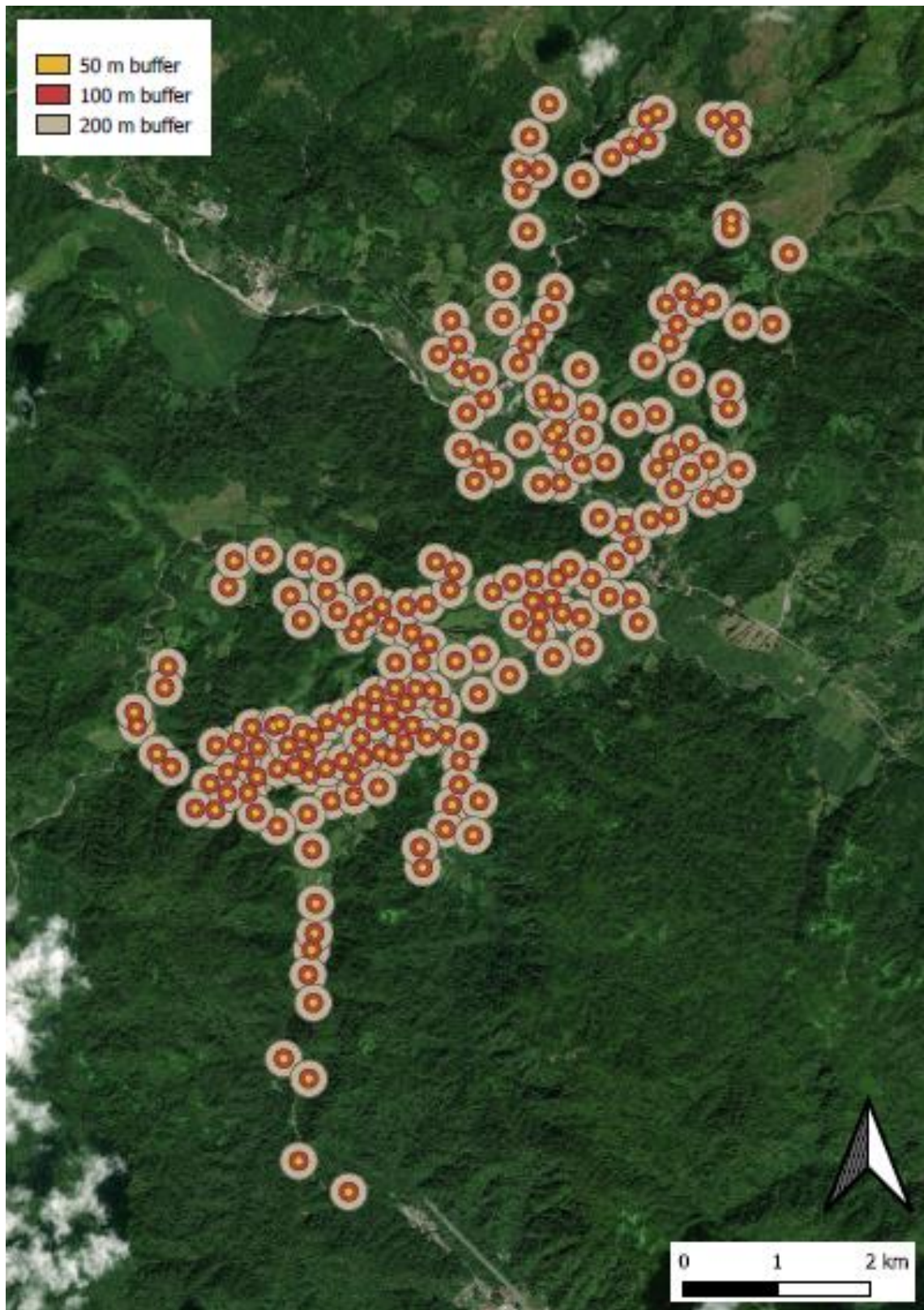


Fig. 3. Map of study area showing all camera trap sites and the 3 considered buffers (50, 100 and 200m) for quantifying habitat composition in the surroundings.

Advantages of camera traps are that they are quiet, they operate continuously, and they are cost effective, all of which are important criteria for researchers (Swan et al. 2010). The used camera model (Cuddleback Digital Silver; Fig. 4) offers a variety of picture and video capturing options. We used a camera speed of 0.25 seconds for each picture and the “no glow” flash option to minimize disturbance of animals. Cameras were programmed to photograph first and then set to record a 20 second video sequence. To enhance likelihood of mammal encounters. A variety of baits (cat food, peanut butter, bananas) was exposed to mammals in front of the cameras. Baits are often used to increase the opportunity to capture wildlife images in rainforest habitats (Norris et al. 2008, Trolle 2003). Bait types as well as the amounts of each bait were kept constant at each site. The importance of standardizing baits is important as these can strongly influence results (Espartosa et al. 2011). Bananas are frequently used due to being cost effective, easy to obtain and have proven to be successful as a bait in rainforest studies (Norris et al. 2008).



Fig. 4. Cuddleback Digital Silver Camera exposed at a site (left) with three different baits placed in front of the cameras: peanut butter, cat food, and banana (right).

Camera traps, which allow images of wildlife to be made with as little human interference as possible, have become increasingly popular among field researchers with improving quality of camera equipment. Each time a new picture or video was taken could have been deemed a new event or occurrence (e.g. Fig. 5 and 6). However, consecutive pictures of one mammal within a three-minute interval were classified as one “event/occurrence”. We decided to use a three-minute interval between pictures before a new “event/occurrence” was recorded. Therefore, a mammal remaining in front of the camera for a given time may be classified as two or more events depending on the length of the stay. This reflects a stronger habitat preference of an individual or group remaining near a trap for a longer time as opposed to one just passing by which would most likely be scored as only a single event/occurrence.

Additionally, direct or indirect personal encounters of animals while placing or retrieving cameras from a site (e.g. tracks and sightings) were documented. Track counts however require a substrate capable of retaining the impression which is not always present in each

of these habitat types (Dirzo & Miranda 1990). In case this data was considered it is mentioned for all respective analyses.

All animals were identified using prior knowledge as well as by using two field guides (Wainwright 2007; Emmons & Feer 1997). Except for a few rat species, identification of ground mammals from photographs is not difficult in the region. Additionally, several bird species and reptiles were also caught on camera (see Appendix Table 22).



Fig. 5. A Northern Tamandua walking past a camera trap on 19 November 2019 at 11:10.



Fig. 6. A family of the Northern Raccoons feeding on provided bait on 26 November 2018 at 12:10.

Assessment of habitat composition around camera traps

To evaluate habitat preferences of the considered mammals, the following 10 habitat types were re-digitalized or newly digitalized based on former habitat mapping projects and new aerial photographs (Google Earth) using the software QGIS: living fences (LF), oil palm plantations (OP), old-growth forest (OF), open cultivated land (OL), roads (RD), settlements and gardens (SG), shrubland (SL), timber plantations (TP), water bodies (WB), and young secondary forest (YF). Subsequently, for each camera trapping site the cover of all habitat types in percent was calculated for areas within buffers of 50m, 100m, and 200m around each camera trap. Additionally, the elevation of each camera trapping site was recorded.

Data analysis

Species richness of the five main habitat types was compared using species accumulation curves calculated with iNEXT Online: Software for Interpolation and Extrapolation of Species Diversity (Chao et al. 2016). iNEXT computes the estimates of the diversities for standardized samples having a common sample size and/or sample completeness. This rarefaction approach aims to compare the diversity estimates for equally large, common sample size or equally complete, common sample coverage of samples. Species lists were created including number of sites, number of occurrences and species accumulation curves were created for each habitat. However, we also extrapolated the species accumulation curves to a sample size of $N = 80$ camera trapping sites.

Similarity of species composition between sites was quantified using Bray-Curtis similarities. Subsequently, one-way ANOSIMs were used to test for differences in species composition between sites, only considering sites with a least 3 and 6 events, respectively. Further, data from all sites belonging to the same habitat type were pooled and a cluster

analysis (a complete linkage cluster) based on Bray-Curtis similarities was calculated to visualize similarities between habitats.

To compare the extent of nocturnal activity of all mammals per habitat a Chi-square test was calculated to test for differences in the ratio of events recorded during day (05:00-17:00) vs. nighttime (17:00-05:00) between habitats. Day and night were classified as the time frame between 5 AM and 5 PM and vice versa.

Subsequently, GLMs were calculated to analyze effects of camera site characteristics (coverage of different habitat types and elevation) on the occurrence of the two most abundant mammals, the Northern Raccoon and the Central American Agouti. In advance, a Spearman correlation matrix was calculated to test for inter-correlations between habitat variables. Strongly correlating variables ($r_s > 0.6$) were not included together in one candidate model. The R package `model.avg` (Barton 2012) was used to calculate the full model-averaged coefficients for all predictor variables as well as a conditional average (for subset of models with $\Delta AICc < 2.00$). We used the full average model for better accuracy but have included the conditional model data in the appendix (Appendix Tables 1, 2 & 3). This full average model was run for each of the 3 buffers of 50m, 100m, and 200m. In addition to habitat coverage data, we included elevation and water body coverage for each site as variables in this model to see if they play a role in the distribution of mammals.

First inspection of our data revealed that raccoon and agouti sightings were not equally distributed across the five habitat types. We then analyzed whether certain habitat structures are related to the presence of raccoons and agoutis. Each of the 200 camera trap sites were located using the GPS coordinates and a land use or habitat use correlation matrix was made to determine if any habitat relationships were significant. Buffers of 50m, 100m, and 200m were defined and by using the GPS and shape files. Habitat and land-use percentages around each trap location were calculated for the 10 distinguishable habitats and structures for each of the 3 buffers at each of the 200 camera trap sites.

Results

Species richness

A total of 21 mammal species were recorded at the 200 study sites. The highest species numbers (14) were recorded in young secondary forests and oil palm plantations, lowest species numbers (3) was found in pastures. The most events (58) were recorded for young secondary forests, fewest events (15) occurred in the pasture habitat. The most common species were Northern Raccoon and Central American Agouti, recorded at 60 and 41 sites, respectively (Table 1).

Table 1. List of all camera recorded mammals and the number of sites with records, provided for each habitat (N = 40 sites per habitat): OGF – old-growth forest, STF – strip forest, YSF – young secondary forest, OPP – oil palm plantation, PAS – pasture.

Species	Habitat type					Total
	OGF	OPP	PAS	STF	YSF	
<i>Central American Agouti (Dasyprocta punctata)</i>	14	2		11	14	41
<i>Nine-Banded Long-Nosed Armadillo (Dasypus novemcinctus)</i>		1				1

Species	Habitat type					Total
	OGF	OPP	PAS	STF	YSF	
White-Nosed Coati (<i>Nasua narica</i>)	2		2	5	5	14
Coyote (<i>Canis latrans</i>)		3				3
Crab Eating Raccoon (<i>Procyon cancrivorus</i>)		1				1
Gray Four-Eyed Opossum (<i>Philander opossum</i>)	1	3		1	1	6
Jaguarundi (<i>Herpailurus yagouroundi</i>)	1				1	2
Kinkajou (<i>Potos flavus</i>)					1	1
Northern Raccoon (<i>Procyon lotor</i>)	4	17	12	13	14	60
Norway Rat (<i>Rattus norvegicus</i>)				1		1
Ocelot (<i>Leopardus pardalis</i>)	2	1			1	4
Common Opossum (<i>Didelphis marsupialis</i>)	1	2		3	2	8
Paca (<i>Agouti paca</i>)	2	1	1	2	3	9
Collared Peccary (<i>Tayassu tajacu</i>)	1	3		3	2	9
Tapiti Rabbit (<i>Sylvilagus brasiliensis</i>)		1				1
Tome's Spiny Rat (<i>Proechimys semispinosus</i>)	1			1	7	9
Variegated Squirrel (<i>Sciurus variegatoides</i>)					1	1
Striped Hog-Nosed Skunk (<i>Conepatus semistriatus</i>)	1			2	1	4
Northern Tamandua (<i>Tamandua mexicana</i>)		1			1	2
Tayra (<i>Eira barbara</i>)	1	4		2	4	11
White-Lipped Peccary (<i>Tayassu pecari</i>)		1				1
Total number of species	12	14	3	11	15	21

The most abundant mammal was the Central American Agouti with 252 events and a total of 268 individuals due to some events with multiple individuals per event. Seven different mammals were recorded only once throughout the entire study. Pastures had the least number of events (29) and individuals (40) (Table 2).

Table 2. Number of events per species in each habitat type and the summed maximum number of individuals at each event to get individual totals. Habitats: OGF – old-growth forest, OPP – oil palm plantation, PAS – pasture, STF – strip forest, YSF – young secondary forest.

Species	Habitat type					Total
	OGF	OPP	PAS	STF	YSF	
Central American Agouti	80/87	17/18		70/71	85/92	252/268
Nine-Banded Long-Nosed Armadillo		1/1				1/1
White-Nosed Coati	2/3		4/4	6/11	7/29	19/47
Coyote		3/3				3/3
Crab Eating Raccoon		1/1				1/1
Gray Four-Eyed Opossum	1/1	11/11		2/2	1/1	15/15
Jaguarundi	1/1				1/1	2/2
Kinkajou					1/1	1/1
Northern Raccoon	7/16	24/35	23/34	21/22	32/41	107/148
Norway Rat				1/1		1/1
Ocelot	2/2	1/1			2/2	5/5
Common Opossum	1/1	10/10		7/7	5/5	23/23
Paca	7/7	5/5	2/2	2/2	5/6	21/22
Collared Peccary	1/1	3/3		3/3	5/5	12/12
Tapiti Rabbit		1/1				1/1
Tome's Spiny Rat	4/4			1/1	22/22	27/27
Variegated Squirrel					1/1	1/1

Species	Habitat type					Total
	OGF	OPP	PAS	STF	YSF	
<i>Striped Hog-Nosed Skunk</i>	1/1			2/2	1/1	4/4
<i>Northern Tamandua</i>		1/1			1/1	2/2
<i>Tayra</i>	2/2	5/5		2/2	4/4	13/13
<i>White-Lipped Peccary</i>		1/1				1/1

Species accumulation curves for the five habitat types show a very similar pattern, independently if only camera trap records were used and also when tracks and observational records were included. We can see pastures appear to show very little species diversity with regards to ground mammals. The other habitat types all show a similar richness (Fig. 7 and 8).

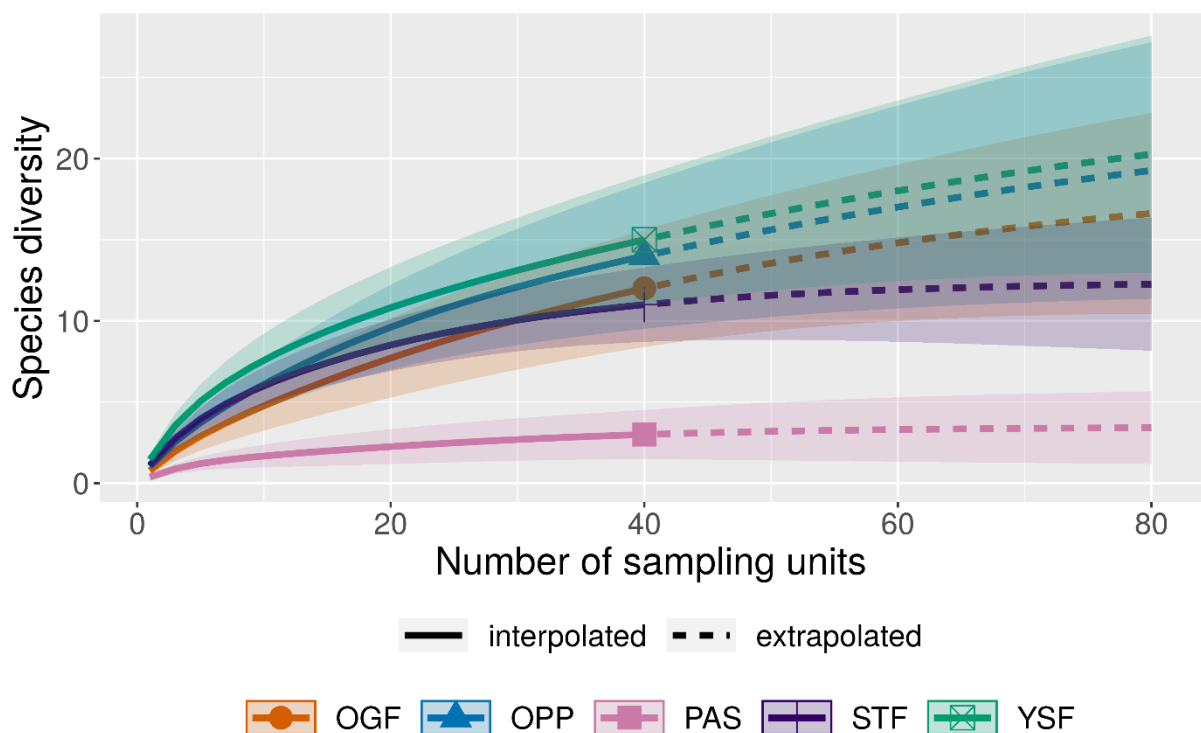


Fig. 7. Species accumulation curves for the five different habitats (OGF – old-growth forest, OPP – oil palm plantation, PAS – pasture, STF – strip forest, YSF – young secondary forest), based on incidence data recorded by camera traps only. Sampling units equal camera trapping sites.

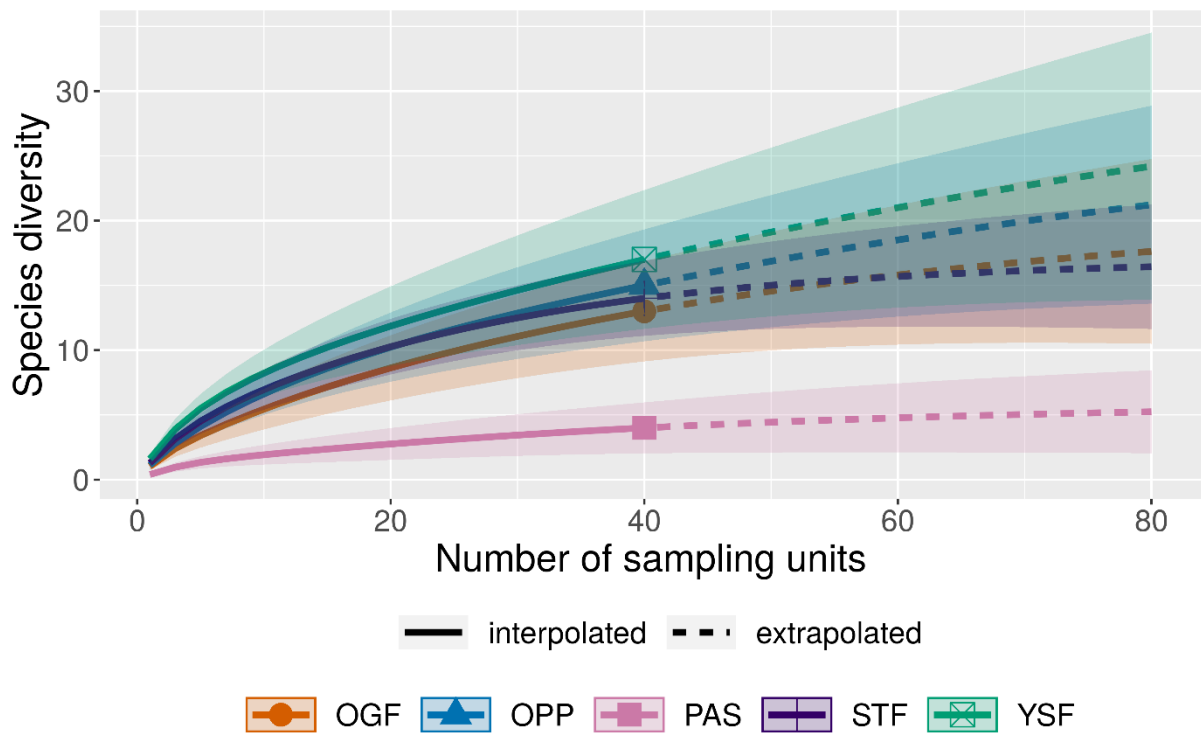


Fig. 8. Species accumulation curves for the five different habitats (OGF – old-growth forest, OPP – oil palm plantation, PAS – pasture, STF – strip forest, YSF – young secondary forest), based on incidence data also including visual sightings and tracks. Sampling units equal camera trapping sites.

Species composition

The composition of mammal assemblages recorded at individual sites (only considering sites with at least 3 events) did not differ significantly between habitat types (one-way ANOSIM: Global $R = 0.003$, $p = 0.372$). Even when only considering sites with at least 6 events, no significant differences could be detected (one-way ANOSIM: Global $R = -0.003$, $p = 0.542$).

However, when pooling sites on the level of habitats and using the species' incidences, a cluster analysis (a complete linkage cluster) based on Bray-Curtis similarities indicates two distinct clusters. One cluster containing the three forest types and a second cluster with the two anthropogenic land-uses systems (pastures and oil palm plantations) (Fig. 9).

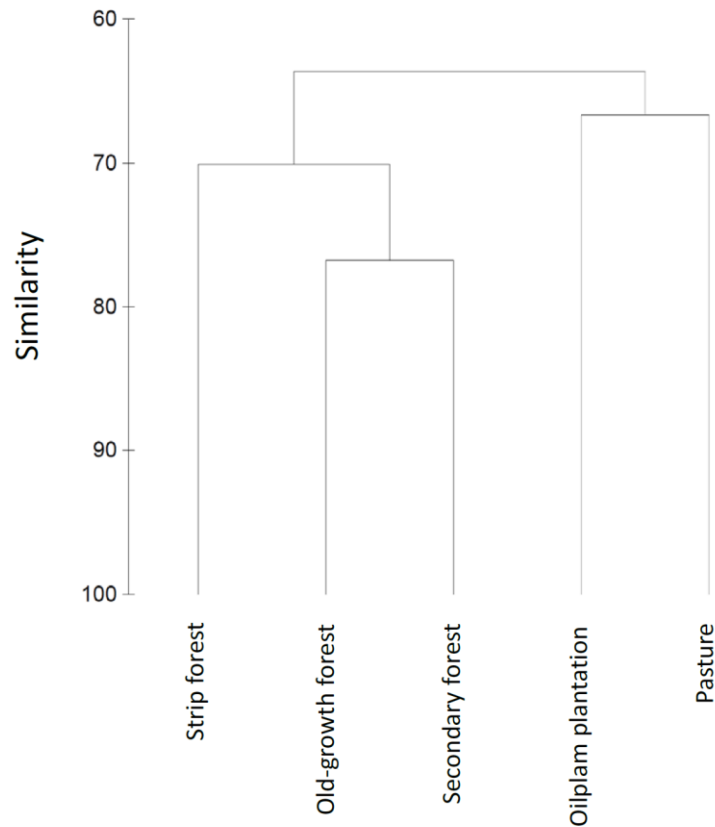


Fig. 9. Cluster analysis (a complete linkage cluster) based on Bray-Curtis similarities visualizing similarity relationships of species assemblages recorded in the five different habitat types.

Habitat specific temporal activity patterns

Percentages of events recorded during day and night-time differed significantly between habitats (Chi-square test: $\chi^2 = 83.1$, $df = 4$, $p < 0.0001$). The majority of events in pastures and oil palm plantations occurred at night (Fig. 10). Also when calculating the number of events per hour, activity peaks in the two land-use systems were found during the night, while highest activity peaks of mammals in all three forest types were recorded during daytime (Fig. 11).

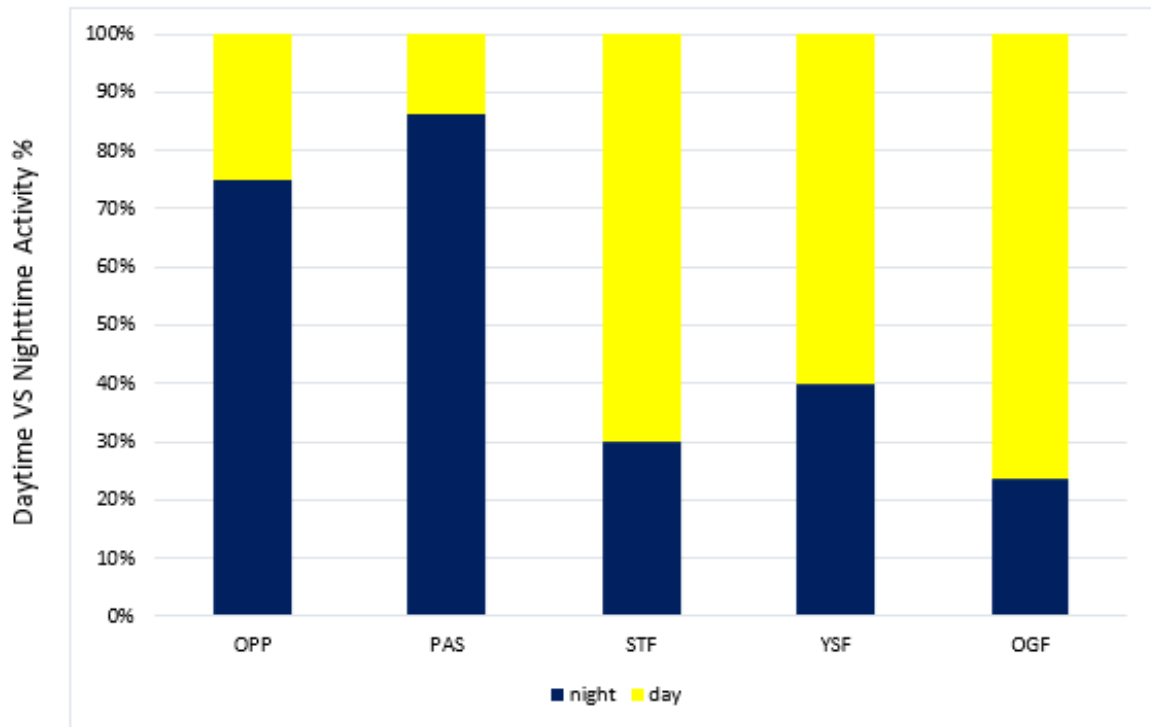


Fig. 10. Ratio of diurnal versus nocturnal activity (= events) of all mammals recorded in the five habitat types using percentages of daytime and nighttime events. (OGF – old-growth forest, OPP – oil palm plantation, PAS – pasture, STF – strip forest, YSF – young secondary forest).

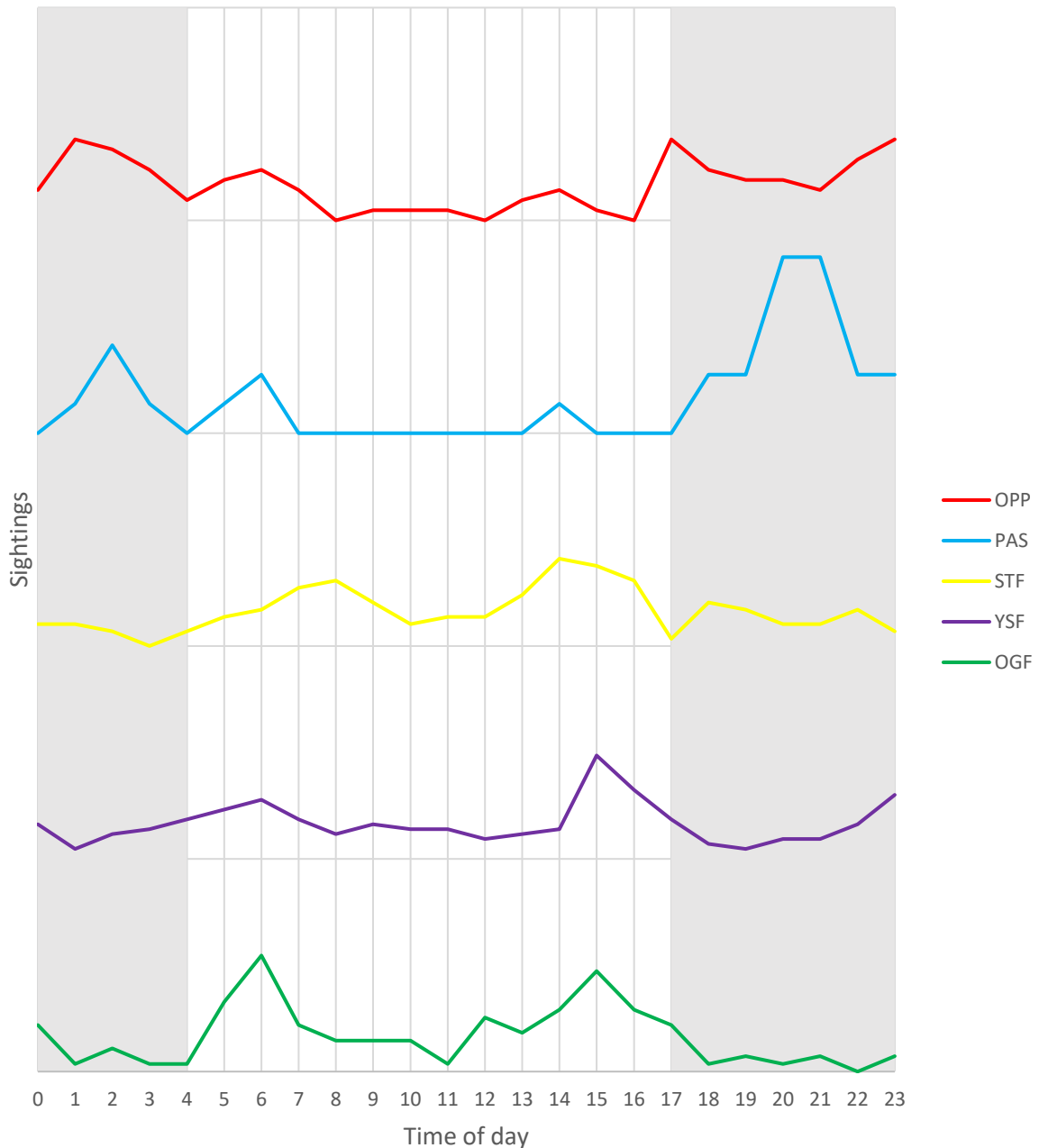


Fig. 11. Change of mammal activity (= number of events per hour) in the course of the day, shown separately for each habitat type (OPP – oil palm plantation, PAS – pasture, STF – strip forest, YSF – young secondary forest, OGF – old-growth forest).

Forest dependency of species

Forest dependency of mammals – quantified as median percentage of forest cover around camera trap sites with records – was strikingly different between species. Within a 200 m buffer, Ocelot and Striped Hog-Nosed Skunk show the highest median forest dependency (apx 85% and apx 75%, respectively), while domestic dog and Common Gray Four-Eyed Opossum have the least (apx 25% and apx 20%, respectively, Fig. 12).

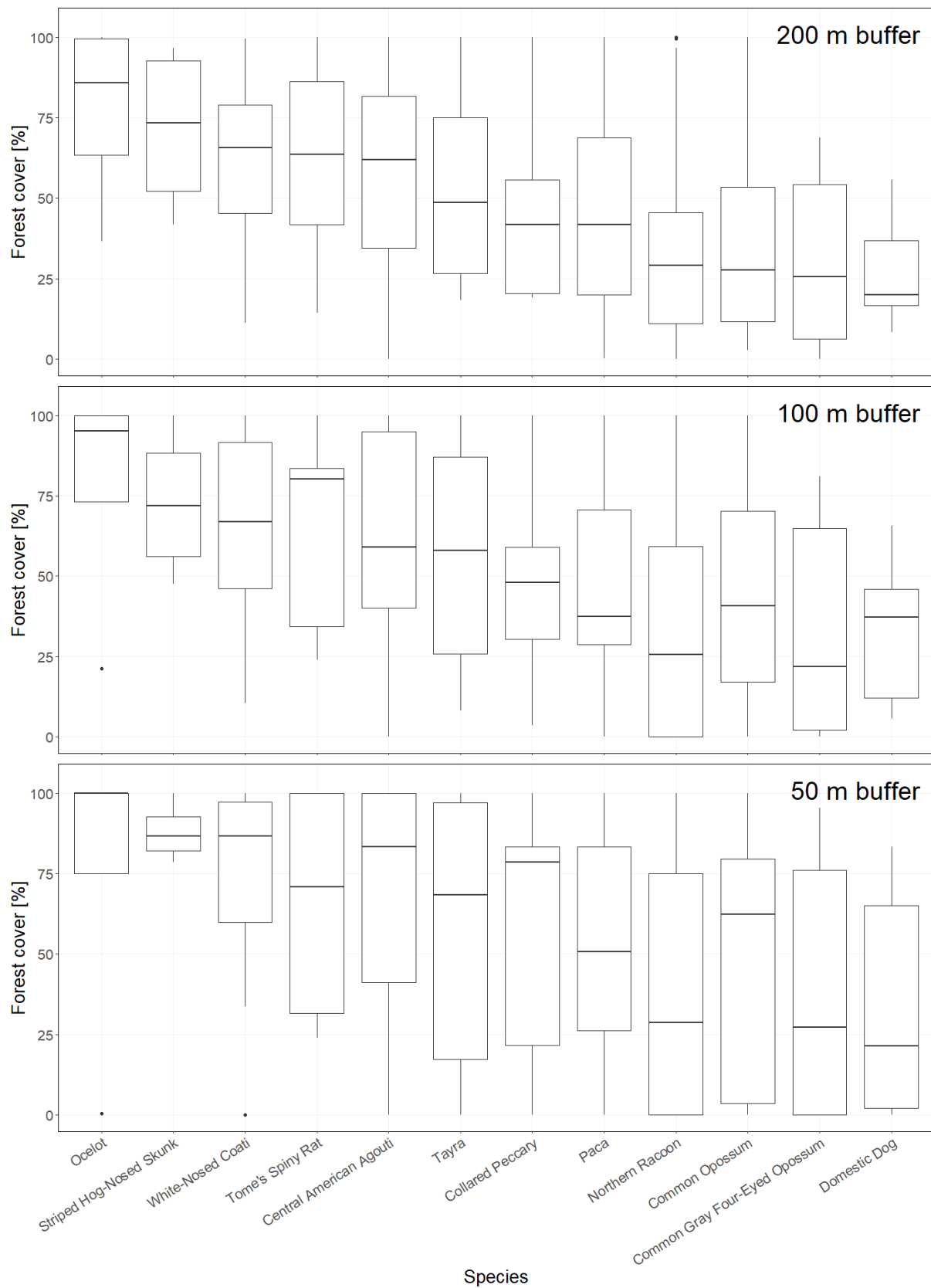


Fig. 12. Forest dependency of the 12 most abundant mammal species, quantified as the median of forest cover percentages at camera trapping sites with records, visualized separately for each of the 3 buffers. The order of mammals from left to right is based on the median forest coverage within the 200 m buffer. Boxes represent the 2nd and 3rd quartiles, whiskers indicate minimum and maximum values.

Habitat preferences of the most abundant species

The two most abundant mammals were the Northern Raccoon and the Central American Agouti, recorded at 32% of all sites with a total of 109 events and at 24% of all sites with a total of 252 events, respectively (Table 1 and 2).

Northern Raccoon

The Northern Raccoon is widespread throughout our study area and can be found in a variety of habitats (Fig. 13). However, it was not equally distributed across the five habitat types (Chi-Square test: $\chi^2 = 10.202$, $df = 4$, $p = 0.0372$, Table 3). Few sightings exist from old growth forests, while all other habitats seem to be of similar importance (Fig. 14).

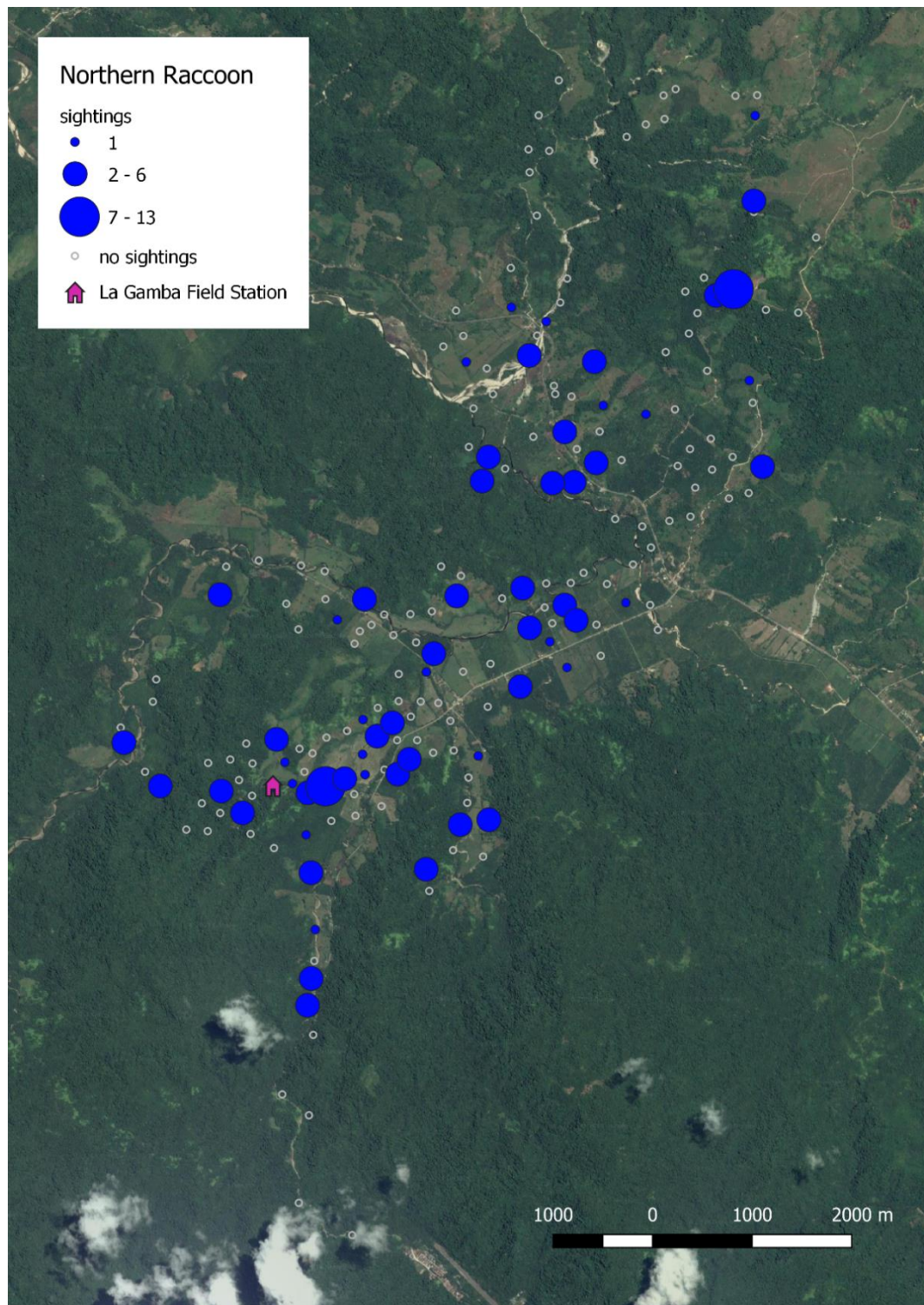


Fig. 13. Map indicating Northern Raccoon records and the number of events at camera trap sites.

Table 3. Number of events and sites with raccoon records per habitat type (N = 40 per habitat).

Habitat type	Number of sites with records	Number of events
Old Growth	4	7
Young Secondary	14	32
Strip	13	21
Pasture	12	23
Palm Oil	17	24

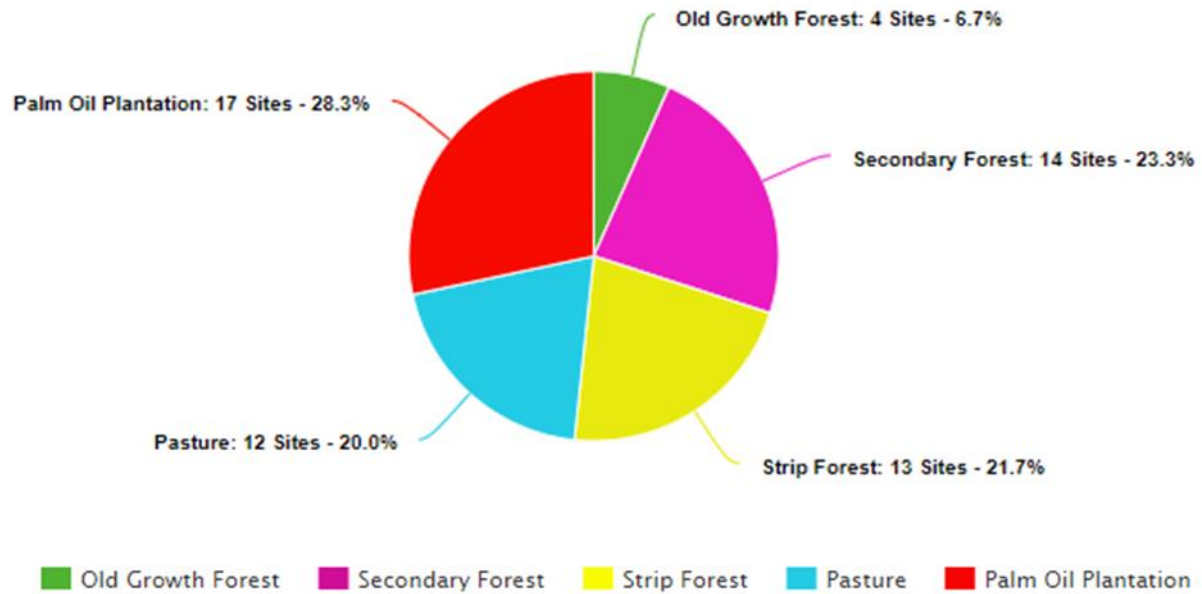


Fig. 14. Fractions of Raccoon sightings based on habitat type and total number of events using cameras, tracks and sightings.

Our models indicate that the likelihood of seeing a raccoon increased with coverage of settlements and gardens, but decreased with roads (Fig. 15). These two variables reach the highest effect size in the 50 m and the 100 m buffer but are only significant at the 50 m buffer size. In the 200 m buffer, settlements and gardens is not significant. When using the same scale on the x axis for all three graphs in Fig. 15, you see that there are hardly any effects remaining for the 200 m buffer. No other tested landscape variable exerted any detectable influence on raccoon sighting probability (Table 4).

Table 4. Model-averaged coefficients: Full Model Average for Northern Raccoon. Significant effects printed bold. RD-Roads, OF-Open Farmland, SH-Shrubland, WB-Water Bodies, YF-Young Forest, OP-Oil Palm Plantation, SG-Settlements and Gardens, OL-Old Growth Forest

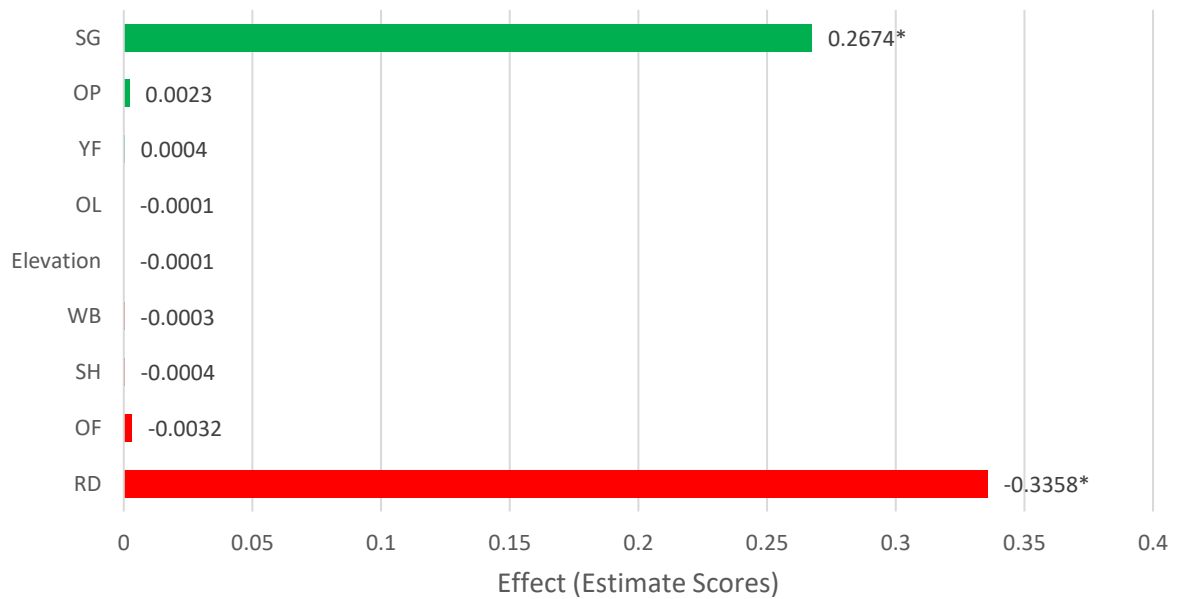
	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
50 m buffer					
(Intercept)	-0.6632	0.2788	0.2798	2.370	0.0178
RD	-0.3358	0.1693	0.1704	1.971	0.0487
OF	-0.0032	0.0043	0.0044	0.730	0.4652
SH	-0.0004	0.0028	0.0029	0.131	0.8957
WB	-0.0003	0.0043	0.0043	0.076	0.9393
Elevation	-0.0001	0.0007	0.0007	0.172	0.8632
OL	-0.0001	0.0021	0.0021	0.050	0.9599
YF	0.0004	0.0022	0.0022	0.186	0.8521
OP	0.0023	0.0039	0.0040	0.582	0.5604
SG	0.2674	0.1314	0.1322	2.022	0.0432
100 m buffer					
(Intercept)	-0.5869	0.3084	0.3094	1.8970	0.0579
RD	-0.1755	0.1505	0.1510	1.1620	0.2452

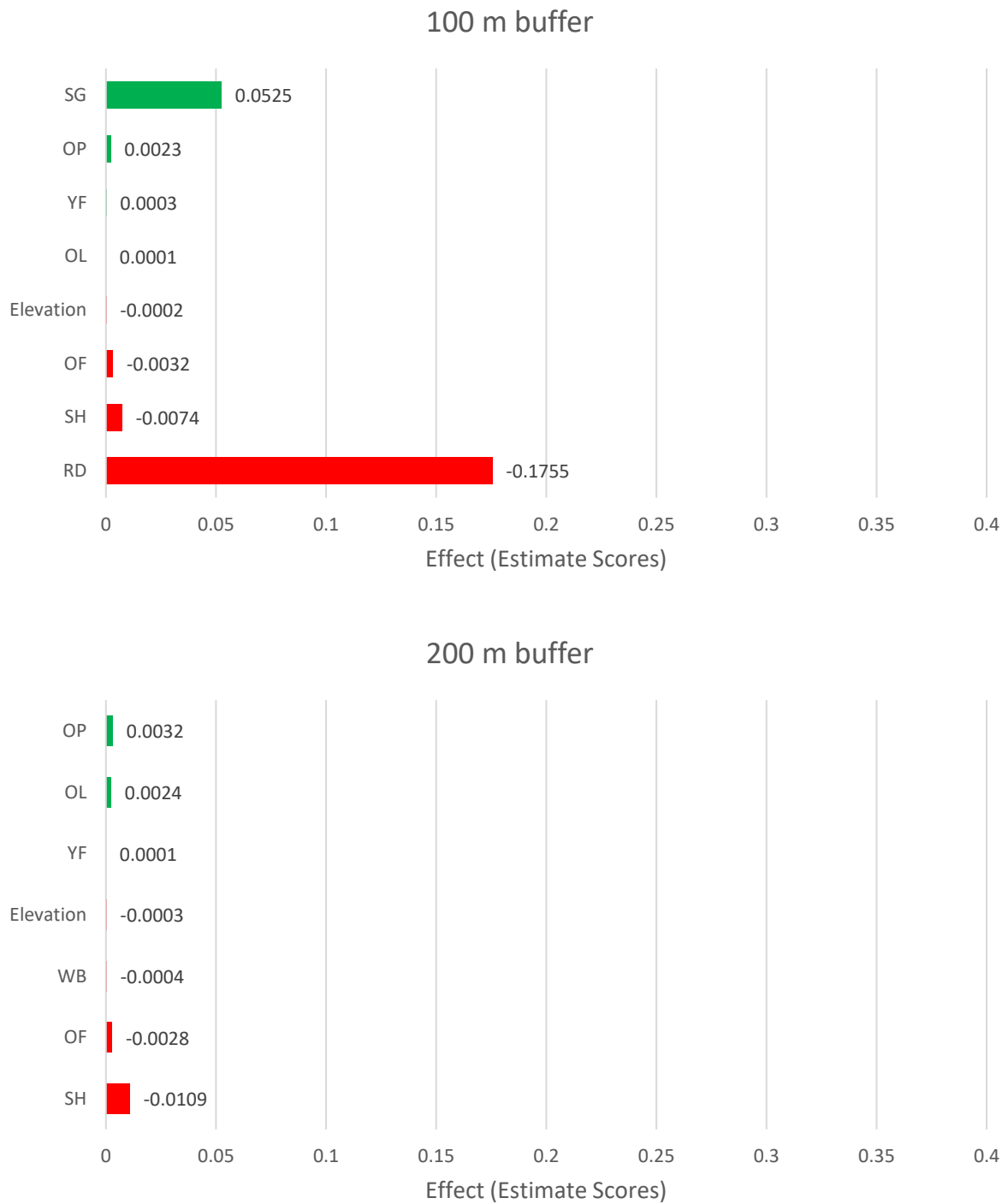
		<i>Estimate</i>	<i>Std. Error</i>	<i>Adjusted SE</i>	<i>z value</i>	<i>Pr(> z)</i>
<i>Elevation</i>	<i>SH</i>	-0.0074	0.0129	0.0129	0.5750	0.5651
	<i>OF</i>	-0.0032	0.0047	0.0048	0.6710	0.5021
	<i>OL</i>	-0.0002	0.0007	0.0007	0.2100	0.8336
	<i>YF</i>	0.0003	0.0023	0.0023	0.1630	0.8703
	<i>OP</i>	0.0023	0.0043	0.0043	0.5430	0.5871
	<i>SG</i>	0.0525	0.0503	0.0505	1.0420	0.2975

200 m buffer

<i>(Intercept)</i>	-0.6952	0.4013	0.4024	1.7280	0.0840
<i>SH</i>	-0.0109	0.0168	0.0168	0.6460	0.5180
<i>OF</i>	-0.0028	0.0049	0.0049	0.5750	0.5650
<i>WB</i>	-0.0004	0.0063	0.0063	0.0700	0.9440
<i>Elevation</i>	-0.0003	0.0010	0.0010	0.3390	0.7350
<i>YF</i>	0.0001	0.0028	0.0028	0.0310	0.9750
<i>OL</i>	0.0024	0.0053	0.0053	0.4490	0.6530
<i>OP</i>	0.0032	0.0057	0.0058	0.5590	0.5760

50 m buffer





*Fig. 15. Estimate scores quantifying the effect size of habitat variables on the occurrence of Northern Raccoons at the camera trap sites, separately shown for each of the 3 buffers. * indicates significant effects. RD-Roads, OF-Old Growth Forest, SH-Shrubland, WB-Water Bodies, YF-Young Secondary Forest, OP-Oil Palm Plantation, SG-Settlements and Gardens, OL-Open Cultivated Land, LF-Living Fences*

Almost all Northern Raccoon records (97 in total, 89%) occurred between 17:00 and 05:00 h, confirming the overwhelmingly nocturnal nature of foraging activities in the focal species (Fig. 16).

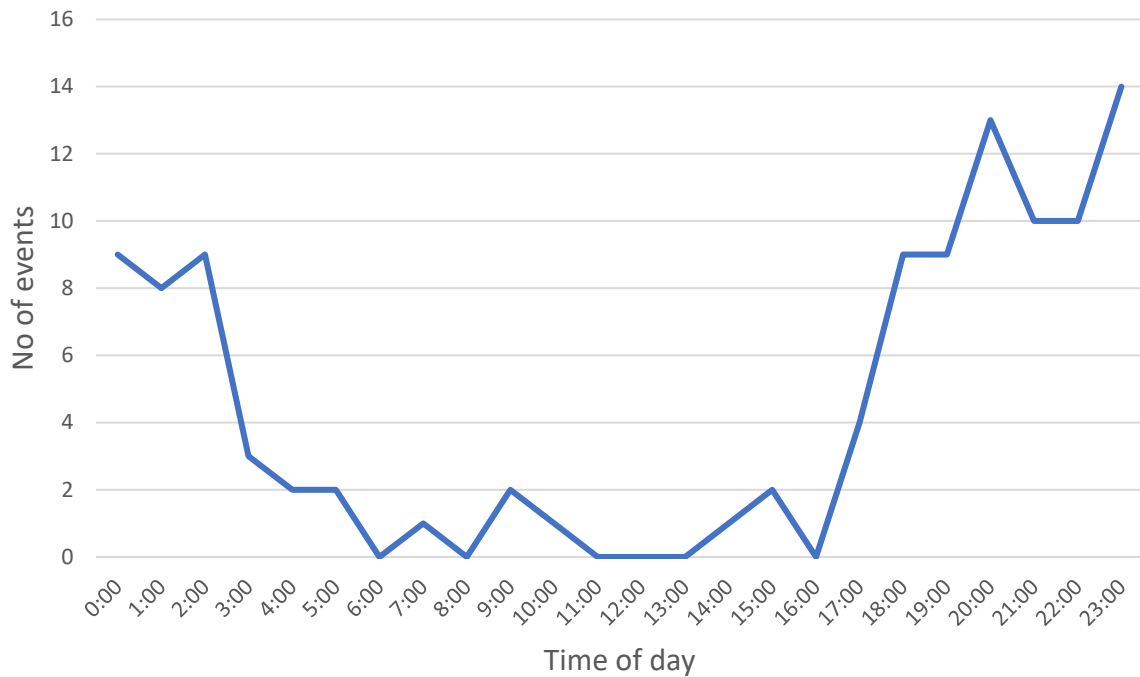


Fig. 16. Graph of Estimate Results of Northern Raccoon events showing hourly activity.

Central American Agouti

The Agouti was the second most common mammal occurring at 41 camera trap sites (Table 1) and also had the highest number of events with a total of 252 events (Table 2). Agoutis prefer the natural forest habitats (Chi-Square test: $\chi^2 = 12.407$, $df = 4$, $p = 0.0282$, Table 5) with 95% of camera trap sites with sightings being from these habitats. They were present at only two plantations and no pasture site, almost completely avoiding the human-dominated habitats.

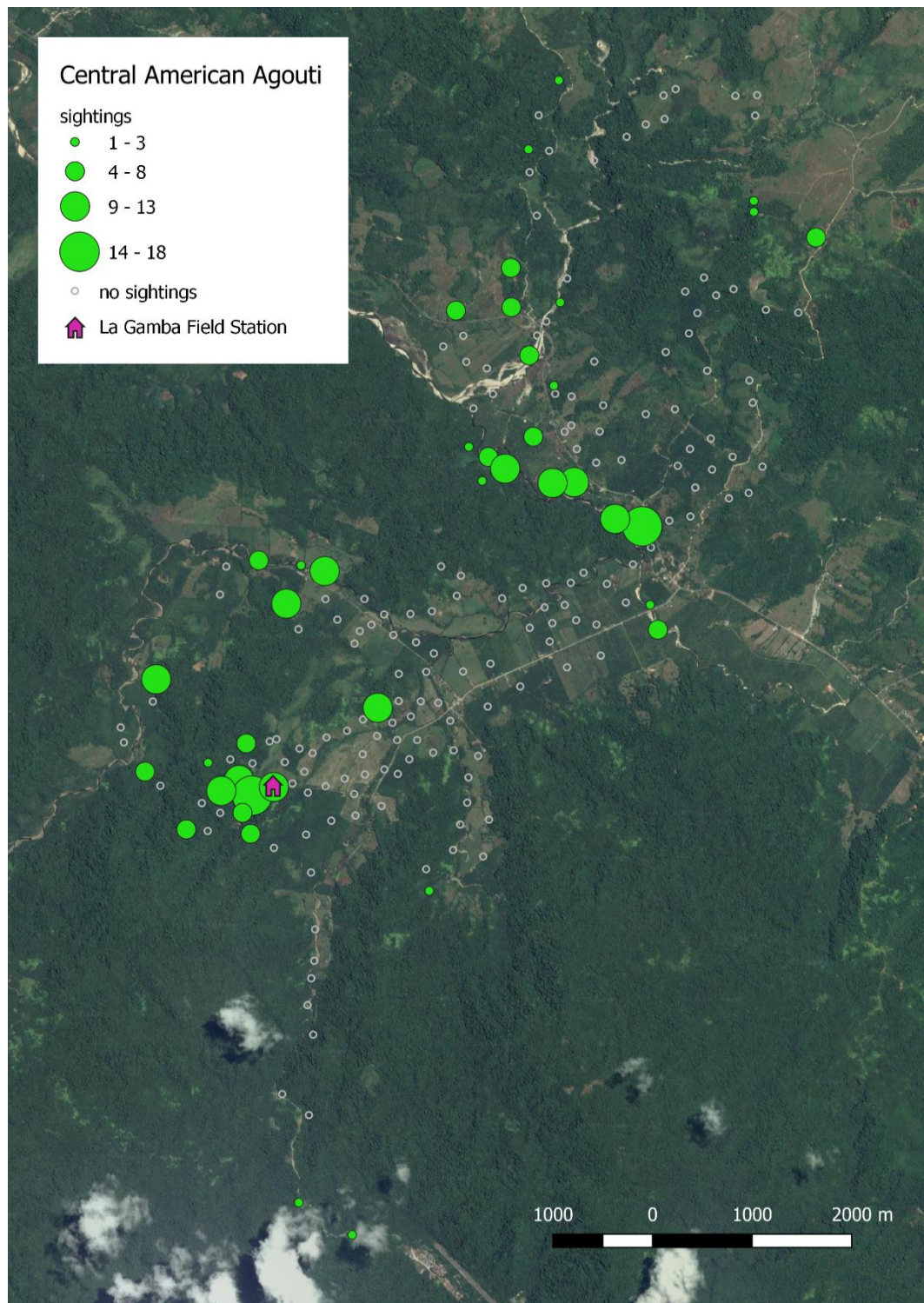


Fig. 17. Map of Central American Agouti sites expressing events per site.

Table 5. Number of events and sites with Agouti records per habitat type (N = 40 per habitat).

Habitat type	Number of sites with records	Number of events
Old Growth	14	80
Young Secondary	14	85
Strip	11	70
Pasture	0	0
Palm Oil	2	17

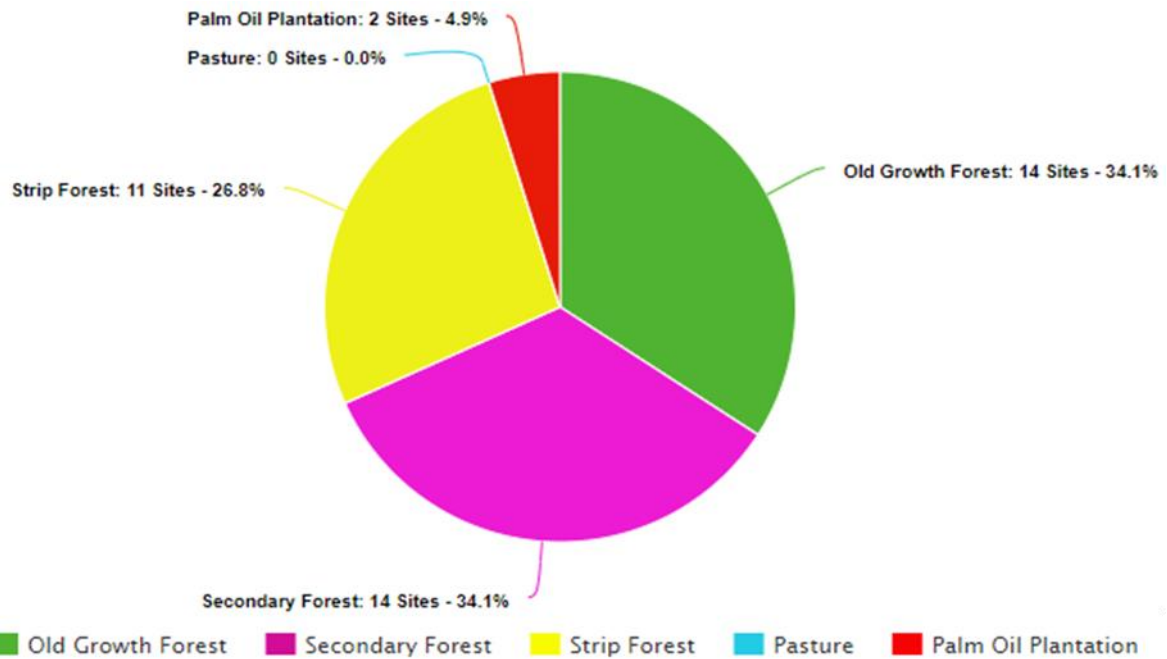


Fig. 18. Fractions of Agouti sightings based on habitat type.

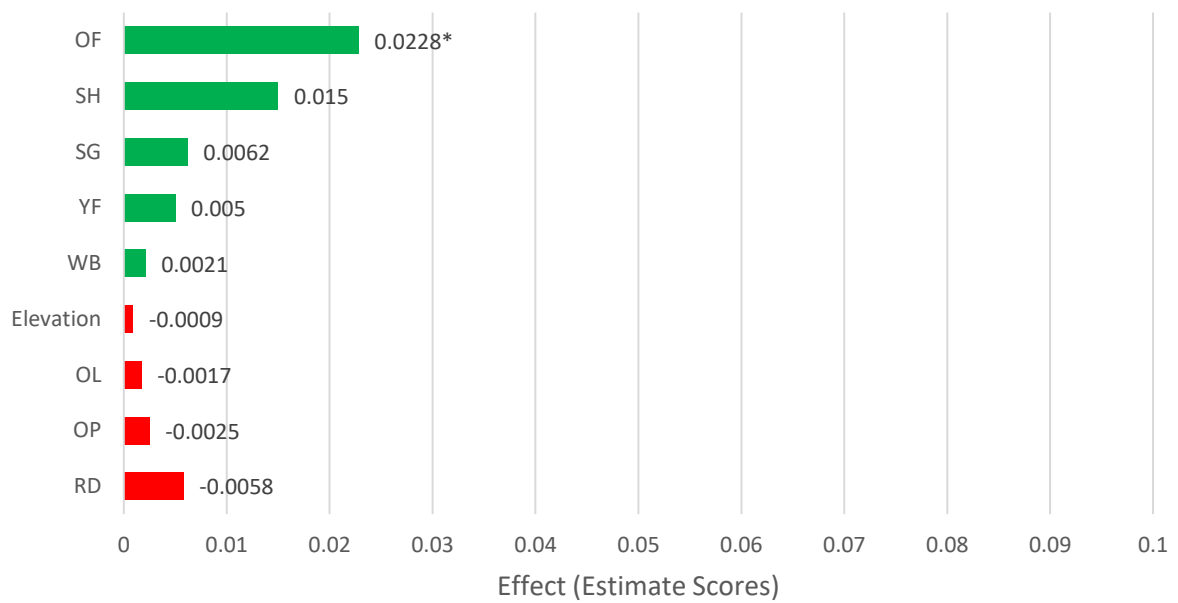
It appears that Agoutis like old growth forest with water nearby. The likelihood of Central American Agouti occurrence was positively affected by high old growth forest cover at all three buffers. Water bodies only showed a significant positive effect on agouti occurrence at the 100 m and 200 m buffers. All other habitat variables did not explain agouti occurrences recorded by camera traps (Table 6).

Table 6. Model-averaged coefficients: Full Model Average for Agouti.

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
50 m buffer					
(Intercept)	-2.3191	0.5964	0.5981	3.877	0.0001
RD	-0.0058	0.0472	0.0475	0.123	0.9024
OP	-0.0025	0.0065	0.0065	0.380	0.7040
OL	-0.0017	0.0056	0.0056	0.299	0.7648
Elevation	-0.0009	0.0017	0.0017	0.512	0.6086
WB	0.0021	0.0085	0.0085	0.247	0.8047
YF	0.0050	0.0083	0.0084	0.602	0.5474
SG	0.0062	0.0297	0.0298	0.206	0.8364
SH	0.0150	0.0127	0.0127	1.178	0.2390
OF	0.0228	0.0069	0.0069	3.283	0.0010
100 m buffer					
(Intercept)	-2.6568	0.4835	0.4858	5.468	< 0.0001
OL	-0.0013	0.0050	0.0050	0.266	0.7900
Elevation	-0.0003	0.0011	0.0011	0.272	0.7860
YF	0.0012	0.0049	0.0049	0.240	0.8110
SG	0.0039	0.0185	0.0186	0.208	0.8350
RD	0.0045	0.0367	0.0368	0.121	0.9040
SH	0.0159	0.0157	0.0158	1.008	0.3130
OF	0.0256	0.0060	0.0060	4.248	< 0.0001
WB	0.0555	0.0245	0.0246	2.257	0.0240

	<i>Estimate</i>	<i>Std. Error</i>	<i>Adjusted SE</i>	<i>z value</i>	<i>Pr(> z)</i>
<i>200 m buffer</i>					
<i>(Intercept)</i>	-2.8847	0.5319	0.5345	5.397	< 0.0001
<i>Elevation</i>	-0.0002	0.0010	0.0010	0.234	0.8152
<i>OL</i>	-0.0002	0.0029	0.0029	0.085	0.9323
<i>OP</i>	0.0003	0.0030	0.0030	0.113	0.9099
<i>SG</i>	0.0086	0.0265	0.0265	0.325	0.7451
<i>SH</i>	0.0184	0.0203	0.0204	0.902	0.3668
<i>OF</i>	0.0284	0.0066	0.0066	4.311	< 0.0001
<i>RD</i>	0.0833	0.1421	0.1425	0.584	0.5590
<i>WB</i>	0.0918	0.0358	0.0360	2.549	0.0108

50 m buffer



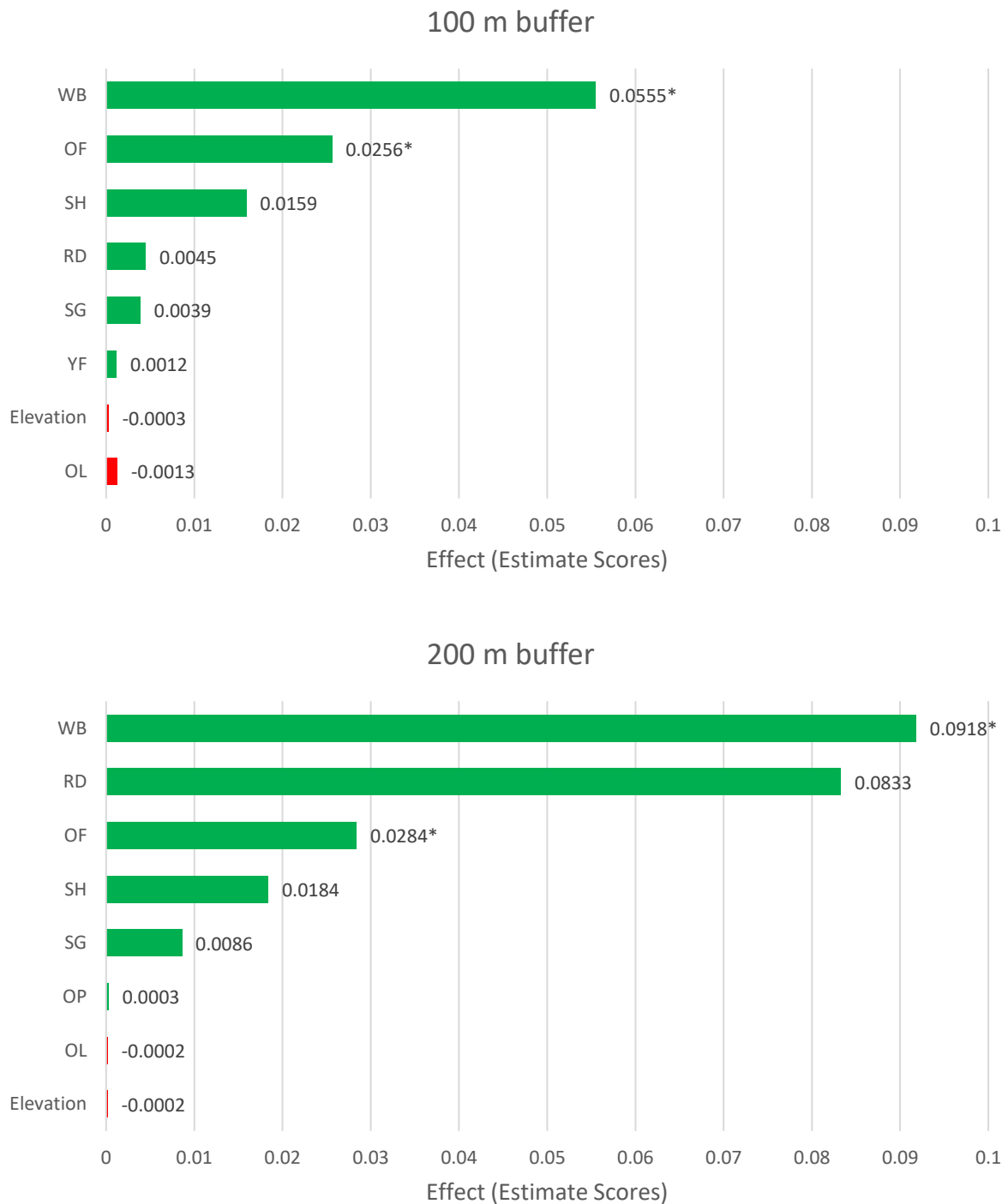


Fig. 19. Estimate scores quantifying the effect size of habitat variables on the occurrence of Central American Agouti at the camera trap sites, separately shown for each of the 3 buffers. * indicates significant effects. RD-Roads, OF-Old Growth Forest, SH-Shrubland, WB-Water Bodies, YF-Young Secondary Forest, OP-Oil Palm Plantation, SG-Settlements and Gardens, OL-Open Cultivated Land, LF-Living Fences

White-Nosed Coati

The White-nosed Coati was the third most common mammal being recorded at 14 camera trap sites (Table 1) with a total of 19 events (Table 2). Notice the habitat locations in the tables below. We can see that there were 47 individuals indicating that many Coati were

travelling in pairs or groups especially in young secondary forests. Coatis were not recorded in palm oil plantations (Table 7).

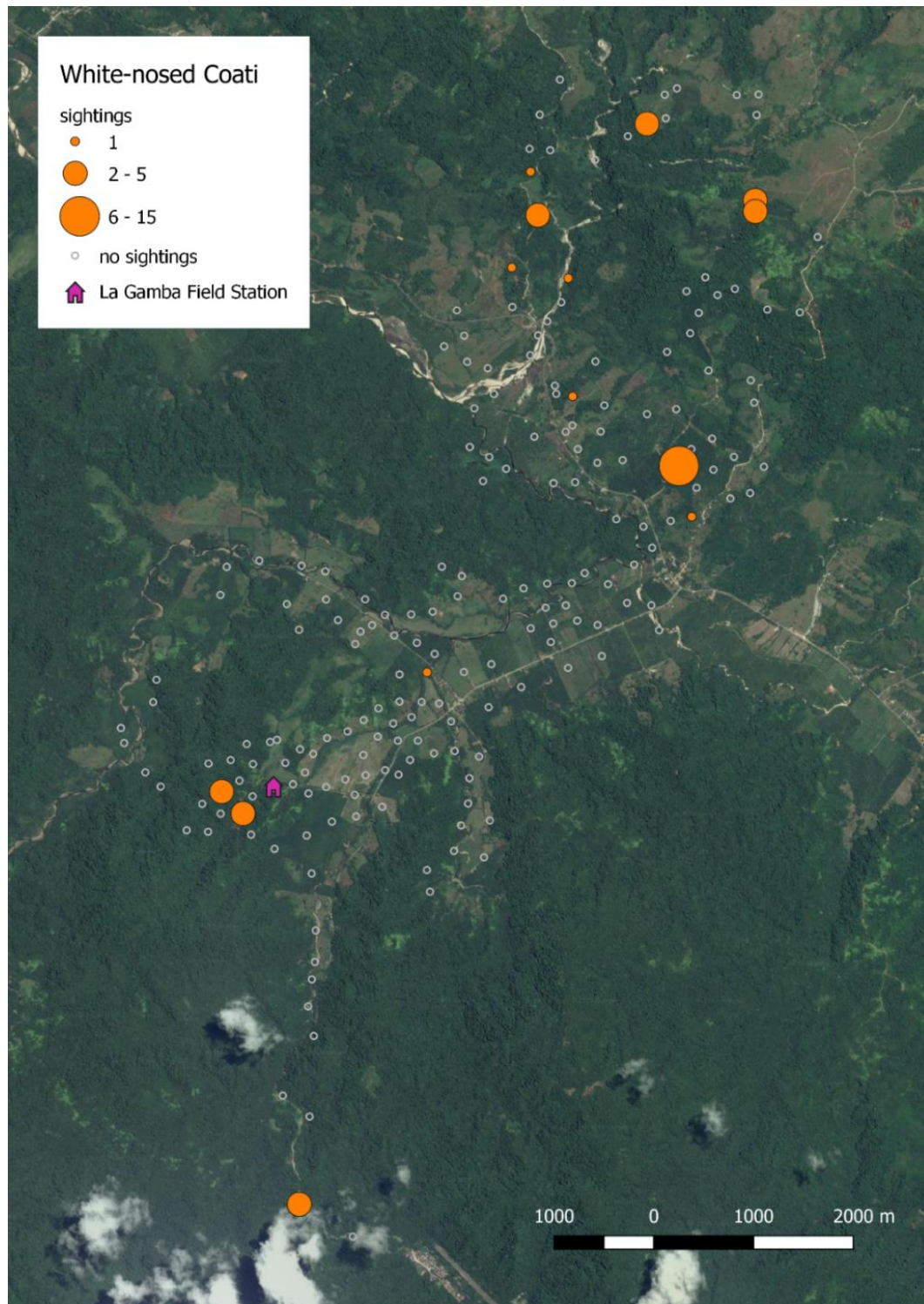


Fig. 20. Map of White-nosed Coati sites expressing events per site.

Table 7. Number of events and sites with White-nosed Coati records per habitat type (N = 40 per habitat).

Habitat type	Number of sites with records	Number of events
Old Growth	2	2
Young Secondary	5	7
Strip	5	6

<i>Habitat type</i>	<i>Number of sites with records</i>	<i>Number of events</i>
<i>Pasture</i>	2	4
<i>Palm Oil</i>	0	0

Tayra

The Tyra was the fourth most common mammal occurring at eleven camera trap sites, (Table 1) with a total of 13 events (Table 2). Notice a total of 13 events and 13 individuals, indicating all Tayra sightings were single individuals. There were no sightings in pastures (Table 8).

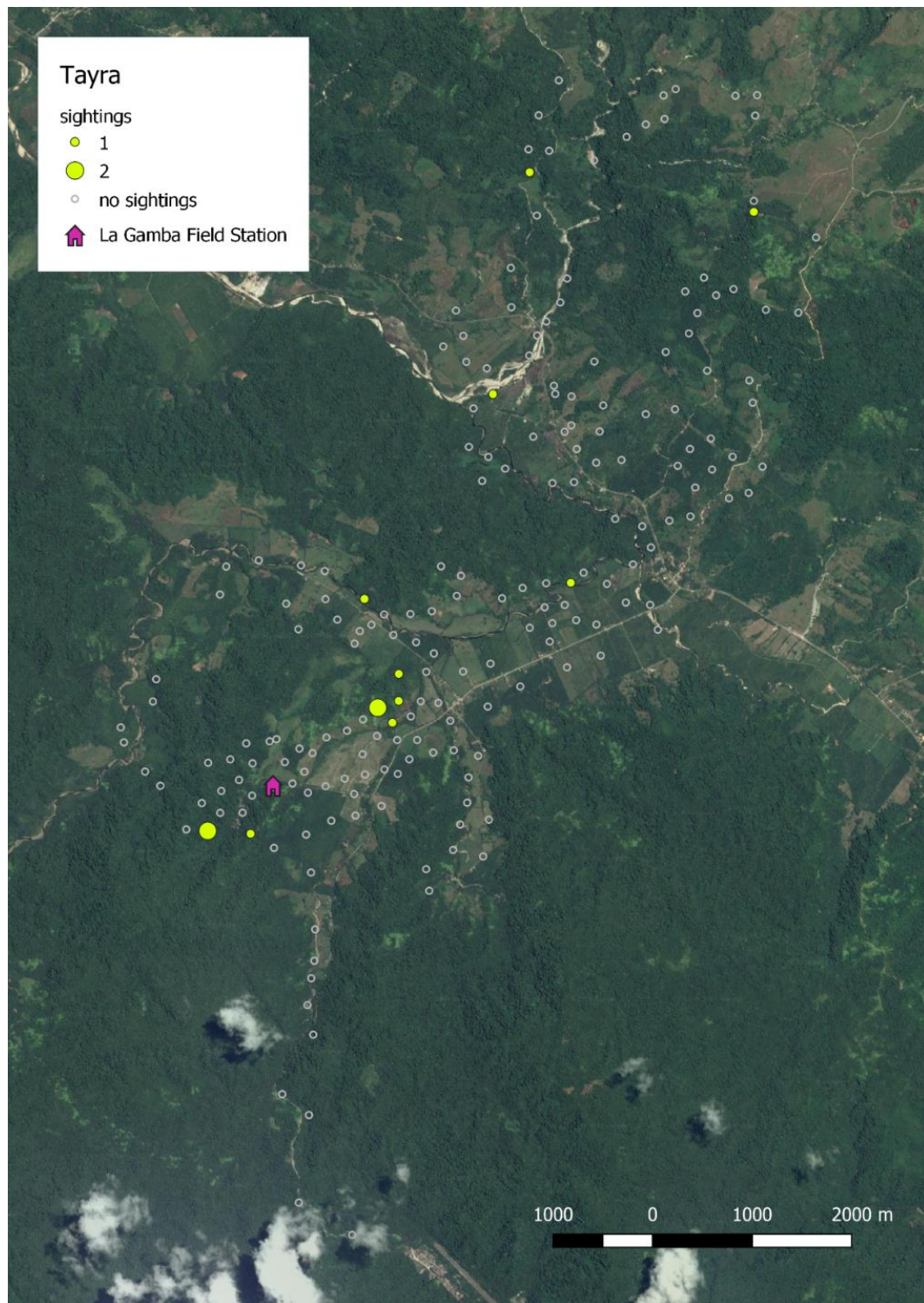


Fig. 21. Map of Tayra expressing amounts per site.

Table 8. Number of events and sites with Tayra records per habitat type (N = 40 per habitat).

Habitat type	Number of sites with records	Number of events
Old Growth	1	2
Secondary	4	4
Strip	2	2
Pasture	0	0
Palm Oil	4	5

Discussion

Species richness

Young secondary forests had the highest species richness of terrestrial mammals, followed by oil palm plantations, old growth forests and strip forests (15, 14, 12 and 11 species, respectively). This is emphasizing the high value of secondary forests for maintaining biodiversity in human-dominated landscapes, as already reported by other studies (Acevedo-Charry O, & Aide T M (2019). Another study from Costa Rica on amphibians showed that even young secondary forest can provide suitable habitats for many amphibian species and that strip forests aid in the biodiversity and colonizing of these areas (Hilje & Aide 2012). This study shows a similar trend of increased mammal diversity in secondary forests and therefore highlights their importance for conservation measures.

With only three recorded species, diversity was lowest in pastures. This large difference in biodiversity could be due to several reasons. Many of the pastures contained domestic horses, cows, dogs and several pastures were also fenced which may represent a barrier for some mammals. Also, the almost complete lack of woody vegetation in pastures could lead to a shortage of places to hide for predators or preys. Our research shows similar results found in other studies suggesting that an increase in pasture habitats has meant a decrease in vertebrate populations (Estrada et al. 1994).

Oil palm plantations were characterized by a slightly higher species richness than strip and old growth forests. This result was surprising, especially as many other studies show a decreased biodiversity in this land-use system (Yue et al. 2015). When an area is converted to an oil palm plantation there are various anthropogenic effects associated with this new habitat (Azhar et al. 2012). These negative effects may include an increase in roadkills as well as disturbance caused e.g. by cattle or domestic and feral dogs. Several other studies of biodiversity in oil palm plantations show trends of reduced species richness compared with old growth and young secondary forests and significant changes in community assemblages (Savilaakso et al. 2014). Many of our oil palm plantations were smaller in size and therefore were located near to natural forest settings which may have contributed to the higher species richness in our study as opposed to others. Mammals may show a decrease in species richness with a decreasing proximity to natural forest habitats (Yue et al. 2015).

Another camera trap study from the Golfo Dulce Region showed that the Lapa Rios Reserve, which suffered less anthropogenic habitat alterations, had a higher species richness (25 sites/18 wild mammal species) compared to the more severely altered area Playa Sandalo (16 sites/9 wild mammal species) (Gutierrez et al. 2019). We had 200 camera trap sites with 21 total species. Species accumulation curves show a similar richness between the Lapa Rios Reserve sites with our young secondary forest sites. The mammal diversity of the Playa Sandalo sites was more similar to the Oil Palm Plantations in our study. Both of these areas may be similar due to some human interference but still having enough resources to harbor some mammals. Though the Playa Sandalo sites showed less diversity it was still more diverse than our pasture sites which had a total of 3 species in 40 total sites. However, there are important differences between both studies. Gutierrez et al. moved the cameras to different locations approximately every seven days, they did not use bait, they placed cameras only at forest sites (with only one exception, compare Fig. 3 in Gutierrez et al. 2019)

and their study areas were much smaller than ours. These differences all could have affected the recorded species richness.

Species composition

When viewing the results, we can come to many conclusions about the distribution of various ground mammals in the Pacific lowlands of Costa Rica, even more specifically, the habitats surrounding La Gamba. When looking at the events and individuals table we can see that most mammals are seen as single individuals with the exception of two species. White-Nosed Coati had 20 events but a total of 47 individuals meaning that many times more than one individual were seen together. Additionally, Northern Raccoons had 107 events with a total of 148 individuals, and many of these pictures captured a mother raccoon with her young. A total of 21 different mammals leading to over 500 events were captured on the camera traps.

Species composition of mammals per camera trap site did not show a significant difference. However, two distinct clusters are seen on the level of habitats, one cluster contains the three forest types and a second cluster the two land-uses systems (pastures and oil palm plantations). If we now consider that these human-dominated land systems are usually associated with less mammalian diversity, we can start to understand the conservation value in these human-dominated areas.

In another study of mammals in Costa Rica, only 3 (11%) of 26 mammal species recorded in all study plots were found in agricultural habitats as opposed to 9 species (35%) in forests and 14 (54%) recorded in both (Daily et al. 2003). The study concluded that species richness did vary greatly between habitats but that agricultural areas closer to forest also expressed more species richness. Additionally, similar to our study, there were some species that were common to the area but not recorded in the study, also some more rare ones including the Jaguar (*Panthera onca*) and Baird's tapir (*Tapirus bairdii*). However, Baird's tapir tracks were recorded at two sites in our study, in an abandoned oil palm plantation (approx. 5 years abandoned) and in a pasture near a strip forest margin (Fig. 22).

Our study also included a few other species worth mentioning. Coyotes (*Canis latrans*) had three events recorded in oil palm plantations only. One plantation landowner was in disbelief despite coyotes being common in southwest Costa Rica because he had not seen them in his plantation before. This underscores the species' secret way of life, possibly especially in habitats with a high degree of human disturbance. Coyotes have the ability to utilize these plantation habitats and this has increased their ability to expand their range further into northeastern and north-central Costa Rica (Cove 2012). The Tapiti Rabbit (*Sylvilagus brasiliensis*) was also recorded one time within an oil palm plantation. This species is rare and only a few papers could be found (Júnior et al. 2005) reporting the occurrence of this species in the study region during the past few decades. Several local biologists reported they had never seen one in this area and were surprised when I showed them our captured photo.



Fig. 22. Baird's tapir (*Tapirus bairdii*) tracks from an oil palm plantation camera trap site.

Temporal activity patterns

Besides differences in species composition between the group of forest habitats and the group of land-use systems, also temporal patterns of mammal activity differed between both groups of habitats. The two human-dominated habitats, pastures and oil palm plantations, were heavily utilized by mammals at night while the forest habitats had highest activity during the day. That mammals shift their daily patterns of activity and increase their nocturnality in response to increased human disturbance is a global phenomenon (Gaynor et al. 2018).

It appears that exclusively diurnal animals have trouble crossing the human-dominated pastures and oil palm plantations, e.g. the Agouti was never recorded in pastures and only twice in oil palm plantations. This could be due to human activity in these habitats during the day. Perhaps the activity of humans, domestic dogs and livestock during day-time hours results in a drastic reduction of mammal activity. On the other hand, nocturnal activity of

predatory cats, such as ocelots, who hunt primarily at night could reduce activity of mammals in forest habitats during the night (Abreu et al. 2008).

Forest dependency

If we take a look at forest dependency of mammals with at least 4 camera trap site locations we can see some trends at the 50m, 100m, and 200m buffers. In this portion of the data analysis we decided to include domestic/feral dog occurrences to view their dependency on forests. To no surprise the dog forest dependency was the least percentage in each buffer (about 25% forest cover within each buffer range) at sites where dogs were captured on camera. Common Opossum and the Gray Four-Eyed Opossum followed showing little forest dependency at each buffer size (about 25%). Studies have shown that the Common Opossum are tolerant of anthropogenically altered environments and will even exploit agricultural and urban environments (Tardieu 2017).

Tayras were found at approximately the 60% forest dependency at all three buffers. The three forest habitats accounted for 7 of the 11 tayra sites, and no tayras were found in the pastures. The data is consistent with other tayras studies that show tayras avoid the open grasslands. A study in the Brazilian Pantanal pertaining to habitat selection of various ground mammals encountered 11 tayras showing a high favorability of a forest habitat selection as opposed to open grasslands (Desbiez et al. 2009).

Ocelots appear to have the largest dependency on forest cover (greater than 75%) at each buffer size. This coincides with previous data that ocelot presence is negatively associated with the intensity of human-use landscapes (Cruz et al. 2018). Following ocelots are the Striped Hog-Nosed Skunk and White-Nosed Coati, each greater than 65% forest dependency at each of the buffers. One study of the Striped Hog-Nosed Skunk using radio collared tracking techniques showed this species spending greater than 60% of the time in forested areas (Esser 2012).

Habitat preferences

A more detailed analysis of landscape variables affecting the occurrence of the most abundant mammals revealed species-specific differences. For example, roads within the 50 m buffer around camera traps reduced the likelihood of observing Northern Raccoons. Perhaps raccoons recognize and avoid disturbances, such as the dangers caused by traffic. Another study in the region showed that wildlife relative abundance at Lapa Rios, Costa Rica, also showed negative correlations with roads (Gutierrez et al. 2019). On the contrary, settlements and gardens increased the likelihood of observing raccoons, perhaps because of access to supplementary food in vicinity to human settlements.

Application of the 100 m buffer showed similar results. However, the P score significance threshold of 0.05 was not met in any of the variables at the 100 m buffer range. Roads had an Estimate score of -0.0176 ($P = 0.2452$), which means that once again Roads have a negative influence on the presence of Raccoons. Roads become less important on a larger spatial scale because they are important as a disturbance factor only with a smaller buffer surrounding them. Similar to 50m, Settlements and Gardens had a positive Estimate score (0.0526; $P = 0.2975$) at 100m which supports a positive influence of this site

characteristic on sightings of Northern Raccoons. As Northern Raccoons were only recorded at 12.5 % of the Old Growth camera trap locations but at least at 30 % of the sites of all other habitat types, it appears as if the species is avoiding closed forest perhaps due to predators such as ocelots and tayras in our study, utilizing this area more than other habitats, or perhaps food sources are fewer here due to other species. Hence, Northern Raccoons may even benefit from land-use and forest disturbance. In fact, at the 100 and 200 m buffer level no significant effect of any of the considered landscape variables could be found. This may emphasize that raccoons are very opportunistic and tolerant against disturbance and habitat conversion.

The importance of strip forests as landscape structure providing habitat and/or structures used for dispersal by forest species was already documented for birds (Seaman & Schulze 2010). As Raccoons utilized every habitat and even showed a slight preference to some human structures such as settlements and gardens, it is not surprising that this linear forest strips did not prove being important.

Oil palm plantations are expanding rapidly in the tropics (Pirker et al. 2016). This study shows that Raccoons also forage in this anthropogenically altered setting as well. Other studies already reported that palm oil plantations are particularly utilized by disturbance tolerant species (e.g. reptiles and amphibians: Gallmetzer & Schulze 2015). Raccoons can be classified as a disturbance tolerant species based on their non-specific habitat preference. Another study from Colombia also documented for mammals that some species are far more vulnerable to oil palm expansion than others, with generalist meso-predators and grazers being relatively tolerant, and many other species being highly vulnerable (Pardo et al. 2018). In general, oil palm plantations have substantially lower mammal biodiversity than the native riparian rainforest and savannas they replace (Pardo et al. 2015). If oil palm plantations continue to increase, biodiversity will decrease. Northern Raccoons however, may even take advantage of this novel habitat.

Northern Raccoons are also considered by many to be clever and various studies have been done to determine their mental abilities (Hohmann et al. 2001). In fact, some studies have found that raccoons have a density of neurons in the cerebral cortex comparable to primates giving an indication of intelligence, problem solving and remembrance (Alvarenga, Jardim-Messeder et al. 2017). One study showed that almost two-thirds of the cerebral cortex area that is responsible for sensory perception is specialized to help interpret tactile impulses, which is a larger proportional amount than in any animal ever studied (Hohmann et al. 2001).

Perhaps all of these physical and mental aspects of Northern Raccoons make them able to persist in a wide variety of habitats and also make it able for them to thrive in this ever-changing human-dominated landscape. There also does not appear to be a habitat preference difference between solitary and families of Northern Raccoons although additional data may prove otherwise, though more data must be collected to study this. Additionally, the predominantly nocturnal life-style of Northern Raccoons may facilitate the utilization of human-dominated landscapes.

Raccoons are considered as a “pest” species that is highly invasive in regions outside their natural range (Canova & Rossi 2009); hence, they are not of conservation concern. Certainly, habitat loss and biodiversity decline are of major concern around the world, but there are also many species benefitting from various human activities, such as Northern Raccoons. In our study area, Northern Raccoons appear to be benefitting from human activities such as the overall conversion of natural habitats into a human-dominated landscape. This change appears to have improved habitat quality for this particular species which is facilitating higher population densities and perhaps expanding ranges. My data shows that these Raccoons are somewhat avoiding old growth forest. I believe that for Northern Raccoons these closed forests represent a dispersal barrier, though partly permeable, though information about this is scarce and more studies need to be done. I believe more research needs to be done for a better understanding of Northern Raccoons in the Pacific Lowlands of Costa Rica.

In contrast to Northern Raccoons, the likelihood of Central American Agouti occurrence was positively affected by old growth forest (in all three buffers) cover and waterbodies (at the 100 and 200 m buffer scale). Since it could not be recorded at pasture sites and only occurred at 2 OPP sites, it appears that agoutis are avoiding human dominated habitats. Another camera trap study in Barra del Colorado Wildlife Refuge, Costa Rica has the Central American Agouti as its most abundant animal (Arroyo-Arce et al. 2017). This strengthens the idea that agoutis prefer forest habitats.

Elevation was also included as variable in this analysis but showed no effect either positive or negative. Other studies of small mammals have shown that elevation, climatic conditions and distance to the cloud cap can all be correlated to patterns of species richness (McCain 2004). We considered elevation as covariate, but it did not prove to explain the likelihood of species' occurrences. This is not surprising as elevational differences between our camera trap sites were very small.

The White-nosed Coati was the third most abundant mammal recorded at 14 of the 200 camera trap sights with a total of 20 events, with a majority of records in forest sites as seen in other studies (Valenzuela & Ceballos 2000). We can see that there were 47 individuals indicating that many Coatis were travelling in pairs or groups especially in the young secondary forest habitat. One site even had 14 individuals travelling together. A four-year study of White-Nosed Coatis in Panama showed a mean foraging group size of 7.2 individuals (Gompper 2009).

The Tayra was the fourth most abundant mammal, 14/40 camera trap sites, with a total of 13 events. Notice a total 13 events and 13 individuals indicating all Tayra sightings were single individuals. Radio tracking data shows that the Tayra is a solitary predator and has a distinct home range that it travels around extensively (Presley 2009). There were not sufficient amounts of data for these mammals to run any reliable statistical analysis and more research should be done. Another large camera trap study recorded fewer terrestrial mammals (11) and the species composition was much different (Arroyo-Arce et al. 2017). This study did not record a single Tayra or Coati, but did record three species of cats, two of which were not captured in our research (*Panthera onca*-Jaguar and *Puma concolor*-Puma). A direct relationship between landscape heterogeneity and the occurrence of jaguars and pumas is very unlikely as both species are not habitat specialists. Human disturbance may be

the main driver shaping the occurrence of both cats. Our research area surrounding La Gamba, Costa Rica has many small patches of various types and sizes, while this other study is located within the Pacuare Nature Reserve and has less heterogeneity in its habitat structure as much of this study area is protected forest which could be the reason for the differences in species recorded.

Conclusion

The habitats considered in this study differed in terms of species richness and species composition. Therefore, the biological corridor benefits from having various habitat types because the greater the heterogeneity the higher the number of species. However, COBIGA should facilitate spatial movements of forest species and not of species tolerant against forest conversion such as Raccoons.

This research was very successful in determining habitat preferences for a few species of Mammals in the Pacific lowlands of Costa Rica in the area surrounding La Gamba and the COBIGA (La Gamba Biological Corridor). We can quantify the success of this study by the information obtained as a whole. An important finding is that strip forests and secondary forests are important structures for improving the permeability of the human-dominated landscape for many forest species. They even resemble old growth forest in terms of species composition (as shown by the cluster analysis). However, even tapirs can cross oil palm plantations, underlining that human disturbance may often be the main factor preventing dispersal movements between forest fragments.

Some mammals appear to prefer natural forest settings, while others do not show an affinity for any one habitat. Therefore, providing structures in the human-dominated habitats would be an extremely useful tool in biodiversity and conservation. This is perhaps why oil palm plantations, though largely dominated in biomass of one tree species, show a much higher species richness than pastures. Trees provide various resources for not only mammals, but reptiles, amphibians and birds.

One way to help biodiversity in pastures, which proved being only utilized by a very small number of mammals, may be to leave some of the trees or plant some trees within the pastures. These “remnant” trees can play an important role in the conservation of biodiversity in pastures (Harvey & Haber 1998). They can provide food, shade, and other various resources for many species. Disturbance may be the main factor for the low conservation value of pastures; hence, even some more trees may not improve their habitat quality for mammals. Maintaining and creating new forest patches and linear forest strips by reforestation measures may be the more successful conservation strategy. Recent studies also can show us the possible corridor routes using a landscape structure analysis (Höbinger et al. 2012). This type of study can be a useful tool to show where our efforts should be focused on to establish corridors with as much connectivity as possible.

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Appendix

Results of Spearman rank correlations testing for relationships between habitat variables

Appendix Table 1. Results of Spearman rank correlations testing for relationships between habitat variables measured at 50 m buffer (r scores below diagonal, p scores above diagonal) (LF = living fences; OP = oil palm plantation, OF = old growth forest, RD = roads, SG = settlements and gardens, SH = shrubland, TP = timber plantation, WB = water bodies, YF = young forest).

	LF	OP	OF	OL	RD	SG	SH	TP	WB	YF
LF		0.929	0.168	0.000	0.537	0.001	0.261	0.532	0.259	0.810
OP	-0.006		<0.001	0.000	0.164	0.614	0.119	0.851	0.042	0.006
OF	-0.098	-0.372		0.000	0.275	0.374	0.672	0.536	0.738	0.000
OL	0.258	-0.257	-0.390		0.516	0.903	0.360	0.768	0.118	0.474
RD	0.044	0.099	-0.077	0.046		0.036	0.882	0.088	0.984	0.035
SG	0.234	0.036	-0.063	0.009	0.148		0.924	0.571	0.083	0.948
SH	-0.080	-0.111	-0.030	0.065	-0.011	-0.007		0.726	0.282	0.431
TP	-0.044	-0.013	-0.044	-0.021	0.121	-0.040	-0.025		0.158	0.652
WB	0.080	-0.144	0.024	0.111	0.001	0.123	0.076	-0.100		0.005
YF	0.017	-0.192	-0.306	0.051	0.149	0.005	0.056	-0.032	0.200	

Appendix Table 2. Results of Spearman rank correlations testing for relationships between habitat variables measured at 100 m buffer (r scores below diagonal, p scores above diagonal) (LF = living fences; OP = oil palm plantation, OF = old growth forest, RD = roads, SG = settlements and gardens, SH = shrubland, TP = timber plantation, WB = water bodies, YF = young forest).

	LF	OP	OF	OL	RD	SG	SH	TP	WB	YF
LF		0.154	0.007	0.000	0.175	0.004	0.063	0.897	0.792	0.631
OP	0.101		0.000	0.040	0.837	0.927	0.025	0.783	0.282	0.003
OF	-0.190	-0.380		0.000	0.806	0.086	0.910	0.529	0.957	0.000
OL	0.274	-0.145	-0.415		0.724	0.143	0.617	0.027	0.016	0.739
RD	0.096	0.015	-0.018	-0.025		0.000	0.439	0.578	0.456	0.081
SG	0.202	0.006	-0.122	0.104	0.487		0.367	0.884	0.266	0.356
SH	-0.132	-0.159	-0.008	0.036	0.055	-0.064		0.689	0.232	0.038
TP	-0.009	-0.020	-0.045	-0.156	0.040	0.010	-0.029		0.047	0.209
WB	0.019	-0.076	-0.004	0.171	0.053	0.079	0.085	-0.141		0.032
YF	-0.034	-0.208	-0.279	0.024	0.124	0.066	0.147	0.089	0.152	

Appendix Table 3. Results of Spearman rank correlations testing for relationships between habitat variables measured at 200 m buffer (r scores below diagonal, p scores above diagonal) (LF = living fences; OP = oil palm plantation, OF = old growth forest, RD = roads, SG = settlements and gardens, SH = shrubland, TP = timber plantation, WB = water bodies, YF = young forest).

	LF	OP	OF	OL	RD	SG	SH	TP	WB	YF
LF		0.007	0.000	0.000	0.000	0.000	0.868	0.105	0.646	0.708
OP	0.192		0.000	0.887	0.205	0.543	0.033	0.947	0.039	0.010
OF	-0.321	-0.492		0.000	0.032	0.002	0.414	0.969	0.064	0.000
OL	0.366	0.010	-0.442		0.131	0.006	0.838	0.000	0.037	0.130
RD	0.277	0.090	-0.152	0.107		0.000	0.509	0.793	0.267	0.053

SG	0.335	0.043	-0.220	0.195	0.575		0.188	0.656	0.123	0.125
SH	-0.012	-0.150	-0.058	0.015	0.047	0.093		0.954	0.170	0.059
TP	-0.115	0.005	-0.003	-0.248	0.019	0.032	0.004		0.000	0.050
WB	0.033	0.146	-0.131	0.148	0.079	0.110	0.097	-0.252		0.144
YF	-0.027	-0.181	-0.330	0.107	0.137	0.109	0.134	0.139	0.104	

Component Models and Conditional Average Model Information (Northern Raccoon)

50 meter buffer

Appendix Table 4. Component models (models with a $\Delta AICc < 0.2$)

Included variables	df	LogLik	AICc	$\Delta AICc$	weight
256	4	-118.67	245.55	-	0.16
456	4	-118.75	245.70	0.15	0.15
56	3	-119.94	246.00	0.44	0.13
2456	5	-118.18	246.68	1.12	0.09
4569	5	-118.37	247.05	1.49	0.08
2356	5	-118.43	247.16	1.61	0.07
2567	5	-118.50	247.31	1.75	0.07
156	4	-119.62	247.44	1.88	0.06
1256	5	-118.61	247.54	1.98	0.06
3456	5	-118.62	247.55	1.99	0.06
2568	5	-118.62	247.55	1.99	0.06

Appendix Table 5. Term codes

Elevation	OF	OL	OP	RD	SG	SH	WB	YF
1	2	3	4	5	6	7	8	9

Appendix Table 6. Conditional Averages

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
(Intercept)	-0.6633	0.2788	0.2799	2.3700	0.0178
OF050	-0.0062	0.0043	0.0043	1.4340	0.1517
RD050	-0.3359	0.1694	0.1704	1.9710	0.0487
SG050	0.2674	0.1315	0.1323	2.0220	0.0432
OP050	0.0061	0.0043	0.0043	1.4040	0.1602
YF050	0.0053	0.0060	0.0060	0.8780	0.3802
OL050	-0.0008	0.0058	0.0058	0.1390	0.8895
SH050	-0.0055	0.0095	0.0096	0.5760	0.5646
Elevation	-0.0009	0.0017	0.0017	0.5510	0.5818
WB050	-0.0055	0.0168	0.0169	0.3260	0.7447

100 meter buffer

Appendix Table 7. Component models (models with a $\Delta AICc < 0.2$)

	df	logLik	AICc	delta	weight
456	4	-121.40	251.01	-	0.06
2567	5	-120.35	251.01	-	0.06
256	4	-121.47	251.14	0.13	0.06
56	3	-122.59	251.30	0.29	0.06

	df	logLik	AICc	delta	weight
27	3	-122.77	251.67	0.66	0.05
567	4	-121.74	251.68	0.67	0.05
257	4	-121.78	251.76	0.75	0.04
4567	5	-120.88	252.06	1.05	0.04
4568	5	-120.89	252.09	1.08	0.04
2	2	-124.03	252.13	1.12	0.04
2456	5	-120.94	252.18	1.17	0.04
25	3	-123.06	252.24	1.23	0.03
4	2	-124.14	252.34	1.33	0.03
3456	5	-121.04	252.38	1.37	0.03
156	4	-122.16	252.52	1.51	0.03
46	3	-123.28	252.67	1.66	0.03
24567	6	-120.13	252.70	1.70	0.03
(Null)	1	-125.37	252.77	1.76	0.03
1456	5	-121.24	252.78	1.77	0.03
7	2	-124.37	252.80	1.79	0.03
1567	5	-121.25	252.82	1.81	0.03
45	3	-123.36	252.84	1.84	0.03
12567	6	-120.21	252.86	1.85	0.03
267	4	-122.34	252.88	1.87	0.03
23567	6	-120.23	252.89	1.88	0.03
5	2	-124.43	252.93	1.92	0.02
1256	5	-121.33	252.97	1.96	0.02
568	4	-122.39	252.99	1.98	0.02

Appendix Table 8. Term codes

Elevation	OF	OL	OP	RD	SG	SH	YF
1	2	3	4	5	6	7	8

Appendix Table 9. Conditional Averages

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
(Intercept)	-0.5869	0.3084	0.3094	1.8970	0.0579
OP100	0.0067	0.0049	0.0049	1.3610	0.1735
RD100	-0.2260	0.1332	0.1340	1.6870	0.0916
SG100	0.0751	0.0438	0.0441	1.7030	0.0886
OF100	-0.0071	0.0047	0.0048	1.4800	0.1388
SH100	-0.0188	0.0144	0.0145	1.2970	0.1948
YF100	0.0062	0.0072	0.0073	0.8520	0.3943
OL100	0.0014	0.0067	0.0068	0.2140	0.8303
Elevation	-0.0011	0.0017	0.0017	0.6830	0.4947

200 meter buffer

Appendix Table 10. Component models (models with a $\Delta AICc < 0.2$)

	df	logLik	AICc	delta	weight
25	3	-123.06	252.25	-	0.08
34	3	-123.16	252.44	0.19	0.07
2	2	-124.26	252.59	0.33	0.07

	df	logLik	AICc	delta	weight
4	2	-124.34	252.75	0.50	0.06
(Null)	1	-125.37	252.77	0.52	0.06
5	2	-124.43	252.91	0.66	0.06
1	2	-124.61	253.28	1.03	0.05
15	3	-123.61	253.35	1.09	0.05
3	2	-124.74	253.53	1.28	0.04
345	4	-122.69	253.58	1.32	0.04
45	3	-123.73	253.59	1.34	0.04
125	4	-122.78	253.77	1.52	0.04
35	3	-123.83	253.78	1.53	0.04
24	3	-123.86	253.84	1.59	0.04
14	3	-123.96	254.04	1.79	0.03
12	3	-123.96	254.04	1.79	0.03
347	4	-122.94	254.09	1.84	0.03
245	4	-122.95	254.10	1.85	0.03
256	4	-122.97	254.15	1.89	0.03
257	4	-122.98	254.17	1.91	0.03
134	4	-123.01	254.22	1.97	0.03
235	4	-123.02	254.24	1.99	0.03

Appendix Table 11. Term codes

Elevation	OF	OL	OP	SH	WB	YF
1	2	3	4	5	6	7

Appendix Table 12. Conditional Averages

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
(Intercept)	-0.6952	0.4013	0.4024	1.7280	0.0840
OF200	-0.0074	0.0054	0.0054	1.3550	0.1750
SH200	-0.0230	0.0178	0.0179	1.2850	0.1990
OL200	0.0083	0.0070	0.0071	1.1730	0.2410
OP200	0.0083	0.0065	0.0066	1.2660	0.2050
Elevation	-0.0015	0.0017	0.0017	0.8960	0.3700
YF200	0.0014	0.0111	0.0112	0.1230	0.9020
WB200	-0.0140	0.0327	0.0329	0.4260	0.6700

Component Models and Conditional Average Model Information (Central American Agouti)

50 meter buffer

Appendix Table 13. Component models

	df	logLik	AICc	delta	weight
27	3	-88.51	183.15	-	0.09
279	4	-87.52	183.25	0.10	0.08
1279	5	-86.49	183.29	0.14	0.08
127	4	-87.74	183.68	0.53	0.07
234	4	-87.96	184.13	0.98	0.05
2	2	-90.08	184.22	1.08	0.05

	df	logLik	AICc	delta	weight
1234	5	-86.99	184.28	1.14	0.05
2789	5	-87.03	184.37	1.22	0.05
278	4	-88.10	184.41	1.26	0.05
247	4	-88.18	184.57	1.43	0.04
267	4	-88.23	184.67	1.52	0.04
2679	5	-87.23	184.76	1.62	0.04
12	3	-89.32	184.77	1.63	0.04
24	3	-89.34	184.80	1.66	0.04
12789	6	-86.23	184.89	1.74	0.04
237	4	-88.35	184.91	1.76	0.04
257	4	-88.36	184.92	1.78	0.04
12679	6	-86.29	185.01	1.86	0.03
1247	5	-87.36	185.03	1.88	0.03
2579	5	-87.37	185.06	1.91	0.03
29	3	-89.49	185.11	1.96	0.03

Appendix Table 14. Term codes

Elevation	OF	OL	OP	RD	SG	SH	WB	YF
1	2	3	4	5	6	7	8	9

Appendix Table 15. Conditional Averages

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
(Intercept)	-2.3191	0.5964	0.5981	3.8770	0.0001
OF050	0.0228	0.0069	0.0069	3.2830	0.0010
SH050	0.0203	0.0105	0.0106	1.9170	0.0552
YF050	0.0131	0.0087	0.0087	1.4970	0.1345
Elevation	-0.0026	0.0020	0.0020	1.2610	0.2072
OL050	-0.0121	0.0099	0.0100	1.2150	0.2242
OP050	-0.0115	0.0096	0.0097	1.1860	0.2355
WB050	0.0164	0.0181	0.0182	0.8970	0.3697
SG050	0.0545	0.0720	0.0724	0.7520	0.4518
RD050	-0.0845	0.1604	0.1614	0.5230	0.6008

100 meter buffer

Appendix Table 16. Component models

	df	logLik	AICc	delta	weight
267	4	-86.56	181.32	-	0.20
27	3	-87.85	181.82	0.50	0.16
2678	5	-86.11	182.52	1.20	0.11
2567	5	-86.22	182.75	1.43	0.10
1267	5	-86.24	182.78	1.46	0.10
2367	5	-86.31	182.92	1.60	0.09
237	4	-87.44	183.08	1.76	0.08
127	4	-87.49	183.18	1.86	0.08
2467	5	-86.45	183.20	1.88	0.08

Appendix Table 17. Term codes

Elevation	OF	OL	RD	SG	SH	WB	YF
1	2	3	4	5	6	7	8

Appendix Table 18. Conditional Averages

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
(Intercept)	-2.6568	0.4835	0.4858	5.4680	< 0.0001
OF100	0.0256	0.0060	0.0060	4.2480	< 0.0001
SH100	0.0235	0.0137	0.0138	1.6970	0.0897
WB100	0.0555	0.0245	0.0246	2.2570	0.0240
YF100	0.0106	0.0107	0.0108	0.9800	0.3270
SG100	0.0391	0.0456	0.0459	0.8510	0.3946
Elevation	-0.0017	0.0021	0.0021	0.7970	0.4254
OL100	-0.0076	0.0097	0.0097	0.7810	0.4346
RD100	0.0564	0.1188	0.1195	0.4720	0.6367

200 meter buffer

Appendix Table 19. Component models

	df	logLik	AICc	delta	weight
278	4	-87.90	184.01	-	0.15
2578	5	-86.88	184.07	0.07	0.14
28	3	-89.11	184.34	0.33	0.13
258	4	-88.11	184.43	0.42	0.12
2678	5	-87.30	184.92	0.91	0.09
268	4	-88.56	185.32	1.31	0.08
1278	5	-87.69	185.69	1.68	0.06
128	4	-88.83	185.87	1.87	0.06
12578	6	-86.72	185.88	1.87	0.06
24578	6	-86.74	185.92	1.91	0.06
2378	5	-87.83	185.96	1.95	0.06

Appendix Table 20. Term codes

Elevation	OF	OL	OP	RD	SG	SH	WB
1	2	3	4	5	6	7	8

Appendix Table 21. Conditional Averages

	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
(Intercept)	-2.8847	0.5319	0.5345	5.3970	< 0.0001
OF200	0.0284	0.0066	0.0066	4.3110	< 0.0001
SH200	0.0297	0.0182	0.0183	1.6220	0.1048
WB200	0.0918	0.0358	0.0360	2.5490	0.0108
RD200	0.2203	0.1525	0.1535	1.4360	0.1511
SG200	0.0505	0.0445	0.0448	1.1270	0.2596
Elevation	-0.0013	0.0021	0.0021	0.6350	0.5255
OP200	0.0059	0.0110	0.0111	0.5350	0.5929
OL200	-0.0045	0.0116	0.0116	0.3840	0.7007

Appendix Table 22. Additional species on camera

Birds
Black Vulture, <i>Coragyps atratus</i>
Little Blue Heron, <i>Egretta caerulea</i>
Cattle Egret, <i>Bubulcus ibis</i>
Crested Caracara, <i>Caracara cheriway</i>
Crested Guan, <i>Penelope purpurascens</i>
Gray-Chested Dove, <i>Leptotila cassini</i>
Clay Colored Thrush, <i>Turdus grayi</i>
Purple Gallinule, <i>Porphyrio martinicus</i>
Great Curassow, <i>Crax rubra</i>
Northern Jacana, <i>Jacana spinosa</i>
Great Kiskadee, <i>Pitangus sulphuratus</i>
Great-Tailed Grackle, <i>Quiscalus mexicanus</i>
Ruddy Quail-Dove, <i>Geotrygon montana</i>
Snowy Egret, <i>Egretta thula</i>
Gray-Necked Wood Rail, <i>Aramides cajaneus</i>
Variable Seedeater, <i>Sporophila corvina</i>
White-Tipped Dove, <i>Leptotila verreauxi</i>
Reptiles
Common Basilisk, <i>Basiliscus basiliscus</i>
Green Iguana, <i>Iguana iguana</i>
Amphibians
Several species of frogs

Zusammenfassung

Das pazifische Tiefland von Costa Rica wurde in den letzten Jahrzehnten von Menschen stark verändert und besteht nun aus einem Lebensraummosaik. Ein Großteil davon ist von Menschen stark geprägt, was die Tiergemeinschaft der Region verändert hat. Um unser Verständnis darüber zu verbessern, wie Landsäugetiere von Menschen dominierte tropische

Lebensräume nutzen, haben wir Kamerafallen auf die fünf wichtigsten Lebensraumtypen (Altwald, junger Sekundärwald, Ölpalmenplantage, Uferwaldstreifen und Viehweiden; N = 50 Kamerafallen pro Lebensraum) unseres 80 km² großen Untersuchungsgebiets (Teil des biologischen Korridors COBIGA) im Tiefland der Bioregion Golfo Dulce im Südwesten Costa Ricas verteilt.

Artenakkumulationskurven zeigen, dass junge Sekundärwälder die höchste Artenvielfalt bodenbewohnender Säugetiere aufwiesen, während Weiden die geringste hatten. Die Zusammensetzung der an einzelnen Standorten aufgezeichneten Säugetiere unterschied sich jedoch nicht signifikant zwischen den Lebensraumtypen. Wenn aber Standorte auf der Ebene der Lebensräume zusammengefasst und die Inzidenzen der Arten verwendet werden, zeigt eine auf Bray-Curtis-Ähnlichkeiten basierende Clusteranalyse zwei unterschiedliche Cluster: einen mit den drei Waldtypen und einen zweiten mit den beiden Landnutzungssystemen, den Weiden und Ölpalmenplantagen. Darüber hinaus wurden diese Landnutzungssysteme nachts stärker genutzt, während sich die Säugetieraktivität tagsüber in Waldlebensräumen als relativ höher erwies.

Ein Modellauswahlansatz wurde verwendet, um die Bedeutung verschiedener Lebensraumstrukturen für das Auftreten der beiden am häufigsten vorkommenden Säugetierarten, dem Waschbär und dem mittelamerikanischen Aguti, unter Berücksichtigung unterschiedlicher räumlicher Skalen (50 m, 100 m und 200 m Puffer um Kamerastandorte) zu bewerten. Das Vorhandensein von Straßen hatte den größten negativen Einfluss auf das Vorhandensein von Waschbären im 50 m Puffer und im 100 m Puffer. Siedlungen und Gärten wirkten sich auf 50 m und 100 m am stärksten positiv aus. Ferner schien der Waschbär Altwald zu meiden. Während die Art in allen anderen Lebensräumen an 30-43 % der Kamerafallenstandorte nachgewiesen wurde, wurde sie nur an 10 % der Altwaldstandorte gefunden. Das Auftreten vom mittelamerikanischen Aguti war hingegen positiv mit dem Vorhandensein von Gewässern (bei allen Puffer-Radien) und von Altwald (beim 100 m und 200 m Puffer) zusammen.

Die Lebensraumpräferenzen von Säugetieren in unserem Untersuchungsgebiet waren sehr unterschiedlich. Einige Arten bevorzugten eine natürliche Waldumgebung, andere zeigen keine Affinität zu einem bestimmten Lebensraumtyp. Vielleicht tragen die relativ hohen Dichten der Uferwaldstreifen, der Schutz der verbleibenden Sekundärwaldflächen und die Umsetzung von Wiederaufforstungsmaßnahmen wesentlich zur Verbesserung der Landschaftsdurchlässigkeit für Waldspezialisten und Generalisten bei und fördern somit die relativ hohe Säugetiervielfalt innerhalb der vom Menschen dominierten Landschaft. Zukünftige Studien sollten räumliche Bewegungen von Tieren analysieren, um die tatsächliche Bedeutung einzelner Lebensraumstrukturen für Säugetiere zu ermitteln. Dies ist eine wichtige Voraussetzung für die Verbesserung der Wirksamkeit biologischer Korridore.

Schlüsselwörter: biologischer Korridor, Kamerafallen, Lebensräume tropischer Landschaften, Lebensraumpräferenzen, Landsäugetiere