Research Article

Integrating occupancy modeling and camera-trap data to estimate medium and large mammal detection and richness in a Central American biological corridor

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Abstract

Noninvasive camera-traps are commonly used to survey mammal communities in the Neotropics. This study used camera-traps to survey medium and large mammal diversity in the San Juan – La Selva Biological Corridor, Costa Rica. The connectivity of the corridor is affected by the spread of large-scale agriculture, cattle ranching, and a growing human presence. An occupancy modeling approach was used to estimate corridor species richness and species-specific detection probabilities in 16 forested sites within four different matrix-use categories: eco-lodge reserves, tree plantations/general reforestation, cattle ranches, and pineapple/agricultural plantations. Rarity had a highly negative effect (β = -1.96 ± 0.65 SE) on the ability to detect species presence. Corridor richness was estimated at 20.4 ± 0.66 species and was lower than that observed in protected areas in the Neotropics. Forest cover was significantly less at pineapple plantations than other land-use matrices. Richness estimates for different land-use matrices were highly variable with no significant differences; however, pineapple plantations exhibited the highest observed richness. Given the limited forest cover at those sites, we believe that this reflects the concentrated occurrence of medium and large mammals in small forest patches, particularly because the majority of pineapple plantation communities were generalist mesopredators. Fragmentation and connectivity will need to be addressed with reforestation and limitations on pineapple production for the region to function as an effective corridor. Occupancy modeling has only recently been applied to camera-trap data and our results suggest that this approach provides robust richness and detection probability estimates and should be further explored.

Key Words: camera-traps, corridor, Costa Rica, detection probability, mammal community, occupancy modeling, San Juan–La Selva Biological Corridor, species richness

Resumen

Cámaras-trampa no invasivas son comúnmente utilizadas para estudiar las comunidades de mamíferos en los Neotrópicos. En éste estudio se utilizaron cámaras-trampa para estudiar la diversidad de mamíferos de tamaños medianos y grandes en el Corredor Biológico San Juan - La Selva en Costa Rica. La conectividad del corredor se ve afectada por la expansión de la agricultura a gran escala, la ganadería y continuo crecimiento poblacional humano. Se desarrolló un modelo de ocupación para estimar la riqueza de especies y especies específicas para el corredor, con probabilidades de detección en 16 localizaciones forestales en cuatro diferentes categorías de uso de la matriz: reservas eco-lodge, plantaciones de árboles / reforestación general, ranchos ganaderos y piñas / plantaciones agrícolas. Rareza tenía un efecto altamente negativo (β = -1,96 ± 0,65 SE) en la capacidad de detectar la presencia de especies. La riqueza de especies en el corredor se estimó en 20,4 ± 0,66 especies y fue menor que la observada en las áreas protegidas en los Neotrópicos. La cubierta forestal fue significativamente menor en las plantaciones de piña que en otras matrices de uso de suelo. Las estimaciones de riqueza para matrices diferentes de uso del suelo fueron muy variables sin diferencias significativas. Sin embargo, las plantaciones de piña exhibieron la mayor riqueza de especies observadas. Dada a la cobertura forestal limitada en estos sitios, consideramos que lo antes mencionado refleja una incidencia concentrada de mamíferos medianos y grandes en pequeños parches de bosque, sobre todo porque la mayoría de las comunidades de las plantaciones de piña sumaron mesodepredadores generalistas. Por esta razón, tendrán que ser abordados con la reforestación y las limitaciones de la producción de piña para que la región bajo estudio pueda funcionar como un corredor eficaz. Modelos de ocupación se han aplicado recientemente a los datos de la cámara-trampa y nuestros resultados sugieren que éste enfoque proporciona un estimado robusto de riqueza de especies y sólida probabilidad de detección, lo cual propone estudiarse a cabalidad en el futuro.

Palabras clave: cámaras-trampa, corredor, Costa Rica, probabilidad de detección, comunidad de mamíferos, modelos de ocupación, Corredor Biológico San Juan-La Selva, riqueza de especies

Introduction

The use of camera-traps for ecological studies has increased dramatically over the past two decades [1-2]. Cameras are often used to estimate abundance and density of large carnivores, particularly large cats [3-4]. Because cameras will photograph many species that pass the infrared sensor, they are also valuable tools for medium and large mammal and terrestrial bird inventories [5-6]. Such inventories are important because they allow the community structure to be examined and compared over time and between geographic regions. Differences can reflect habitat suitability and forest integrity, and also the impact of expanding human development [7].

Large mammals are often considered keystone species and serve critical roles in maintaining balanced community structure [8]. In the absence of large carnivores, mesopredators can become abundant as suggested by the Mesopredator Release Hypothesis (MRH, [e.g. 9-10]), while herbivores can also become abundant due to release from predation [7, 11-12]. Large herbivores such as tapirs and social artiodactyls (e.g. peccaries) play important roles in forest plant communities through seed dispersal and seed and plant consumption [13-14]. Entire community changes are common because large mammals are often the first species to disappear upon human encroachment [7], typically due to agricultural land cover changes, hunting, and poaching in the Neotropics.

Given that many mammals are elusive and difficult to detect, the objective of most medium and large mammal inventories is to maximize the area covered and confidently estimate the number of species present while minimizing the time requirements [1]. For several decades ecologists have incorporated detection probability parameters when estimating individual abundance by using a capture-recapture modeling framework [15-16]. This framework also underlies many species richness models [5]. Recently, the approach was modified for use in species occupancy modeling, which utilizes presence/absence data to estimate the probability of occurrence (Ψ) by incorporating the additional parameter of detection probability ($\hat{p}$), both of which can be affected by habitat and survey-specific covariates [15, 17]. This modeling approach can also be applied to community data to estimate species-specific detection probabilities and appropriately estimate species richness for an area [15, 17-18]. Although occupancy modeling has been used extensively in recent years, there have been few studies applying this approach to camera-trap data [19]. Following the recommendations of O'Brien [19], Tobler *et al*. [6, 20] reanalyzed their community camera-trap data using the occupancy modeling approach. Their subsequent occupancy-based richness models performed well compared to other richness estimators, but they did not include or explore the effects of species-specific covariates.

In this study, we used camera-traps to survey medium- and large- mammal diversity in a fragmented biological corridor and used an occupancy approach to estimate species richness within the corridor. Specifically, we explored how different species' traits affect their detection. We then explored and

compared medium and large mammal richness and individual species-specific occurrence among forest sites in variable matrix land-uses within the corridor.

Methods

Study area

The San Juan–La Selva Biological Corridor is the northernmost portion of the Mesoamerican Biological Corridor in Costa Rica (Fig. 1). This 2,425 km² corridor links the Indio-Maíz Biological Reserve of southeastern Nicaragua to the Braulio Carrillo National Park of central Costa Rica [21-22]. Although deforestation still occurs within the corridor, government incentives (Forestry Law no. 7575) have encouraged reforestation and tree plantations, which have maintained forest cover [22]. The majority of the land within the corridor is private, and many villages and private groups have established reserves and eco-lodges to mitigate small-scale agriculture and farming. However, the spread of large-scale pineapple plantations and cattle ranches has become prevalent in the corridor and surrounding landscape [23].
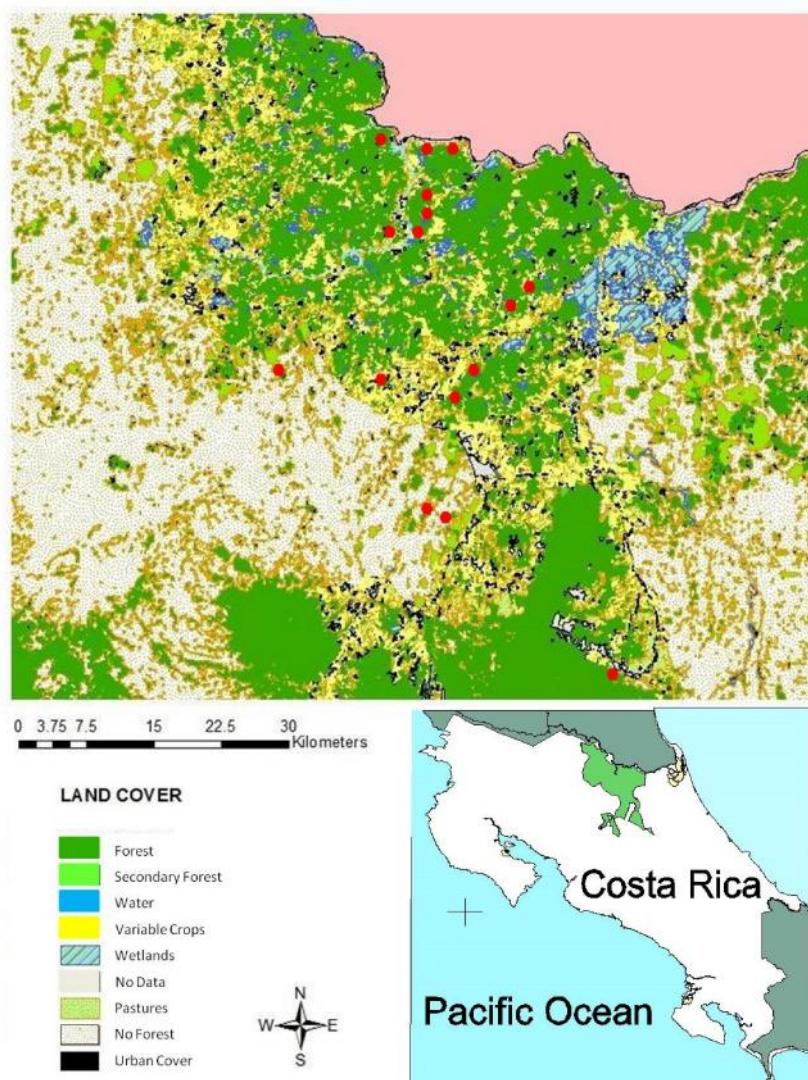

Fig. 1. Map of the San Juan – La Selva Biological Corridor and surrounding landscape with medium and large mammal survey locations (red dots)

Our study sites were forested patches of primary and secondary forest located on private land within or adjacent to four different matrix land uses: eco-lodge forest reserves, tree plantations/general reforestation, cattle ranches, or pineapple/agricultural plantations (Fig. 2). The matrix categories were representative of the major land uses for the entire corridor and surrounding landscape. Cattle ranches and eco-lodges were located within or directly adjacent to two protected areas, Maquenque Mixed-Use National Wildlife Refuge and Braulio Carrillo National Park, whereas the tree plantations and pineapple plantations were outside of these protected areas. Fragmentation and ownership issues precluded the use of a typical grid system for site selection, hence we selected 16 sites with four sites in each of the four dominant land-use categories, based on accessibility (<5km from access point), landowner permission, and forest size (>75 ha). The forest patch size was based on the lower limit of typical community-based forest reserves in agricultural lands, and we *a priori* hypothesized that smaller patches would likely provide little conservation value for medium and large mammals. Over two field seasons (July-August 2009 and June-August 2010), we surveyed a total of 14 forest sites in the San Juan – La Selva Biological Corridor and surrounding area, Costa Rica. Two additional sites were surveyed by a field technician from October to November 2009. Although our data collection occurred over multiple seasons, each site was only surveyed once and sites were not revisited, so we did not violate any of the assumptions of a single-season model because it is improbable that richness changed over the course of the year [15, 17].

Fig. 2. Four representative matrix land-use types within the San Juan – La Selva Biological Corridor. From left to right: pineapple plantation, cattle ranch, tree plantation, eco-lodge reserve.

Camera-trap surveys

To avoid the pitfalls of site inference from a single camera [24], we placed multiple cameras at each of the 16 sites. Each site consisted of a central camera station and three additional camera stations surrounding the central station spaced at >250 m apart, for a total of four cameras in the 2009 surveys. Cameras were arranged in a grid of six spaced >250 m apart in the 2010 surveys. Although we systematically placed cameras in an array, we also loosely defined our grids to allow for optimal placement. Other camera-trap studies set cameras along human trails and roads [6, 25]; however, we avoided areas of high human use due to a lack of security measures (i.e. lock boxes or chains) and focused survey efforts on animal game trails. Each camera station consisted of a remotely triggered passive-infrared camera (Scout Guard SG550, HCO Outdoor Products, Norcross, GA, USA) or a remotely triggered traditional flash camera (Stealth CamSniper Pro Camera 57983, Stealth Cam, LLC, Grand Prairie, TX, USA) secured to a sturdy tree 0.25-0.5 m off the ground. The camera was directed at an opposing tree, 3-4 m away, and baited with a secured can of fish (sardines) 1-1.5 m off the ground. Because we *a priori* hypothesized that felids would be difficult to detect, we also used hanging compact discs or small portions of carpet sprayed with cologne at a subset

of cameras at each site to increase felid detections [26]. Cameras were left at each site for 24-38 d and checked weekly (or as often as possible due to logistics) for rebaiting and battery changes.

Data analyses

After the surveys were complete, we combined all photos from both field seasons to organize and manage binary detection histories for each species detected (1 = species detected, 0 = species not detected). We calculated detection frequency for each species as the number of independent detections/1000 trapnights for comparison to previous camera studies in the Neotropics [6].

We then used an occupancy modeling approach, as described by Mackenzie *et al*. [15, 17], to estimate species richness and individual species detection probabilities for the corridor. The modeling process requires an *a priori* list of species and treats each species as a 'site' to determine the proportion of species present (Ψ) corrected by incorporating species-specific detection probability [17-18]. The *a priori* list of species contained 29 terrestrial mammal species [21, 27]. We excluded all arboreal species including primates, some small carnivores, and arboreal marsupials, because these species rarely come to the forest floor and most likely go undetected by cameras. We then ranked each species in five *a priori* categories to examine and account for species-specific parameter effects on detection and occurrence. Each species was categorized as either large (>10 kg) or medium (<10 kg). The species were also categorized as rare or common and hunted/poached if the species was targeted by humans [M. Cove *pers. obs*., 27-28]. Coyotes (*Canis latrans*) have only recently invaded northeastern Costa Rica [29], so we considered them to be rare even though they are considered common in other regions of Costa Rica. Finally, we categorized animals by diet as herbivores, omnivores, or carnivores. Obligate insectivores, northern tamandua (*Tamandua mexicana*) and giant anteater (*Myrmecophaga tridactyla*), were classified as carnivores due to their highly specialized diet.

Each detection history was partitioned into 5-d survey blocks for a maximum total of seven repeat surveys. These detection histories and species covariates (categories) were the input for a single-season occupancy model in the program PRESENCE 4.3 [30]. The assumption for the corridor richness model is that species traits (i.e. rarity, hunted/poached, etc.) affect local abundance and therefore affect detection, but do not remove species from the corridor. We used five *a priori* models to estimate species richness and species-specific detection probabilities, including a global model containing all covariates. The best approximating models were selected based on the Akaike Information Criterion, corrected for small sample size (AIC_c) and Akaike weights (w_i). We then selected the 95% confidence set and conducted model averaging [31] using spreadsheet software designed by B. Mitchell (www.uvm.edu/%7Ebmitchel/software.html) to estimate species-specific detection probabilities and effects of covariates in multiple models. We used the estimated detection probabilities per sample unit to predict the total trap effort (number of trapnights) required to detect each species with 95% confidence.

We had anticipated estimating richness for each individual forest site for multiple comparisons, but detection rates were too low to reliably estimate such parameters; instead, we pooled the data from the four sites within each of the land-use matrix categories. Because all sites were at least 2 km apart, we measured the proportion of forest cover within a 1km radius circular buffer surrounding the cameras at a site for each matrix in ArcGIS 10.0 (ESRI, 380 New York Street, Redlands, CA 92373, USA). The buffer size ensured independence between sites and served as an index of forest integrity and connectivity (i.e. higher forest cover proportion has more conservation value) for the different land-use matrices adjacent to forest sites [7, 32]. We also measured the mean distance to nearest village at each site as an index of human disturbance, which is also a landscape component affecting richness and detection within matrix types [7, 32]. We then compared these measures for each land-use matrix with a one-way ANOVA and a post-hoc Tukey's Honest Significant Difference Test. Forest proportions and mean distances were log-transformed and α-value was set to 0.05. Geographic information system (GIS) data were derived from Landsat imagery with field validation data [23].

Prior to the individual land-use matrix analyses, we conducted an analysis to determine if number of cameras (4 vs. 6) and duration of the survey (24-36 d) affected detection probability. Because no single model contained significant support, we did not include number of cameras per site or survey length as covariates in our candidate models. Survey length was accounted for in the detection histories as missing values, which are accommodated by the occupancy modeling approach [17]. We used the significant detection covariates from the primary analysis as the constant detection model and implemented the same preliminary richness models, except with covariates affecting richness (Ψ) for each of the four land-cover matrix categories. Model selection and model averaging among those models followed the same procedure as for the corridor analysis. We compared model-based richness estimates with observed richness via a one-sample t-test and determined estimates to be significantly different if confidence intervals did not overlap.

All animal research was in accordance with the guidelines established by The American Society of Mammalogists [33]. The camera-trapping protocol was approved by the University of Central Missouri Institutional Animal Care and Use Committee (IACUC -- Permit No. 10-3202).

Results

From 2,286 trapnights, we detected 17 native medium and large mammal species (Appendix 1 – species with capture frequencies). The model-averaged estimate (± SE) for species richness of the corridor was 20.4 ± 0.66 species and was significantly different from the naïve (observed) richness estimate (P < 0.001), suggesting that we missed 3-5 species due to detection bias. The top three models contained > 95 % of the support for corridor richness (Table 1), leading to the model averaged β-coefficients in Table 2. Rarity was the only covariate that was contained in all three top models and had a strong model-averaged negative effect (β_1 = -1.96 ± 0.65) on mammal detection probability. Although hunted/poached and diet also had negative effects (β_3 = -1.50 ± 0.98, β_5 = -1.54 ± 1.10, respectively) on detection, the coefficients were not significant in that 95% confidence intervals strongly overlapped 0. Other coefficients were also not significantly different from 0 effects. For this reason, we only included rarity as a detection covariate in the subsequent land-use matrix models.

Table 1. Model selection statistics for richness and detection probability estimates derived from occupancy analysis for mammalian camera-trap surveys in the San Juan - La Selva Biological Corridor, Costa Rica, 2009-2010. Included are the Akaike information criteria corrected for small sample size (AIC_c), the information distance from the highest ranked model (ΔAIC_c), Akaike weight (w_i), number of parameter (K), and -2 log-likelihood ($-2\log(£)$).

Model	AIC_c	ΔAIC_c	w_i	K	$-2\log(£)$
$\Psi(.),p$(global)	195.12	0.00	0.73	7	175.79
$\Psi(.),p$(rarity)	197.69	2.57	0.20	3	190.73
$\Psi(.),p$(rarity + size + hunted)	200.25	5.13	0.06	5	187.65
$\Psi(.),p$(diet)	203.83	8.71	0.01	4	194.17
$\Psi(.),p$(.)	207.93	12.81	0.00	2	203.47
$\Psi(.),p$(hunted)	209.98	14.86	0.00	3	203.02
$\Psi(.),p$(size)	210.30	15.18	0.00	3	203.35

Predicted detection probabilities (Appendix 1) ranged from very low 0.12 ± 0.13 for jaguar (*Panthera onca*), puma (*Puma concolor*), and white-lipped peccary (*Tayassu pecari*) to very high 0.88 ± 0.06 for the Central American agouti (*Dasyprocta punctata*). The estimated trap effort required to catalogue a species using camera-traps with 95% certainty ranged from 395 trapnights to detect agouti to 2,929 trapnights to detect jaguar, puma, and white-lipped peccary. Capture frequencies were computed for detected species for general comparisons to other previously published camera surveys (Appendix 1).

Table 2. Model-averaged estimates of coefficients for covariates with 95% confidence intervals derived from occupancy analysis for mammalian camera-trap surveys in the San Juan - La Selva Biological Corridor, Costa Rica, 2009-2010. Abbreviations: diet1 and diet2 are binary covariates to differentiate among carnivores, omnivores, and herbivores. The bolded entry is significant in that the confidence interval excludes 0.

Species covariate	β estimate	SE	Confidence Interval	
Intercept	2.32	1.12	0.13	4.52
Occupancy (Ψ)	0.87	0.61	-0.33	2.07
Rarity	**-1.96**	**0.65**	**-3.25**	**-0.67**
Size	0.31	0.51	-0.69	1.31
Hunted/poached	-1.50	0.98	-3.43	0.42
Diet1	0.05	0.62	-1.16	1.27
Diet2	-1.54	1.10	-3.70	0.62

Forest cover at our sites varied significantly among the matrix land-use categories (One-way ANOVA: $F_{3,12}$ = 13.05; P < 0.001). Forest patches located adjacent to pineapple plantations had significantly less forest cover (33.8% ± 6.07 SE) within their buffers than the other three matrix land-use categories (Tukey HSD; P< 0.01). Forest sites adjacent to the other land-use categories maintained >75% forest cover within site buffers. Distance to nearest village was marginally significantly different (One-way ANOVA: $F_{3,12}$ = 3.38; P= 0.05), with post-hoc comparisons of forest sites in pineapple matrices occurring >1km closer to villages than sites adjacent to cattle ranches (Tukey HSD; P= 0.07) and >1km closer than sites located in eco-lodge forest reserves also approaching significance (Tukey HSD; P= 0.08). In the detection analysis to examine survey effects, no model contained significant support, so the number of cameras per site and the duration of camera survey were excluded as covariates in further analyses (Table 3).

Table 3. Model selection statistics for preliminary detection analysis examining the effects of number of cameras and survey length on detection of medium- and large- mammals from camera-trap surveys in the San Juan-La Selva Biological Corridor, Costa Rica, 2009-2010. Included are the Akaike information criteria corrected for small sample size (AIC$_c$), the information distance from the highest ranked model (ΔAIC$_c$), Akaike weight (w_i), number of parameter (K), and -2 log-likelihood ($-2\log(£)$).

Model	AIC$_c$	ΔAIC$_c$	w_i	K	$-2\log(£)$
Ψ(.),*p*(survey length)	1082.01	0.00	0.29	3	1075.96
Ψ(.),*p*(no. cameras + survey length)	1082.09	0.08	0.28	4	1074.00
Ψ(.),*p*(.)	1082.27	0.26	0.26	2	1078.24
Ψ(.),*p*(no. cameras)	1083.10	1.09	0.17	3	1077.05

Mammal richness estimates within the four different matrix land-uses were low and variable, but not significantly; no richness estimates were significantly different from the observed richness (Table 4). The constant richness model was the top ranking for eco-lodges and pineapple plantations, while a rarity effect was most supported in the cattle and tree plantation richness models (Table 4); however, after model averaging no covariates had significant effects on species richness among sites. Detection probabilities and observed and estimated richness were highest for forest sites located adjacent to pineapple plantations.

Four mesopredators, ocelot (*Leopardus pardalis* – Fig. 3), tayra (*Eira Barbara* – Fig. 3), white-nosed coati (*Nasua narica*), and common opossum (*Didelphis marsupialis*) were detected at sites within all land-use matrix categories. Two other species were detected at all sites: nine-banded armadillo (*Dasypus novemcinctus*) and Central American agouti (*Dasyprocta puntata*). Several species were only detected at sites adjacent to pineapple plantations: northern tamandua, coyote, greater grison (*Galictis vittata*), striped hog-nosed skunk (*Conepatus semistriatus*), and margay (*Leopardus wiedii*). The Baird's tapir (*Tapirus bairdii* – Fig. 3) is the only species occurring in the corridor that is classified as endangered by the IUCN and was detected at forest sites adjacent to all matrix land-use types except pineapple plantations.

Table 4. Model selection statistics, observed richness, and estimates for richness derived from occupancy analysis for mammalian camera-trap surveys in the San Juan - La Selva Biological Corridor, Costa Rica, 2009-2010. Included are the four land-use cover change categories and the information distance from the highest ranked model (ΔAIC_c - Bolded 0.00 represents the highest ranked model), and number of parameter (K) for each model. All models contain a covariate of rarity on detection. Missing information is result of non-convergence in models.

Model	K	Pineapple	Cattle	Plantation	Eco-Lodge
$\Psi(.)$	3	**0.00**	3.71	5.88	**0.00**
Ψ(rarity)	4	2.30	**0.00**	**0.00**	0.87
Ψ(hunted)	4	0.21	5.68	8.31	-
Ψ(size)	4	0.09	5.70	8.39	-
Ψ(diet)	5	5.62	4.01	5.64	3.98
Ψ(rarity + size + hunted)	6	5.38	3.49	5.40	-
Ψ(global)	8	-	6.29	-	-
Observed Richness	-	14	9	10	9
Richness Estimate ($\Psi \pm$ SE)	-	19 (4.08)	11 (3.60)	12 (3.42)	20 (4.67)

Discussion

Our observed and estimated richness for the entire study area are less than those observed in other Neotropical camera surveys [6, 20, 28]. Tobler *et al*. [6, 20] used multiple species richness estimators including an occupancy modeling approach, but did not incorporate species-specific covariates. They estimated species richness to be 25 species and 24 species from their occupancy analysis, given 36 d of sampling effort in 2005 and 2006, respectively. Our estimate of 20 species in the corridor suggests that only 2/3 of the native medium and large mammal community is represented in the corridor. This suggests richness is negatively affected by habitat changes associated with human development in the region compared to more contiguous protected areas [6]. Although pineapple plantations had the highest observed and estimated richness among other land-use categories, the other land-use matrices currently provide substantially more forest cover in their site buffers, with higher potential for connectivity and protection. Cattle ranches often reduce forest cover on a large scale, but the sites that we surveyed adjacent to cattle ranches were located within and connected to two state-protected areas, which likely

play a role in the reduced deforestation at those sites compared to the agricultural plantations. We believe that the heightened richness observed in pineapple landscapes is a consequence of higher detection rates due to a concentrating effect when animals are relegated to small remnant forest patches within agricultural land versus the larger forest patches of the other land-use categories. Detection biases have been observed to yield misleading community dynamics in other studies within fragmented landscapes [34].

It is encouraging that the endangered Baird's tapir was detected at three of the four matrix land-use categories; however, its absence as well as the absence of collared peccary (*Pecari tejacu* – Fig. 3) in forests adjacent to pineapple plantations reveals a relative weakness when comparing richness among sites without examining composition. Pineapple production may support many medium mammals, but the fragmentation and edge effects severely limit the habitat for large herbivorous/frugivorous mammals that are often responsible for maintaining natural plant communities [7]. Other influences on herbivores are most likely hunting and poaching pressures. In their study of ungulates in Peru, Licona *et al*. [32] determined that passive protection from hunters and poachers is mainly due to the inaccessibility of forest reserves. The fragmented nature of the San Juan–La Selva Biological Corridor allows easy access into the forest and may not afford such protection for game species such as collared peccary and paca (*Cuniculus paca*).

Fig. 3. Photos of two mesopredators, (a) tayra and (b) ocelot, encountered at all four land-cover types, and two large ungulates, (c) Baird's tapir and (d) collared peccary, encountered at land-cover types except pineapple plantations.

Rarity was the only strong predictor of species-specific detection probability for the corridor. This is biologically plausible because rare species inherently occur at low densities with patchy distributions [35]. Both of these factors affect our ability to detect species using camera-traps at a landscape-scale. Rarity was also a negative though not significant factor in individual site richness estimates. Rare species such as

tapirs, jaguars, and other charismatic mammals are also typically the species of interest in conservation assessments or may serve as umbrella and flagship species [36], so allotting survey effort to increase detections of these community members is vital to assessing habitat suitability and community composition. Allocating the appropriate survey effort may be accomplished by increasing camera coverage or extending the survey length [37], particularly to reach the predicted trap effort required to detect flagship and umbrella species.

Our derived detection probabilities were similar to another Neotropical survey with large cats (jaguar) and white-lipped peccary exhibiting low detection probabilities, while medium-sized rodents and armadillos exhibited high detection probabilities, and other ungulates exhibited moderate detection probabilities [38]. Zeller *et al*. [38] observed higher detection probabilities than those in our study, but we believe this is because the authors used interview-based occupancy modeling as opposed to camera-traps. The use of interviews about wildlife trends is useful, but the assumption that repeat surveys (multiple interviews) are independent may be inaccurate. People within the villages and communities most likely communicate with each other and influence the perceived presence/absence of species in the area, leading to higher detection probabilities than observed with camera-traps.

We did not detect jaguar, puma, or white-lipped peccary during our sampling period, but we observed field evidence, cattle depredations, and reported sightings of both big cat species and white-lipped peccaries at the northern portion of the corridor. The lack of detections for these species may be an artifact of sampling design, because we did not set camera stations along roads or heavily-used human trails. In a critique of camera-trap studies for the large cats [39], the authors suggest that roads and human trails are often heavily used by large predators and camera placement can highly affect detection rates. However, we selected camera locations based on apparent use by other animals, particularly prey species, and used felid-specific attractants, so the lack of detections might more appropriately reflect the true rarity of large cats in the corridor and hence their low detection probabilities. Other non-detected species such as red brocket deer (*Mazama americana*), forest rabbit (*Sylvilagus brasiliensis*), Neotropical river otter (*Lutra longicaudis*), and water opossum (*Chironectes minimus*) are most likely present but difficult to detect with cameras due to local hunting pressure for the first two and preference for waterways for the latter. The giant anteater is very rare in Costa Rica and may have been extirpated [27], so they are most likely absent from the study area.

With the apparent rarity of large carnivores in our surveys and in the different land-use matrices, mesopredators were the most commonly detected guild at all sites. Although this may provide evidence for the MRH, this is likely a consequence of concentrated populations of the smaller carnivores and the effect of scent lures at cameras [40]. Additionally, mesopredators may be tolerant of habitat disturbance and utilize agricultural food resources. This highlights the difficulties in comparing indices such as capture frequencies for landscape associations of mesopredators, because landscape influences and concentration of individuals in forest fragments have been observed to affect detection probability and inference [40].

Mesopredators accounted for 64% of the medium and large mammal community observed at forest sites located near pineapple plantation landscapes, with four of those species only observed in that matrix-use. This is most likely an effect of additional food resources from pineapple production leading to higher local abundance or concentrated foraging activities in pineapple-forest edge habitats. The fruits provide direct food resources, and other food resources may be indirectly provided from pineapple pests such as small rodents, insects, and ground-nesting birds [27, 41]. The expansion of pineapple plantations, as well as other export crops, has also decreased reforestation rates [23] which may have facilitated the invasion of the coyote to Caribbean slope, which may affect the rest of the community [29]. This also highlights the negative influences of pineapple production, even though richness appears to be higher than other habitats. Given that pineapple production, as well as other export crops, have increased dramatically in recent years in the region [23], the resultant forest patches in those matrices may be carrying a high

extinction debt (i.e. local extinction is imminent) if connectivity is reduced to prevent immigration and emigration [42, 43].

The occupancy modeling approach applied in this study demonstrates the usefulness of this tool to estimate species richness and habitat use when all species exhibit different detection probabilities. By using an *a priori* species list, this approach can also be applied to other taxonomic groups with data collected from repeated surveys [15, 17]. Investigators in multiple ecological disciplines can benefit from occupancy analysis to estimate species richness and detection probabilities from their community survey data, particularly with regard to continuously shifting baselines of diversity into the future [44]. Further standardization will also allow more robust comparisons over time and between regions and should be explored further in biodiversity assessments.

Implications for conservation

The camera trapping protocol, as well as the occupancy modeling approach, provide a standardized analytical framework for monitoring medium and large mammal diversity in the region and throughout the Neotropics. Although large cats and white-lipped peccaries were not directly observed and appear absent or very rare, field evidence as well as our richness estimates suggest that these species likely occur at low densities and are thus very difficult to detect. Although forests within pineapple plantation matrices had the highest observed and estimated medium and large mammal richness estimates, we suggest that this is not a good indicator of a healthy mammal community. Of the mammals observed in pineapple plantations, the majority were opportunistic mesopredators and an invasive mesopredator, which have less community value than flagship species such as the Baird's tapir [45], peccaries, or large carnivores. Our monitoring protocol will help to further evaluate the effects of inherent species rarity, as well as hunting, agricultural expansion, and the loss of connectivity as potential limiting factors influencing the mammal community within the San Juan - La Selva Biological Corridor.

Acknowledgements

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Appendix 1. Model-averaged predicted detection probability estimates with standard error, capture frequencies (CF --captures/1000 trapnights) for detected species, species traits (Spec Traits --binary covariates for rarity, size, hunted/poached, and diet), and predicted trap effort (trapnights) required to detect each species with 95% confidence derived from occupancy analysis for medium and large mammal camera-trap surveys in the San Juan - La Selva Biological Corridor, Costa Rica, 2009-2010.

Order Common Name	Species	$\hat{p}$	SE	CF	Spec Traits	Effort required
Didelphimorphia						
Common opossum	*Didelphis marsupialis* (Linnaeus)	0.69	0.07	10.1	00001	509
Brown four-eyed opossum	*Metachirus nudicaudatus* (Geoffroy)	0.24	0.11	–	10001	1465
Grey four-eyed opossum	*Philander opossum* (Linnaeus)	0.69	0.07	0.4	00001	509
Water opossum	*Chironectes minimus* (Zimmermann)	0.24	0.11	–	10001	1465
Xenarthra						
Giant anteater	*Myrmecophaga tridactyla* (Linnaeus)	0.31	0.12	–	11011	1134
Northern tamandua	*Tamandua mexicana* (Saussure)	0.25	0.10	0.4	10011	1406
Northern naked tailed Armadillo	*Cabassous centralis* (Miller)	0.24	0.11	–	10001	1465
Nine-banded armadillo	*Dasypus novemcinctus* (Linnaeus)	0.69	0.07	15.3	00001	509
Rodentia						
Central American agouti	*Dasyprocta punctata* (Gray)	0.88	0.06	18.8	00000	395
Paca	*Cuniculus paca* (Linnaeus)	0.25	0.14	8.3	10100	1406
Lagomorpha						
Forest rabbit	*Sylvilagus brasiliensis* (Linnaeus)	0.59	0.20	–	10000	596
Carnivora						
Coyote	*Canis latrans* (Say)	0.30	0.12	0.4	11001	1172
Northern raccoon	*Procyon lotor* (Linnaeus)	0.69	0.07	3.1	00001	509
White-nosed coati	*Nasua narica* (Linnaeus)	0.69	0.07	14.4	00001	509
Long-tailed weasel	*Mustela frenata* Lichtenstein	0.25	0.10	–	10011	1406
Greater grison	*Galictis vittata* (Schreber)	0.25	0.10	0.4	10011	1406
Tayra	*Eira barbara* (Linnaeus)	0.69	0.07	10.1	00001	509
Striped hog-nosed skunk	*Conepatus semistriatus* (Boddaert)	0.24	0.11	0.9	10001	1465
Neotropical river otter	*Lutra longicaudis* (Olfers)	0.25	0.10	–	10011	1406
Margay	*Leopardus wiedii* (Schinz)	0.25	0.10	0.4	10011	1406
Ocelot	*Leopardus pardalis* (Linnaeus)	0.31	0.12	7.4	11011	1134
Jaguarundi	*Puma yagouaroundi* (Geoffroy)	0.25	0.10	–	10011	1406
Puma	*Puma concolor* (Linnaeus)	0.12	0.13	–	11111	2929
Jaguar	*Panthera onca* (Linnaeus)	0.12	0.13	–	11111	2929
Perissodactyla						
Baird's tapir	*Tapirus bairdii* (Gill)	0.65	0.18	3.9	11000	541
Artiodactyla						
Collared peccary	*Pecari tejacu* (Linnaeus)	0.40	0.20	1.7	01101	879

White-lipped peccary	*Tayassu pecari* (Link)	0.12	0.13	–	11101	2929
Red brocket deer	*Mazama americana* (Erxleben)	0.75	0.12	–	01100	469
White tailed deer	*Odocoileus virginianus* (Zimmermann)	0.75	0.12	1.3	01100	469