More trees with your coffee? Diversity and habitat associations of terrestrial medium- and large-sized mammals in shade-grown coffee plantations of the highlands of Guatemala

¿Más árboles con su café? Diversidad y asociaciones de hábitat de mamíferos terrestres medianos y grandes en plantaciones de café bajo sombra en el altiplano de Guatemala

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ABSTRACT. Agricultural practices can have detrimental impacts on biodiversity, but some studies have shown the benefits of agroforestry practices like shade-grown coffee to bird communities and, to a lesser extent, to mammal

communities. To better understand whether shade-grown coffee plantations can contribute to the conservation of mammal communities, we deployed camera traps in private reserves with a matrix of shade-grown coffee plantations and forest in the highlands of Guatemala. At each reserve we estimated species richness of terrestrial medium- and large-sized mammals. We also estimated mammal relative abundance and occupancy probabilities as proxies for mammalian habitat associations and evaluated how these were affected by key landscape features (e.g., land-use type, asphalt roads, and distance to protected areas). We used hierarchical multi-species Bayesian abundance models that account for imperfect detection to estimate our parameters of interest and model the influence of landscape features on site-level species richness and species relative abundance. We detected 14 species across all reserves and found a strong influence of land use and presence of asphalt roads on mammalian relative abundances and species richness. More species used areas around the camera traps in forest than in shade-grown coffee plantations and far from asphalt roads. Our study shows that reserves with shade-grown coffee plantations can harbor terrestrial mammalian communities of conservation interest. Our results also suggest that to maintain mammalian diversity and abundances in our study area, shade-grown coffee crops should be mixed in with natural forests and the presence of asphalt roads within these should be avoided or minimized.

Keywords: agroforestry; bayesian hierarchical abundance model; camera trapping; Central America; private reserves; shade-grown coffee management

RESUMEN. Las prácticas agrícolas pueden tener impactos perjudiciales en la biodiversidad, pero algunos estudios han demostrado beneficios de prácticas agroforestales, como el café bajo sombra, para comunidades de aves y, en menor medida, comunidades de mamíferos. Para entender mejor si las plantaciones de café bajo sombra pueden contribuir a la conservación de comunidades de mamíferos, colocamos cámaras trampa en reservas privadas con plantaciones de café bajo sombra y bosque en el altiplano de Guatemala. En cada reserva estimamos la riqueza de especies de mamíferos medianos y mayores. También estimamos la abundancia relativa y probabilidad de ocupación como aproximaciones a las asociaciones de hábitat de mamíferos y evaluamos cómo estas son afectadas por características clave de paisaje (p.ej. tipo de uso de suelo, carreteras y distancia a áreas protegidas). Utilizamos modelos jerárquicos bayesianos multiespecies de abundancia que consideran que la detección de especies es imperfecta para estimar nuestros parámetros de interés y modelar la influencia de características del paisaje en la riqueza y abundancia relativa de especies a nivel de sitio. Detectamos 14 especies en todas las reservas y encontramos una fuerte influencia del uso de la tierra en la abundancia relativa y la riqueza de especies de mamíferos. Más especies utilizaron áreas cercanas a las cámaras trampa en el bosque que a las plantaciones de café bajo sombra y lejos de carreteras. Nuestro estudio demuestra que las plantaciones de café bajo sombra pueden albergar comunidades de mamíferos terrestres de interés para la conservación. Nuestros resultados también sugieren que para mantener la diversidad y abundancia de mamíferos en el área de estudio, las plantaciones de café bajo sombra deben estar mezcladas con bosques nativos diversos, así como que la presencia de carreteras debe ser evitada o reducida.

Palabras clave: sistemas agroforestales; modelos jerárquicos bayesianos; fototrampeo; Centroamérica; reservas privadas; manejo de café bajo sombra

INTRODUCTION

Agricultural activities can have detrimental impacts on biodiversity and ecosystem services (Firbank *et al.*, 2008). However, evidence suggests that certain agricultural activities, such as tree-shaded coffee plantations are compatible with biodiversity conservation (Etana *et al.*, 2021). Research on the benefits of coffee plantations to biodiversity has shown that maintaining native tree canopies, forest cover (Chang *et al.*, 2018) and structurally diverse locations near forest edges (Rodrigues *et al.*, 2018) provide benefits to the conservation of birds; shade-grown coffee has also been proven to provide a buffer area in fragmented habitats that can contribute to the conservation of invertebrates (Iwasaki, 2010; Sosa-Aranda *et al.*, 2018). There is also evidence that maintaining shade tree richness, mature shade trees and preserving forested areas in landscapes with shade-grown coffee provides important refuge and habitat for mammals (Caudill *et al.*, 2014; Caudill & Rice, 2016; Guzmán *et al.*, 2016). However, most research on the conservation benefits of landscapes dominated by coffee production for threatened vertebrates focus on bird species (Caudill & Rice, 2016) and few studies examine mid- and large-sized terrestrial mammal assemblages. Furthermore, there are gaps in the scientific literature for overlooked or rarely studied regions such as the highlands of Guatemala.

Mammals are particularly threatened due to their dependence on large tracts of undisturbed natural areas and their sensitivity to human induced threats such as hunting, fragmentation, and habitat loss (Ceballos & Ehrlich, 2002). Due to the prevalence and expansion of agricultural lands, forests in protected areas should not be the only strategy used for conservation of biodiversity (Caudill & Rice, 2016). These areas have been shown to be ineffective at halting processes such as habitat loss and degradation (Leisher *et al.*, 2013) that can impact mammal diversity and populations. A complementary strategy is to manage agricultural lands, such as coffee farms, in a way that contributes to habitat and wildlife preservation (Caudill & Rice, 2016). Major coffee production areas such as those found in Mesoamerica overlap significantly with biodiversity hotspots (Hardner & Rice, 2002; Caudill & Rice, 2016). These agroforestry systems can help, not only to protect biodiversity, but also to provide ecosystem services to farmers (Donald, 2004; Tscharntke *et al.*, 2011). As a result, coffee plantations have the potential to contribute to mammal conservation in highly diverse tropical systems if managed correctly (Gallina *et al.*, 1996; Williams-Guillén *et al.*, 2006; Guzmán *et al.*, 2016). Thus, a better understanding of mammal diversity and the factors that contribute to mammal occurrence and persistence in rural shade-grown coffee farm landscapes is essential to guide management of these agroforestry systems considering the rapid rate of agricultural expansion across the world and its effects on biodiversity and ecosystem services.

Our main objective was to determine whether shade-grown coffee plantations contribute to terrestrial mammal conservation and to evaluate habitat associations (e.g., land use type and road presence) of mammal local relative abundance patterns (used as a proxy for site preference) and species richness in shade grown coffee farms of the highlands of Guatemala. We conducted mammal surveys with camera traps in three nature reserves with shade-grown coffee plantations in the Lake Atitlan buffer zone. We used a Bayesian hierarchical multi-species relative abundance model (Yamaura *et al.*, 2011; Beesley *et al.*, 2014) that accounts for imperfect detection across species to examine the association between local relative abundances and species richness with environmental and management attributes (i.e., land use type, distance to asphalt road and protected areas). We hypothesized species-specific abundances and species richness at camera trap locations would be higher in forests without coffee crops compared to coffee plantation areas

and positively associated to distance from human infrastructure (i.e., roads) and negatively associated to distance to protected areas.

MATERIALS AND METHODS

Study area. We conducted this study in three private nature reserves that maintain native forests alongside shade-grown coffee plantations. The soil types of the region are volcanic and sandy loam, and the elevation varies between 760 and 2500 masl. The average annual rainfall is between 1450 and 3000 mm (Bressani *et al.*, 2004) and the vegetation found in this area is humid evergreen broadleaf forest, with broadleaf-conifer forest in higher and less humid areas (Eisermann *et al.*, 2011). The farms are: Pampojila Pena Flor (PPF), San Jeronimo Miramar (SJM), and SantoTomas Pachuj (STP), and are located within the Multipurpose Reserve of Lake Atitlan Basin (RUMCLA) (Fig. 1), an area located in the southwestern part of Guatemala (Consejo Nacional de Áreas Protegidas, 2007). The main coffee varieties grown in these farms are bourbon caturra, catuai, pacas, robusta, and catimor. PPF covers a total area of 345.1 ha, of which 203.6 are forests and 141.5 are coffee plantations (Díaz *et al.*, 2004), while SJM has an estimated total area of 486 ha, of which 277 are forests intended for conservation and approximately 83.26 are used for shade-grown coffee (Bressani *et al.*, 2004; Burge *et al.*, 2004), and STP has an estimated total area of 378 ha, with 3.08 km^2 of forest and 70 ha of shade-grown coffee (Díaz *et al.*, 2004).
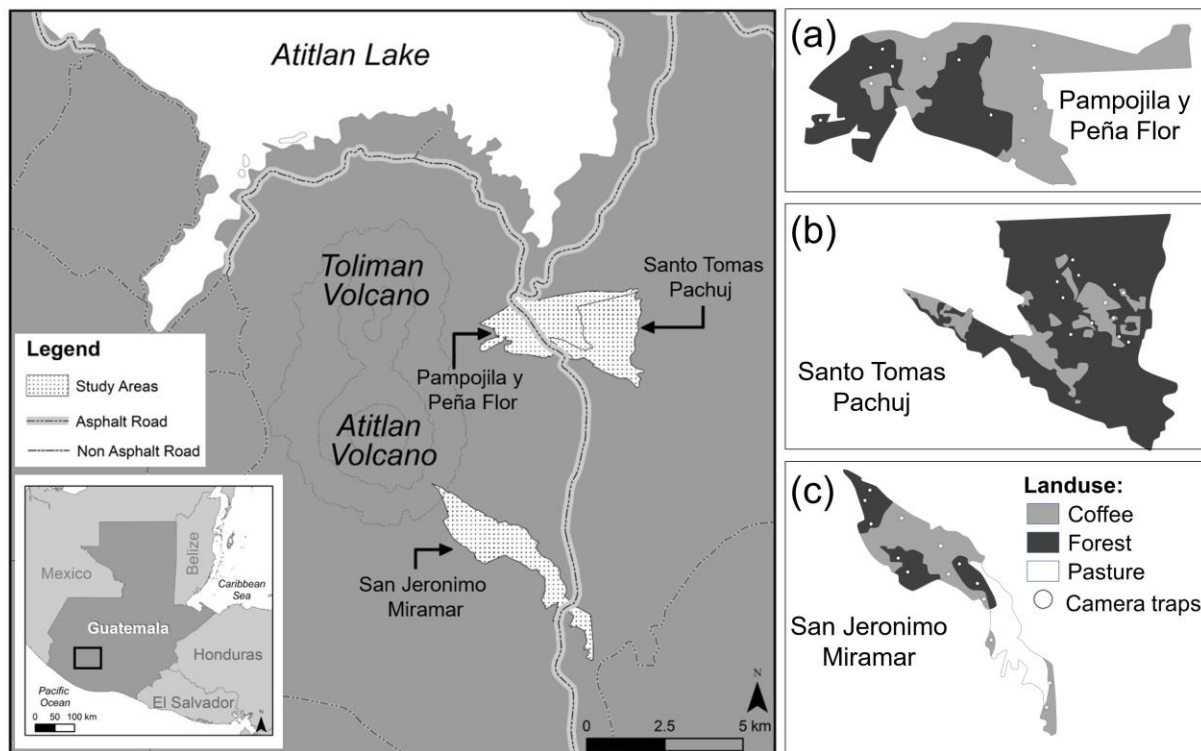
Figure 1. Map of study area location and depiction of camera trap setup within each reserve. Insert map in main figure shows location of private reserves surveyed in Guatemala March-May 2014. Both Toliman and Atitlan Volcanoes are designated as protected areas.

Camera trap surveys. We conducted camera trap surveys from March to May 2014. We deployed 7 cameras [Bushnell, 8MP Trophy Cam] in trails along forest sites without coffee crops

and 7 cameras in sites with shade-grown coffee plantations of each reserve during non-harvest months for 15 days at each reserve (i.e., 15 sampling occasions per site). Minimum distance between camera traps was 200 mt. Thus, our data consisted of a matrix of 0's and 1's (0 = not observed, 1 = observed), where the columns represented a species detected and the rows the sites surveyed. Camera locations were selected based on high probability of mammal capture (trails, sites with mammal signs). To increase probability of detecting carnivores in our study, we placed a lure in 4 of the 7 camera sites in each land use type. As a lure, we used men's cologne (Obsession by Calvin Klein Men), which has been used in previous studies to attract carnivores (Arroyo-Arce *et al.*, 2014; Clayton & Shrock, 2020; Dean & Nielsen, 2007; Marker & Dickman, 2003). The use of lures was assigned randomly to the camera sites. Cameras were strapped to trees 50 cm above ground and programmed to be active 24 h/day and to take a sequence of 3 pictures once activated. We calculated the sampling effort by adding the days that each camera remained active (Monroy-Vilchis *et al.*, 2011) and we considered independent records when one hour or more had passed between pictures of a species.

Covariates included in the model. We modeled the effects of covariates we believed would have the most influence on species-specific local abundances and species richness. The covariates are land use (natural forest without coffee or shade grown coffee plantation), distance to the asphalt road and the nearest protected area. The latter two covariates were estimated using ArcGIS 10.7 (Environmental Research Systems Institute, 2018). We used land use as a covariate because we believed there would be differences in the use of forest with and without coffee crops due to differences in vegetation structure and the types of resources each land use type provides. We used distance to the nearest protected area because they are the only large blocks of protected intact forest acting as a potential source of wildlife and thus the mammals present in the sites closer to the protected areas may be a result of spillover dynamics between these large blocks of forest and the reserves (Tscharntke *et al.*, 2012). We used distance to the main highway because wildlife spatial ecology has been shown to respond negatively to roads (Gaston & Spicer, 1998). Although there are smaller inner dirt roads within each reserve, we did not include these in our model because they are not heavily trafficked, and we did not conduct our study during the harvest season, which is when they are used more intensively. We did not include the covariate distance to nearby towns because of high correlation between distance to the main highway (r = 0.83) and distance to the protected area (r = 0.65) that could potentially lead to multicollinearity in the model.

To model detection probability, we used land use type because coffee plantations consist of more open understory vegetation where this parameter may be higher. We also modeled detection probability of each species as a function of lure use. We standardized all continuous covariates to mean zero and a standard deviation of 1.

Model Structure. We used a Bayesian hierarchical model that estimates multi-species abundances and accounts for imperfect and variable species detection probabilities (Beesley *et al.*, 2014). Relative abundances are interpreted as intensity of use of a survey site *j* by species *i*. The multi-species framework of our model specifies species-specific parameters as random effects drawn from hyperdistributions governed by hyperparameters under the assumption that patterns in species abundances are neither equivalent nor independent but related according to distributional assumptions (i.e., random effects). Thus, information is shared among species in the community, potentially increasing statistical power and allowing for species-specific parameters (i.e., abundance) and community-level parameters (i.e., species richness) to be estimated simultaneously. Our model also describes the data collection process for each species with an

abundance submodel, that represents the ecological process of interest, and a detection submodel, that represents the observation process. This allows our hierarchical model to disentangle the confounding influence of variation in abundance and the variation in detection probability on our incidence data.

In our model, species-specific abundance is assumed to be a latent random variable that conforms to a Poisson distribution as $N_{i,j} \sim \text{Poisson}(\lambda_{ij})$, where λ_{ij} is the Poisson mean for species *i* at site *j*. We model our incidence data as binomial outcomes $y_{i,j} \sim \text{Binomial}(k, p_{ij})$, where k is the number of replicate samples (i.e. days of sampling at a site) and $p_{i,j}$ is the probability of detecting one or more individuals of species *i* at site *j*. Our abundance model is linked to the detection model by assuming a relationship between $p_{i,j}$ and $N_{i,j}$ following Royle and Nichols (2003) as, $p_{ij} = 1 - (1-r_{ij})N_{ij}$, where $r_{i,j}$ is the detection probability on the individual scale (i.e., the average probability of any individual being detected). This equation describes the probability of detecting at least one individual as a saturating function of abundance, where $p_{i,j} = 0$ when $N_{i,j} = 0$ and $p_{i,j}$ approaches an asymptote of one as $N_{i,j}$ increases.

We incorporated covariates into the abundance model to account for their effects on species-specific abundances with a log link as:

$$\log(\lambda_{i,j}) = \lambda 1_i + \lambda 2_i \, landuse_j + \lambda 3_i \, road_j + \lambda 4_i \, pa_j$$

where $\lambda 1i$ is the species-specific intercept and $\lambda 2_i - \lambda 4_i$, are the species-specific regression coefficients for each covariate. Landuse is a categorical variable that indicates whether a site was located within a forest or a coffee plantation, road is the distance of site *j* to the main asphalt road, and pa is the distance of site *j* to the nearest protected area.

We modeled detection probability ($r_{i,j}$) as a function of two covariates: landuse (similar to the variable used to model species-specific abundances) and lure, a categorical variable indicating whether a lure was used at site *j*. These covariates of detection probability ($r_{i,j}$) were incorporated into the detection model with a logit link as:

$$\text{logit}(r_{i,j}) = \varphi 1_i + \varphi 2i \, landuse_j + \varphi 3_i \, lure_j$$

where $\varphi 1i$ represents the species-specific intercept and $\varphi 2_i - \varphi 3_i$ are the regression coefficients for each covariate.

For ease of interpretation, we transformed the species-specific abundance estimate into an estimate of occupancy probability (Ψ) averaged across all sites as follows: $\Psi_{i,j} = 1 - \exp(\lambda_{i,j})$ (Royle & Nichols, 2003).

Species richness per site (n_j) was estimated as the sum of species with abundance greater than zero in each site (i.e., $n_j = \sum i \, (N_{i,j} > 0)$). We evaluated the relationship between species richness and distance to road and protected area by calculating the slope between the log of n_i and these distances for each posterior sample of n_i, resulting in the derived posterior sample of each slope.

We evaluated whether the credible interval of the posterior estimates of the covariate effects on abundance and detection probabilities overlapped zero to determine the statistical significance of species-level covariate effects on these parameters. To determine the direction of the association with each covariate, we assessed the position of the distribution with regards to zero. Similarly, to determine the effects of distance to the main road and the protected area on species-richness, we evaluated whether the credible interval of the posterior estimates overlapped zero and the position of the distribution with regards to zero to assess direction of the association. Bayesian models were implemented in software JAGS (Plummer, 2003). We ran three parallel chains with a length of 400 000 after a burn-in of 200 000 iterations and a thinning rate of 200. Convergence was assessed using the Gelman-Rubin statistic, which considers values <1.1 acceptable (Brooks & Gelman, 1998).

We also analyzed fit of the full model, including all covariates, using a Bayesian p-value (*Bp*) that is based on Pearson's discrepancy (Kéry, 2010). The Bayesian p-value, a posterior-predictive check, provides a measure of under- or over-dispersion of the data relative to the model (Kery, 2010). We simulated the detection data (i.e., number of detections across 15 replicate days at each site) for each Markov Chain Monte Carlo iteration. The discrepancy between the simulated and expected values and observed and expected values was calculated with a Pearson residual as, $[(o-e)/\sigma^2]$, where *o* is either the observed or simulated number of detections, *e* is the expected value (i.e., $e = kp_{i,j}$), and σ^2 is the variance of *e* (i.e., $\sigma^2 = kp_{i,j}(1-p_{i,j})$). Because the simulated data are generated directly from the model they are considered "perfect" and, thus, the resultant Pearson residual represents the fit of the model when all model assumptions are met (Kery, 2010). We then created a fit metric that is equal to one when the Pearson residual was greater for the observed data than the simulated data and is equal to zero, otherwise. We then calculated the *Bp* as the mean of the posterior sample of the fit metric for each species, where a mean of 0.5 indicates perfect model fit and a mean approaching 0 or 1 indicates under- or over-dispersion, respectively.

RESULTS

We detected 14 species across the three reserves with a sampling effort of 630 camera trap-days (Monroy-Vilchis *et al.*, 2011) and a total of 426 independent records (Table 1). The mammalian order with the highest number of species detected was carnivores (n = 7), followed by rodents (n = 3), whereas all other orders (Ungulata, Marsupialia, Xenarthra and Pilosa) where represented by only one species (Table 1).

Table 1. Number of independent records and mammal species detected in camera trapping surveys in three reserves with coffee plantations of the highlands of Guatemala (March-May 2014). NIR, Number of independent records.

Species	Common name	Order	NIR	STP	SJM	PPF
Odocoileus virginianus	White-tailed deer	Cetartiodactyla	4		X	
Puma concolor	Puma	Carnivora	4	X	X	
Leopardus wiedii	Margay	Carnivora	12	X	X	
Urocyon cinereoargenteus	Gray fox	Carnivora	54	X	X	X
Eira barbara	Tayra	Carnivora	5	X	X	
Procyon lotor	Northern raccoon	Carnivora	12	X		
Nasua narica	White-nosed coati	Carnivora	31	X	X	X
Mephitis macroura	Hooded skunk	Carnivora	1		X	
Cuniculus paca	Paca	Rodentia	19	X	X	X
Dasyprocta punctata	Central American Agouti	Rodentia	141	X	X	X
Sciurus variegatoides	Variegated squirrel	Rodentia	38	X	X	X
Tamandua mexicana	Northern tamandua	Pilosa	2	X	X	
Dasypus novemcinctus	Nine-banded armadillo	Cingulata	9		X	X
Didelphis virginiana	Virginia opossum	Didelphimorphia	84	X	X	X

Rhat values (max Rhat = 1.01; mean Rhat =1.00) indicated adequate convergence across all chains and Bayesian p values showed an adequate model fit for all species (*Bp* range = 0.34 – 0.74; Table 2). Occupancy probabilities across the entire study site ranged from 0.09 (the hooded

skunk, *Mephitis macroura* Lichtenstein, 1832) to 0.77 (the Central American agouti, *Dasyprocta punctata* (Gray, 1842)); Table 2). The species with the highest occupancy probabilities was a rodent, the Central American agouti and a marsupial, the Virginia opossum (*Didelphis virginiana* (Kerr, 1792)) (Table 2). Occupancy probabilities for these species were six to seven times higher than large-bodied mammals (i.e., white-tailed deer, *Odocoileus virginianus* (Zimmermann, 1780)) and carnivores such as the puma (*Puma concolor* (Linnaeus, 1771)), tayra (*Eira barbara* (Linnaeus, 1758)), hooded skunk, and northern raccoon (*Procyon lotor* (Linnaeus, 1758)). Occupancy probabilities for the margay (*Leopardus wiedii* (Schinz, 1821)), gray fox (*Urocyon cinereoargenteus* (Schreber, 1775)) and white-nosed coati (*Nasua narica* (Linnaeus, 1766)), were intermediate across the study area (0.39 – 0.47). The paca (*Cuniculus paca* (Linnaeus, 1766)), a medium-sized rodent preferred by hunters (El-Bizri *et al.*, 2017), also showed an intermediate value of occupancy probability (0.27).

Table 2. Mammals detected in camera trapping surveys in three reserves with shade grown coffee plantations of the highlands of Guatemala (March-May 2014) along with their naïve occupancy estimates, mean occupancy estimate (Ψ) across the three coffee farms, mean detection probability (p) and their standard deviations (SD). Model fit was evaluated with the Bayesian *p*-value (BP) for the species model, where values between 0.05 and 0.95 indicate adequate fit and a mean of 0.5 indicates perfect model fit.

Common name	**Naïve Occupancy**	**Mean Occupancy Ψ (SD)**	**Mean detection probability P (SD)**	**BP**
		Model Estimates		
White-tailed deer	0.05	0.11 (0.13)	0.04 (0.03)	0.56
Puma	0.07	0.16 (0.16)	0.04 (0.03)	0.57
Margay	0.21	0.39 (0.31)	0.04 (0.02)	0.57
Gray fox	0.33	0.47 (0.31)	0.05 (0.02)	0.43
Tayra	0.05	0.13 (0.15)	0.05 (0.03)	0.47
Northern raccoon	0.07	0.12 (0.12)	0.05 (0.03)	0.50
White-nosed coati	0.29	0.47 (0.32)	0.06 (0.03)	0.34
Hooded skunk	0.02	0.09 (0.15)	0.04 (0.03)	0.74
Paca	0.17	0.27 (0.17)	0.07 (0.03)	0.53
Central American agouti	0.52	0.77 (0.49)	0.09 (0.03)	0.39
Variegated squirrel	0.31	0.49 (0.27)	0.07 (0.03)	0.39
Northern tamandua	0.05	0.14 (0.15)	0.04 (0.03)	0.60
Nine-banded armadillo	0.10	0.18 (0.18)	0.05 (0.03)	0.53
Virginia opossum	0.38	0.60 (0.34)	0.08 (0.03)	0.42

Relative abundance per species and their association to covariates. Relative abundance estimates of five species (margay, tayra, paca, the Central American agouti, the variegated squirrel [*Sciurus variegatoides* Ogilby, 1839], and the Virginia opossum) were positively associated to forest cover (as opposed to coffee plantation; Table 3; Fig. 2). Relative abundance estimates of three species (margay, Central American agouti and the Virginia opossum) were positively associated to distance to roads. Relative abundance estimates of one species, the gray fox, was negatively associated to roads. While we found no association between relative abundances and distance to protected areas for any species (Table 3; Fig. 2).

Detection probabilities and their association to covariates. Detection probabilities ranged from 0.04 to 0.09 (Table 2), indicating low detection probabilities across all species and sites. Detection probabilities of three species (gray fox, northern raccoon, and paca) were negatively associated to land use (Table 4), suggesting higher probability of detection in sites located within more open coffee plantations. Detection probability of only one species (gray fox) increased when lure was used.

Species richness and its association to covariates. Species richness per sampling site in all three reserves was higher in forest land use than in coffee plantations (Fig. 3). Species richness showed a positive and significant association with distance to the main road (Fig. 4), indicating this parameter was higher at sites farther from the road. We found no significant trend between species richness and distance to protected area.
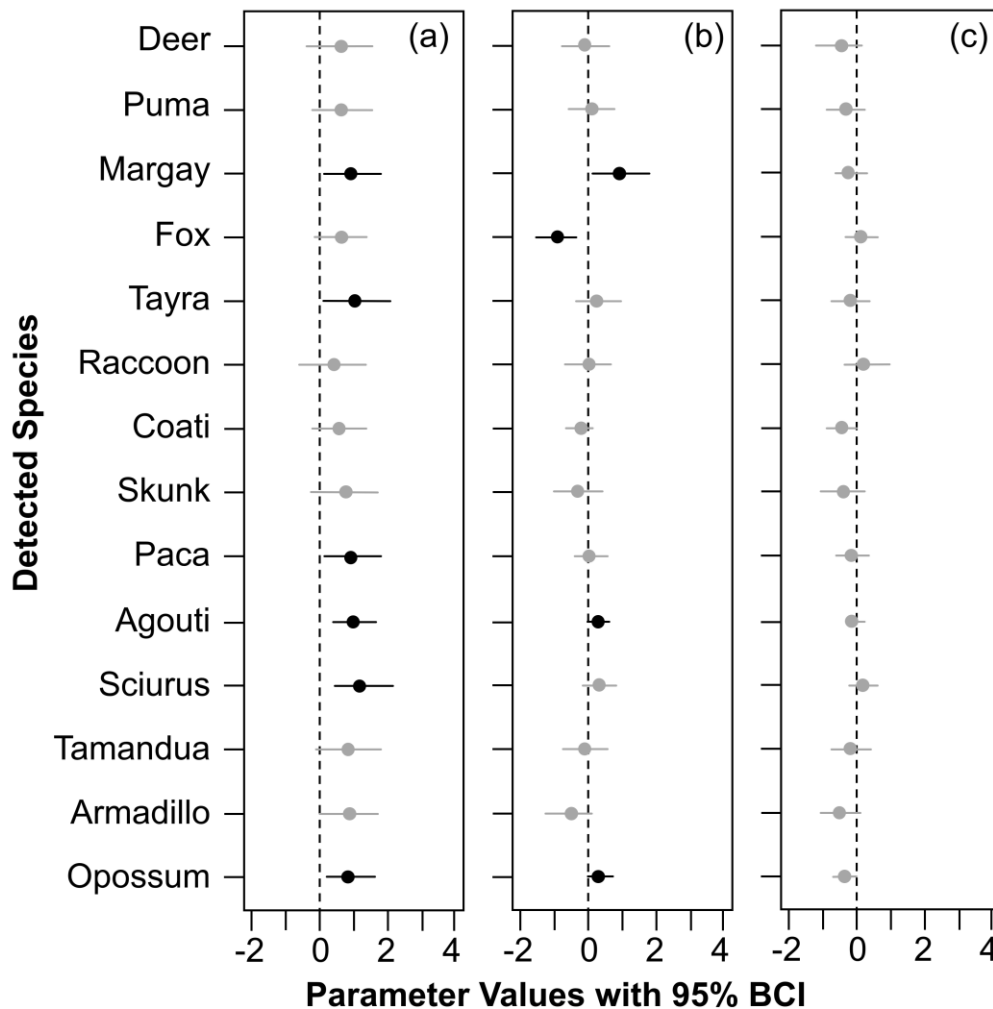

Figure 2. Posterior summaries of the effects of (a) land use (forest vs. coffee plantations); (b) distance to asphalt road; and (c) distance to protected area on local relative abundances of terrestrial mammals detected in camera trap surveys in three reserves with coffee plantations of the highlands of Guatemala (March-May 2014). Dotted vertical line represents the mean of the posterior distributions while the lines along x-axis represent 95% Bayesian credible intervals. The grey dots and lines indicate parameters that are not statistically different than zero (95% credible intervals include zero). Black dots and lines indicate statistical significance. The x-axis is the parameter value; units on the x-axis are interpreted as one unit of occurrence on the log scale for every one standard deviation of the covariate.

Table 3. Summary of mean model coefficients and their 95% credible intervals for species-level relationships between relative abundance estimates (λ) and model covariates and the direction of the effect of statistically significant covariates. Measures for mammals detected in camera-trapping surveys conducted during March-May 2014. Statistical significance is based on 95% credible interval non-overlap with zero. * and † indicate a positive and negative association respectively to covariate.

Species	Land use	Distance to road	Distance to protected area
White-tailed deer	0.64 (-0.39, 1.54)	-0.05 (-0.73, 0.59)	-0.41 (-1.11, 0.15)
Puma	0.68 (-0.24, 1.57)	0.12 (-0.49, 0.72)	-0.23(-0.81, 0.32)
Margay	0.95 (0.12, 1.84)*	0.48 (0.03, 0.96)*	-0.16 (-0.63, 0.30)
Gray fox	0.64 (-0.13, 1.38)	-0.88 (-1.48, -0.32)†	0.15 (-0.26, 0.62)
Tayra	1.05 (0.14, 2.11)*	0.30 (0.34, 0.98)	-0.13 (-0.72, 0.44)
Northern raccoon	0.48 (-0.58, 1.37)	0.06 (-0.58, 0.70)	0.26 (-0.32, 0.94)
White-nosed coati	0.64 (-0.19, 1.41)	-0.15 (-0.57, 0.24)	-0.36 (-0.82, 0.06)
Hooded skunk	0.79 (-0.17, 1.72)	-0.23 (-1.01, 0.46)	-0.28 (-0.97, 0.31)
Paca	0.96 (0.15, 1.84)*	0.09 (-0.40, 0.58)	-0.12 (-0.59, 0.35)
Central American agouti	1.01 (0.38, 1.71)*	0.32 (0.02, 0.65)*	0.02 (-0.33, 0.28)
Variegated squirrel	1.22 (0.43, 2.14)*	0.34 (-0.11, 0.79)	0.21 (-0.18, 0.62)
Northern tamandua	0.85 (-0.10, 1.84)	-0.05 (-0.75, 0.61)	-0.13 (-0.73, 0.45)
Nine-banded armadillo	0.85 (-0.01, 1.71)	-0.47 (-1.17, 0.15)	-0.42 (-1.06, 0.12)
Virginia opossum	0.89 (0.19, 1.65)*	0.38 (0.05, 0.73)*	-0.32 (-0.65, 0.01)

DISCUSSION

Our study shows that areas of the highlands of Guatemala still hold relatively intact terrestrial mammalian assemblages and that shade-grown coffee plantations are likely playing an important role in their conservation. The detection of large-bodied species such as the puma, margay and of species that are vulnerable to hunting (e.g., white-tailed deer, paca, and Central American agouti) suggest that these agroforestry systems provide habitat with suitable conservation status and adequate resources for the protection of Neotropical wildlife (Escobar-Anleu *et al.*, 2017; Winnie & Creel, 2017).

Our findings highlight the need to study overlooked and unique ecosystems, even in fragmented or human-dominated landscapes (Morales-Rivas *et al.*, 2020). We consider the mammal communities found in study systems like ours have most likely been isolated for decades from other large intact Neotropical forests and this makes them particularly vulnerable and an important genetic pool for these species. Mammals isolated in small areas are more vulnerable to human-induced mortality than to stochastic processes and have a higher probability of local extinction (Pacifici *et al.*, 2013; Woodroffe & Ginsberg, 1998).

We found that although forest sites without coffee were more used by native mammal species, shade-grown coffee plantations also provide habitat for them. These results agree with recommendations from other authors regarding shade-grown coffee and the importance of maintaining natural forests in agroforestry system landscapes to benefit mammal diversity (Caudill *et al.*, 2014; García-Burgos *et al.*, 2014; Caudill & Rice 2016; Guzmán *et al.*, 2016). Although some studies have found little difference in diversity metrics between shade coffee sites and forests (Cruz-Lara *et al.*, 2004; Mendoza-Sáenz & Horváth, 2013), our results confirm our hypothesis that medium- and large-sized mammals used forest sites more than coffee plantation sites. Though we did not evaluate vegetation structure and composition directly, the distinct differences between

forests and shade-grown coffee plantations can be considered a factor explaining these patterns of site preferences. For example, in Kodagu, India, Caudill *et al.* (2014) found that small mammal species richness and abundance increased with greater amounts of herbaceous ground cover (<5 cm in height) and in coffee habitats in Costa Rica, small mammal richness and abundance were higher in sites with greater amounts of lower strata vegetation (from 5 cm to 1 m tall) (Caudill, 2013).
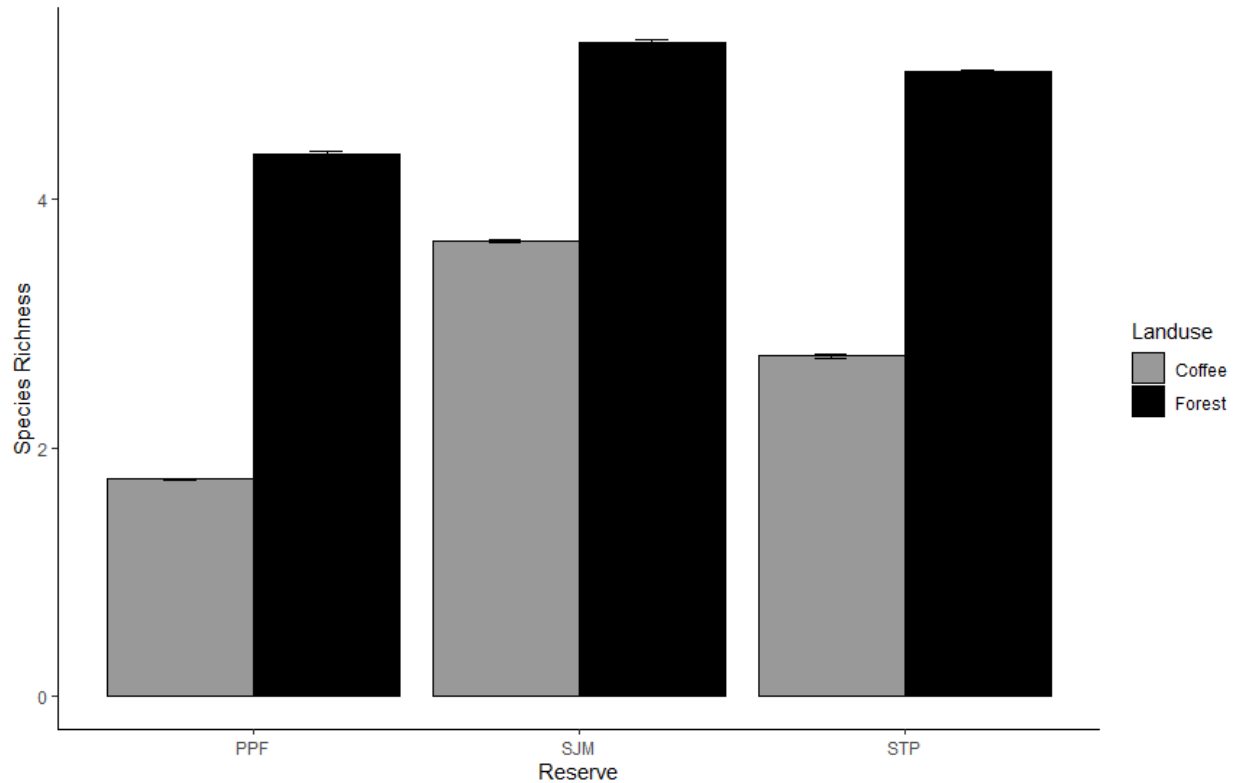
Figure 3. Average species richness estimates per reserve according to land use type (forest cover or coffee plantation) of terrestrial mammals detected in camera trap surveys in three reserves with shade grown coffee plantations of the highlands of Guatemala (March-May 2014). The reserves are: STP: Santo Tomas Pachuj; PPF: Pampojila Pena Flor; and SJM: San Jeronimo Miramar.
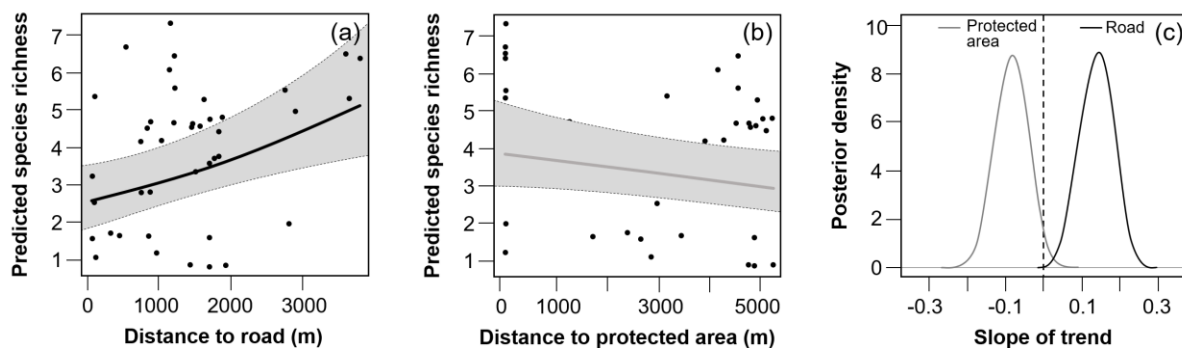
Figure 4. Sampling site species richness versus distance to asphalt road and the protected area. Estimates are for reserves with shade-grown coffee plantations in the highlands of Guatemala surveyed with camera traps during March-May 2014.

Table 4. Summary of mean model coefficients and their 95% credible intervals for species-level relationships between probability of detection (*p*) and model covariates and the direction of the effect of statistically significant covariates. Measures for mammals detected in camera-trapping surveys conducted during March-May 2014. Statistical significance is based on 95% credible interval non-overlap with zero. * and † indicate a positive and negative association respectively to covariate. Reference covariate for land use covariate is forest (in contrast with coffee plantation), while for the lure covariate the reference covariate was use of lure.

Species	Land use	Lure
White-tailed deer	-0.80 (-1.88, 0.19)	0.15 (-0.68, 0.93)
Puma	-0.66 (-1.65, 0.031)	0.24 (-0.50, 1.00)
Margay	-0.30 (-1.20, 0.79)	0.34 (-0.34, 1.02)
Gray fox	-0.83 (-1.59, -0.08) †	0.62 (0.00, 1.29) *
Tayra	-0.05 (-1.66, 0.75)	0.48 (-0.37, 1.46)
Norhern raccoon	-1.04 (-2.21, -0.08) †	-0.07 (-0.93, 0.65)
White-nosed coati	-0.48 (-1.24, 0.29)	0.22 (-0.37, 0.80)
Hooded skunk	-0.56 (-1.63, 0.52)	0.39 (-0.38, 1.25)
Paca	-1.46 (-2.55, -0.53) †	0.28 (-0.49, 1.02)
Central American agouti	-0.51 (-1.18, 0.18)	0.19 (-0.31, 0.65)
Variegated squirrel	-0.59 (-1.44, 0.35)	-0.01 (-0.65, 0.57)
Northern tamandua	-0.52 (-1.56, 0.58)	0.32 (-0.44, 1.13)
Nine-banded armadillo	-0.84 (-1.79, 0.06)	0.47 (-0.27, 1.33)
Virginia opossum	-0.47 (-1.18, 0.28)	0.38 (-0.14, 0.92)

Species that showed a preference for forest sites have mostly frugivorous-omnivorous opportunistic feeding habits (i.e., pacas, Central American agouti, variegated squirrel, and the Virginia opossum), and although they have been found in agricultural areas, our results suggest that they are still dependent on forest remnants. For example, pacas have been shown to survive in small fragments of forest that remain between large fragments of agricultural areas (Gallina *et al.*, 2012). Even when they can find food to survive in these areas, these rodents can also move great distances from the forest fragments in search of food resources (Zucaratto *et al.*, 2010; Harmsen *et al.*, 2018). In addition, previous studies have also found this species in cacao (Benavides *et al.*, 2017) and coffee plantations (Ramírez-Bravo & Hernández-Santín, 2012), suggesting that agroforestry systems may offer this species food resources throughout the year (Benavides *et al.*, 2017).

Similarly, even though the Central American agouti frequents forested areas, it can also be found in disturbed areas (Orjuela & Jiménez, 2004). On the other hand, although the Virginia opossum is thought to depend on anthropogenic resources in some areas (Kanda *et al.*, 2009) and that its range expansion is explained with its ability to use these resources, we found this species to also prefer forest sites over coffee plantations sites. Beatty *et al.* (2014) found that, contrary to their predictions, areas near a forest and with high-forest edge density were selected all year-round, indicating native habitats are used broadly by this species, showing that forest remains are a critical habitat in fragmented landscapes, even for species that are considered generalists.

The preference of two carnivore species (the margay and tayra) for natural forest cover can be associated to two factors: 1) higher prey abundance (Burton *et al.*, 2012); and 2) greater cover for stalking their prey and avoiding human contact (Balme *et al.*, 2007; Esparza-Carlos *et al.*, 2018).

As mentioned above small mammal diversity and abundances increase with ground cover (Caudill, 2013; Caudill *et al.*, 2014), benefitting carnivores that feed regularly on them.

The Neotropics is one of the most diverse regions in the world but is also one of the most threatened due to anthropogenic factors (Brown, 2014). Previous studies for multiple taxa and ecosystems around the world have identified disturbance as a determinant and driver of changes on diversity measures, such as functional diversity (Biswas & Mallik, 2011). In our study disturbances such as the asphalt road reduced local scale species richness and relative abundances of three species (margay, Central American agouti and the Virginia opossum). This may ultimately impact diversity at a larger scale. Roads can increase access for hunters (Espinosa *et al.*, 2018), alter interactions between predators and their prey (DeMars & Boutin, 2018), and increase mortality through vehicle collisions (Jaeger *et al.*, 2005).

Not all species responded in the same manner though, as one species, the gray fox, showed a positive association to the asphalt road. This species is less common in evergreen forest and frequents edges of forest and farmland, with previous studies showing it uses road areas next to them (Gallina *et al.*, 2016; Deuel *et al.*, 2017), and urban zones (Deuel *et al.*, 2017; Riley, 2006). Roads have the potential to provide an alternative source of food (road-killed carrion) in fragmented landscapes (DeVault *et al.*, 2011; Olson *et al.*, 2012). Consequently, the high adaptability of the gray fox (Gallina *et al.*, 2016; Villalobos-Escalante *et al.*, 2014) and the proximity to adjacent forest remnants (Kapfer & Kirk, 2012) could explain its association to the road in our study area.

Contrary to what was found by other authors (Bali *et al.*, 2007), our hypothesis of higher diversity and abundances near protected areas was not supported. This may be due to the small scale of the study and relatively large home ranges of most species detected (Grant *et al.*, 2005), indicating connectivity is still intact in this human dominated landscape, at least for our study sites. Furthermore, the reserves in this study are close to human presence and thus they may be acting as refuges where disturbance and hunting are low (Monsarrat *et al.*, 2019). This suggests a high value of these reserves to biodiversity conservation. However, to better determine the effects of distance to protected areas, more coffee plantation reserves representing a wider range of distances should be surveyed.

Detection probability increased for some species in shade-grown coffee plantations, potentially due to the more open nature of the understory. The use of lures such as men's cologne has been found to attract carnivores (Gelin *et al.*, 2017; Mills *et al.*, 2019) and may increase their detectability in studies such as ours. We found this to be the case for one of the carnivores detected in our study, the gray fox. However, due to the limited number of sampling sites of our study and potentially low carnivore populations in the area, we cannot infer with certainty on the effects of lure on carnivore detectability in the area.

In our study, one of the reserves is certified by Rainforest Alliance™. The Rainforest Alliance™ certification indicates that a plantation has been audited to meet standards that require environmental sustainability, reducing or eliminating negative environmental factors (Haggar *et al.*, 2017). Coffee certification programs are also implemented to guarantee coffee under shade contributes to biodiversity conservation (Cruz-Angón & Greenberg, 2005; Gobbi, 2000). The certified reserve in our study, maintained its coffee crops under a diverse, native tree canopy with minimum intervention. More species and a richness increase (ants, birds and butterflies) has been linked to a decrease in management intensity in certified coffee farms (Cruz-Lara *et al.*, 2004; Philpott *et al.*, 2007). This suggests there may be ecological benefits to maintaining high native and natural (as opposed to cultivated) tree diversity in agricultural landscapes to use these as

shade for coffee crops. Although we caution interpretation of these results due to our small sample size.

Our study contributes with increasing our understanding of terrestrial medium- and large sized mammalian diversity and their habitat associations within an agroforestry system. However, generalization and the scope of inference of our results should be interpreted with caution due to our small sample size (3 reserves with coffee plantations) and limited temporal sampling. Our results suggest that shade-grown coffee plantations within private reserves in our study area have the potential to conserve native mammal communities, as has been suggested by other studies (Williams-Guillén *et al.*, 2006; Guzmán *et al.*, 2016). Furthermore, with our analyses of habitat associations, we provide preliminary guidelines for landscape configuration management that may benefit medium- and large-sized mammals in our study site. For example, we show that mammal diversity and abundances for several species increased in natural forests and in sites that are distant from asphalt roads. Therefore, to maximize mammalian diversity and local abundances, it is necessary to maintain natural native forest patches as shade for coffee plantations and these should be located at a distance from human infrastructure such as asphalt roads as well as consider mitigation measures on the roads to protect wildlife.

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