

# Tropical timber plantations as habitat for ground-dwelling mammals: A camera-trapping assessment in Central Panama

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## Abstract

Reforestation projects in the tropics often consist of plantations, typically monocultures of non-native timber species. It has been questioned whether such plantations are suitable as wildlife habitat, but empirical evidence is scarce, especially on plantations embedded on highly disturbed landscapes. Here, we compare species richness and occupancy of ground-dwelling mammals between five types of plantations within a single area in Central Panama, the narrowest tract of the Mesoamerican Biological Corridor. We deployed camera traps at stratified random points and followed a hierarchical modeling approach to compare community composition and occupancy between plantation types. We found a total of 16 ground-dwelling mammals in the area, most of which were small-bodied and short-lived, and the majority of species' occupancy probabilities were below 0.5 at any given plantation. Teak (*Tectona grandis*) plantations, which covered the largest area in the study, had the lowest estimated richness and occupancy, with occupancy probabilities exceeding 0.5 for just three species. Conversely, plantations of the native *Pachira quinata* and the non-native *Gmelina arborea*, covering an area four and nineteen times smaller than Teak, respectively, had higher richness and occupancy. Occupancy values were intermediate in the *Acacia* and mixed plantation types. Our findings suggest that plantations embedded in lowland tropical landscapes have limited conservation value for large-bodied mammals, and are ecologically constrained habitats for small- and medium-sized mammals.

## KEYWORDS

fine-scale studies, forest restoration, hierarchical models, landscape mosaic, occupancy estimates, Panama Canal Watershed, small-bodied mammals

## 1 | INTRODUCTION

Between 2010 and 2015, natural forest areas decreased at a rate of 3.3 Mha/year globally, and the highest forest loss occurred in the tropical domain (Hansen et al., 2013; Keenan et al., 2015). The

remaining tree cover increasingly consists of plantations (Verheyen et al., 2016). In the tropics, the total area covered by tree plantations reached 32.2 Mha between 2000 and 2012 (Fagan et al., 2022). Plantations nowadays are important components of climate change mitigation efforts and ecosystem restoration projects (Hall

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et al., 2011; Sinacore et al., 2023), and plantations of *Pinus*, *Tectona*, *Acacia*, *Hevea*, or *Eucalyptus* (Carle et al., 2002), which provide commercial timber, are widely used to “reforest” large tracts of cleared or degraded landscape (Lamb, 1998; Silva et al., 2019).

Timber plantations are also widely used for the creation of buffer zones and biological corridors, which should enhance forest connectivity and support landscape-level biodiversity (Chazdon, 2008; Hall, Murgueitio, et al., 2015). Here, the implicit assumption is that these plantations provide wildlife with sufficient ecological resources to function as habitats, or at least provide connectivity between natural forest remnants. However, while timber plantations usually restore the first stages of landscape productive capacity, it is not clear how much they contribute to the recovery of biological diversity (Lamb, 1998; Wang et al., 2022) and multifunctionality (Messier et al., 2021). It has been argued that plantations do not provide sufficient resources to serve as habitat for wildlife (Kanowski et al., 2005; Mendes-Oliveira et al., 2017). Indeed, a global review, using biodiversity and abundance as indicators, reported that monocultures and exotic plantations harbored less biodiversity than primary forests and secondary succession forests (Wang et al., 2022).

Mammals are a prime conservation target for forest corridors, because their large body size, low reproductive rates, and forest-dependent life histories are especially vulnerable to landscape modification (Daily et al., 2003; Grilo et al., 2010). Forest mammals may thus be useful indicators of habitat quality in plantations, regarding resource availability, their use as refuges and corridors, and their landscape-scale functions. Further, biodiversity assessments on unprotected areas (i.e., fragmented landscapes and timber plantations) are particularly relevant because protected areas alone cannot prevent biodiversity loss (Santangeli et al., 2023).

A number of studies comparing non-volant mammals on timber plantations against natural habitats reported low species richness and/or abundance in plantations (i.e., on teak plantations, Méndez-Carvajal, 2012; Sánchez-Londoño et al., 2021; eucalyptus, Almeida-Maués et al., 2022; Coelho et al., 2014, Piña et al., 2019; oil palms, Almeida-Maués et al., 2022; Mendes-Oliveira et al., 2017; Pardo et al., 2018; pine, Iezzi et al., 2018, 2020; Sánchez-Londoño et al., 2021). All of these studies compared single monoculture plantation types against a nearby or adjacent natural habitat; most of these plantations were established for commercial purposes in large-scale landscapes, while implicitly contributing to reforestation strategies (Sinacore et al., 2022). Conversely, plantations may be small (i.e., 3 ha), situated in highly disturbed habitats, and owned by local landholders (Iezzi et al., 2020; Sinacore et al., 2023). Their degree of embedding within the landscape, and consequently their impacts on wildlife, may differ from large-scale plantations. More insights in the value of these small-scale plantations as habitat replacement for wildlife are needed.

In this study, we assessed the value of different types of timber plantations to ground-dwelling mammals in a single region, as a way to minimize background variation that could otherwise confound inferences of species utilization. We deployed camera traps in a mosaic of timber plantations surrounding a small-scale industrial

area in the Panama Canal Watershed, located in a highly deforested landscape within the narrowest part of the Mesoamerican wildlife corridor that connects the forests of North and South America (Hall, Cerezo, & Entem, 2015). Camera trapping is a useful tool for studying habitat occupancy and the composition of ground-dwelling mammal communities, including elusive species (Agha et al., 2018; Rovero et al., 2013). We assessed the level of habitat use by mammals using occupancy modeling (Royle & Nichols, 2003), a current standard for investigating species-habitat associations, which accounts for imperfect detection (Sollmann, 2018).

Our goals were to evaluate ground-dwelling mammal species diversity and their intensities of use in a fine-scale mosaic of timber plantations. We did not have prior expectations for differences between plantation types. Thus, our analyses can be viewed as an informal test of the hypothesis that the plantations are equivalent in terms of their use by ground-dwelling mammals. We used hierarchical models to estimate species richness and occupancy by plantation type, so that the presence or absence of each species and their intensity of use could be compared.

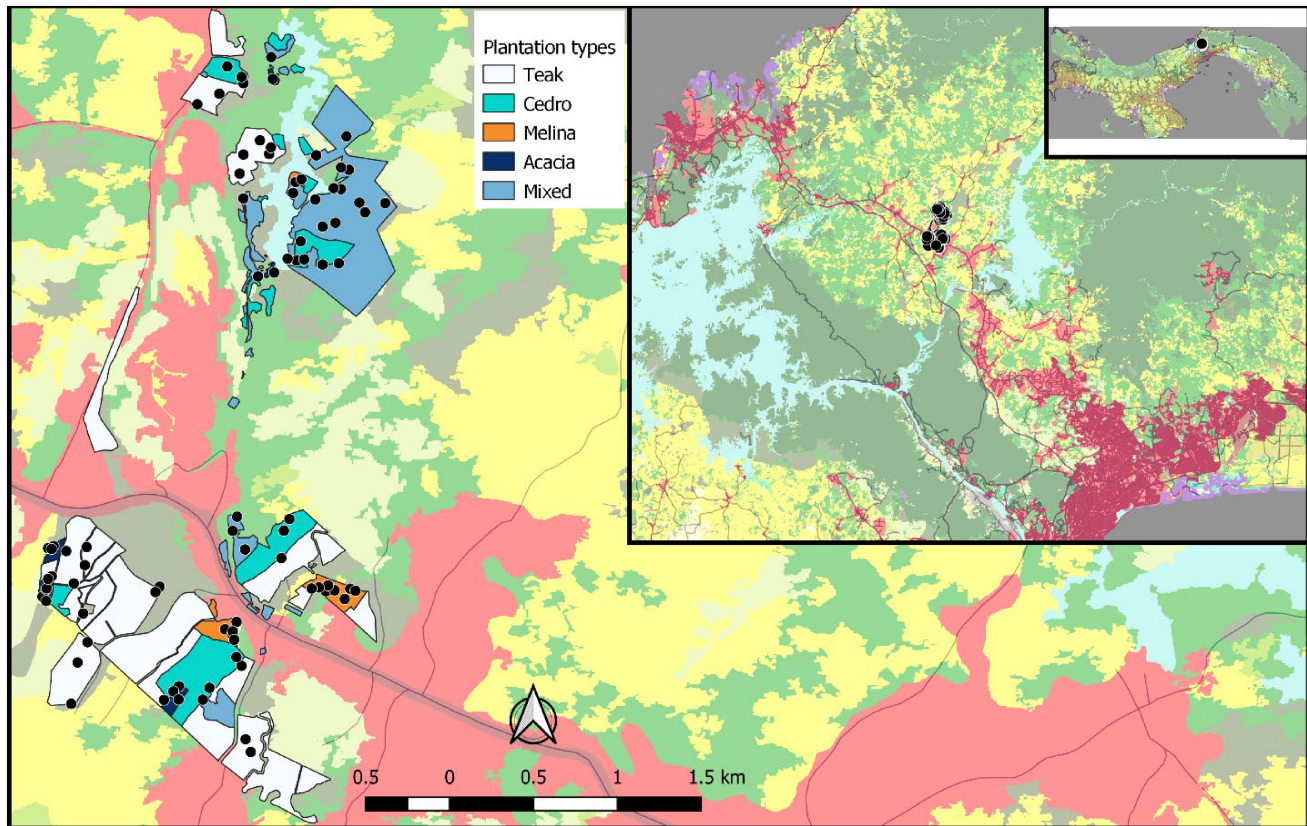
## 2 | METHODS

### 2.1 | Study area

Our fine-scale survey took place in a plantation area located at Nuevo San Juan, Colon (Lat: 9°15'56.4" N, Long: 79°39'24.5" W, Figure 1) in the eastern region of the Panama Canal Watershed on the grounds of the ARGOS cement plant.

The plantations cover a total area of ~223-ha, and consist of monocultures of the non-native timber species *Tectona grandis* (136-ha), *Gmelina arborea* (7-ha), *Acacia* sp. (4.8-ha), *Pachira quinata* (36-ha), and 45-ha of a mix of various native and non-native species, hereafter referred to as Teak, Melina, Acacia, Cedro, and Mixed, respectively (Table 1). The five plantation types were initially established as an environmental mitigation. They consist of a total of 66 lots that vary in size and age, where 83% were planted between 1991 and 1999, 12% in 1962 (1 lot) and 1977 (7 lots). Age was unknown for 5% of the lots. Further, the lots are embedded in a multifunctional anthropogenic landscape including human settlements (i.e., houses, school, public clinic, sport fields, and agricultural fields), commercial activities, and roads.

Two distinct groups of lots could be distinguished, a group to the north of the cement plant and a group to the south. The north group includes lots of Teak, Mixed, and Cedro, which were separated by a dammed river that creates a small artificial lake (the light-blue color in map of Figure 1). These lots are adjacent to human houses, a secondary paved road, fields of Panama Canal grass, patches of native forest and more timber plantations (from a different owner and not included in our study). In contrast, the south group includes lots of Teak, Cedro, Melina, Acacia, and Mixed, which are bisected by the Trans-Isthmus Highway (Transistmica), a main road connecting Panama City with Colon City. The south group was adjacent to more



**FIGURE 1** Map showing the spatial distribution of the camera traps throughout the study period, and the position of the plantation in respect to the landscape. Additional colors in the map are as follows: thin black lines, paved, and unpaved roads; shaded black line, highway; red, human settlements; light green, secondary forest patches of varying ages; light blue, lakes; beige and yellow, Panama Canal grass, field of crops (agriculture or timber plantations); and dark green, protected forest.

**TABLE 1** Characteristics of the five plantation types and their sampling at Argos, Central Panama. Specifications of camera-trapping surveys conducted in these sites.

Plantation type	Size (ha)	Number of camera sites	Total effort (days)
Teak	136	17	731.8
Cedro	36	16	611.1
Mixed	45	19	734.2
Melina	7	15	681.5
Acacia	4.8	15	554.8

houses than the north group, as well as sport fields, a clinic, a school, and secondary paved and unpaved roads.

The elevation ranged between 40 and 200masl (Yamazaki et al., 2017), but the majority of the camera sites for this study were below 100m. Plantation areas had typically been cleared before planting, and in subsequent years, fires had been set by local residents (not for silvicultural practices) to control canal grass progressing into the Teak plantations, mostly on the south group. The plantations are therefore structurally distinct, with the Teak plantations most often lacking an understory. Although the ARGOS plantations were not established with scientific purposes in mind,

we can nonetheless take advantage of relative similarities in background conditions to compare wildlife use across plantations, as for a natural experiment.

The area is assumed to help provide connectivity for wildlife between Soberanía National Park (western side) and Chagres National Park (eastern side), as part of a “Mesoamerican Biological Corridor” along the Isthmus of Panama. This Mesoamerican corridor is particularly important for medium-to-large sized forest species such as Baird’s tapir (*Tapirus bairdii*), jaguar (*Panthera onca*), puma (*Puma concolor*), white-nosed coati (*Nasua narica*), giant anteater (*Myrmecophaga tridactyla*), white-tailed (*Odocoileus virginianus*) and red-brocket deer (*Mazama temama*), and collared (*Pecari tajacu*) and white-lipped peccaries (*Tayassu pecari*) (Meyer et al., 2015).

## 2.2 | Camera trap survey

Unbaited camera traps were deployed at computer-generated random points between July 2014 and June 2015 to assess use by ground-dwelling vertebrates. The randomized points were stratified by the five plantation types to ensure that the sample was approximately balanced, in terms of number of camera traps and sampling time. Camera traps (Reconyx PC900 Hyperfire – Reconyx, Inc., WI,



USA) were mounted on tree stems in steel security enclosures at knee height, and programmed to take 10 images upon each trigger with no delay between triggers (hereafter events), yielding sequences of multiples of 10 photos. Cameras were programmed to also take a time-lapse image every 12h to enable distinguishing absence of wildlife from camera malfunction. At each sampling point, we used the “walk-test function” of the camera traps to measure the maximum distance at which a human triggered the camera, as a measure of each camera's sensitivity (Zimmermann & Rovero, 2016), by walking in front of the camera at installation, and noting the farthest distance from which the camera's infrared sensor could be activated by hand waving (Monteza-Moreno et al., 2020). This camera-level detection distance is influenced by undergrowth vegetation, and serves as a proxy for the local understory density.

At any given time during the study period, two or three cameras within each plantation type were simultaneously deployed (which we called a *round*), making up to 15 camera traps in the study area per round. Rounds one to four took place in the rainy season of 2014, round five was during the dry season of 2015, and the remaining rounds covered the 2015 rainy season until 1 year of sampling was completed in July. The cameras remained in the field for 40 days on average and were then moved to a new random point. By our sampling protocol, adjacent random points were never sampled simultaneously. Over the course of this study, one camera was stolen and no camera malfunctioned. The median pairwise distance between cameras, among cameras deployed at the same time, was 1564 m, with minimum and maximum distance being 41 and 4117 m, respectively. A total of eight pairs of cameras, among cameras deployed at the same time, were separated by less than 75 m.

In total, we surveyed 79 camera sites over a cumulative 3165 camera-trapping days (Table 1). Photo sequences were processed and annotated with the camera-trap platform Agouti (Casaer et al., 2019; Kays et al., 2009). Species identifications were based on Reid (2009). Birds, reptiles, and domesticated species were excluded from the analyses.

## 2.3 | Data analysis

We took a hierarchical modeling approach to species counts and occupancy, treating camera deployments as the basic sampling units. The temporally and spatially randomized deployments, with plantation types as spatial strata, supported modeling assumptions that deployments are conditionally exchangeable given plantation type, season, and other covariates (Webb et al., 2010). Adjustments within our models for potential confounders, along with the assumption that landscape-level, background conditions are similar across plantations, allowed us to interpret the ARGOS survey as a kind of natural experiment, with plantation types as treatments (Craig et al., 2017).

We first assessed our sampling effort by producing species accumulation curves per plantation type and for the entire site, using the “specaccum” function in the R library *vegan* (Oksanen et al., 2013). This was done in three different ways: based on the number of

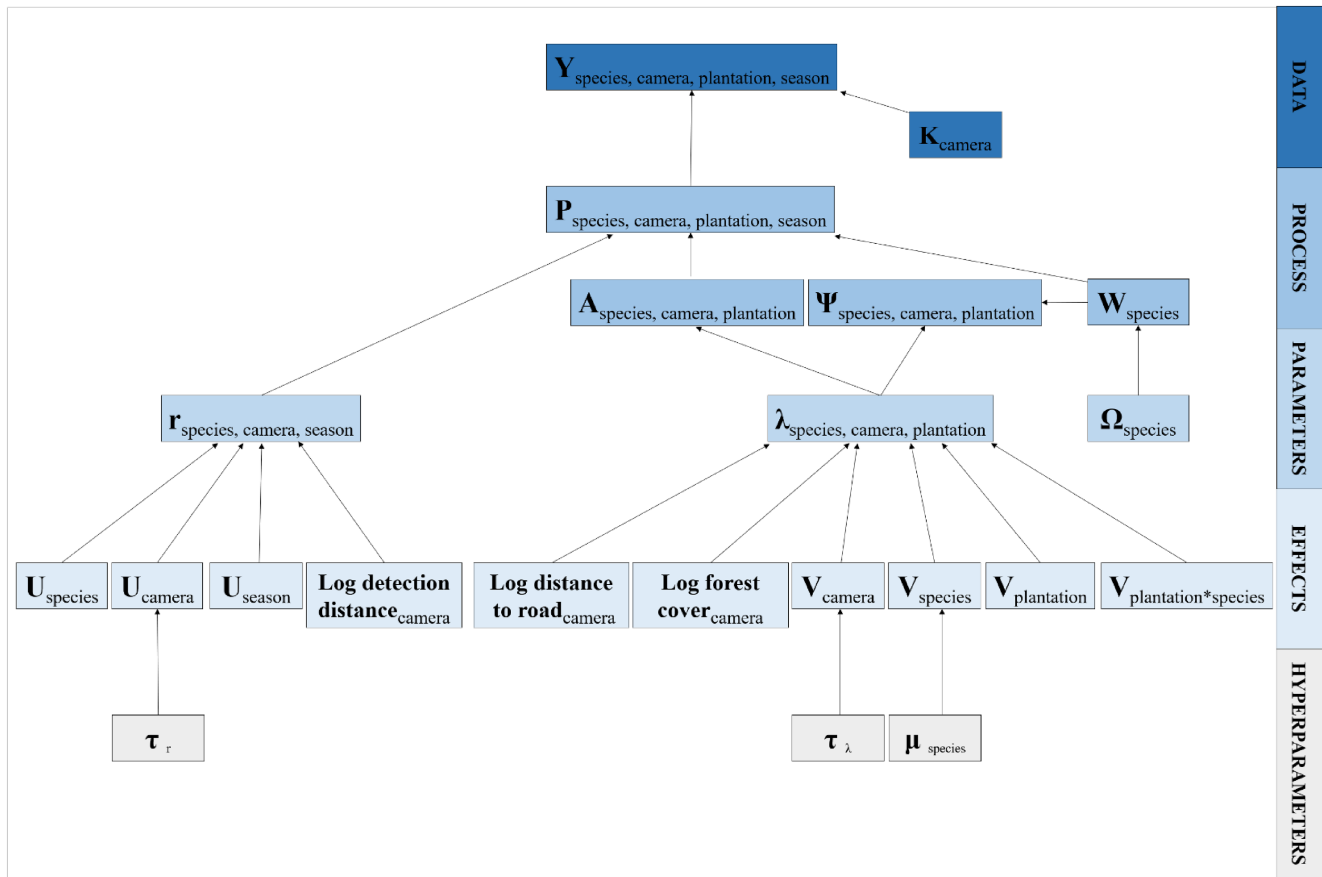
camera sites, length of deployment (number of days), and number of events.

Species counts (“richness”) per camera deployment for each plantation type were modeled using a likelihood-based Poisson regression method, implemented in the library *glmmADMB* (generalized linear mixed model AD model builder; Skaug et al., 2013) of the R Statistical Language (R Core Team, 2021). Varying intercepts (“random effects”) for camera deployments gave the model hierarchical structure. We adjusted for seasonal effects (rainy season in 2014, dry and rainy seasons in 2015), mean forest cover (Hansen et al., 2013), distance to nearest road, and sampling effort, calculated as the product of camera deployment duration and detection distance, measured in meter-days (Ramirez et al., 2023). Each of the continuous covariates was log-transformed. The factorial covariate, season, allows for the possibility that species counts may vary systematically across yearly wet and dry periods, and the logarithm of effort adjusts for the effect of differing deployment durations and detection distances among cameras. Additionally, to check the sensitivity of the results to our choice of *camera deployment* as the key clustering variable for hierarchical structure, we fitted an alternative Poisson regression model with random intercepts for *lots* instead of for camera deployments. For both the primary and alternative models, we examined Pearson residual plots to check for goodness of fit.

To investigate how different plantation types were used by different species, we adopted a multispecies Royle–Nichols Occupancy Model (Royle & Nichols, 2003). Figure 2 shows the model graphically, following the approach of Hobbs and Hooten (2015), and Table 2 gives definitions of the variables, parameters and prior distributions. The observations used to fit the model are the number of sampling occasions per deployment during which each species was detected (i.e., the number of *successful occasions for each species*), out of the total number of occasions per deployment. For our model, an occasion was a 24-h day: this acknowledges the circadian rhythms of many mammal species and balances between animals that visited sites repeatedly during the day and/or night and those that visited less frequently. The detection probability was therefore the probability that a species was observed by a given camera within a 24-h day.

We included effects on local abundance of species and plantation types along with their interactions. Inclusion of these interactions allowed us to investigate the occupancy of each species in each plantation type. As in the model for species richness, we adjusted for mean forest cover (Hansen et al., 2013), distance to nearest road, detection distance, and seasonality. In the model, occupancy is defined for each species as the probability that the local abundance of the species is one individual or greater, given that the species occurs on the landscape (MacKenzie et al., 2002; Royle & Nichols, 2003). The occupancy model therefore concerns a species' use of the local area around a camera, in contrast to the local species richness. We coded the Royle–Nichols model in JAGS (Plummer, 2003), using the library *R2jags* (Su & Yajima, 2016). We sampled 260K iterations from four chains, thinning at 2000 iterations, after a burn-in of 10,000 iterations, to generate 500 posterior samples for inference. We used





**FIGURE 2** Graphical description of the occupancy model structure. At the data level,  $Y$  is the number of sampling occasions in which a given species was detected (i.e., the number of *successes*), and  $K$  is the number of sampling occasions for the camera. At the process level,  $P$  is the success probability per occasion,  $\Psi$  is the occupancy probability,  $A$  and  $W$  are latent variables for the local abundance and presence or absence of the species, respectively.  $r$ ,  $\lambda$ , and  $\Omega$  are parameters of the process-level variables  $P$ ,  $A$ , and  $W$ , respectively. At the effects level,  $U_{\text{species}}$ ,  $U_{\text{camera}}$ , and  $U_{\text{season}}$  are effects of species, camera and season on the detection probability, and log detection distance is an offset.  $V_{\text{camera}}$ ,  $V_{\text{species}}$ ,  $V_{\text{plantation}}$ , and  $V_{\text{plantation*species}}$  are effects of camera, species, plantation, and the interaction of plantation and species, on the local abundance. Log distance to road and log forest cover are camera-specific predictors of local abundance. Finally,  $\tau_r$ ,  $\tau_\lambda$ , and  $\mu_{\text{species}}$  are parameters of the prior distributions for  $U_{\text{camera}}$ ,  $V_{\text{camera}}$ , and  $V_{\text{species}}$ . Informative priors were created for  $V_{\text{species}}$  by varying  $\mu_{\text{species}}$  according to how common the species is in typical Panamanian lowland forests (Table S1). Regularizing priors were used for the remaining effects. Further details are found in Table S1.

diagnostic checks implemented in the *coda* library (Gelman-Rubin diagnostics; Plummer et al., 2006) and examined Pearson residuals from the model to check for mixing and goodness of fit. As for the Poisson regression model for species richness, we checked our assumptions about camera-level effects by fitting an alternative occupancy model, using random intercepts for lots,  $U_{\text{lot}}$  and  $V_{\text{lot}}$ , instead of  $U_{\text{camera}}$  and  $V_{\text{camera}}$  (Table 2, Figure 2), following this with the diagnostic checks mentioned above.

### 3 | RESULTS

#### 3.1 | Richness and composition

With a total sampling effort of 3165 camera-trapping days, we recorded 16 ground-dwelling mammals of 11 families (see Table S1 for record counts). Of these, two were large mammals, seven were

medium-sized, and seven small-sized, according to the classification of Peres (2000, see Table S1). The Central American agouti (*Dasyprocta punctata*), common opossum (*Didelphis marsupialis*), and paca (*Cuniculus paca*) were the most commonly observed species among all five plantation types. No species of mammals of local conservation concern (i.e., due to illegal hunting) were found (i.e., jaguar, puma, Baird's tapir, red-brocket deer, giant anteater, and collared peccary) (Meyer et al., 2020). Moreover, several species that are relatively common in protected forests of Central Panama, such as ocelot (*Leopardus pardalis*), red-brocket deer, white-tailed deer, collared peccary, and tayra (*Eira barbara*) (Meyer et al., 2015), were not detected.

Over all plantations combined, the accumulation curves flattened after a sampling effort of approximately 60 camera traps, 2000 days or 900 events (Figure 3). *Acacia* was the only plantation type for which accumulation curves flattened with all three measures of effort (10 camera traps, 300 days or 100 events), followed

$Y_{\text{species,camera,plantation,season}}$	Observed data: The number of sampling occasions in which a species was detected
$K_{\text{camera}}$	The number of sampling occasions for a given camera
$P_{\text{species,camera,plantation,season}}$	Success probability per occasion for a given species, camera, plantation, and season
$r_{\text{species,camera,season}}$	Detection probability per occasion for a given species, camera, and season
$A_{\text{species,camera,plantation}}$	Integer latent variable: local abundance for a given species, camera, and plantation
$\Psi_{\text{species,camera,plantation}}$	Occupancy: the probability that A is greater than or equal to one
$W_{\text{species}}$	Binary latent variable: the presence or absence of a given species on the landscape
$\lambda_{\text{species,camera,plantation}}$	Poisson parameter for A, the expected local abundance
$\Omega_{\text{species}}$	Probability of species presence on the landscape
U, V	Random effects of species, camera, season, and plantation on detection probability and local abundance, respectively
<i>Description of the distributions</i>	
$Y \sim \text{Binomial}(K, P); P = 1 - (1 - r)^{A + W}$	
$A \sim \text{Poisson}(\lambda)$	
$W \sim \text{Bernoulli}(\Omega)$	
$U_{\text{camera}} \sim \text{Normal}(0, 1/\tau_r^2)$	
$V_{\text{camera}} \sim \text{Normal}(0, 1/\tau_\lambda^2)$	
$V_{\text{species}} \sim \text{Normal}(\mu_{\text{species}}, 4)$	

TABLE 2 Data and parameters of the model.

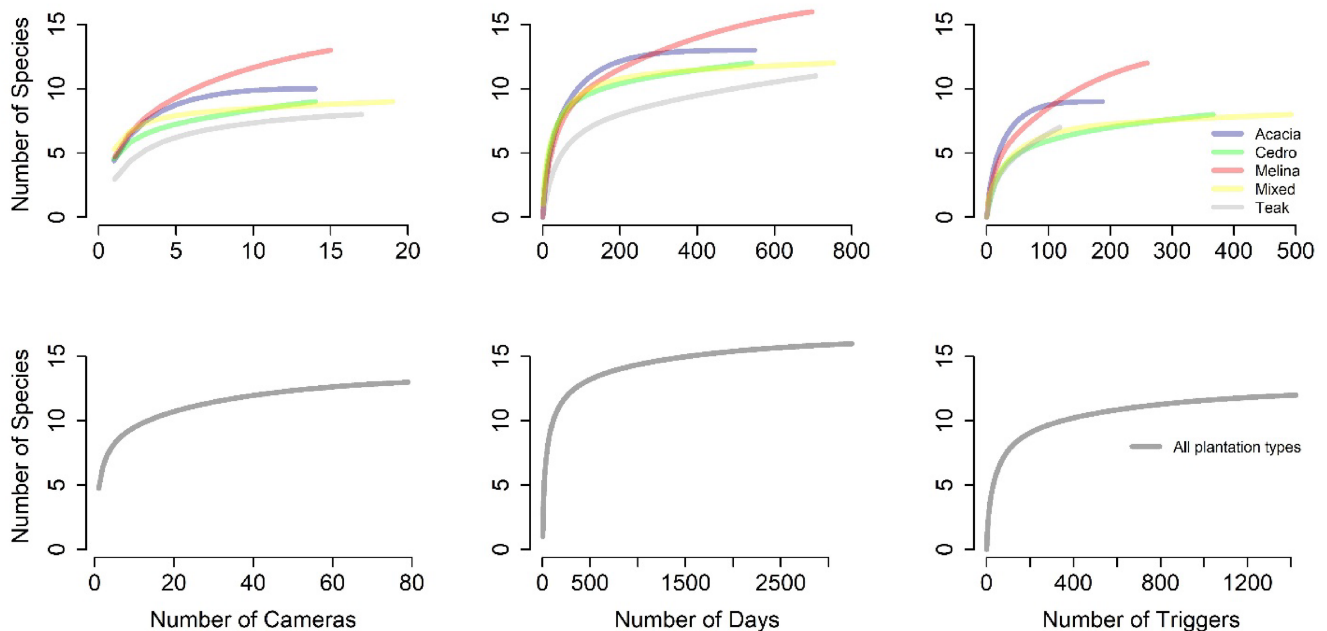


FIGURE 3 Rarefaction curves of mammal species richness based on camera trap data for five plantation types and all five plantations combined at ARGOS, Central Panama. Curves shown are based on the number of camera stations at each plantation type, total number of surveyed days and number of events produced by all non-volant mammals.

by the Mixed plantation, where accumulation curves nearly flatten at the maximum effort under this study. Despite a similar sampling effort, Cedro, Melina, and Teak had so few captures that accumulation curves did not flatten.

The empirical species richness over all cameras—the count of unique species occurrences—was highest in Melina ( $S=16$ ), followed by Acacia ( $S=13$ ), Cedro ( $S=12$ ), Mixed ( $S=12$ ), and Teak ( $S=11$ ). These counts are not adjusted for covariates. Based on the

Poisson regression model, Cedro, Mixed, and Melina had the highest average species richness per camera and were broadly similar (Figure 4). Teak had the lowest richness per camera, where the majority (15 out of 17) of the cameras detected just three or fewer species. Species counts were highly variable across cameras (Figure 4), and estimated average counts were not dramatically different. The overlap between confidence intervals was noticeable, indicating uncertainty about the differences between plantation types. The alternative model using *lot* as the clustering variable for hierarchical structure produced qualitatively the same results (Figure S1) as our primary model.

### 3.2 | Occupancy

Species' occupancy probabilities—broadly, the chance that at least one individual of a given species inhabits the area near a camera—were very heterogeneous across plantations, and ranged from  $\psi=0.016$  for the greater grison to  $\psi=0.991$  for the common opossum (Table 3, Figure 5). The common opossum had the highest occupancy probabilities in all plantation types except Cedro. Most species' occupancy probabilities were below 0.5 at any given plantation. Across all species, Teak had the lowest occupancy

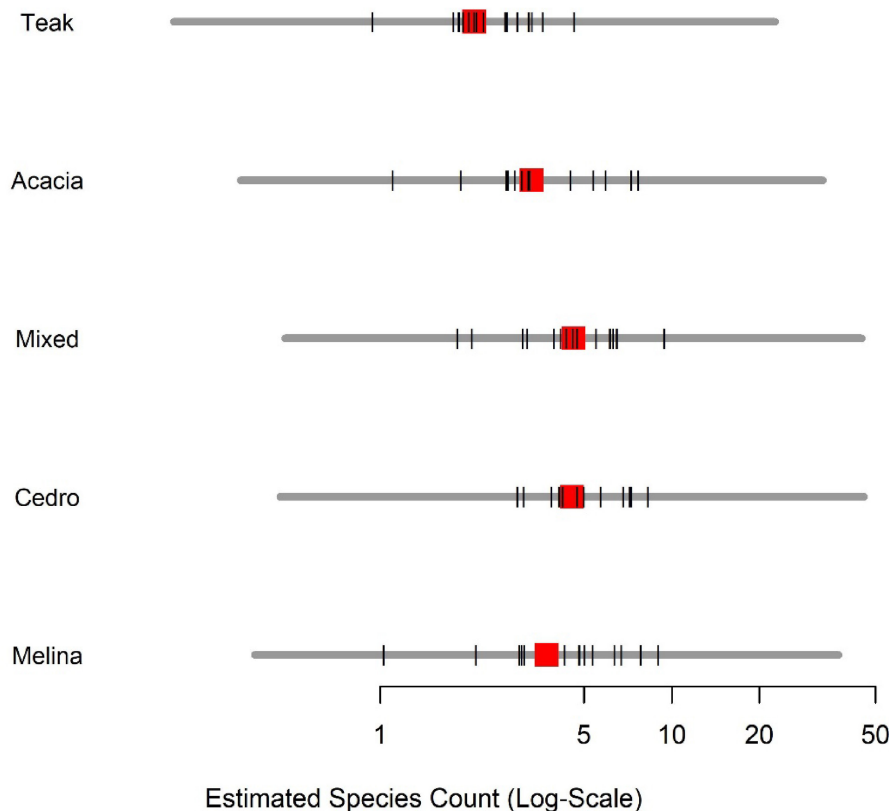
probabilities, where only the nine-banded long-nosed armadillo (*Dasypus novemcinctus*), the common opossum and the forest rabbit (*Sylvilagus brasiliensis*) had occupancy probabilities above 0.5. In contrast, in Cedro, agouti, brown four-eyed opossum (*Metachirus nudicaudatus*), common opossum, forest rabbit, nine-banded long-nosed armadillo, northern tamandua (*Tamandua mexicana*), paca and white-nosed coati had occupancy probabilities above 0.5.

Overall, the estimated detection probabilities were below 0.05 for all ground-dwelling mammal species except agouti and paca (Table 3, Figure S2). Detection probabilities ranged from  $r=0.007$  for the northern tamandua to  $r=0.088$  for agouti.

As for the species richness model, the alternative occupancy model using *lot* as the clustering variable for hierarchical structure produced qualitatively the same results (Figures S3 and S4).

## 4 | DISCUSSION

Reforestation projects in the tropics often consist of plantations, typically monocultures, of non-native timber species (Hall et al., 2011; Sinacore et al., 2022). It has been questioned whether such plantations are suitable as wildlife habitat or corridors. This study took advantage of an informal natural experiment to assess species richness



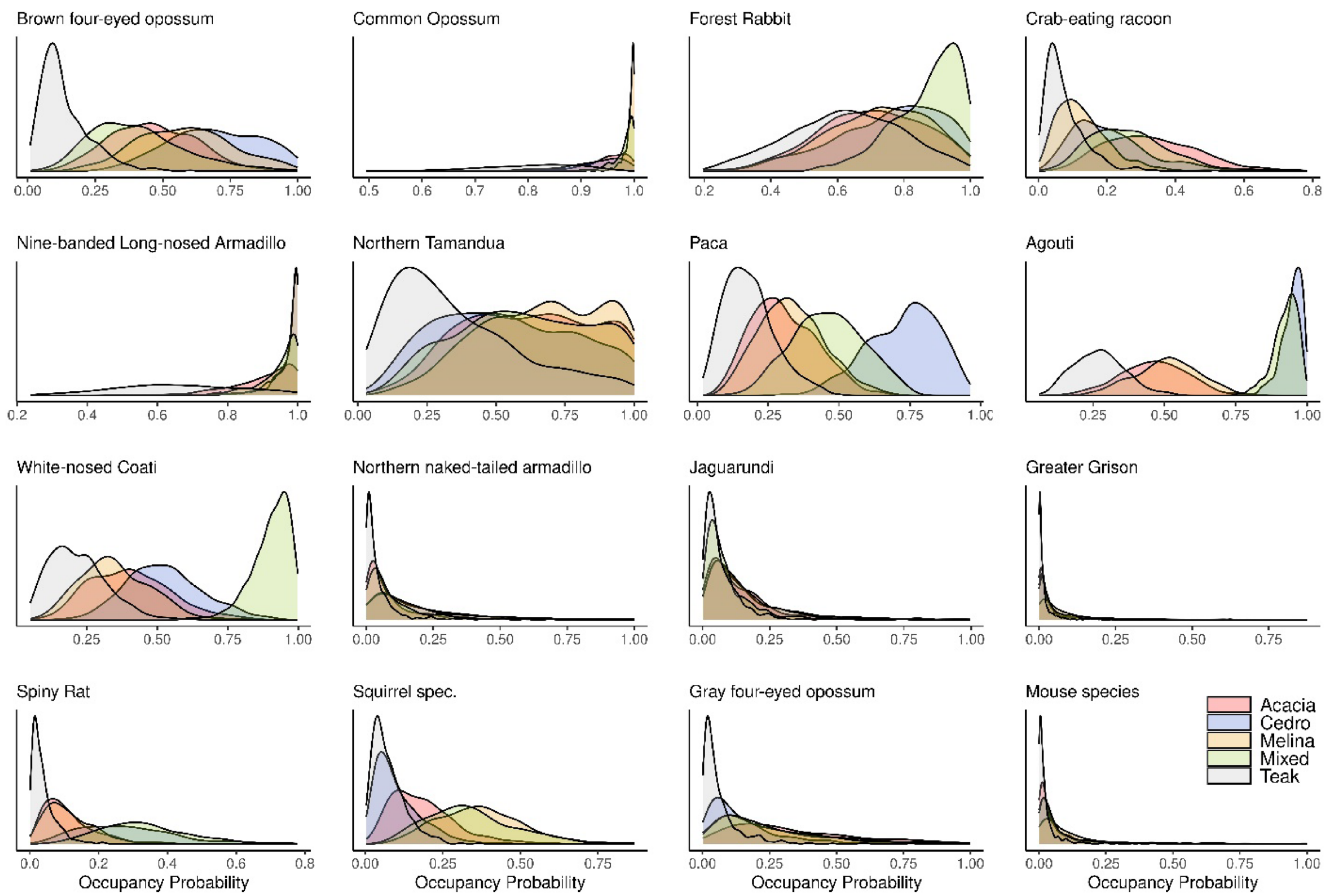
**FIGURE 4** Model estimates for species richness, along with empirical richness captured by each camera station (vertical tick marks), for five plantation types. The red squares show the estimated mean richness per camera in each plantation type on a log-scale, and the gray horizontal lines give 95% confidence intervals for the means. Estimates are for the rainy season of 2015, assuming a sampling effort of 150m-days, forest canopy cover 80%, and distance to the nearest road 450m. Vertical marks show the number of unique species observed over the sampling period at each camera station. The species counts have been numerically jittered to prevent overstrikes in the graph.



**TABLE 3** Estimates of occupancy probability (SD) for all ground-dwelling mammals in five timber plantation types at Argos, Central Panama, and overall detection probability (SD) per species.

Species	Occupancy probability ( $\Psi$ )					Detection probability ( $r$ )
	Acacia	Cedro	Melina	Mixed	Teak	All plantations
Agouti	0.464 (0.119)	0.946 (0.038)	0.510 (0.113)	0.924 (0.044)	0.272 (0.089)	0.088 (0.014)
Brown four-eyed opossum	0.466 (0.161)	0.694 (0.168)	0.583 (0.172)	0.406 (0.172)	0.136 (0.091)	0.023 (0.008)
Common opossum	0.946 (0.045)	0.921 (0.062)	0.991 (0.013)	0.981 (0.022)	0.809 (0.091)	0.029 (0.007)
Crab-eating racoon	0.331 (0.133)	0.211 (0.118)	0.131 (0.08)	0.268 (0.118)	0.076 (0.06)	0.04 (0.013)
Forest rabbit	0.703 (0.157)	0.759 (0.159)	0.719 (0.155)	0.871 (0.1)	0.626 (0.166)	0.014 (0.005)
Gray four-eyed opossum	0.336 (0.229)	0.167 (0.173)	0.257 (0.214)	0.248 (0.195)	0.065 (0.083)	0.01 (0.007)
Greater grison	0.039 (0.068)	0.053 (0.094)	0.087 (0.121)	0.045 (0.068)	0.016 (0.03)	0.014 (0.015)
Jaguarundi	0.143 (0.144)	0.159 (0.158)	0.146 (0.133)	0.094 (0.099)	0.071 (0.082)	0.017 (0.013)
Mouse species	0.061 (0.095)	0.082 (0.134)	0.140 (0.189)	0.081 (0.128)	0.031 (0.059)	0.021 (0.023)
Nine-banded long-nosed armadillo	0.902 (0.096)	0.967 (0.052)	0.969 (0.043)	0.944 (0.066)	0.661 (0.176)	0.013 (0.005)
Northern naked-tailed armadillo	0.103 (0.139)	0.184 (0.179)	0.195 (0.199)	0.107 (0.128)	0.051 (0.086)	0.009 (0.009)
Northern tamandua	0.625 (0.236)	0.542 (0.248)	0.670 (0.22)	0.610 (0.241)	0.355 (0.233)	0.007 (0.005)
Paca	0.306 (0.115)	0.726 (0.125)	0.334 (0.115)	0.462 (0.126)	0.183 (0.089)	0.051 (0.011)
Spiny rat	0.186 (0.106)	0.106 (0.08)	0.370 (0.136)	0.340 (0.144)	0.075 (0.053)	0.042 (0.013)
Squirrel species	0.132 (0.099)	0.344 (0.160)	0.151 (0.094)	0.315 (0.116)	0.054 (0.048)	0.037 (0.011)
White-nosed coati	0.404 (0.141)	0.525 (0.133)	0.351 (0.123)	0.904 (0.067)	0.219 (0.099)	0.031 (0.008)

Note: Occupancy probabilities assumed a road distance of 450m, a forest cover of 80%, and detection probabilities assumed a detection distance of 4.5m.



**FIGURE 5** Posterior densities of occupancy probabilities for each species and plantation type at ARGOS, Central Panama. In each graph, the horizontal axis gives the probability that the local abundance of the species is one or greater. The probabilities were estimated assuming that forest canopy cover is 80% and distance to the nearest road is 450m.

and occupancy of ground-dwelling mammals in five plantation types in Central Panama, the American continent's biological bottleneck. The community composition of mammals (i.e., small-bodied mammal species) in this area was characteristic of disturbed forest fragments rather than protected forests (Meyer et al., 2015), and no species of conservation concern were found. The habitat features driving this similarity to forest fragments are understudied, but could include properties such as the quality of the patch matrix and/or patch size. Overall, our findings indicate that these plantation types may provide ecologically constrained habitats for the ground-dwelling mammals of Central Panama.

#### 4.1 | Species richness

Species counts obtained from camera traps do not distinguish whether individuals inhabit the plantations or are merely passing through them. Nevertheless, across all ARGOS plantation types, the observed species richness and composition of terrestrial mammals ( $S=16$ ) was fairly similar to that of forest fragments surveyed with camera traps (Meyer et al., 2015) at distances less than 10km from ARGOS. In contrast to nearby protected forest (Meyer et al., 2015), such as Soberania National Park and Barro Colorado Nature Monument, species richness was relatively lower at ARGOS and the composition was markedly different. Species that are relatively common in the protected forests of Central Panama, such as ocelot, red-brocket deer, white-tailed deer, collared peccary, and tayra (Meyer et al., 2015), were not detected at ARGOS.

In our survey, 14 out of 16 species were small to medium-bodied generalist mammals, characterized by their broad niche tolerance (Pacifici et al., 2020). What are features that promote, and those that constrain, mammals' presence at timber plantations? This question is of particular interest to improve sustainable practices on monoculture plantations. Some studies have identified a number of extrinsic factors that positively contributed to species richness (i.e., percent of forest, lezzi et al., 2020; Pardo et al., 2018; canopy cover, Pardo et al., 2018; Piña et al., 2019; understory vegetation, Pardo et al., 2018; and age, lezzi et al., 2020), others found negative effects (i.e., livestock; lezzi et al., 2020; Pardo et al., 2018), and no effect (i.e., age, Piña et al., 2019; and distance to patch and tree height, Pardo et al., 2018). These mixed results suggest a context-dependent scenario and warrant attention, especially when timber plantations are embedded in geographically narrow landscapes (i.e., Isthmus of Central America). Similarly, the low number of carnivore observations in our results (Table S1), as well as in previous studies of timber plantations (i.e., Pardo et al., 2018; Piña et al., 2019), or fragmented patches of native forests (Meyer et al., 2015), could be explained by different trade-offs such as human-related risks (i.e., hunting), low prey availability, and landscape features (i.e., permeability and plantation size). However, additional studies will be required to understand how animals use timber plantations and navigate landscape mosaics containing them.

Despite a sustained sampling effort in this study, we documented relatively lower species richness in Teak ( $S=11$ ), compared to the

other plantation types at ARGOS. For instance, plantations of Melina and Cedro at ARGOS are, respectively, 20 and 4 times smaller than the Teak plantation, and their average species richness per camera (Figure 4) was nearly three times greater than Teak. However, the wide confidence intervals in our species richness model (Figure 4) beg caution in the interpretation of our results. The Teak plantations at ARGOS were also outperformed, with respect to species richness of mammals, by forest fragments that are 2–65 times smaller (Meyer et al., 2015), located in the same landscape mosaic. Similarly, a contemporaneous study at ARGOS found that species richness of butterflies was two times greater in Cedro than in Teak (Basset et al., 2017). Other studies, both in Neotropical and Pantropical landscapes, have also reported lower community diversity in Teak plantations for birds (Bennett et al., 2018; Didas et al., 2022; Lamb, 1998), anurans (Hinde et al., 2001), and mammals (Bonnington et al., 2009).

Factors that potentially limit the performance of Teak as wildlife habitat include plantation age, proximity to natural forest, low food resources availability, and canopy openness (Harikrishnan et al., 2012; Healey & Gara, 2003; Jenkins et al., 2003). Additionally, fire is potentially the most common understory management practice in Teak plantations (Idrees et al., 2021; Kaosa-ard, 1995), and this may create structural differences contributing to lower species captures. For instance, during this study, fire occurred in two out of the five Teak plantations at ARGOS.

Teak's performance as a species harbor is of particular concern for conservation, because monocultures of this exotic timber species are the most common type of plantation in the Panama Canal Watershed (Emanuelli et al., 2017; Heckadon-Moreno, 1999) and in Central America (Kollert & Cherubini, 2012). For instance, in Panama, Teak monocultures account for as much as 65% of the timber plantations (ANAM, 2008). Definitive claims about how ground-dwelling mammals fare in Teak plantations are difficult to make, and there is a need to investigate whether Teak plantations allow or constrain ecosystem functioning, especially in countries where Teak-growing exceeds 5000m<sup>3</sup>/year (i.e., Costa Rica, Panama, Colombia, and Ecuador) (Kollert & Walotek, 2015) and which are biodiversity hotspots (Raven et al., 2020).

#### 4.2 | Occupancy and detection

Our methods cannot distinguish between persistent and ephemeral uses of these plantations. On the one hand, the small home ranges of most detected species, except for greater grison (*Galictis vittata*) and jaguarundi (*Herpailurus yagouaroundi*), are more or less the same sizes as these plantations. On the other hand, the mere presence of the detected species in these plantations supports their viability as corridors and/or temporary refuges, though the network of roads and human settlements embedded in the landscape, as well as distances greater than 9km to natural forests, might represent obstacles to migration.

It is possible that our study missed some rare species, even though we used 15–19 cameras per plantation type, which is near the

threshold for obtaining precise occupancy estimates of common species (i.e., those with true occupancy greater than 0.75) in small-scale tropical studies as suggested by Kays et al. (2020). Of the common forest mammals in Central Panama, only paca, white-nosed coati, agouti, and nine-banded long-nosed armadillo had confidently high occupancies at ARGOS. Notably, species expected to inhabit, and exhibit a relatively high occupancy in, a functional forest in Central Panama such as ocelot, collared peccary, and white-tailed deer (see Figure 5, Meyer et al., 2015), were not detected at ARGOS. For the rest of the recorded common species of Central Panama (Meyer et al., 2015), most of their occupancy values at ARGOS were below 0.40, and for all of them the lowest values were in the Teak plantation.

The mammal community at ARGOS is distinctly different from that of nearby natural forests (see Meyer et al., 2015), with more species of disturbed and open landscapes. Species uncommon in natural habitats—such as the common opossum and the forest rabbit (Kays et al., 2009; Meyer et al., 2015; Tobler et al., 2015)—appear to be relatively common in the ARGOS plantations. In fact, the occupancy estimates were above 0.750 for the common opossum in all plantation types, and for the forest rabbit in Cedro, Melina, and Mixed (Table 3).

The relatively high occupancy estimates of the common opossum, which is reported to be more terrestrial than arboreal (Adler et al., 2012), could be explained by a noted reduction in canopy connectivity and lianas in these plantations (Basset et al., 2017). However, the common opossum is understood to have high behavioral flexibility and has been frequently observed in forest fragments (Meyer et al., 2015; Urquiza-Haas et al., 2009). Although forest rabbit is not commonly observed via camera traps (Kays et al., 2009; Meyer et al., 2015), this herbivore-grazer exhibited relatively high occupancy at ARGOS, perhaps because the open canopy of the plantation created favorable conditions for grass growth (Basset et al., 2017; Parrotta & Knowles, 1999).

The mammal community of the ARGOS plantations was also functionally different from nearby lowland tropical forests, including Soberania National Park and Barro Colorado Nature Monument (see Meyer et al., 2015). Of the seven recorded frugivore-granivore and frugivore-omnivore species (paca, agouti, common opossum, white-nosed coati, spiny rat, crab-eating raccoon (*Procyon cancrivorus*), and squirrels (*Sciurus* spp.)) that are important for forest ecosystem services including seed dispersal (Medellin, 1994; Mittelman et al., 2021; Quintela et al., 2014; Wright et al., 2000), only the common opossum had relatively high occupancy estimates ( $\psi > 0.750$ ) in all plantation types. Occupancy estimates of agouti—the most common frugivore-granivore (Robinson & Redford, 1986) in Central Panama—were generally two to three times lower in the plantations at ARGOS than on Barro Colorado Island (Kays et al., 2020).

Detection probability ( $r$ ) estimates were lower than 0.04 for most species at ARGOS, suggesting that animals did not return to the same locations with much regularity. The only two species with detection probability  $> 0.05$  were agouti ( $r = 0.088$ ;  $SD = 0.014$ ) and paca ( $r = 0.051$ ;  $SD = 0.011$ ). Nevertheless, the detection probabilities for agouti and paca were two to three times lower at the ARGOS plantations than in the Peruvian Amazon (Tobler et al., 2015), and detection

probabilities for agouti, armadillo, paca, and coati were four or more times lower at ARGOS than at Volcan Barva, a natural habitat in Costa Rica (Ahumada et al., 2013). Two possible explanations for infrequent detections are that species required the use of the whole plantation to gather enough resources for survival, or that the plantations are used as corridors and/or temporary refuges. Indeed, to affirm that animals are resident in timber plantations, tracking individuals (i.e., GPS and/or capture-recapture) would be necessary.

We recorded three elusive species—jaguarundi, greater grison and northern naked-tailed armadillo—at low frequencies (Table S1). Given the life histories of jaguarundi and greater grison (i.e., home ranges and rareness; Escobar-Lasso & Guzmán-Hernández, 2014; Giordano, 2016; Kasper et al., 2016; Yensen & Tarifa, 2003), we suggest that these species might be using the ARGOS plantation as a corridor. Conversely, the highly fossorial northern naked-tailed armadillo (Abba & Superina, 2010) may be resident.

### 4.3 | Limitations

Camera trapping is a highly efficient method for surveying ground-dwelling mammals in natural habitats (Kays et al., 2020; Si et al., 2014; Tobler et al., 2008). However, despite global increases in plantation land cover (FAO, 2020; Keenan et al., 2015), there is little guidance on how to conduct species inventories in these human-modified landscapes, which vary greatly in size, age, management, proximity to native forest and other characteristics.

Our cumulative sampling effort across all plantation types was sufficient to obtain a representation of the ground-dwelling mammal community at ARGOS as a whole (Figure 3, bottom row), but not for each plantation type separately. This challenge may be typical of fragmented areas (Meyer et al., 2015). Because of the variation in rarefaction curves, the low number of events (Table S1), and bearing in mind the guidelines in Kays et al. (2020) in the context of occupancy estimation, more extensive sampling is advisable in future surveys of monoculture plantations, as even common species may take longer to appear.

Our observations of species occurrence were taken from camera deployments randomized in space and time, mitigating spatiotemporal biases that have been shown to arise from relatively opportunistic or unplanned data collection efforts (Birsan et al., 2017). The hierarchical models used here furthermore adjusted for the level of replication afforded by repeated deployments within plantation types. Although our study benefited from replication within plantations, all of the plantations were in the same location (i.e., ARGOS) and thus replication at the landscape level is lacking. Our study was further limited in the range of biophysical covariates that could be feasibly incorporated: potentially useful covariates include distance from camera to water, food availability, time since the last controlled burn, and a fine-scale measure of human impact. For instance, we photographed some poachers in the area, however, our sampling method, deploying off-trail camera traps, does not provide data that are adequate for investigation of the effects of poaching on animal



habitat use. Finally, we did not observe predominantly arboreal species with our ground camera traps. Therefore, our findings represent a restricted snapshot of tropical forest biodiversity.

Our study suggests that timber plantations are inadequate harbors for large-bodied mammals in Central Panama – a biogeographical bottleneck—especially those of conservation concern (i.e., jaguar, puma, ocelot, collared peccary, tapir, and red-brocket deer). Especially Teak—the most common plantation type in Central America (Kollert & Cherubini, 2012)—had a low value to mammals in terms of both species' richness and composition. However, our limited spatial scope within the landscape begs caution when interpreting our results. A problem for estimating the value of timber plantations to wildlife conservation, is that they vary greatly in size, location, species composition, and management practices, making replication difficult. For instance, while many plantations (i.e., Teak) are blocks of ~100 hectares, others, farmed via concessions, are in the range of >1000 hectares. Furthermore, some timber plantations are adjacent to natural forests, while others are embedded in landscape mosaics. Thus, data from unreplicated timber plantation surveys must be interpreted with caution: wildlife found in plantations adjacent to forests might be a consequence of source-sink effects; while those found in plantations located away from forests might be a result of colonization (Leibold et al., 2004). Broader-scale studies at a variety of locations are needed to shed light on the conservation value of plantations.

#### AUTHOR CONTRIBUTIONS

Conceptualization: CMM, PAJ, and JSH; Data curation: CMM, and MNG; Formal analysis: CMM, MNG, and PAJ; Funding acquisition: JSH and CMM; Investigation: CMM and PAJ; Methodology: CMM, MNG, and PAJ; Project administration: CMM, PAJ, and JSH; Resources: JSH and PAJ; Software: CMM and MNG; Supervision: PAJ and JSH; Validation: CMM and MNG; Visualization: CMM and MNG; Writing—original draft: CMM and MNG; Writing—review and editing: All authors.

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#### CONFLICT OF INTEREST STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

#### DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in Mendeley Data at DOI:[10.17632/88p8dhjthv.1](https://doi.org/10.17632/88p8dhjthv.1).

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#### REFERENCES

- Abba, A. M., & Superina, M. (2010). The 2009/2010 armadillo red list assessment. *Edentata*, 11(2), 135–184.
- Adler, G. H., Carvajal, A., Davis-Foust, S. L., & Dittel, J. W. (2012). Habitat associations of opossums and rodents in a lowland forest in French Guiana. *Mammalian Biology*, 77(2), 84–89.
- Agha, M., Batter, T., Bolas, E. C., Collins, A. C., Gomes da Rocha, D., Monteza-Moreno, C. M., Preckler-Quisquater, S., & Sollmann, R. (2018). A review of wildlife camera trapping trends across Africa. *African Journal of Ecology*, 56(4), 694–701.
- Ahumada, J. A., Hurtado, J., & Lizcano, D. (2013). Monitoring the status and trends of tropical forest terrestrial vertebrate communities from camera trap data: A tool for conservation. *PLoS One*, 8(9), e73707.
- Almeida-Maués, P. C., Bueno, A. S., Palmeirim, A. F., Peres, C. A., & Mendes-Oliveira, A. C. (2022). Assessing assemblage-wide mammal responses to different types of habitat modification in Amazonian forests. *Scientific Reports*, 12(1), 1797.
- Autoridad Nacional del Ambiente (ANAM). (2008). Plan Nacional de Desarrollo Forestal: Modelo Forestal Sostenible.
- Basset, Y., Barrios, H., Ramirez, J. A., Lopez, Y., Coronado, J., Perez, F., Arizala, S., Bobadilla, R., & Leponce, M. (2017). Contrasting the distribution of butterflies and termites in plantations and tropical forests. *Biodiversity and Conservation*, 26(1), 151–176.
- Bennett, R. E., Leuenberger, W., Bosarreyes Leja, B. B., Sagone Caceres, A., Johnson, K., & Larkin, J. (2018). Conservation of Neotropical migratory birds in tropical hardwood and oil palm plantations. *PLoS One*, 13(12), e0210293.
- Bîrsan, C. C., Iosif, R., Székely, P., & Cogălniceanu, D. (2017). Spatio-temporal bias in the perceived distribution of the European pond turtle, *Emys orbicularis* (Linnaeus, 1758), in Romania. *Acta Zoologica Bulgarica*, 2017, 37–41.
- Bonnington, C., Weaver, D., & Fanning, E. (2009). The use of teak (*Tectona grandis*) plantations by large mammals in the Kilombero Valley, southern Tanzania. *African Journal of Ecology*, 47(2), 138–145.
- Carle, J., Vuorinen, P., & Del Lungo, A. (2002). Status and trends in global forest plantation development. *Forest Products Journal*, 52(7/8), 12–23.
- Casaer, J., Milotic, T., Liefting, Y., Desmet, P., & Jansen, P. (2019). *Agouti: A platform for processing and archiving of camera trap images*. Biodiversity Information Science and Standards.
- Chazdon, R. L. (2008). Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science*, 320(5882), 1458–1460.
- Coelho, M., Juen, L., & Mendes-Oliveira, A. C. (2014). The role of remnants of Amazon savanna for the conservation of Neotropical mammal communities in eucalyptus plantations. *Biodiversity and Conservation*, 23, 3171–3184. <https://doi.org/10.1007/s10531-014-0772-9>
- Craig, P., Katikireddi, S. V., Leyland, A., & Popham, F. (2017). Natural experiments: An overview of methods, approaches, and contributions to public health intervention research. *Annual Review of Public Health*, 38, 39–56.

- Daily, G. C., Ceballos, G., Pacheco, J., Suzán, G., & Sánchez-Azofeifa, A. (2003). Countryside biogeography of neotropical mammals: Conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology*, 17(6), 1814–1826.
- Didas, N. G., Geoffrey, S., & Kirari, M. P. (2022). Effects of the establishment of large-scale teak plantations on bird assemblages in Kilombero Valley, Tanzania. *Sustainability and Biodiversity Conservation*, 1(1), 25–41.
- Emanuelli, P., Milla, F., Szejner, M., & Vergara, L. (2017). *Diseño del Inventario Forestal Multipropósito en la Cuenca del Canal de Panamá*.
- Escobar-Lasso, S., & Guzmán-Hernández, C. F. (2014). El registro de mayor altitud del Hurón Mayor *Galictis vittata*, con notas sobre su presencia y conservación dentro del departamento de Caldas, en la región andina de Colombia. *Therya*, 5(2), 567–574.
- Fagan, M. E., Kim, D. H., Settle, W., Ferry, L., Drew, J., Carlson, H., Slaughter, J., Schaferbien, J., Tyukavina, A., Harris, N. L., Goldman, E., & Ordway, E. M. (2022). The expansion of tree plantations across tropical biomes. *Nature Sustainability*, 5(8), 681–688.
- Food and Agriculture Organization of the United Nations (FAO). (2020). *Global Forest Resources Assessment 2020: Main report*.
- Giordano, A. J. (2016). Ecology and status of the jaguarundi *Puma yagouaroundi*: A synthesis of existing knowledge. *Mammal Review*, 46(1), 30–43.
- Grilo, C., Bissonette, J. A., & Cramer, P. C. (2010). In S. R. Jones (Ed.), *Mitigation measures to reduce impacts on biodiversity*. Construction, Management, and Maintenance. Nova Science Publisher's.
- Hall, J. S., Ashton, M. S., Garen, E. J., & Jose, S. (2011). The ecology and ecosystem services of native trees: Implications for reforestation and land restoration in Mesoamerica. *Forest Ecology and Management*, 261, 1553–1557.
- Hall, J. S., Cerezo, A., & Entem, A. (2015). Managing the Panama Canal watershed. In V. Kirn & E. Yanguas-Fernandez (Eds.), *Hall, J.S* (pp. 92–106). *Managing Watersheds for Ecosystem Services in the Steepland Neotropics*.
- Hall, J. S., Murgueitio, E., Calle, Z., Raudsepp-Hearne, C., Stallard, R. F., & Balvanera, P. (2015). Implications of climate and land use change. In V. Kirn & E. Yanguas-Fernandez (Eds.), *Hall, J.S* (pp. 58–66). *Managing Watersheds for Ecosystem Services in the Steepland Neotropics*.
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, 342(6160), 850–853. <https://glad.earthengine.app/view/global-forest-change>
- Harikrishnan, S., Vasudevan, K., Udhayan, A., & Mathur, P. K. (2012). Biodiversity values of abandoned teak, *Tectona grandis* plantations in southern Western Ghats: Is there a need for management intervention? *Basic and Applied Ecology*, 13(2), 139–148.
- Healey, S. P., & Gara, R. I. (2003). The effect of a teak (*Tectona grandis*) plantation on the establishment of native species in an abandoned pasture in Costa Rica. *Forest Ecology and Management*, 176(1–3), 497–507.
- Heckadon-Moreno, S. (1999). *La Cuenca del Canal: deforestación, urbanización y contaminación*.
- Hinde, R., Corti, G., Fanning, E., & Jenkins, R. K. (2001). Anurans in the Kilombero Valley, Tanzania: Comparison between miombo woodland, evergreen forest and teak plantations. *African Journal of Herpetology*, 50(1), 35–39.
- Hobbs, N. T., & Hooten, M. B. (2015). *Bayesian models: A statistical primer for ecologists*. Princeton University Press.
- Idrees, M. O., Folaranmi, D. B., Omar, D. M., Yusuf, A. G., & Babalola, A. (2021). Planted forest fire burn area and impact assessment using sentinel-2: Case study of the University of Ilorin Teak Plantation. *IOP Conference Series: Earth and Environmental Science*, 620(1), 012013.
- Iezzi, M. E., Cruz, P., Varela, D., De Angelo, C., & Di Bitetti, M. S. (2018). Tree monocultures in a biodiversity hotspot: Impact of pine plantations on mammal and bird assemblages in the Atlantic Forest. *Forest Ecology and Management*, 424, 216–227.
- Iezzi, M. E., De Angelo, C., & Di Bitetti, M. S. (2020). Tree plantations replacing natural grasslands in high biodiversity areas: How do they affect the mammal assemblage? *Forest Ecology and Management*, 473, 118303.
- Jenkins, R. K., Roettcher, K., & Corti, G. (2003). The influence of stand age on wildlife habitat use in exotic teak tree *Tectona grandis* plantations. *Biodiversity and Conservation*, 12, 975–990.
- Kanowski, J., Catterall, C. P., & Wardell-Johnson, G. W. (2005). Consequences of broadscale timber plantations for biodiversity in cleared rainforest landscapes of tropical and subtropical Australia. *Forest Ecology and Management*, 208(1–3), 359–372.
- Kaosa-ard, A. (1995). Management of Teak Plantations. In *In teak for the future proceedings of the second regional seminar on teak*. Teaknet publication (No. 1).
- Kasper, C. B., Schneider, A., & Oliveira, T. G. (2016). Home range and density of three sympatric felids in the southern Atlantic Forest, Brazil. *Brazilian Journal of Biology*, 76(1), 228–232.
- Kays, R., Arbogast, B. S., Baker-Whitton, M., Beirne, C., Boone, H. M., Bowler, M., Burneo, S. F., Cove, M. V., Ding, P., Espinosa, S., & Gonçalves, A. L. S. (2020). An empirical evaluation of camera trap study design: How many, how long and when? *Methods in Ecology and Evolution*, 11(6), 700–713.
- Kays, R., Kranstauber, B., Jansen, P., Carbone, C., Rowcliffe, M., Fountain, T., & Tilak, S. (2009). Camera traps as sensor networks for monitoring animal communities. In *2009 IEEE 34th conference on local computer networks* (pp. 811–818). IEEE.
- Keenan, R. J., Reams, G. A., Achard, F., de Freitas, J. V., Grainger, A., & Lindquist, E. (2015). Dynamics of global forest area: Results from the FAO global Forest resources assessment 2015. *Forest Ecology and Management*, 352, 9–20.
- Kollert, W., & Cherubini, L. (2012). Teak resources and market assessment 2010. *FAO Planted Forests and Trees Working Paper FP/47/E*, Rome, 206.
- Kollert, W., & Walotek, P. J. (2015). Global teak trade in the aftermath of Myanmar's log export ban. *Planted Forests and Trees Working Paper*, 49(49), 20.
- Lamb, D. (1998). Large-scale ecological restoration of degraded tropical forest lands: The potential role of timber plantations. *Restoration Ecology*, 6(3), 271–279.
- Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., & Loreau, M. (2004). The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters*, 7(7), 601–613.
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8), 2248–2255.
- Medellin, R. A. (1994). Seed dispersal of *Cecropia obtusifolia* by two species of opossums in the Selva Lacandona, Chiapas, Mexico. *Biotropica*, 26, 400–407.
- Mendes-Oliveira, A. C., Peres, C. A., Maués, P. C. R. D. A., Oliveira, G. L., Mineiro, I. G., de Maria, S. L. S., & Lima, R. C. (2017). Oil palm monoculture induces drastic erosion of an Amazonian forest mammal fauna. *PLoS One*, 12(11), e0187650.
- Méndez-Carvajal, P. (2012). Estudio de diversidad de mamíferos en cuatro hábitats de transición asociados a una plantación de teca (*Tectona grandis*) dentro de la cuenca del canal de Panamá, Las Pavas, Chorrera, Panamá. *Tecnociencia*, 14(2), 55–83.
- Messier, C., Bauhus, J., Sousa-Silva, R., Auge, H., Baeten, L., Barsoum, N., Bruelheide, H., Caldwell, B., Cavender-Bares, J., Dhiedt, E., & Eisenhauer, N. (2021). For the sake of resilience and multifunctionality, let's diversify planted forests! *Conservation Letters*, 15(1), e12829.

- Meyer, N. F., Esser, H. J., Moreno, R., van Langevelde, F., Liefing, Y., Oller, D. R., Vogels, C. B., Carver, A. D., Nielsen, C. K., & Jansen, P. A. (2015). An assessment of the terrestrial mammal communities in forests of Central Panama, using camera-trap surveys. *Journal for Nature Conservation*, 26, 28–35.
- Meyer, N. F., Moreno, R., Sutherland, C., de la Torre, J. A., Esser, H. J., Jordan, C. A., Olmos, M., Ortega, J., Reyna-Hurtado, R., Valdes, S., & Jansen, P. A. (2020). Effectiveness of Panama as an intercontinental land bridge for large mammals. *Conservation Biology*, 34(1), 207–219.
- Mittelman, P., Dracxler, C. M., Santos-Coutinho, P. R., & Pires, A. S. (2021). Sowing forests: A synthesis of seed dispersal and predation by agoutis and their influence on plant communities. *Biological Reviews*, 96(6), 2425–2445.
- Monteza-Moreno, C. M., Crofoot, M. C., Grote, M. N., & Jansen, P. A. (2020). Increased terrestriality in a Neotropical primate living on islands with reduced predation risk. *Journal of Human Evolution*, 143, 102768.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., Simpson, G. L., Solyomos, P., Stevens, M. H. H., Wagner, H., & Oksanen, M. J. (2013). Package 'vegan'. *Community Ecology Package, Version*, 2(9), 1–295.
- Pacifici, M., Rondinini, C., Rhodes, J. R., Burbidge, A. A., Cristiano, A., Watson, J. E., Woinarski, J. C., & Di Marco, M. (2020). Global correlates of range contractions and expansions in terrestrial mammals. *Nature Communications*, 11(1), 2840.
- Pardo, L. E., Campbell, M. J., Edwards, W., Clements, G. R., & Laurance, W. F. (2018). Terrestrial mammal responses to oil palm dominated landscapes in Colombia. *PLoS One*, 13(5), e0197539.
- Parrotta, J. A., & Knowles, O. H. (1999). Restoration of tropical moist forests on bauxite-mined lands in the Brazilian Amazon. *Restoration Ecology*, 7(2), 103–116.
- Peres, C. A. (2000). Effects of subsistence hunting on vertebrate community structure in Amazonian forests. *Conservation Biology*, 14(1), 240–253.
- Piña, T. E., Carvalho, W. D., Rosalino, L. M. C., & Hilário, R. R. (2019). Drivers of mammal richness, diversity and occurrence in heterogeneous landscapes composed by plantation forests and natural environments. *Forest Ecology and Management*, 449, 117467.
- Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, 124(125.10), 1–10.
- Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: Convergence diagnosis and output analysis for MCMC. *R News*, 6(1), 7–11. <https://journal.r-project.org/archive/>
- Quintela, F. M., Iob, G., & Artioli, L. G. (2014). Diet of *Procyon cancrivorus* (Carnivora, Procyonidae) in restinga and estuarine environments of southern Brazil. *Iheringia. Série Zoologia*, 104, 143–149.
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Ramirez, J. I., Poorter, L., Jansen, P. A., den Ouden, J., Siewert, M., & Olofsson, J. (2023). Top-down and bottom-up forces explain patch utilization by two deer species and forest recruitment. *Oecologia*, 201(1), 229–240.
- Raven, P. H., Gereau, R. E., Phillipson, P. B., Chatelain, C., Jenkins, C. N., & Ulloa Ulloa, C. (2020). The distribution of biodiversity richness in the tropics. *Science Advances*, 6(37), eabc6228.
- Reid, F. A. (2009). *A field guide to the mammals of Central America and Southeast Mexico*. Oxford University Press.
- Robinson, J. G., & Redford, K. H. (1986). Body size, diet, and population density of Neotropical forest mammals. *The American Naturalist*, 128, 665–680.
- Rovero, F., Zimmermann, F., Berzi, D., & Meek, P. (2013). "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. *Hystrix*, 24(2), 9–17.
- Royle, J. A., & Nichols, J. D. (2003). Estimating abundance from repeated presence-absence data or point counts. *Ecology*, 84(3), 777–790.
- Sánchez-Londoño, J. D., Botero-Cañola, S., & Villada-Cadavid, T. (2021). Mamíferos silvestres en plantaciones forestales: ¿Una oportunidad para su conservación? *Caldasia*, 43(2), 343–353.
- Santangeli, A., Weigel, B., Antão, L. H., Kaarlejärvi, E., Hällfors, M., Lehtikoinen, A., Lindén, A., Salemaa, M., Tonteri, T., Merilä, P., & Saastamoinen, M. (2023). Mixed effects of a national protected area network on terrestrial and freshwater biodiversity. *Nature Communications*, 14, 5426. <https://doi.org/10.1038/s41467-023-41073-4>
- Si, X., Kays, R., & Ding, P. (2014). How long is enough to detect terrestrial animals? Estimating the minimum trapping effort on camera traps. *PeerJ*, 2, e374.
- Silva, L. N., Freer-Smith, P., & Madsen, P. (2019). Production, restoration, mitigation: A new generation of plantations. *New Forests*, 50(2), 153–168.
- Sinacore, K., García, E. H., Finkral, A., van Breugel, M., Lopez, O. R., Espinosa, C., Miller, A., Howard, T., & Hall, J. S. (2023). Mixed success for carbon payments and subsidies in support of forest restoration in the neotropics. *Nature Communications*, 14(1), 8359.
- Sinacore, K., García, E. H., Howard, T., van Breugel, M., Lopez, O. R., Finkral, A. J., & Hall, J. S. (2022). Towards effective reforestation: Growth and commercial value of four commonly planted tropical timber species on infertile soils in Panama. *New Forests*, 54(1), 125–142.
- Skaug, H., Fournier, D., Bolker, B., Magnusson, A., & Nielsen, A. (2013). Generalized linear mixed models using AD model builder. *R package version 0.7.7*.
- Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. *African Journal of Ecology*, 56(4), 740–749.
- Su, Y. S., & Yajima, M. (2016). R2jags: Using R to run JAGS; 2015. *R package version 0.5-7*. <https://CRAN.R-project.org/package=R2jags>
- Tobler, M. W., Carrillo-Percegué, S. E., Pitman, R. L., Mares, R., & Powell, G. (2008). An evaluation of camera traps for inventorying large- and medium-sized terrestrial rainforest mammals. *Animal Conservation*, 11(3), 169–178.
- Tobler, M. W., Zúñiga Hartley, A., Carrillo-Percegué, S. E., & Powell, G. V. (2015). Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *Journal of Applied Ecology*, 52(2), 413–421.
- Urquiza-Haas, T., Peres, C. A., & Dolman, P. M. (2009). Regional scale effects of human density and forest disturbance on large-bodied vertebrates throughout the Yucatán peninsula, Mexico. *Biological Conservation*, 142(1), 134–148.
- Verheyen, K., Vanhellemont, M., Auge, H., Baeten, L., Baraloto, C., Barsoum, N., Bilodeau-Gauthier, S., Brulheide, H., Castagnyrol, B., Godbold, D., & Haase, J. (2016). Contributions of a global network of tree diversity experiments to sustainable forest plantations. *Ambio*, 45(1), 29–41.
- Wang, C., Zhang, W., Li, X., & Wu, J. (2022). A global meta-analysis of the impacts of tree plantations on biodiversity. *Global Ecology and Biogeography*, 31(3), 576–587.
- Webb, J. A., Stewardson, M. J., & Koster, W. M. (2010). Detecting ecological responses to flow variation using Bayesian hierarchical models. *Freshwater Biology*, 55(1), 108–126.
- Wright, S. J., Zeballos, H., Domínguez, I., Gallardo, M. M., Moreno, M. C., & Ibáñez, R. (2000). Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical Forest. *Conservation Biology*, 14(1), 227–239.
- Yamazaki, D., Ikeshima, D., Tawatari, R., Yamaguchi, T., O'Loughlin, F., Neal, J. C., Sampson, C. C., Kanae, S., & Bates, P. D. (2017). A high-accuracy map of global terrain elevations. *Geophysical Research Letters*, 44(11), 5844–5853.



- Yensen, E., & Tarifa, T. (2003). *Galictis vittata*. *Mammalian Species*, 2003(727), 1–8.
- Zimmermann, F., & Rovero, F. (2016). *Camera trapping for wildlife research*. Pelagic Publishing Ltd.

### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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