



## Mammal diversity and composition are not affected by certified timber extraction in Suriname

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### ABSTRACT

Increasing knowledge of species occurrence and assemblage composition is crucial to uncover the impacts of human activities on biodiversity. Here we investigate the effects of certified selective logging on assemblages of medium- and large-sized mammals in central Suriname. Using camera traps set in logged and unlogged parts of two logging concessions, we estimated mammal richness and assemblage composition within them and compared the results to other sites across Suriname obtained from a literature search. Then, using Bayesian multi-species occupancy models, we investigated if selective logging affects the richness, composition, and probabilities of habitat use and detection of mammals in the study sites. We recorded 27 mammal species in total, of which four are threatened globally. The study areas were amongst the richest concerning mammalian diversity throughout Suriname in response to the larger sampling effort employed. However, assemblage composition was overall similar to other sites previously sampled in the country, with variation in species richness mainly driven by sampling effort. Species richness and assemblage composition were similar concerning logged and unlogged parts of the concessions. At the species level, only a minor influence was observed in the probabilities of detection and habitat use of mammals. Most species presented positive responses to logging status, i.e., increasing their detection and habitat use probabilities in logged sites. Therefore, we conclude that selective logging to the extent practiced in the managed sites may fulfill the criteria of sustainability. Due to the continuous nature of Suriname's landscape, which allows for a constant flow of species from managed to unmanaged sites, it may act as a buffer to hamper the secondary and indirect impacts of selective logging.

### 1. Introduction

To combine economic benefits, social justice, and ecosystem integrity, economic activities should strive to mitigate their environmental impact at a regional level (CBD, 2004; Dasgupta, 2021). Though applicable to all kinds of human activities, the Convention on Biological Diversity (CBD) is best known in the context of the exploitation of tropical forest products, particularly timber. Following the guidelines provided in the CBD, timber exploitation should follow the principles of

sustainable forest management, as laid down in standards and principles for certified timber extraction (FSC, 2015; PEFC, 2017) or in the International Tropical Timber Organization (ITTO) criteria and indicators for sustainable forest management (ITTO, 2016). An important component of forest management is selective logging, defined as the extraction of individual trees, typically targeting large hard-wooded species with commercial potential, leaving most of the canopy and residual vegetation standing (Bousfield et al., 2020). In contrast to other land-use activities, such as the conversion of forests to agricultural land or mining,

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selective logging holds some potential to combine economic benefits and biodiversity conservation (Burivalova et al., 2014; Johns, 1992; Polisar et al., 2017; Tobler et al., 2018).

Biodiversity conservation as well as certification of timber extraction require monitoring of the persisting biodiversity. Large vertebrates can provide crucial information on biodiversity status by serving as umbrella species and indicators of overall ecosystem functioning, especially in little-known systems (Lacher Jr. et al., 2019; Magioli et al., 2021; Terborgh, 1988), besides being widely impacted by defaunation (Dirzo et al. 2014). Another advantage of focusing on larger vertebrates is the

possibility of using methodologically feasible, standardized, and cost-effective sampling protocols based on camera traps (e.g., Carvalho Jr et al., 2021; Granados et al., 2016; Polisar et al., 2017; Sollmann et al., 2017; Tobler et al., 2018).

The tropical forests of South America keep declining despite international conventions aiming for their protection (Bullock et al., 2020; Stewart et al., 2020). In this regard, Suriname stands out as 93% of its land surface is still covered by forests. The annual deforestation rate is between 0.03 and 0.04 percent (MLTDE, 2012), which is very low compared to most other Amazonian countries (Peres et al., 2010). In

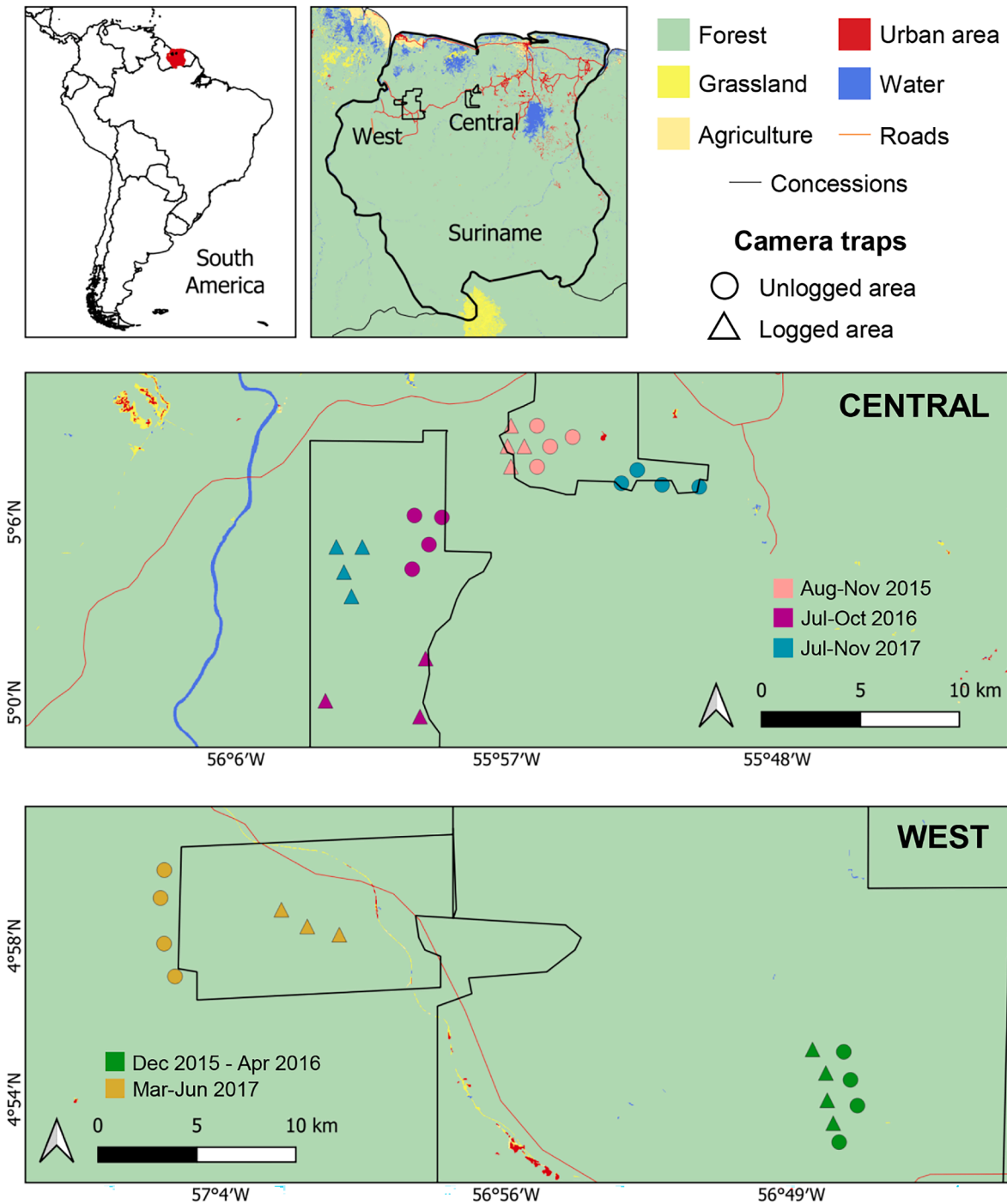


Fig. 1. Location of the camera traps at the logging concessions in Suriname depicting the main land use classes (MapBiomias Amazonia Project 2021). Colored symbols depict the location of the camera traps in logged (triangles) and unlogged parts (circles) per sampling campaign.

Suriname, about 4.5 million ha of lowland forest are categorized as production forests, including 2.8 million ha destined for timber extraction. Early on, the country applied the policy of sustainable forest management on the basis of “Reduced Impact Logging” (Playfair, 2007; Werger, 2011). Based on previous research, a permissible harvest rate of  $25 \text{ m}^3\text{ha}^{-1}$  (equivalent to 6–10 trees per ha) and a felling cycle of 25 years were assumed to allow sustainable revenue and biodiversity conservation, i.e., an annual growth rate of  $1 \text{ m}^3\text{ha}^{-1}$  (SBB, 2019; Tropenbos International, 2011). Logging concessions are issued only for the forest belt where timber extraction is permitted and is monitored by the local forest supervisory authority through the awarding and monitoring of concessions. These unique circumstances make Suriname’s forests a useful laboratory for the evaluation of the consequences of selective logging on mammals.

Assessments of the impacts of human activities on biodiversity, such as the effects of selective logging require basic knowledge of species occurrence and distribution. The Neotropical region holds an impressive amount of biodiversity, but there are still many gaps in our knowledge about their occurrence and distribution (Oliveira et al., 2016), a situation that is reflected in the small number of published studies on Suriname mammals, for example. Therefore, acquiring primary data through inventories and compiling the available information is crucial to increase knowledge on biodiversity and the impacts they are subject to, also serving as subsidies to local and regional conservation strategies.

Here, we investigate the effects of selective logging on assemblages of medium- and large-sized mammals of the lowland tropical rainforest in central Suriname. We rely on data from camera traps set in both logged and unlogged parts of two logging concessions in order to 1) estimate mammal richness and assemblage composition within concessions and compare those to results from other studies across Suriname, and 2) investigate whether or not selective logging affects the richness, composition, and probabilities of habitat use and detection of mammals as an indication of disturbance (MLTDE, 2012).

## 2. Materials and methods

### 2.1. Study site

The study was conducted in two logging concessions (Central and West) of the Greenheart operations in the tropical rainforest of central Suriname, northern South America (Fig. 1). The Central concession comprises a total area of 34,945 ha, and the West concession has an area of 137,022 ha (SBB, 2019), both located in lowland forests about 70 km inland. According to the Köppen classification, the Suriname climate is “Af” (Tropical Rainforest Climate), with a mean annual temperature is  $27.2^\circ\text{C}$  and annual rainfall amounts to 2225 mm. The climate is seasonal with most of the annual rainfall falling in a short-wet season from February to March and a long-wet season from August to November (Nurmohamed and Naipal, 2006). The concessions were certified by the Forest Stewardship Council during the time of the study. Selective logging occurred about one year before each camera trapping campaign. Logging intensity was between 4 and 7  $\text{m}^3/\text{ha}$ , which is below the logging intensity permitted by Suriname’s harvesting code of  $25 \text{ m}^3\text{ha}^{-1}$  of timber per hectare within a rotation interval of 25 years (SBB, 2011).

### 2.2. Camera trapping

We conducted five sampling campaigns from 2015 to 2017, three in the Central concession and two in the West concession, each comprising eight single-camera sampling stations distributed between unlogged and logged parts, totaling 38 stations (Fig. 1; missing stations in campaigns from Jul-Oct 2016 and Mar-Jun 2017 were due to camera failure). The average distance between stations at any site was 1.4 km and the minimum distance was 0.8 km. Camera traps (Bushnell Trophy Cam model 119636C) were installed on tree trunks, mostly at knee height, programmed to take three-photo bursts at one-second intervals once

triggered, and operate 24/h-day for an average of 90 days. The total sampling effort was 3,383 trap-days (West = 1,353; Central = 2,030).

### 2.3. Data analysis

We used specialized literature (Emmons and Feer, 1997; Oliveira and Cassaro, 2006) to identify medium (from 1 to 7 kg; Chiarello, 2000) and large-sized mammals ( $>7 \text{ kg}$ ; Emmons and Feer, 1997). We included small mammal species ( $<1 \text{ kg}$ ) that could be identified reliably (e.g., *Guerlinguetus aestuans*). We followed the list of the Brazilian Society of Mammalogy (Abreu et al., 2022) as a taxonomic authority and the IUCN Red List for threat categories (IUCN, 2022). All analyzes were performed in R 4.2.2 (R Core Team, 2022), and graphical implementation was done using the ggplot2 package (Wickham, 2016).

#### 2.3.1. Local and site-level comparisons

First, at the local level, we compared the observed species richness (excluding primates) between logging concessions using the Wilcoxon rank-sum test; data normality was assessed with the Shapiro-Wilk test. At the site level, in order to compare the species richness of our study sites with other sites across Suriname, we performed a literature search on Google Scholar and Web of Science searching for the keywords “mammals”, “inventory”, and “Suriname” in the titles and abstracts of published articles. We also performed a Google search with the same keywords. We included studies published in indexed and non-indexed journals, and gray literature (Ph.D. dissertation), and checked the geographic coordinates in Google Earth Pro. We compiled eight studies (from 2005 to 2022) totaling information from 16 different sites in Suriname (Table A.1). Using data from studies that relied on camera trapping (five studies and 14 sites), we assessed the relationship between species richness and the corresponding sampling effort (log-transformed) by fitting a linear regression. Further, in order to evaluate possible spatial variation in community composition, we evaluated assemblage composition using a principal coordinates analysis (PCoA).

#### 2.3.2. Selective logging effects

We employed a Bayesian multi-species occupancy model to unravel the effects of selective logging on species richness and probabilities of detection and occupancy (Devarajan et al., 2020). This approach combines community and species-level attributes in a single framework that accounts for imperfect detection and provides better parameter estimates than conventional, single-species occupancy methods (Dorazio et al., 2006; Kéry and Schaub, 2012; Zipkin et al., 2010). We assumed the probability of occupancy as habitat use due to possible non-independency among camera trap stations following Mackenzie et al., (2006). In the model, the latent state variable “occurrence of species  $i$  at site  $j$ ” is specified as a Bernoulli outcome governed by the habitat use probability of species  $i$  at site  $j$ :  $z_{i,j} \sim \text{Bern}(\psi_{i,j})$ . To account for imperfect detection, the observation process is specified as a Bernoulli outcome governed by  $z_{i,j}$  times detection probability for species  $i$  at site  $j$  during sampling occasion  $k$ :  $y_{i,j,k} \sim \text{Bern}(z_{i,j} \times p_{i,j,k})$  (Kéry and Royle, 2008; Kéry and Schaub, 2012). We considered five days of sampling as one sampling occasion. The predictor variable for  $\psi$  and  $p$  was implemented using logit link functions (Dorazio et al., 2006; Kéry and Schaub, 2012). We evaluated the effect of selective logging status on species habitat use and detection, including the sampling campaign as a random effect to control for spatial and temporal autocorrelation, using the following specifications:

$$\text{logit}(\psi_{i,j}) = \alpha_0 + \alpha_1\text{campaign}_b + \alpha_2\text{status}_j \quad (1)$$

$$\text{logit}(p_{i,j,k}) = \beta_0 + \beta_1\text{campaign}_b + \beta_2\text{status}_j \quad (2)$$

We used the parameter-expanded data augmentation technique to estimate species richness while accounting for unobserved species (Kéry and Schaub, 2012). We added 11 additional all-zero observation histories, corresponding to “potential” undetected species, to the dataset

and fitted a zero-inflated version of the model to it. These “dummy” species were assigned based on the total number of species expected to occur in Suriname based on a literature review ( $N = 50$ ; see Table A.2), excluding those with records not favored by camera trap sampling (i.e., species with arboreal (except squirrels) and semi-aquatic habits). We added an indicator variable  $w_i$  to the occurrence process so that  $z_{i,j}$  became a Bernoulli outcome governed by  $\psi_{i,j} \times w_i$ , where  $w_i$  is a Bernoulli outcome governed by the inclusion probability  $\Omega$ :  $w_i \sim \text{Bern}(\Omega)$  (Kéry and Schaub, 2012; Zipkin et al., 2010). We then estimated global and local species richness by summing the estimated  $w_i$  from all “species” in the augmented dataset (Kéry and Schaub, 2012; Zipkin et al., 2010).

From our species pool, we removed records from primates and those identified only to the genus level (*Dasyops* sp., *Mazama* sp., and *Leopardus* sp.), thereby, including 24 species in the analysis. We fitted the model in JAGS (Plummer, 2017) using the R2jags package (Su and Yajima, 2021). We used non-informative priors for all the parameters and ran three chains with 100,000 Markov Chain Monte Carlo (MCMC) iterations with a burn-in of 50,000 and a thinning rate of 100. We evaluated parameter convergence using the Gelman-Rubin diagnostic (Gelman and Shirley, 2011) and visual inspection of trace plots. All chains showed R-hat values  $< 1.05$  for all parameters, indicating convergence. We considered that there was support for a predictor effect when the 95% posterior credible interval (CI) for the parameter did not include zero.

To compare the mammal assemblages between logged and unlogged parts, we employed two calculations based on the probability of habitat use estimated by the Bayesian multi-species occupancy models: the dissimilarity index and diversity profiles. The dissimilarity index is a modification of the Bray-Curtis index, which calculates the dissimilarity between a reference and a focal assemblage (Giacomini and Galetti, 2013). Here, we used an adapted version of the index proposed by Tilker et al. (2020), which uses the probability of occupancy (habitat use probability, in our case) instead of density or presence/absence data. We considered the unlogged parts as the reference assemblage since, in theory, they are less disturbed than logged ones. Dissimilarity values range between  $-1$  and  $1$ , in which negative values indicate a higher probability of habitat use by the focal assemblage in comparison to the reference, zero indicates no difference between assemblages, and positive values indicate a lower probability of habitat use by the focal assemblage related to the reference.

The diversity profiles (Hill numbers) summarize multiple diversity indices along a gradient  $q$ , which assesses the impact of rare species on assemblage diversity (Leinster and Cobbold, 2012). This calculation includes the most common diversity indexes, e.g.,  $q = 0$  represents the species richness, which accounts for the assemblage diversity irrespective of the species being rare or not. As the  $q$  value increases, the contribution of rare species to diversity diminishes, showing a pronounced decline in diversity for assemblages composed of a few dominant species. When  $q = 1$ , it represents the Shannon index, and  $q = 2$ , represents the inverse of the Simpson index, both of which accounts for the impact of rare species on assemblage diversity. Here, we used an adaptation of the diversity profiles proposed by Abrams et al. (2021) which uses the probability of occupancy (habitat use probability, in our case) instead of relative abundance data.

### 3. Results

#### 3.1. Species list

In total, we recorded 27 mammal species (West = 24; Central = 25), belonging to eight orders and 16 families (Table 1, Fig. A.1), including records of three primates (*Sapajus apella*, *Pithecia pithecia*, and *Saimiri sciureus*). Four species are listed as ‘Vulnerable’ to worldwide extinction (IUCN, 2022): giant anteater (*Myrmecophaga tridactyla*), giant armadillo (*Priodontes maximus*), lowland tapir (*Tapirus terrestris*), and white-lipped

**Table 1**

Medium and large-sized mammals recorded at the logging concessions in Suriname, including global threat categories according to IUCN (2022) and the number of records per species at each concession.

Taxon	Common name	Threat category	West	Central
DIDELPHIMORPHIA				
DIDELPHIDAE				
<i>Didelphis imperfecta</i> Mondolfi & Pérez-Hernández, 1984	Guianan white-eared opossum		20	30
PILOSA				
MYRMECOPHAGIDAE				
<i>Myrmecophaga tridactyla</i> Linnaeus, 1758	Giant anteater	VU	7	6
<i>Tamandua tetradactyla</i> (Linnaeus, 1758)	Southern tamandua		1	4
CINGULATA				
CHLAMYPHORIDAE				
<i>Priodontes maximus</i> (Kerr, 1792)	Giant armadillo	VU	–	2
DASYPODIDAE				
<i>Dasyops novemcinctus</i> Linnaeus, 1758	Nine-banded armadillo		34	24
<i>Dasyops kappleri</i> Krauss, 1862	Greater long-nosed armadillo		35	25
<i>Dasyops</i> sp. Linnaeus, 1758	Armadillo		82	43
PERISSODACTYLA				
TAPIRIDAE				
<i>Tapirus terrestris</i> (Linnaeus, 1758)	Lowland tapir	VU	14	27
ARTIODACTYLA				
CERVIDAE				
<i>Mazama americana</i> (Erxleben, 1777)	Red brocket deer		49	84
<i>Mazama nemorivaga</i> (F. Cuvier, 1817)	Brown brocket deer		35	62
<i>Mazama</i> sp. (Erxleben, 1777)	Deer		30	65
TAYASSUIDAE				
<i>Dicotyles tajacu</i> (Linnaeus, 1758)	Collared peccary		33	44
<i>Tayassu pecari</i> (Link, 1795)	White-lipped peccary	VU	4	6
PRIMATES				
CEBIDAE				
<i>Sapajus apella</i> Linnaeus, 1758	Black-capped capuchin		1	–
<i>Saimiri sciureus</i> (Linnaeus, 1758)	Guianan squirrel monkey		1	1
PITHECIIDAE				
<i>Pithecia pithecia</i> (Linnaeus, 1766)	White-faced saki		7	–
CARNIVORA				
CANIDAE				
<i>Speothos venaticus</i> (Lund, 1842)	Bush dog		–	1
FELIDAE				
<i>Herpailurus yagouaroundi</i> (É. Geoffroy Saint-Hilaire, 1803)	Jaguarundi		4	7
<i>Leopardus pardalis</i> (Linnaeus, 1758)	Ocelot		13	17
<i>Leopardus wiedii</i> (Schinz, 1821)	Margay		7	7
<i>Leopardus</i> sp. Gray, 1842	Small spotted cat		7	5
<i>Panthera onca</i> (Linnaeus, 1758)	Jaguar		2	3
<i>Puma concolor</i> (Linnaeus, 1771)	Puma		3	11
MUSTELIDAE				
<i>Eira barbara</i> (Linnaeus, 1758)	Tayra		9	37
PROCYONIDAE				
<i>Nasua nasua</i> (Linnaeus, 1766)	South American coati		4	4
<i>Procyon cancrivorus</i> (G. Cuvier, 1798)	Crab-eating raccoon		–	1

(continued on next page)



Table 1 (continued)

Taxon	Common name	Threat category	West	Central
RODENTIA				
CUNICULIDAE				
<i>Cuniculus paca</i> (Linnaeus, 1766)	Lowland paca		56	124
DASYPROCTIDAE				
<i>Dasyprocta leporina</i> (Linnaeus, 1758)	Red-humped agouti		280	264
<i>Myoprocta acouchy</i> (Erxleben, 1777)	Red acouchi		63	92
SCIURIDAE				
<i>Guerlinguetus aestuans</i> Linnaeus, 1766	Guianan squirrel		8	6
<b>Total</b>	<b>27</b>	<b>4</b>	<b>24</b>	<b>25</b>

peccary (*Tayassu pecari*). The red brocket deer (*Mazama americana*) is considered 'Data Deficient' (IUCN, 2022).

3.2. Local assessment

The observed species richness was similar between logging concessions (Welch two-sample t-test,  $t = -0.14$ ,  $p = 0.89$ ), as was assemblage composition, in which they shared 87.5% of all species recorded ( $N = 21$ ). The giant armadillo (*P. maximus*), the bush dog (*Speothos venaticus*), and the crab-eating raccoon (*Procyon cancrivorus*) were recorded only in the Central concession. The red-rumped agouti (*Dasyprocta leporina*), armadillos (*Dasybus* sp.), and the red acouchi (*Myoprocta acouchy*) were the most frequently recorded species in the west concession; the red-rumped agouti, the lowland paca (*Cuniculus paca*), and the red acouchi were the most recorded in the central concession (Table 1).

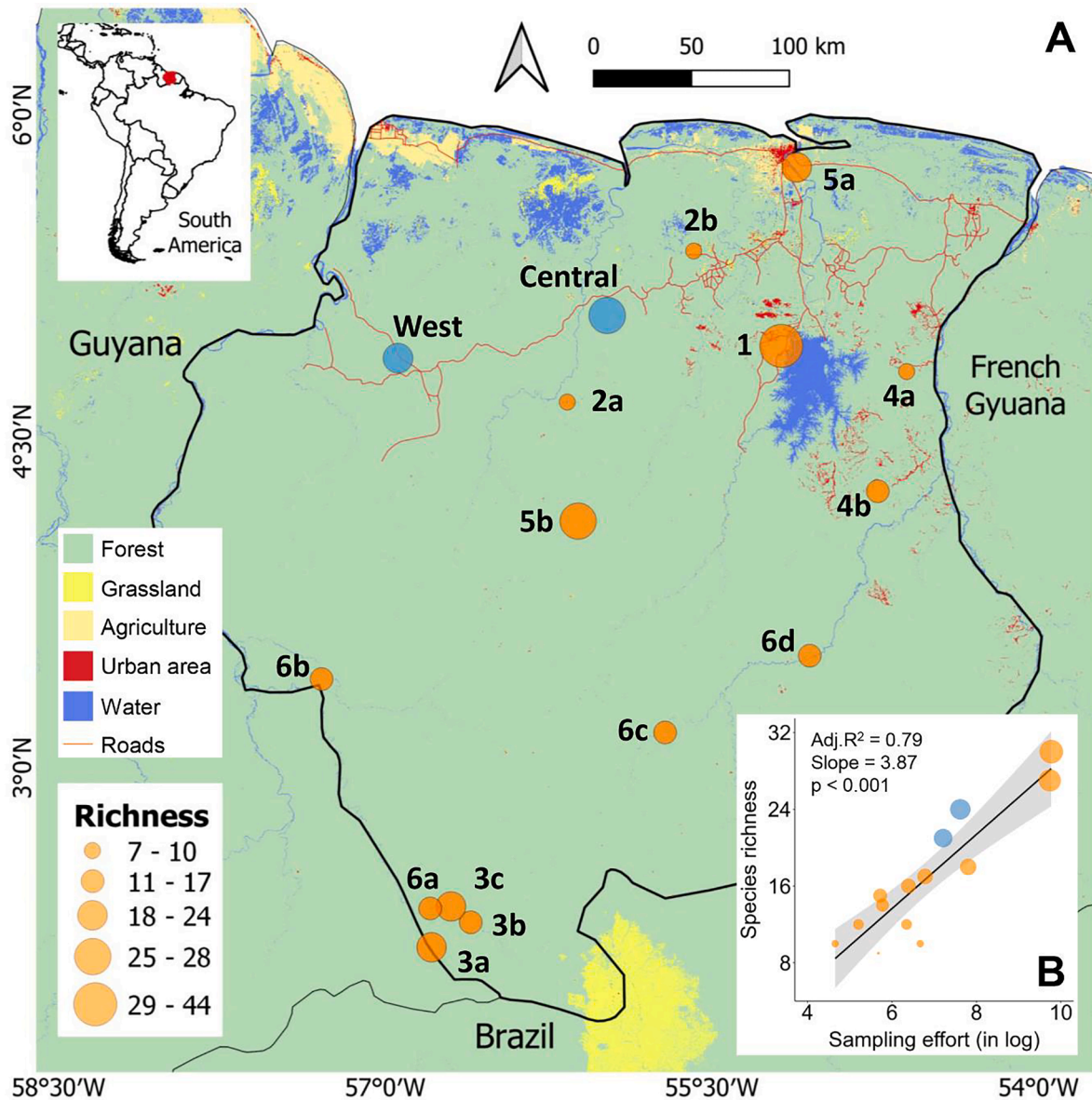


Fig. 2. A) Richness of mammal species among different sites in Suriname depicting the main land use classes (MapBiomias Amazonia Project 2021). Central and West concessions are highlighted in blue. [1] Lim et al. (2005) and Ouboter et al. (2021); [2a-b] Ouboter et al. (2011); [3a-c] Gajapersad et al. (2012); [4a-b] Solari and Pinto (2007); [5a] Schuttler et al. (2021); [5b] Ahumada et al. (2011) and Vath (2008); [6a-d] van Kuijk et al. (2022). Small case letters indicate the different sites assessed per study. B) Relationship between mammal richness and sampling effort (trap-days in log) for studies that used camera trapping. Dot size indicates the species richness of each site. The shaded area represents the 95% confidence interval of the regression. More details on study sites are in Table A.1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 3.3. Site-level comparison

Richness among the 16 sites in the dataset varied widely (from 7 to 44 species), with an average value of  $19.1 \pm 9.1$  species, and the number of threatened species varied from 0 to 6 (Table A.1). Compared to other sites in Suriname including all species recorded, and accounting for the sampling effort, our study sites were among those with more records (Fig. 2A). Considering only the records from studies that used camera trapping (14 sites; Table A.1), variation in species richness diminished (from 9 to 30 species), with an average value of  $16.8 \pm 6.6$ . Expectedly, we observed a strong relationship between assemblage richness and sampling effort (Adj.R2 = 0.79,  $p < 0.001$ , Slope = 3.87; Fig. 2B), which varied from 104 to 17,520 trap-days. Assemblage composition was overall similar among studied sites, however, also showed sites with higher sampling effort to be more similar among them compared to sites with lower effort (Fig. A.2).

### 3.4. Selective logging effects

The average estimate of total species richness based on the multi-species occupancy model was 25.5 species (95% CI: 24 to 29), while the average estimate per trapping station was 17.1 species (95% CI: 8–25). The bush dog (*S. venaticus*) and the crab-eating raccoon (*P. cancrivorus*) were recorded only once in unlogged parts. The credible intervals of the logged and unlogged diversity profiles overlapped, indicating no significant differences in species richness or Shannon and Simpson indexes, and the curves decline was small and smooth, suggesting a low influence of the occurrence of rare species (Fig. 3A). The dissimilarity index mean value was negative but credible intervals included zero ( $-0.02 \pm 0.06$ ), indicating no significant difference in assemblage composition between logged and unlogged areas (Fig. 3B).

We observed that the estimates of the probability of habitat use and detection of species were similar between logged and unlogged parts (Fig. 4A and 4B), which on average were slightly higher for most species in logged parts. The probability of habitat use of most species (87.5%) presented a positive response to logging status, although none of them was significantly different from zero (Fig. 4C). Detection probability

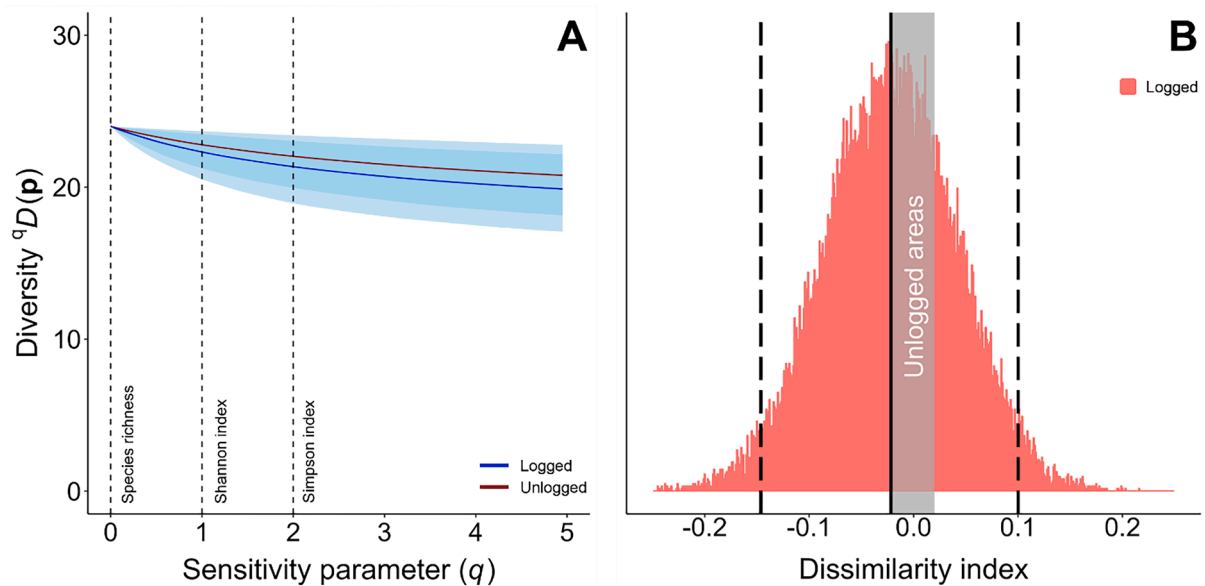
varied slightly more among species in response to logging status, with 17 responding positively and seven negatively, but most were non-significant. The red acouchi (*M. acouchi*) showed a significant positive response (95% CI: 0.03 to 0.69), and a marginally significant positive response was observed for the greater long-nosed armadillo (*Dasyaps kappleri*) (95% CI:  $-0.01$  to 0.91) (Fig. 4D).

## 4. Discussion

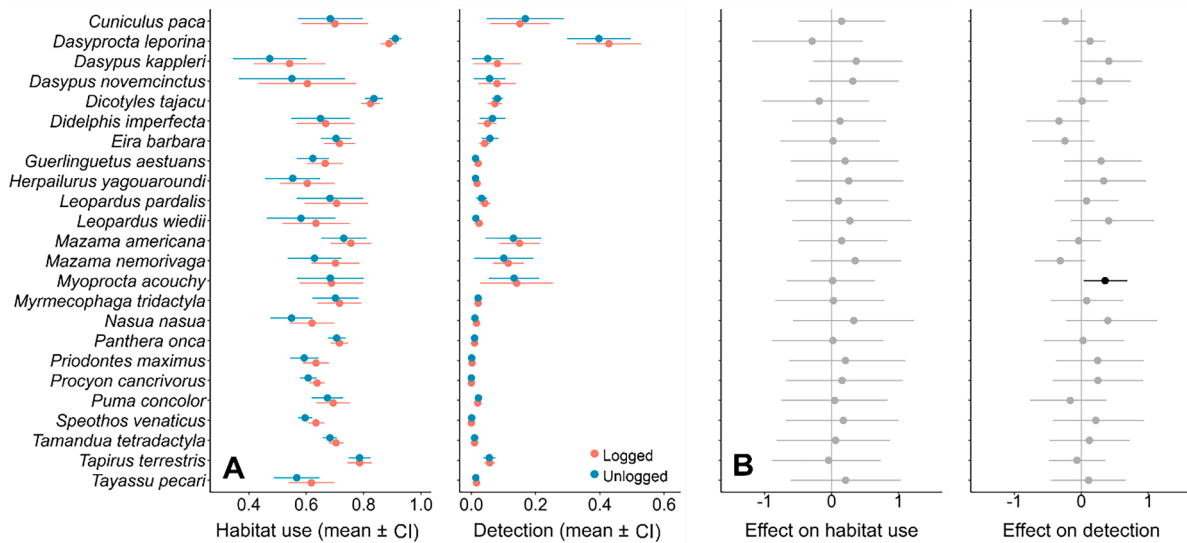
To our knowledge, this is the first study to evaluate the effects of selective logging on mammals in Suriname and our results contribute to the debate about the sustainability of this low-impact activity. Mammal richness and composition were very similar between logging concessions, including the record of rare and threatened species. Although subject to selective logging, the study sites were among the richest in mammal diversity throughout Suriname, which is likely a product of the large sampling effort, and showed overall similarity in assemblage composition compared to unmanaged sites. We observed no substantial influence of selective logging on the diversity and composition of mammal assemblages between logged and unlogged parts of the concessions. Logging status had only a minor influence on the probabilities of habitat use and detection of species, indicating that the certified selective logging practiced in the study area does not have substantial impacts on the species level.

### 4.1. Local and site-level comparison

Besides the high species richness recorded, other species are expected to occur in the study sites, such as the capybara (*Hydrochoeris hydrochaeris*), the greater grison (*Galictis vittata*), and the lesser naked-tailed armadillo (*Cabassous unicinctus*) (see Tables A.1 and A.2, and references therein). The non-detection of these species in our study can be explained by the fact that some of them are naturally rare (e.g., *G. vittata*, *Leopardus tigrinus*) while others are not well sampled by ground-level camera traps, such as arboreal species (e.g., *Potos flavus*, *Coendou* sp., and primates), or the place where cameras were deployed, such as for semi-aquatic species (e.g., *H. hydrochaeris*, *Lontra longicaudis*,



**Fig. 3.** A) Species diversity profiles calculated from estimates of habitat use probability for 24 medium and large-sized mammals recorded in logged and unlogged parts of the logging concessions in Suriname. Vertical dotted lines depict the species richness ( $q = 0$ ), the Shannon index ( $q = 1$ ), and the Simpson index ( $q = 2$ ). Blue shadings indicate the standard deviations. B) Dissimilarity index based on estimates of habitat use probability of mammal species in logged and unlogged parts of the logging concessions. The black solid line represents the mean value, the black dotted lines represent the 95% Bayesian credible intervals, and the histogram (red) shows the posterior distribution of the dissimilarity index. Unlogged parts were used as reference site (gray bar). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 4.** Panels synthesizing the results of the Bayesian multi-species occupancy model for 24 medium and large-sized mammals recorded in the logging concessions in Suriname. A) Average estimates of the probability of habitat use and detection of each species in logged and unlogged parts. B) Magnitude and direction (Bayesian mean  $\pm$  95% credible interval) for the posterior distribution of logging predictor effect on habitat use and detection probabilities of each species. Values in black indicate effects with significant statistical support.

and *Pteronura brasiliensis*) or those associated with water (e.g., *P. cancrivorus*).

Yet, we also recorded several species that are naturally rare throughout their wide distribution across South and Central Americas, such as the giant armadillo (*P. maximus*), the bush dog (*S. venaticus*), and the crab-eating raccoon (*P. cancrivorus*) (Carter et al., 2016; DeMatteo et al., 2011; Reid et al., 2016). The globally threatened giant armadillo (Anacleto et al., 2014) was recorded twice, in both logged and unlogged parts, but apparently occurs in low densities in Suriname (Walsh and Gannon, 1967). The population trend for the bush dog in the Guianas is unknown, and due to its semi-nomadic movement patterns (DeMatteo et al., 2011), records of the species are scarce across its distribution. The crab-eating raccoon, in agreement with other studies, is rarely recorded across most of the Amazon (Cheida et al., 2013), mainly attributed to the species associated with water and the use of the arboreal strata for foraging and resting (Cheida et al., 2013; Emmons and Feer, 1997). Large-sized species such as jaguar (*Panthera onca*), white-lipped peccary (*T. pecari*), and giant anteater (*M. tridactyla*), the latter two threatened globally (IUCN, 2022), had also only a few records, a common outcome of most studies in Suriname (Ouboter et al., 2021; Schuttler et al., 2021; van Kuijk et al., 2022).

Our results strengthen that richness estimates based on camera trapping are highly dependent on sampling effort (Antunes et al., 2022), which calls attention to the importance of the implementation of sufficient camera traps and/or days of trapping in inventorial studies. The sampling effort of our study was among the highest applied in mammal studies in Suriname to date and corroborated results of high mammal richness as shown by high-effort studies in Central Suriname Nature Reserve (N = 27; Ahumada et al., 2011) and Brownsberg Nature Reserve (N = 30; Ouboter et al., 2021). The high dependency on sampling effort indicates that the low richness detected in some studies may be due to insufficient sampling (and not to the absence of mammal species), particularly considering that Suriname is mainly composed of natural forests. Although study sites with similar efforts resulted also in more similar assemblages, sampling effort seems to have a much lower influence on assemblage composition. This result indicates that detection probabilities of mammals are non-random among sampling sites, leading to the same species being detected with higher probability at all sites (likely due to higher regional abundances).

#### 4.2. Selective logging effects

We observed no difference neither in species richness nor in the assemblage composition between logged and unlogged parts of the concessions. This is consistent with previous studies showing no substantial effect on mammalian diversity in continuous tracks of tropical forests subjected to selective logging (e.g., Burivalova et al., 2014; Carvalho et al., 2020; Carvalho Jr et al., 2021; Granados et al., 2016; Johns, 1992; Sollmann et al., 2017; Tobler et al., 2018). These results are corroborated by a recent analysis of the dynamics of logged forests (Malhi et al., 2022). In managed sites, the disturbance created by selective logging increases primary net production, which increases food resource availability (i.e., herbaceous plants and fast-growing trees), thereby in turn attracting species (especially herbivores) and increasing overall species richness in comparison to unmanaged sites (Malhi et al., 2022). Logging effects are non-linear. While at low logging intensities, there may be positive effects or no change between selectively logged and unlogged sites (Burivalova et al., 2014; Carvalho Jr et al., 2021), the native species richness is expected to decline with increasing logging intensity. “Low” and “high” logging intensity (as measured by the standard measurements of  $m^3/ha$ ) and their effects depend on stand structure and productivity and should not be applied in any formalized way.

As for individual species responses, although non-significant, most species presented slightly higher habitat use probabilities in logged compared to unlogged parts. This is probably due to an increase in local environmental heterogeneity and food resource availability at logged sites (Malhi et al., 2022). Most species tend to recover from the effects of selective logging within a decade after tree removal (Brodie et al., 2015), and it is possible that the mammal assemblage in our study is still recovering from past disturbance since camera trapping occurred about one year after timber extraction. This effect was also observed in other tropical forests subject to selective logging around the world, which may increase not only species richness but also their detection and occupancy probabilities (e.g., Clark et al., 2009; Burivalova et al., 2014; Granados et al., 2016; Tobler et al., 2018; Malhi et al., 2022).

Regarding the detection probability, most species (70.8%) tended to respond positively to logging status, with seven species presenting an opposite response, but all were non-significant. Only the red acouchi (*M. acouchy*) and the greater long-nosed armadillo (*D. kappleri*) had



statistical support in their positive responses. Both species seem to avoid disturbed areas (Patton et al., 2015; Aya-Cuero et al., 2019) as those created by selective logging. Higher detection probabilities at logged sites may indicate increased abundance or increased activity levels (McCarthy et al., 2013; Neilson et al., 2018). For frugivore/herbivore species, habitat disturbance might create more opportunities to forage on saplings and regenerating plants as understory vegetation increases locally (e.g., Clark et al., 2009; Malhi et al., 2022; Tobler et al., 2018). Nonetheless, some large-sized herbivore/frugivore species presented average negative responses to logging, which might be related to the loss of large fruit-bearing trees at logged sites (Carvalho et al., 2022).

For most of the medium and large-sized mammals of our study, due to the larger home ranges of terrestrial species (Broekman et al., 2023), different logging status may not represent distinct spatial units, but a fine-grained habitat where logged sites add just another component to the natural environmental heterogeneity. The absence of negative effects on the probability of habitat use for most species detected in this study indicates that the selective logging to the extent practiced in the managed sites (between 4 to 7 m<sup>3</sup>/ha) may fulfill the criteria of sustainability, at least regarding the assemblage of medium to large-sized mammals. Moreover, the increased detection and habitat use probabilities in the logged parts for sensitive species, suggest that the overall habitat quality was maintained with the current model employed for timber extraction. Given that several species analyzed in this study can be characterized as umbrella species, particularly charismatic, large-sized, and threatened ones (e.g., *P. onca*, *M. tridactyla*, *P. maximus*, and *T. terrestris*), and thereby indicate habitat integrity for a series of other species, this inference might be extendable to other taxonomic groups.

#### 4.3. Limitations

We recognize analytical limitations for species from the genus *Dasybus*, *Mazama*, and *Leopardus*, which presented a substantial number of records that could not be identified to species level due to poor photo quality, possibly resulting in an underestimation of the occurrence for the respective species in this study (i.e., *D. novemcinctus*, *D. kappleri*, *M. americana*, *M. nemorivaga*, *L. pardalis*, and *L. wiedii*). One alternative to soften this limitation is to group species by genera, as ecospecies (e.g., Peres 1997), considering that congener species have complementary functional roles, therefore, increasing the number of individual records available for analysis. However, despite the loss of individual record numbers, we find it important to obtain species-specific responses to generate more accurate results on the effects of logging.

#### 4.4. 5.4 Conclusions and recommendations

The result of low impacts of selective logging is in line with other studies that demonstrate the possibility of integrating selective logging or even mosaics of more drastic forest exploitation with effective biodiversity conservation (e.g., Johns, 1992). However, only the correct implementation of “Reduced Impact Logging” techniques can help achieve both conservation and economic goals. They should take into account the forest dynamics, area-specific requirements, and ecological processes, in order to avoid long-term and irreversible effects on forests (Gräfe et al., 2020; Landburg et al., 2021). Nevertheless, there may be gradual changes in ecosystem responses that cannot be measured with our methods and/or species in focus, and the study especially of smaller organisms remains necessary (e.g., Burivalova et al., 2014). Moreover, apart from the direct effects of selective logging, it is known that the establishment of secondary impacts may have more pervasive consequences for biodiversity (Zimmerman and Kormos, 2012). Opening roads and trails for timber extraction and establishing settlements might facilitate potentially impacting activities such as poaching, illegal logging, fires, and invasion and/or introduction of non-native species (both plants and animals). These possible secondary impacts of selective logging might be still absent in the study sites due to the continuous nature

of Suriname’s landscape which allows for a constant flow of species from managed to unmanaged sites and act as a buffer to hamper secondary impacts due to the distance and difficulty accessing the logging sites.

#### CRediT authorship contribution statement

**Marcelo Magioli:** Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Elildo A.R. Carvalho:** Formal analysis, Writing – original draft, Writing – review & editing. **Ricardo Sampaio:** Formal analysis, Writing – original draft, Writing – review & editing. **Thomas Püttker:** Writing – original draft, Writing – review & editing. **Svenja Arlt:** Writing – review & editing. **Wedika Hanoeman:** Conceptualization, Writing – review & editing. **Rewie Mattai:** Writing – review & editing. **Ariane Ooms:** Conceptualization, Writing – review & editing. **Anne-Maria Schweizer:** Writing – review & editing. **Miriam Scriba:** Writing – review & editing. **Michael Köhl:** Writing – review & editing. **Jörg U. Ganzhorn:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

Data will be made available on request.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121080>.

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