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EFFECTS OF HISTORICAL LOGGING ON SQUIRREL MONKEY (*SAIMIRI MACRODON*) POPULATION DENSITY AND PRIMATE SPECIES RICHNESS IN THE PERUVIAN AMAZON

John Rowland[1,*], Richard Bodmer[1,2], Miguel Antunez[2], Dave Seaman[1]

[1]Durrell Institute of Conservation and Ecology, School of Natural Sciences, University of Kent, Canterbury, Kent CT2 7NS, United Kingdom. [*]E-mail: jr701@kent.ac.uk
[2]FundAmazonia, Museum of Amazonian Indigenous Cultures, 332 Malecon Tarapaca, Iquitos, Peru

Abstract

Primates in the Amazon are threatened by the expansion of human activities, including logging. Here, we investigate how primate communities are affected by different forest use and disturbance histories in two adjacent indigenous territories. We assess how logging in the recent past has changed primate community composition. One of the territories was protected from selective commercial logging activities, whilst the other had decades of selective logging before starting the process of becoming an indigenous territory in 2012. The past logging has left forest gaps and secondary forests, and was accompanied by small agricultural plots. Using line transect surveys and distance sampling analysis, we compared primate species richness between the two territories, and the density of the ecologically dominant squirrel monkey species, *Saimiri macrodon*. Villa Belén, the territory with more recent and more intense logging supported a higher population density of squirrel monkeys (192 indiv./km^2) than Jaldar (107 indiv./km^2), the territory with a less intense and more distant logging history. We found no difference in squirrel monkey group size between the forests of Villa Belén and Jaldar. Primate species richness declined as logging pressure and anthropogenic disturbance increased with an estimated richness of seven species in Villa Belén, compared to 11 species in Jaldar. Our findings suggest that squirrel monkeys can persist in tropical forests with high levels of historical logging pressure and at greater densities than in less disturbed areas with higher overall primate species richness.

Keywords: Anthropogenic disturbance, distance sampling, indigenous lands, population density, primate communities

Resumen

Los primates de la Amazonía se encuentran amenazados por la expansión de las actividades humanas, incluida la tala forestal. En este estudio, investigamos cómo las comunidades de primates se ven afectadas por diferentes historiales de uso y perturbación del bosque en dos territorios indígenas adyacentes. Evaluamos cómo la tala ocurrida en el pasado reciente ha modificado la composición de las comunidades de primates. Uno de los territorios estuvo protegido de actividades de tala comercial selectiva, mientras que el otro experimentó décadas de extracción selectiva de madera antes de iniciar su proceso de constitución como territorio indígena en el año 2012. La tala histórica generó claros en el bosque y áreas de bosque secundario, además de estar asociada con pequeñas parcelas agrícolas. Mediante muestreos por transectos lineales y análisis basados en muestreo por distancia, comparamos la riqueza de especies de primates entre ambos territorios, así como la densidad poblacional de la especie de mono ardilla ecológicamente dominante, *Saimiri macrodon*. Villa Belén, el territorio con una historia de tala más reciente e intensa, presentó una mayor densidad poblacional de monos ardilla (192 individuos/km^2) que Jaldar (107 individuos/km^2), territorio con un historial de tala menos intenso y más antiguo. No encontramos diferencias en el tamaño de los grupos de monos ardilla entre los bosques de Villa Belén y Jaldar. La riqueza de especies de primates disminuyó conforme aumentaron la intensidad de la tala y la perturbación antropogénica, registrándose una riqueza estimada de siete especies en Villa Belén, frente a las 11 presentes en Jaldar. Nuestros resultados sugieren que los monos ardilla pueden persistir en bosques tropicales sometidos a una elevada presión histórica de tala y alcanzar densidades mayores que en áreas menos perturbadas, donde existe una mayor riqueza general de especies de primates.

Palabras clave: Comunidades de primates, densidad poblacional, muestreo de distancias, perturbación antropogénica, territorios indígenas

Introduction

Non-human primates around the world are threatened by human activities such as overexploitation, habitat destruction and fragmentation, and a changing climate (Young et al., 2016). Indigenous territories, areas governed, managed, and used by indigenous peoples, have been shown to be a land use system that contributes to

conserving biodiversity, including primates (Blackman et al., 2017). However, not all indigenous territories are managed by the people in the same way, and differences in land and resource use have different impacts on primates. The responses of primate populations to these differences must be studied if we are to understand their impacts and provide data for evidence-based conservation strategies (Paim et al., 2019).

The traditional approach to biodiversity conservation is the designation and management of protected areas, to provide sanctuaries for primates and other wildlife and relief from the pressure of human activities (Anaya and Espírito-Santo, 2018). However, there is strong debate as to their effectiveness and morality, and Laurance et al. (2012) suggest that only half of protected areas in tropical forests worldwide perform well in conserving biodiversity. In the Peruvian Amazon, strictly protected areas are less effective at conserving biodiversity and preventing deforestation than mixed-use protected areas, as the former results in conflict with the traditional lands of indigenous territories (Bodmer et al., 2008; Miranda et al., 2016).

Primates in the Amazon are threatened by the expansion of human activities such as logging (da Silva et al., 2022) and agricultural expansion (Pereira et al., 2020). These activities result in the clearance of primary rainforest and loss of space for wildlife to inhabit, adversely affecting ecosystem functioning and services (Balvanera et al., 2006). Approximately 20% of the Amazon rainforest is currently exploited for timber, typically by selective harvest (Piponiot et al., 2019). In the Peruvian Amazon most of the timber extraction is low level selective logging removing targeted trees for timber (Putz et al., 2008). Inevitably, such removal causes effects on biodiversity (Bicknell et al., 2014). These effects must be studied if we are to better understand the impact logging has on different species, especially as timber concessions are now a major land-use strategy in tropical forests.

Logging can also induce ecological alterations beyond physical disturbance. For instance, selective tree removal alters floristic composition by favouring fast-growing pioneering and secondary tree species, altering canopy openness, understorey density, and spatial distribution of fruiting and flowering trees (Bousfield et al., 2023), leading to a greater availability of early-successional food plants. Such modifications affect resource availability for primates, with varying impacts on species depending on dietary guild (i.e. folivory vs. frugivory). Consequently, logged forests may favor small, generalist species capable of exploiting patchy and diverse resources, while reducing habitat suitability for larger, specialized, or canopy-dependent primates (Almeida-Rocha et al., 2017). These ecological shifts can therefore drive measurable demographic responses such as changes in primate population density, group size, and movement patterns, and alter community-level species richness as adaptable species expand while sensitive taxa decline.

Here, we investigate how primates are affected by different forest use in two adjacent indigenous territories to understand how logging in the recent past has impacted the primate community composition. Primarily, our investigation is centered on the population dynamics of an ecologically dominant species, the squirrel monkey (*Saimiri macrodon*), including population density, group size, and encounter rate. Furthermore, we assess the difference in estimated primate species richness between the two territories. One of the territories was protected from commercial selective logging activities, whilst the other had decades of selective logging before starting the process of becoming an Indigenous Territory in 2012. The past logging has left forest gaps and secondary forests, and was accompanied by small agricultural plots and hunting.

Saimiri is a genus of small platyrrhine primate native to the forests of South and Central America (Ruiz-García et al., 2015). They are diet generalists, consuming fruit and flowers, as well as arthropods and small vertebrates taken from arboreal foliage (Boinski, 1999). Squirrel monkeys are most often observed in large groups of 25–75 individuals (Boinski, 1999). Smaller all-male alliance groups may also be observed migrating between larger breeding groups, whereas females are philopatric (Mitchell, 1994). This social organisation may be driven by high predation, despite the resulting cost of higher within-group competition for feeding resources (Mitchell et al., 1991).

Methodology

Study area and focal species

Data were collected in the Lower Yarapa *várzea* forests between the Pacaya-Samiria National Reserve and the Tamshiyacu-Tahuayo Community Reserve, located in the Marañon-Ucayali subsidence area of the Ucamara depression, Peru. The focal species of squirrel monkey in this study area was *Saimiri macrodon* (see Link et al., 2021). These forests make up part of the largest area of *várzea* flooded forests in the Western Amazon, extending over an area of 120,000 km^2 in the Department of Loreto, Peru. The study was based at the FundAmazonia research station situated on the Yarapa channel (Figure 1).

Amazonian *várzea* forests are floodplains that are seasonally inundated by the flooding of white-water rivers, resulting in distinct seasons of high-water and low-water (Parolin et al., 2004). The high-water season at the study site typically lasts from December-June, coinciding with periods of heavy rainfall, with the low-water season running from July-November (Bodmer et al., 2014). Large quantities of nutrient-rich sediments drain from Andean landscapes and are deposited in the *várzea* forests, resulting in fertile soils (Irion 1978; Räsänen et al., 1987).

The study site included two indigenous territories, Villa Belén and Jaldar, and their territories are divided by the Ango Canal (Figure 1). The Jaldar territory is a 'Comunidad Nativa' that the community has managed since the late 20th century. The area of Villa Belén has recently begun the designation of their territory, and only over the past decade have they begun to manage it.

We ascertained the extent of logging in each territory since the 1950s using semi-structured interviews to gain insights from local people. Interviews were led by FundAmazonia staff, and information was provided by Villa Belén and Jaldar authorities.

Villa Belén

Villa Belén is at the mouth of the Lower Yarapa channel. From 1999–2013, the forests were logged yearly. Over this period, ~700 tree trunks were removed from the territory of approximately 4,000 ha, with commercial tractors being used to remove timber on two occasions.

The trees most often taken from this area were the 'capinuri' (*Monteverdia laevis*) and 'capirona' (*Calycophyllum spruceanum*), making up around half of all the trunks that were removed. As of 2013, commercial timber concessions have not been allowed into Villa Belén, and timber has only been removed for the needs of local people.

Jaldar

Jaldar territory borders Villa Belén to the south and is in the middle section of the Lower Yarapa channel. The territory of Jaldar did not allow commercial timber extraction. Timber was removed selectively prior to Jaldar becoming an indigenous territory at a low rate between the 1950s and 1999. Since then, the people of Jaldar have not allowed any commercial logging in their territory and only use timber for local village infrastructure. The forests of Jaldar show less evidence of anthropogenic disturbance, according to the authorities of each territory.

Study design and data collection

We conducted line-transect surveys to observe primates in the two territories, according to the distance sampling methodologies set out by Buckland et al. (2001). Seven transects were used, four in Villa Belén and three in Jaldar (see Table 1), and were walked on rotation between July and September 2022. All trails were either disused hunting paths once used by the local communities or placed in targeted areas specifically for wildlife research. The mean transect length was 1.78 km, and each started on the bank of the Yarapa, entering the forest perpendicular to the Yarapa channel (see Figure 1).

The survey team consisted of 2–4 people observing the primates, including one local field assistant and 1-3 biologists. Occasionally, there were other people at a distance from the observers who would help measure

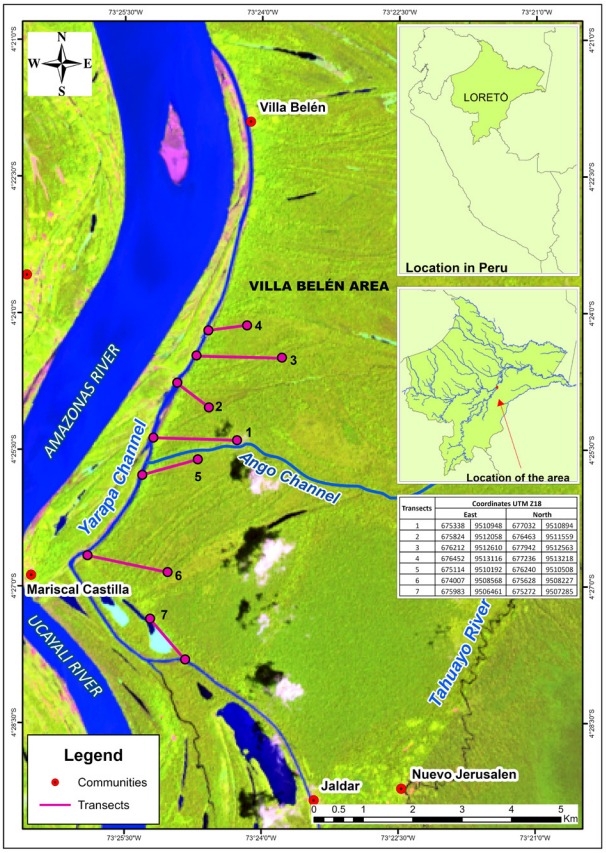

Figure 1. Location of study area and transects within Villa Belén and Jaldar territories, Loreto, Peru.

distances and record GPS and habitat data. We walked at approximately 1 km/h, between 07:00 and 12:00 and 14:00 and 17:00 to avoid the hottest period of the day when primate activity is reduced (Campos and Fedigan, 2009). Transects were not walked during heavy rain or poor visibility. In detection of primates, we recorded the time, species, distance walked along the transect, and the geographical coordinates of the location using a handheld GPS. One lead observer counted the number of individuals within the group, and this number was recorded as the group size. Perpendicular distance was measured from the trail to the location where the first individual was detected. We measured distances up to 20 m with a tape measure, and distances greater than 20 m were estimated. After each sighting, no new records for the same species were made within 150 m to ensure independence of observations (Leca et al., 2013). At the end of each transect route, we waited 15 minutes before undertaking the reverse journey, terminating at the same point as the start. We collected data on both the outward leg and the return leg of the transect.

Data analysis

Population density calculation

We used Distance software version 7.5 (Thomas et al., 2010) to estimate population densities for *Saimiri*

macrodon and calculate the effective strip width (*w*). The data for Villa Belén and Jaldar were pooled to calculate a value for *w* across the entire study area due to an insufficient number of observations in Jaldar for separate analysis. Examination of histograms generated in Distance revealed heterogeneity in the detection distances; therefore, the data were aggregated into five groups at 10 m intervals. Primate observations with a perpendicular distance of greater than 50 m were omitted to avoid the influence of outliers.

Table 1. Summary of location and length (in km) of each transect.

Transect number	Territory	Length (one way)
1	Villa Belén	2.2
2	Villa Belén	1
3	Villa Belén	2.2
4	Villa Belén	1.3
5	Jaldar	1.3
6	Jaldar	2.5
7	Jaldar	2

We then fitted models with every combination of key function (i.e., uniform; half normal; hazard rate) and series expansion (i.e., cosine; simple polynomial; hermite polynomial) to our data. We took multiple steps to compare and verify which of these models were the most appropriate for our dataset. Firstly, we screened out ill-fitting models using the chi-square goodness-of-fit test values, coefficient of variation, and visual inspections of the histograms and Q-Q plots generated by each model. The remaining models were compared using Akaike's Information Criterion (AIC) and the Delta AIC to determine the best-fitting model for our data, with the value of *w* being derived from the best-fitting model.

We obtained population density (*D*) using the formula:

where *n* is the total number of individuals observed on each transect, and *L* is the length of the transect. The value of *w* is multiplied by 2 in the equation to account for the strip width, both left and right of the transect. Due to the insufficient number of observations per transect, results were pooled to calculate a single value of population density in each territory.

$$D = \frac{n}{2wL}$$

Statistical analysis

Squirrel monkey group size values were normally distributed after a log10 transformation (Kolmogorov-Smirnov p=0.09 and p=0.13 respectively), and we used a 2-tailed independent t-test to compare the mean squirrel monkey group sizes observed in Villa Belén and Jaldar. All statistical analyses were performed in IBM SPSS Statistics 27. Means were presented ±SD.

Species accumulation and richness estimates

We plotted the total cumulative number of primate species observed against the survey effort in terms of the number of transects walked using Microsoft Excel to produce a species accumulation curve for each territory. We then added a logarithmic trend line for each territory to the scatter graph and simulated an extension of our survey effort to 60 transects walked per territory. We used the asymptote of the resulting trend curves as an estimation of total primate species richness in the territories (Ugland et al., 2003).

Results

Saimiri macrodon

We observed 1,291 squirrel monkeys over 54 transect repeats, with a total survey effort of 178.6 km. These totals comprised 853 individuals observed in Villa Belén over a total length of 93.2 km, and 438 individuals observed in Jaldar over 85.4 km.

Population density

According to the AIC and Delta AIC values for each model fitted using Distance software, the best-fitting model was derived from a combination of half-normal key function and cosine series expansion. The distribution of perpendicular distances (Figure 2) showed that most *Saimiri macrodon* detections occurred close to the transect line, with the number of records declining steadily up to the 50-m truncation distance. The fitted half-normal detection function with cosine adjustment provided a good visual fit to the data, indicating that detectability decreased smoothly with increasing distance. The absence of irregular peaks or gaps in the histogram suggests that distance measurements were consistent and that the dataset met the assumptions of distance sampling analysis.

Across the entire Lower Yarapa region, we estimated 151 squirrel monkeys per km^2 (Table 2). The territory with the higher population density was Villa Belén with 192 individuals per km^2, compared to 107 individuals per km^2 in Jaldar (Figure 3).

Group size and encounter rate

Across the Lower Yarapa forests, we observed 66 groups of squirrel monkeys, ranging in size from 1–70 individuals (mean±SD: 19.56±15.13). In the Jaldar territory, we observed 21 groups at an encounter rate of 0.25 groups/km. The group encounter rate was almost twice as high in Villa Belén, where we observed 45 groups, at 0.48 groups/km. There was no difference in group size between the two territories (t64=0.53, p=0.6). In fact, the mean group sizes were remarkably similar between Villa Belén (18.96±14.57) and Jaldar (20.86±16.56; see Table 3).

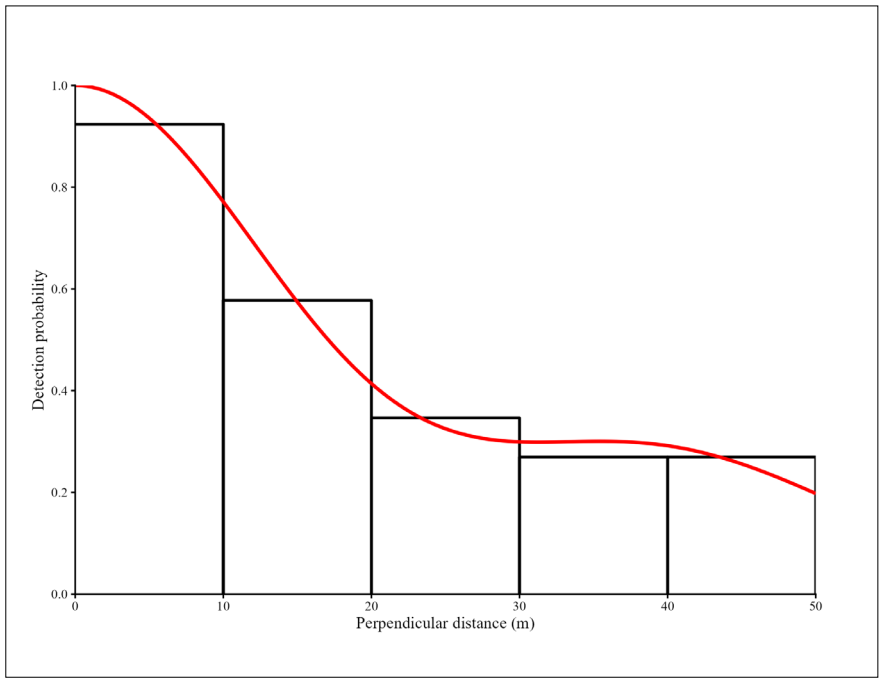

Figure 2. Histogram of *Saimiri macrodon* detections by perpendicular distance (black bars) with the fitted half-normal detection function (red line). Observations beyond 50 m were truncated prior to model fitting.

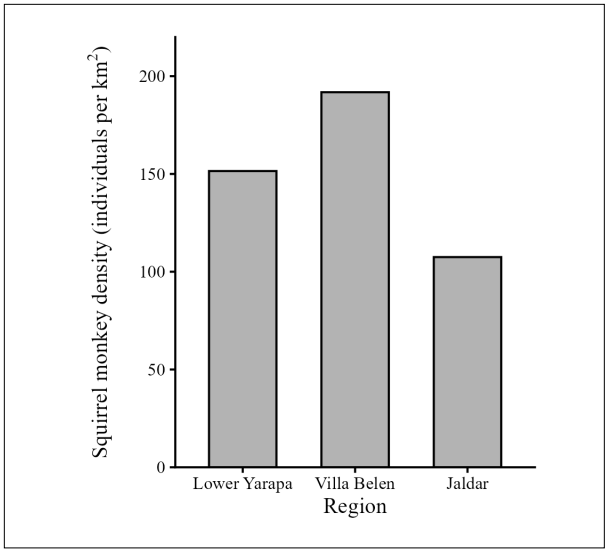

Figure 3. Density of squirrel monkeys (individuals per km^2) for the entire Lower Yarapa forests, as well as Villa Belén and Jaldar territories specifically.

The transect with the highest mean group size was transect #6 in the Jaldar territory, with a mean group size of 24.64±18.82 individuals. Transect #6 was also the transect where the largest group was observed, with 70 individuals.

Primate species richness

Across the 178.6 km walked in the Lower Yarapa forests, we observed eight species of primates including the squirrel monkey, large-headed capuchin (*Sapajus macrocephalus*), white-faced capuchin (*Cebus unicolor*), pygmy marmoset (*Cebuella niveiventris*), moustached tamarin (*Tamarinus mystax*), saddleback tamarin (*Leontocebus nigrifrons*), coppery titi monkey (*Plecturocebus cupreus*), and red howler monkey (*Alouatta seniculus*).

Across the 93.2 km that we walked in Villa Belén territory, we observed six of the eight species (*Saimiri macrodon, Sapajus macrocephalus, Cebus unicolor, Cebuella niveiventris, Tamarinus mystax* and *Plecturocebus cupreus*), over the course of 28 transect repeats divided across the four transect routes (see Table 2 for survey effort per transect). Using the logarithmic trendline on a species accumulation curve, we extrapolate an estimated species richness in Villa Belén territory of seven primates (Figure 4). In neighbouring Jaldar, we observed all eight of the species, across a total of 85.4 km and 25 transect repeats divided along the three transect routes. Using the logarithmic trendline on a species accumulation curve, we extrapolate an estimated species richness in Jaldar territory of 11 primates (Figure 4).

Discussion

We produced squirrel monkey population density estimates across two indigenous territories with differing historic resource uses, including logging. Villa Belén, the territory with a more recent and more intense logging intensity (yearly commercial logging between 1999-2013), had a higher population density of squirrel monkeys (192 individuals per km^2) than Jaldar (107 individuals per

Table 2. Summary of squirrel monkey population density calculated per territory, and survey effort per transect.

Territory	Transect number	Individuals observed	Total survey effort (km)	Effective strip width (m)*	Population density (ind/km²)
Villa Belén	1-4	853	93.2	23.86	191.79
	1	221	30.8		
	2	195	16		
	3	149	30.8		
	4	288	15.6		
Jaldar	5-7	438	85.4	23.86	107.48
	5	54	23		
	6	345	41.6		
	7	39	20.8		
Lower Yarapa Total	**1–7**	**1,291**	**178.6**	**23.86**	**151.48**

*Effective strip width calculated within Distance software 7.5 (Thomas et al. 2010).

Table 3. Summary of squirrel monkey group size per transect.

Territory	Transect	Mean group size (individuals)
Villa Belén	1–4	18.96
	1	18.42
	2	16.25
	3	21.29
	4	20.57
Jaldar	5-7	20.86
	5	18
	6	24.64
	7	9.75
Lower Yarapa total	**1–7**	**19.56**

km²), the territory with a less intense and more distant logging history (low-level local use only since the 1950s).

Our results suggest that areas of forest with a higher historical logging pressure support a higher population density of squirrel monkeys than the less disturbed surrounding forests. There are various ecological aspects of logged forests that could lead to a higher density of a primate species in a habitat conventionally described as degraded. Firstly, *Saimiri* species are generalist feeders (Boinski 1999) and are more able to adapt to a shift in food type availability from anthropogenic pressures than specialist feeders. For example, Oliveira-Silva et al. (2018) demonstrated that *S. sciureus* continued to thrive and contribute to the natural recovery of a highly anthropogenically disturbed Atlantic Forest in Brazil,

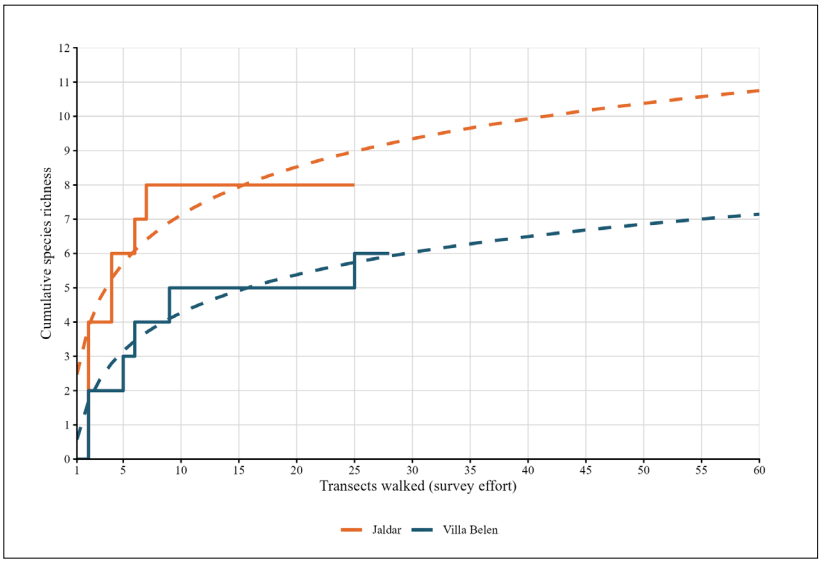

Figure 4. Extrapolated species accumulation curve showing estimated primate species richness in Villa Belén (blue line) and Jaldar (orange line) after 60 transects in each region.

despite the fact that the population was illegally released outside of its natural range. The forest gaps left by commercial timber concessions will likely not prevent squirrel monkeys from feeding, as they can support a greater variety and higher abundance of invertebrates (Watkins et al., 2017; Hill et al., 2001), and squirrel monkeys were regularly observed foraging for and consuming insects, myriapods, and arachnids during this study.

Another aspect of logged forests, which may explain the higher density of squirrel monkeys, is the development of a complex 3-D understory structure. Figueira et al. (2008) demonstrated that forest gaps created by selective logging promoted regrowth of small (10–35 cm DBH) and medium (35–55 cm DBH) sized trees, creating a complex understory with a higher density of trees than areas with a dense canopy cover limiting light availability to the forest floor. This dynamic and complex forest structure is beneficial to squirrel monkeys due to the reduced pressure of avian predation. Squirrel monkeys in Peru face predation from large birds such as harpy eagles (*Harpia harpyja*), and observations by Boinski et al. (2003) suggest that squirrel monkeys in habitats with a more complex understory are victims of fewer successful avian attacks than those in areas with an intact canopy. Studies of harpy eagle foraging ecology also support this theory, as adult harpy eagles require a clear flight path towards their prey, and struggle to locate and retrieve arboreal prey from dense foliage (Touchton et al., 2002).

The higher density of squirrel monkeys in Villa Belén may be related to a decrease in interspecific competition for resources. In tropical ecosystems, primate species richness declines as logging pressure and anthropogenic disturbance increase (Almeida-Rocha et al., 2017), a conclusion corroborated by our observations of an estimated richness of seven species in Villa Belén, compared to 11 species in Jaldar. Villa Belén may support fewer primate species due to more recent and intense degradation of the forest, creating vacant niches in the ecosystem. Squirrel monkeys can fill vacant niches due to their generalist diet and opportunistic adaptability to disturbed landscapes (Estrada et al., 2012). Members of the Villa Belén and Jaldar communities are subsistence hunters as permitted by wildlife management plans, primarily focussing on species with higher reproduction rates, such as collared peccary (*Pecari tajacu*) and lowland paca (*Cuniculus paca*). Hunting of primates is prohibited (Mahabale et al., 2025). Due to this prohibition, very few of primates are hunted in the Lower Yarapa forests each year, and this does not have any appreciable impact on the primate community composition or population densities in each territory (Mahabale et al., 2025).

We found no difference in squirrel monkey group size between the forests of Villa Belén and Jaldar. In fact, with mean group sizes of 18.96 and 20.86, respectively, the socio-ecological aspects of squirrel monkey distribution are similar in Villa Belén and Jaldar. Group size in social primates is generally determined by predation, food availability, and competition (Janson and Goldsmith, 1995). Large group sizes are beneficial for squirrel monkeys because they enable them to retain access to productive fruit trees, as competing primate species are not able to successfully expel them in the same way they would with a small group (Terborgh and Janson 1986). This may have contributed to the observation of the largest group size also occurring on the transect with the highest number of primate species observed.

The results of our study provide an insight into the ecological benefits of the self-governance and land management of indigenous territories. The contrast between the neighbouring territories in terms of primate species richness allows us insight into the potential ecological benefits of land management strategies – in this case, the prevention of any further commercial timber extraction being allowed. Of the two indigenous territories analysed here, Jaldar was the first to place a strict ban on timber extraction in 1999. Therefore, the forests of Jaldar were able to recover at a natural rate for 23 years until the point of data collection, and support a greater diversity of primates. In contrast, Villa Belén was only free from commercial logging for 9 years, to the point of data collection after banning commercial operations in 2013, meaning it had only 39.1% of the time to recover when compared to Jaldar. This difference demonstrates that, over time, indigenous territories may have beneficial consequences for biodiversity.

Pantropical reviews have revealed that formally protected areas may not be the only tool to create effective protection for biodiversity and the function of tropical rainforests. Indigenous territories perform well to protect areas in terms of conserving rainforest structural integrity, and support 71% of all primate species across the globe, while receiving a fraction of formal biodiversity conservation funding (Sze et al., 2022, 2024). These benefits demonstrate, in this case, an enormous contribution made by indigenous people towards the conservation of primates, and the recent management of the Lower Yarapa forests by the people of Villa Belén and Jaldar preventing commercial timber workers or loggers from destroying primate habitat, is an example of this contribution. These trends highlight the importance of developing community-based conservation strategies alongside indigenous people as major stakeholders, to create landscapes within which both human and non-human primates can prosper.

Overall, our findings suggest that squirrel monkeys can persist at high densities in tropical forests with greater levels of historical logging pressure. However, this increase in population density may come at the expense of other primates, and squirrel monkeys may simply be

filling the vacant niche available to them via the habitat becoming unsuitable for other species.

Acknowledgments

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