ORIGINAL ARTICLE

A high-diversity primate community in a mid-elevation flooded forest, the Jungla de Los Monos Community Reserve, Peru

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Abstract

The Alto Mayo region in the Peruvian department of San Martin has one of the highest levels of deforestation and fragmentation in the country. Historically, San Martin was home to at least 20 primate species, of which at least 14 persist in the Alto Mayo Valley. We surveyed primate populations in the "Jungla de Los Monos", a locally protected remnant of a naturally diverse primate community in one of the last remaining mid-elevation (800 m a.s.l.) seasonally flooded forests in the region. We recorded seven primate species, with a further two species reported to have been extirpated from the area. By far the most common species was *Saimiri macrodon*. Half of the primate biomass was made up of a single species, *Alouatta seniculus,* with *S. macrodon* accounting for another quarter. The endemic *Plecturocebus oenanthe* was only detected once in forest interior, but was observed in edge and riverine forest, as well as neighboring fragments. The area holds a surprisingly high diversity and density of primates considering its proximity to population centers, thanks primarily to self-imposed hunting bans and logging control by local communities.

Introduction

The Amazon is home to one of the highest diversities of primate species in the world, with the western Amazon particularly important (Haugaasen and Peres 2005b; Wilson et al. 2013; Aquino et al. 2014). This is represented in emblematic areas such as the Manu, Pacaya-Samiria, and Yasuni parks in Peru and Ecuador (Janson and Emmons 1990; Pozo-R and Youlatos 2005; Allgas et al. 2018). In such areas, primate species sympatry is exceptionally high (Soini 1986; Janson and Emmons 1990; da Silva et al. 2005; Pozo-R and

Youlatos 2005; Allgas et al. 2018), with up to 14 species reported for the Tamshiyacu-Tahuayo Communal Reserve (Puertas and Bodmer 1993; Puertas et al. 1995). As well as their protected status, the sheer size of these parks, > 2 million ha in the case of Pacaya-Samiria National Reserve, is one of the most important factors in maintaining these high diversities (Harcourt and Doherty 2005; Marshall et al. 2010; Benchimol and Peres 2013, 2014).

The continuing and accelerating destruction of natural primate habitats across the globe (Estrada et al. 2017) means many species are becoming restricted to heavily fragmented habitats in anthropogenic landscape matrices (Blanco 2013; Marsh and Chapman 2013; Benchimol and Peres 2014; da Silva et al. 2015). As such, the preservation of remaining fragments and their functional connectivity within the landscape are of primary importance for conservation (Benchimol and Peres 2014; da Silva et al. 2015). Several studies have shown the persistence of diverse primate communities in fragments of varying sizes (Lopes and Ferrari 2000; Stone et al. 2009; Sampaio et al. 2010), highlighting their importance for conservation. State-run protected areas in highly populated areas, such as the northern Peruvian region of San Martin, are often insufficient for species protection and should be complemented by community-led, landscape-level

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conservation strategies (Margules and Pressey 2000; García et al. 2005; Bergl et al. 2007; Shanee et al. 2015, 2017; Muench and Martinez-Ramos 2016).

Historically, San Martin, in the far western Amazon, had one of the most diverse primate faunas in Peru; with a probable 18 extant species (Shanee et al. 2013), several of which are endemic to Peru and/or listed as Threatened by the IUCN (Shanee et al. 2013, IUCN 2017). The Critically Endangered San Martin titi monkey (*Plecturocebus oenanthe*) is completely restricted to the region (IUCN 2011; Shanee et al. 2011; Decreto Supremo No 004-2014-MINAGRI) and is commonly used as a conservation flagship species. San Martin is also one of the most deforested regions of Peru (Llactayo et al. 2013a, 2013b; IBC 2016) due to massive immigration from Andean regions such as Cajamarca and Piura (Shanee 2012a; Shanee and Shanee 2016). Population growth, along with associated deforestation, fragmentation, and hunting has increased in line with immigration (Shanee 2012a, b; Shanee and Shanee 2016). The Alto Mayo valley in the north of San Martin region is a sub-center of species diversity and endemism, with 14 extant primate species (Shanee et al 2013). The entire Alto Mayo covers an area of just under 8000 km^2 of which ~40% has already been deforested, predominantly in the flat valley floor.

We conducted census surveys in the "Jungla de Los Monos" community-run reserve (JdlM), where self-imposed community-wide hunting and clear-cutting bans have been put in place by community members. Monitoring of primate communities was undertaken as a measure of habitat quality and anthropogenic pressure to be incorporated into management strategies (Yoccoz et al. 2001; Balmford et al. 2003; Paim et al. 2019). Preliminary observations prior to the start of the study suggested high primate diversity and densities in the area, which, if confirmed, would in turn highlight the importance of this and similar relict landscape components.

Methods

The JdlM is located near the village of El Tambo, between the Romero and Negro rivers, approximately 10 km north of the city of Rioja (Fig. 1). The site is characterized by seasonally flooded *aguajal* forests, dominated by Aguaje palms (*Mauritia flexuosa*) at ~800 m a.s.l. (above sea level). We carried out diurnal surveys using line transect methodology (Marshall et al. 2008; Buckland et al. 2010). Transect walks were carried out by researchers and trained local co-investigators. Eight transects, totaling 7500 m (average 0.94 km/transect) were opened, measured, and tagged with foresters' tape. Transects were cut parallel to each other, at least 200 m apart (Fig. 1). Depending on weather conditions, each transect was walked four times each month for 4 months during the dry season

and 4 months during the wet season. Two transects were walked each day. Transects were sampled twice between 7:00 and 9:00 am and twice between 4:00 and 6:00 pm each month. Observers maintained a speed of ~1 km/h on all walks to increase detection probabilities. Only observations on the outbound walk were used in density estimates. Repeat walks on the same transect were made no less than 72 h apart, and neighboring transects were not surveyed on the same day. This was done to ensure independence of detections and avoid issues of pseudo-replication. Habitat characterization and phenological data were recorded separately from transect walks.

Data recorded during primate detections included: date, start and end times of transect walks and detection events, weather conditions, species identity, group size, sighting location, perpendicular distance from the approximate group center to the transect, group spread, activity, height in tree, and, when possible, age/sex class of primates. Distances were measured using a laser range finder or estimated by eye; angles were measured with a compass/protractor. The locations of detections were recorded with hand-held GPS units. Interspecific associations, ad-lib behavioral observations, and vegetation features were also recorded. Prior to analysis, we tested for differences in observer detection rates, detection rates of local field guides, detections per transect, and detection rates between transects.

Density estimates were made using Distance 7.2 software (Buckland et al. 1993; Thomas et al. 2009) for the primate community as a whole (Biomass) and for individual species. Estimates using Distance were calculated for overall primate density and for individual species (Table 1). We fit different models to the data (Supplementary Fig. 1) and used Delta AIC, AIC, and coefficient of variance values to evaluate which model fit best (Burnham and Anderson 1998; Burnham et al. 2011) choosing those with the lowest AIC and coefficient of variation (Buckland et al. 1993). We also used Krebs' (1999) formula:

$$\text{Group density} = G_t / \left(L_t 2(\text{ESW})\right)$$

wherein G_t=total number of sightings, L_t=total sampling effort, and ESW=estimated strip width (calculated as the average adjusted perpendicular distance). Crude biomass estimates were calculated using the formula:

$$\text{Bio}_c = W \times D$$

where Bio_c=crude biomass, W=average adult body weight (kg), and D=population density of species (/km^2). We used average adult body weights from published studies and assumed that half the members of each group were immature individuals and that immature individuals weigh half that of mature individuals (Ford and Davis 1992; Peres 1993; Ford 1994; Boinski 1999; Lu 1999; Allgas et al 2018).
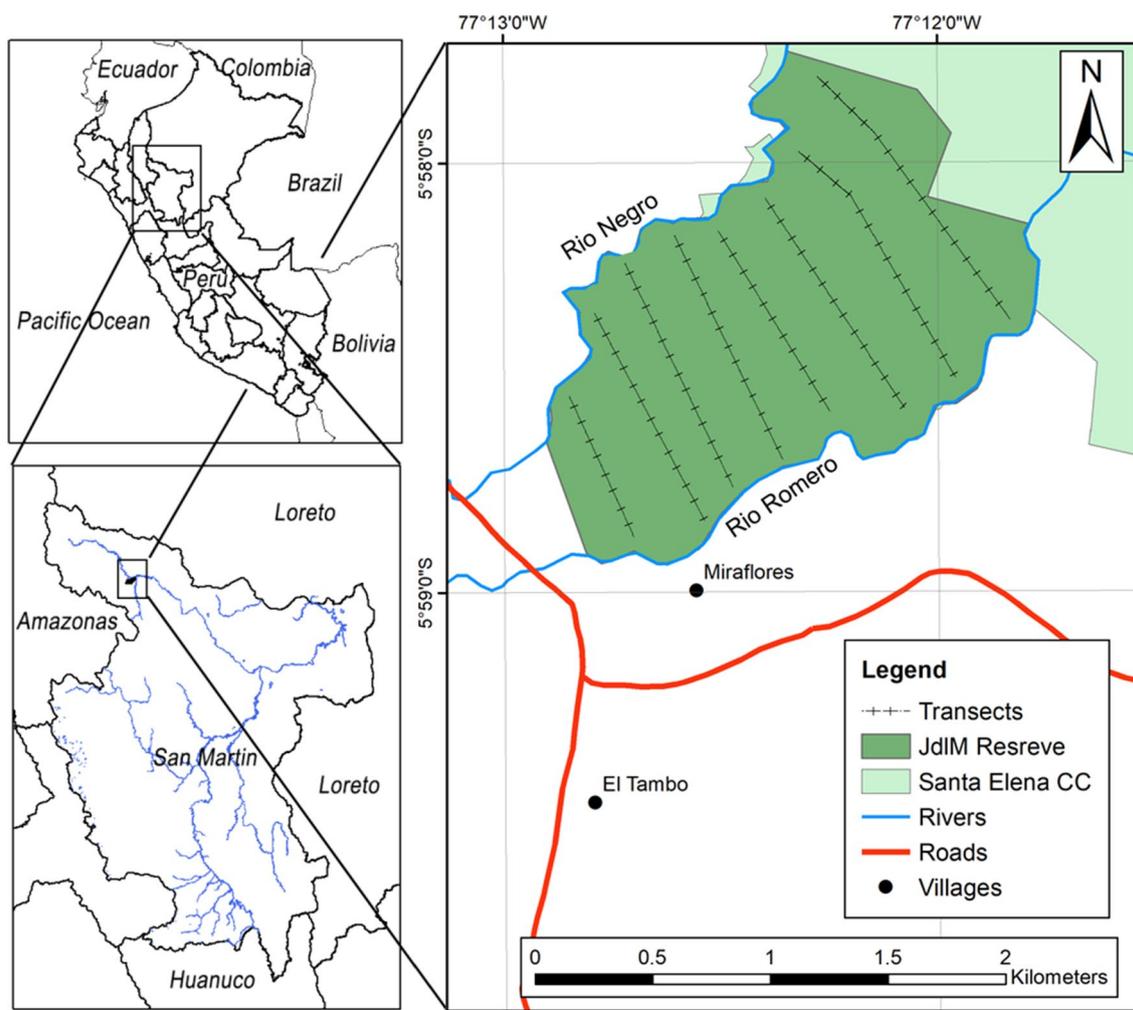
Fig. 1 Map showing study sight location within Peru and transects used in surveys

We made habitat descriptions using point-quarter method (Krebs 1999) on the same transects as census walks (Fig. 1). Samples were taken every 50 m along each transect. At each point, we established four quadrants, divided between the cardinal compass points. We used a radial cut-off distance of 25 m around each point, not sampling trees at greater distances. In each quadrant, we measured the distance from the center to the nearest tree and a second measurement from the first tree to its nearest neighbor (Allgas et al. 2017). We included all trees of trunk diameter at breast height (DBH) > 10 cm, recording DBH, height, and crown spread for each.

We also made additional presence/absence surveys of *P. oenanthe* using visual and audio detection cues. Surveys were carried out in riverine forests and forest fragments in the areas immediately around the study site. Similarly, we made nocturnal surveys to confirm the presence/absence of *Aotus* cf. *nancymaae* in the reserve. We carried out nocturnal surveys at 12 points along four of the transects used in diurnal surveys

(Fig. 1). For nocturnal surveys, we used adapted point transect sampling methods, waiting for 20 min at points established every 200 m along the transects. Although due to the extreme difficulty of night surveys along flooded transects, we abandoned nocturnal surveys.

Ethical note

This research adhered to all relevant laws of Peru and was conducted under research permit No 173-2016-SERFOR/DGGSPFFS. Research protocols followed the American Society of Primatologists' Principles for the Ethical Treatment of Non-human primates.

Table 1 Species expected/encountered during surveys, showing conservation status, notes on detections, group sizes, and comparative density and biomass estimates

Species	Red List status	CITES appendix	DS004-2014MINA-GRI	Recorded during surveys	Detections (n)	Average group size	Avg body weight (kg)	Encounter rate (Gp/km)	Krebs (1999) Strip width	Gp/km²	Ind./km²	Biomass (kg/km²)	Distance Key function	Series expansion	Strip width	Ind./km²	Delta AIC	AIC	CV	Biomass (kg/km²)
Alouatta seniculus	LC	II	VU	Yes	92	6.11	6.5	0.33	43.3	7.74 (0.08)	47.28 (0.47)	307.32	Half normal	Cosine	30.46	64.76 (0.65)	0.00	296.93	0.148	420.93
Aotus cf. nancymaae	VU	II	–	Yes	2	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ateles belzebuth	EN	II	EN	No[c]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cebus yuracus	NT	II	–	Yes	22	7.91	2.7	0.09	42.96	1.86 (0.02)	14.75 (0.15)	39.83	Hazard rate	Simple polynomial	38.99	16.6 (0.17)	0.00	72.97	0.270	44.82
Plecturocebus oenanthe	CR	II	CR	Yes[a]	7	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leontocebus leucogenys	VU	II	–	Yes	28	5.86	0.39	0.10	33.72	3.02 (0.03)	17.72 (0.18)	6.91	Half normal	Cosine	23.29	26.73 (0.27)	0.00	78.01	0.272	10.42
Lagothrix lagotricha	EN	II	EN	No[b]	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sapajus macrocephalus	LC	II	–	Yes	47	6.26	2.91	0.17	45.30	3.78 (0.04)	23.65 (0.24)	68.82	Hazard rate	Simple polynomial	38.8	28.07 (0.28)	0.00	147.94	0.184	81.70
Saimiri cf. macrodon	LC	II	–	Yes	97	18.95	2.91	0.35	44.66	7.91 (0.08)	149.81 (1.50)	140.82	Half normal	Cosine	30.52	220.74 (2.21)	4.82	326.49	0.136	207.29
Primate community	–	–	–	–	286	3.0	–	1.09	43.08	24.26 (0.24)	256.43 (2.56)	563.70	Hazard rate	Simple polynomial	33.67	333.15 (3.33)	1.11	920.35	0.098	765.36

[a] Not recorded during transect surveys

[b] Reported by local guides; not confirmed

[c] Reported by local guides as previously present but probably extirpated within living memory

Results

Primate surveys

We made a total of 173 good transect walks (274.7 km total effort). We detected primates on 287 occasions. The species with the highest encounter rates were *Saimiri macrodon* (0.35 groups/km) and *Alouatta seniculus* (0.33 groups/km). The species with the lowest encounter rates were *P. oenanthe*, only one detection, and *Aotus* cf. *nancymaae*, with only two detections (during diurnal transect surveys). No significant differences were found between observer detection rates ($X^2 = 10$, df 10, p 0.44), guide detection rates ($X^2 = 5$, df 5, p 0.42), detections per transect ($F = 8$, df 6, $p = 0.26$), or detection rates between transects (ANOVA, all > 0.05).

Using Krebs' (1999) formula, densities of primates varied widely (Table 1). *Saimiri macrodon* was by far the most common species with an estimated 150 individuals/km^2, followed by *A. seniculus* with just under 50 individuals/km^2. Overall primate density was 256.43 individuals/km^2, using the same formula (Krebs 1999), with an estimated biomass of 563.70 kg/km^2 (Table 1). Over half of the estimated primate biomass was made up by *A. seniculus*, with a further quarter made up by *S. macrodon* (Table 1).

Densities calculated using Distance (Buckland et al. 1993; Thomas et al. 2009) also varied widely between primate species, but were consistently higher than estimates using Krebs' (1999) formula. Again, *S. macrodon* was the species found at the highest density, accounting for roughly one-third of all primates at the study site, and over half of all primate biomass was made up of *A. seniculus* (Table 1). Overall primate density was 333.15 individuals/km^2, using Distance (Buckland et al. 1993; Thomas et al. 2009), with an estimated biomass of 765.36 kg/km^2 (Table 1).

Aotus cf. *nancymaae* was not encountered during any of the night surveys (although we did record the species during diurnal surveys, see above). We did not calculate density estimates for *A*. cf. *nancymaae*.

Habitat description

A total of 508 trees were sampled between the eight transects (average 63.5 per transect, Supplementary Table 1), which represented a total of 30 different species. Average tree height was 18.28 (± 3.43) m, average DBH was 109.19 (± 16.57) cm, average crown projection was 6.23 (± 0.87) m, and average relative tree diversity score was 0.26 (± 0.09). No significant differences were found in habitat characteristics between transects (all $p > 0.05$).

Plecturocebus oenanthe

We only recorded the presence of *P. oenanthe* once during transects surveys in forest interior. We did observe this species on several occasions in forests along riverbanks when traveling to or from the study site. During presence/absence surveys of *P. oenanthe* in surrounding forest patches, we confirmed its presence in five of the seven patches we surveyed. We also recorded the presence of *P. oenanthe* in several riverine forests along the borders of the JdlM and nearby rivers (Supplementary Fig. 2).

Interspecific associations

Interspecific associations were recorded for all primate species (except *Plecturocebus oenanthe* and *Aotus* cf. *nancymaae*). By far the most common species parings were between *S. macrodon* and *Sapajus macrocephalus* (Supplementary Table 2). The only species pairs not observed were *Leontocebus leucogenys* with either *C. yuracus* or *S. macrocephalus*, or between the two capuchin species themselves (Supplementary Table 2).

Discussion

This is the first census of a primate community undertaken in mid-elevation flooded forests of the Alto Mayo valley, one of the most deforested areas in Peru (Llactayo et al. 2013a, b; IBC 2016). Our results suggest that the primate community is fairly intact, with seven species confirmed in the area. Two primates that may historically have been present, the two largest-bodied species, *Ateles belzebuth* and *Lagothrix lagotricha*, were not found. These species are often the first to disappear due to anthropogenic hunting pressure (Endo et al. 2010; Benchimol and Peres 2014). Interviews with local residents suggest the possible continued persistence of *L. lagotricha*, which was still present at the site within living memory. *Ateles belzebuth* was probably extirpated much earlier (the foundation of nearby cities beginning as early as 1540) and no local informants mentioned their persistence. Hunting is also common in the nearby *Awajun* native communities, with large-bodied primates being principle targets of hunters.

Current species diversity at El Tambo is comparable to much larger and better conserved areas, such as the emblematic Yasuní National Park in Ecuador, with nine species (Pozo-R and Youlatos 2005), although lower than areas of Peru such as Pacaya Samiria National Reserve, 15 species (Neville et al. 1976; Allgas et al. 2018), Tamshiyacu-Tahuayo Communal Reserve, 14 species (Puertas and Bodmer 1993; Puertas et al. 1995), and Manu National Park, 13 species (Janson and Emmons 1990; da

Silva et al. 2005). The fact that this area has been able to maintain such a high primate diversity within a 15-min drive from relatively large urban areas such as Rioja, Nueva Cajamarca, and Moyobamba (populations ~ 25,000, 30,000, and 50,000 respectively), and with no official protection, is very surprising and gives hope for conservation of the area.

Average group sizes for primates recorded during this survey were all within the ranges expected from previously published studies, although all towards the low end (Supplementary Table 3). *Saimiri macrodon* was an exception with substantially lower average group size, ~ 19 at El Tambo, and minimum 25 from the literature. Highly mobile, small-bodied primate species that live in large groups, such as *Saimiri* spp., are notoriously hard to obtain reliable group counts for. However, counts in these cases would tend to underestimate group sizes, and therefore lead to underestimation of densities. In our results, *S. macrodon* was by far the most common species, however still much lower than estimates for the Brazilian endemic *S. vanzolini* in the Mamirauá Sustainable Development Reserve, of 359 individuals/km[2] (Paim et al. 2019). Even though our study site is at a much higher elevation than lowland Amazonian *Varzea* forests, its annual flooding regime is similar to such nutrient-rich areas, which have much higher primate densities than non-flooded, *terra firme*, Amazonian forests (Haugaasen and Peres 2005a). This is especially true for generalist species (Haugaasen and Peres 2005a; Paim et al. 2019). As habitat and dietary generalists, and not the focus of anthropogenic hunting pressure, densities of *Saimiri* spp. could be high at our site, as dispersal opportunities are limited and most natural predators have been all but eliminated (during surveys we found little evidence of possible terrestrial predators).

Our biomass estimates for El Tambo are the highest in the literature for South American primates (Supplementary Table 4). Even higher than those found in the western side of the Pacaya Samiria National Reserve by Bodmer et al. (1997), an area with healthy populations of large-bodied Atelids including *L. lagotricha* and *A. belzebuth* (Bodmer et al. 1997), and Chocha Cashu, in Manu National Park (Janson and Emmons 1990), again an area with *L. lagotricha* and *A. chamek*. Over half of the primate biomass at El Tambo is made up of *A. seniculus*, which is expected, as they are the only large-bodied species we recorded, and have small home ranges and generally high population densities (Supplementary Table 3). What was surprising was that nearly a quarter of the primate biomass came from *S. macrodon* (Table 1). However, as mentioned above, this could be from natural causes. For both species, density compensation due to the lack of some species, and low densities of others, could have led to increased densities. Also, hunting and deforestation in outlying areas are probably pushing animals to seek refuge in remaining habitats.

Primate density at El Tambo was high, double that of Katakari in the Pacaya Samiria National Reserve, Peru (Allgas et al. 2018), and higher than average primate densities at many hunted and un-hunted sites in the western Amazon, 168 and 132 ind./km[2], respectively (Peres 1990). Density of *A. seniculus* at El Tambo was within the limits found in the literature (Supplementary Table 3), but much lower than found in Guarico state, Venezuela, between 112 and 223 ind./km[2] (Crockett 1984; Rudran and Fernandez-Duque 2003). Similarly, densities of *S. macrocephalus* and *C. yuracus* at El Tambo were within the limits of previous studies, although *C. yuracus* was at the higher limit of previous estimates (Supplementary Table 3). Densities of *L. leucogenys* were within the range from the literature, but much higher than those reported by Allgas et al. (2018) and Freese et al. (1982) of 6.6 and 2.4 ind./km[2] respectively.

Habitat in the area was found to be fairly homogenous, with no significant differences found in average tree height, DBH, crown projection, or species diversity between the eight transects (Supplementary Table 1). Although subject to selective logging, the site has conserved characteristics appropriate for healthy populations of the species found in the site's interior, with some found at high densities relative to other areas (Supplementary Tables 3 and 4). If habitat in the area continues to remain relatively intact, it should ensure the persistence of the primate community for the future, as long as hunting can be controlled (Peres 1990). The habitat characteristics we found were not however appropriate for *P. oenanthe*, the only Critically Endangered species at the site (IUCN 2011), which was found primarily in riverine and edge habitat, as reported previously for titi monkeys (Peres 1993; Ferrari et al. 2000; Van Roosmalen et al. 2002). At Pucuncho, a secondary forest site with a high density of *P. oenanthe*, habitat characteristics were very different to the El Tambo site, with much smaller average DBH (18.1 cm), tree height (9.7 m), and crown spread (4.6 m) (Allgas et al. 2017).

Many interspecific associations between Amazonian primate species have been recorded in the literature (Haugaasen and Peres 2009). These associations can serve as behavioral adaptions to increase access to food resources, and as antipredator strategies (Schluter 1984; Haugaasen and Peres 2009; Levi et al. 2013). We observed interspecific associations for all primate species at El Tambo (Supplementary Table 2), with the exception of *Plecturocebus oenanthe* and *Aotus* cf. *nancymaae*. It is possible that some associations exist between *P. oenanthe* and other primate species, but that we did not detect them due to the very low number of encounters with this species. In their study of interspecific interactions in Amazonian primates, Haugaasen and Peres (2009) found that only three of the 12 species at their study sites did not form interspecific associations with other primates. Similar to our findings, these included *Plecturocebus*

cupreus and *Aotus* cf. *nigriceps,* the other was *Ateles chamek* (Haugaasen and Peres 2009). Interactions between *S. macrodon* and *Sapajus macrocephalus* were common (Supplementary Table 2). This species pairing has been observed previously (Podolsky 1990; Haugaasen and Peres 2009; Leonardi et al. 2009; Levi et al. 2013; pers. obs.; Allgas et al. 2018), where squirrel monkeys take advantage of foraging opportunities created by the larger-bodied capuchins (Haugaasen and Peres 2009; Levi et al. 2013). There were no associations observed between the two capuchin species, possibly because of their similar ecological niche requirements.

We chose to place transects in forest interior to avoid edge effects from being too close to rivers (Fischer and Lindenmayer 2007). Locating transects in this way may have been inappropriate for surveys of *P. oenanthe* at this site. *Plecturocebus oenanthe* was fairly common in surrounding forest patches (present in five of the seven we surveyed) and along river edges, meaning that, even though almost never recorded during transect walks, this area is important for its conservation. This species has been noted to prefer edge and secondary forests (Mark 2003; van Kuijk et al. 2015), an observation corroborated by our results, with all but one detection of *P. oenanthe* being along river edges or forest borders (Supplementary Fig. 2). Another possibility for the low encounter rate with *P. oenanthe* in forest interior was the presence *S. macrocephalus* and *C. yuracus*. It was reported locally that capuchins are often aggressive towards titi monkeys, with reports of capuchins even killing them, as has been observed at other sites (Lawrence 2003; Sampaio and Ferrari 2005).

The presence of high densities of aguaje (*M. flexuosa*), a commonly harvested fruit with local market value (Manzi and Coomes 2009), has aided in the JdlM's protection. The area is also a source of timber for local communities, giving further incentive to its preservation. These uses, as well as local impetus for conservation by the *Ronda Campesina* (Shanee 2013, 2019; Shanee et al. 2015) have led to the area being guarded by villagers from El Tambo, with protection from communal hunting and deforestation bans. These initiatives are common in Peru, and a vital addition to Peru's protected areas system (Shanee et al. 2017).

The combination of formal and informal conservation initiatives is the most efficient way to conserve fragmented, anthropogenic landscapes, and private and communal reserves often provide better protection to wildlife than state reserves (Vuohelainen et al. 2012). Peruvian legislation for the formalization of private and communal conservation areas is increasingly complex and often ignores or even obstructs informal conservation initiatives (Shanee 2019). The JdlM shows that these small, local, initiatives can conserve high-diversity primate assemblages in some of the last refuges of natural forests in highly deforested areas, almost solely because of the efforts of local communities.

The proximity of the JdlM to major cities and towns makes it a priority for conservation and a good candidate for primate focused eco-tourism as an alternative income stream for local people. Further efforts should be made to replicate this kind of initiative in areas with relict habitats and threatened primate communities.

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