SECONDARY FORESTS MATTER: BOTANICAL DIVERSITY AND STRUCTURE SUPPORTING *Plecturocebus oenanthe* PERSISTENCE IN FRAGMENTED SAN MARTÍN FORESTS, PERU

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ABSTRACT

Plecturocebus oenanthe (Callicebinae) is Critically Endangered and restricted to fragmented premontane forests of San Martín, Peru. Severe habitat loss and altered forest structure threaten population persistence, and baseline ecological knowledge of habitat requirements is lacking. We characterized floristic composition and forest structural attributes across occupied habitats to identify botanical and structural features essential for species persistence. We conducted the first systematic characterization across nine forest plots in five fragments, combining one-hectare inventories in extensive areas with transect-based sampling in reduced patches. We recorded 237 morphospecies (161 identified to species level) across 53 families, dominated by Lauraceae (27 species), Moraceae (24), Leguminosae (21), and Melastomataceae (19). Alpha diversity indices (Shannon-Wiener: 3.89–5.78; Simpson: 0.89–0.98) indicated medium-to-high biodiversity, whereas low intersite floristic similarity (Jaccard: 0.08–0.21) reflected microhabitat heterogeneity. Extensive fragments exhibited inverted-J diameter distributions and taller, continuous canopies (mean height 15.5–17.5 m; crown height 4.9–5.8 m; basal area 16.69–27.28 m^2/ha), whereas reduced fragments were dominated by small stems (88.14% in the 2.5–10 cm class), lower stature (mean 6.6–9.4 m), and reduced basal area (9.17–36.48 m^2/ha). Pioneer species (*Cecropia concolor, Jacaranda macrocarpa, Miconia* spp., *Pourouma guianensis, Vochysia ferruginea*) dominated across fragments. P. oenanthe exploits secondary patches through ecological flexibility; however, persistence depends critically on retained vertical complexity, crown continuity, and botanical diversity, enabling safe arboreal movement and dietary breadth. Effective conservation requires maintaining canopy closure, height uniformity, and structural recovery through protection from extraction and forest restoration in both primary and secondary stands.

Keywords: Callicebinae, Forest fragmentation, canopy structure, floristic composition, habitat suitability.

INTRODUCTION

Conservation decisions in rapidly fragmented tropical landscapes hinge on habitat diagnostics that translate vegetation composition and architecture into operational criteria for species persistence (Johnson et al., 2023), moving beyond broad habitat labels to measurable attributes that guide actions (Garshelis, 2000). Such diagnostics are most informative when they identify combinations of floristic composition and structural features—canopy height and continuity, basal area, and diameter profiles—associated with species' occupancy and performance, because these attributes can be monitored, restored, and used to prioritize patches and corridors under limited budgets (Arroyo-Rodríguez & Fahrig, 2014; Fahrig, 2017). In regions dominated by secondary forests and small remnants, this approach aligns local management (protection, enrichment, and connectivity) with landscape-level- planning aimed at retaining habitat amount and permeability for arboreal mammals.

Plecturocebus oenanthe is a monkey species Critically Endangered and restricted to the premontane forests of San Martín, Peru, where forest loss and structural simplification threaten its persistence (Shanee et al., 2013; Vermeer & Shanee, 2020). This species occurs in primary and secondary forests and in human-modified- mosaics, indicating behavioral and dietary flexibility (B. C. Aldrich et al., 2008; Bóveda-Penalba et al., 2009; DeLuycker, 2006; Mark, 2003; Shanee et al., 2013). However, the fine-scale- floristic and structural requirements that define functional habitats within the landscape of small, disturbed fragments remain poorly resolved, limiting targeted planning for population persistence (Estrada & Garber, 2022; Torres-Romero et al., 2023). Clarifying these requirements is essential to move from presence records to management benchmarks that maintain safe arboreal movement and reliable resource access (Arroyo-Rodríguez & Fahrig, 2014; Estrada & Garber, 2022).

Habitat fragmentation drives biodiversity decline, but its impacts vary with species' adaptability and forest architecture that supports locomotion and foraging (Benitez-Malvido & Arroyo-Rodríguez, 2008; Fahrig, 2003, 2017). For *P. oenanthe*, the use of secondary patches suggests ecological flexibility; however, small home ranges constrain dispersal and increase vulnerability to stochastic events and genetic isolation, focusing attention on crown height and continuity, basal area, and diameter structure as potential limiting dimensions of habitat quality (DeLuycker, 2007; Schaffer-Smith et al., 2016). Distinguishing the roles of habitat amount versus configuration and emphasizing matrix-mediated- connectivity can therefore improve conservation effectiveness in fragmented landscapes (Arroyo-Rodríguez & Fahrig, 2014; Hortal et al., 2015).

Regionally, premontane forests in San Martín have undergone extensive deforestation and agricultural conversion, with recent decades of forest cover- loss altering floristic composition and vertical structure and reducing understory complexity (B. Aldrich, 2006; DeLuycker, 2007; MINAM, 2015; Shanee et al., 2013). A growing body of work in tropical systems indicates that secondary forests and even small patches can retain conservation value when structural conditions recover within functional ranges (Deere et al., 2020), supporting a pragmatic emphasis on protecting and managing these elements to restore canopy continuity and height needed by arboreal primates. Recent evidence from forest restoration studies demonstrates that three-dimensional habitat structure, including canopy height, vertical complexity, and connectivity, is the primary driver of tropical primate persistence in degraded landscapes (Johnson et al., 2023). This study aims to (1) quantify floristic composition and forest structure across fragments used by *P. oenanthe* and (2) identify botanical species and structural features associated with persistence by comparing extensive (≥2.5 ha) and reduced (<2.5 ha) fragments to derive operational indicators of habitat quality.

METHODS

Study Area

The study was conducted in the Zona de Conservación y Recuperación de Ecosistemas (ZoCRE) Morro de Calzada, located in the districts of Calzada and Yantaló, Moyobamba Province, San Martín Department, Peru (6.0200°S, 77.0400°W; WGS84 datum). The protected area encompasses approximately 1,247.60 hectares of Tropical Premontane Humid Forest (Holdridge, 1971) within the Selva Alta ecoregion (Brack Egg & Mendiola Vargas, 2000), at elevations ranging from 800 to 1,400 m above sea level. The climate is characterized by high annual precipitation, mean temperature of 23.1°C, and relative humidity of 83.3%. Geology comprises Quaternary alluvial and residual deposits interspersed with coarse-grained, cross-bedded sandstones of the Cushabatay Formation (INGEMMET, 1998), representing fluvial-deltaic deposits of the Cretaceous Oriente Group. Vegetation in extensively forested areas is dominated by pioneer species including *Byrsonima spp., Cecropia spp., and Jacaranda macrocarpa*, with frequent canopy gaps colonized by lianas and epiphytic hemiparasites. Anthropogenic areas adjacent to the ZoCRE contain cultivated fruit trees, particularly *Mangifera indica, Psidium guajava,* and *Theobroma cacao*.

Site Selection and Fragment Classification

Five forest fragments were selected based on known home ranges of *Plecturocebus oenanthe* family groups identified through ethological observations (Proyecto Mono Tocón, unpublished data). Fragments were categorized by size: extensive fragments (>2.5 ha), CAL01 (6.8 ha of continuous forest) and YAN01 (2.7 ha); and reduced fragments (<2.5 ha), CAL02 (1 ha), CAL03 (1.1 ha), and YAN02 (1.58 ha). The selection accounted for varying levels of anthropogenic disturbance and fragment isolation to capture habitat heterogeneity (Figure 1).

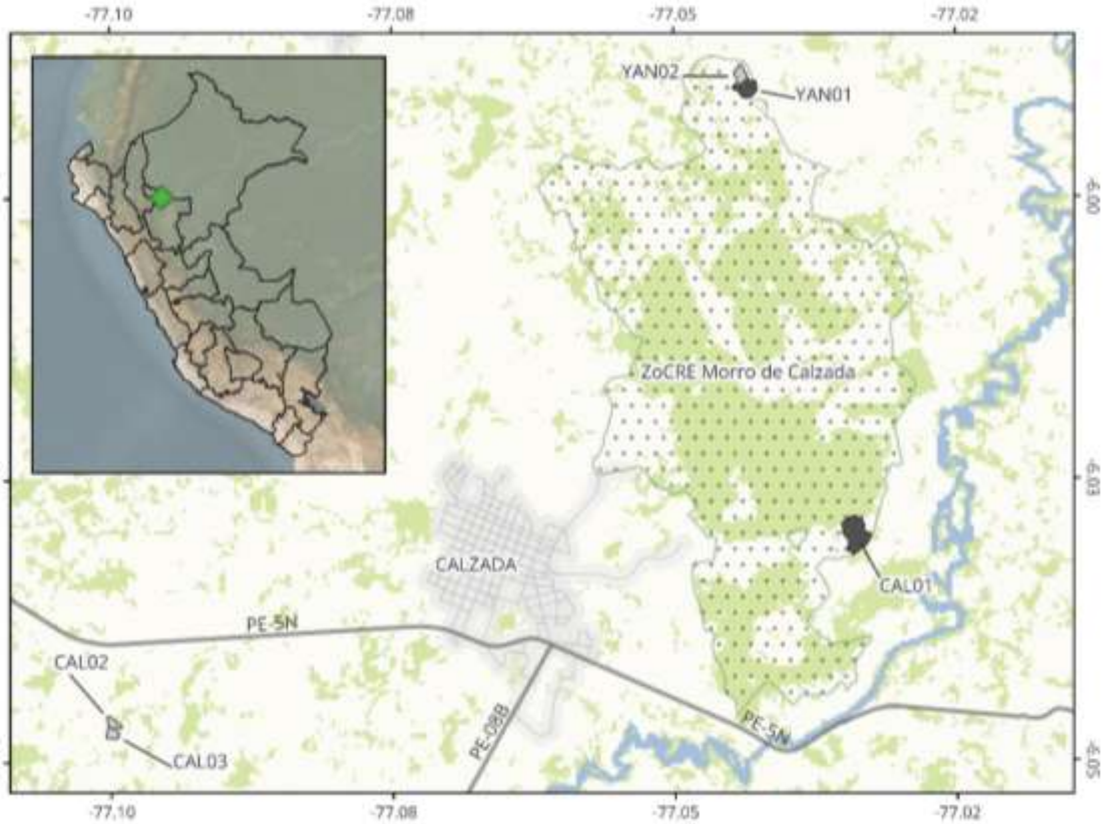

Figure 1. Study area and fragment locations within the ZoCRE Morro de Calzada, San Martín, Peru. The map shows the five sampled fragments—CAL01, YAN01 (extensive), and CAL02, CAL03, and YAN02 (reduced)—and an inset showing the location of ZoCRE within Peru.

Sampling Design and Vegetation Inventory

In extensive fragments, one-hectare plots (100 × 100 m) were established following the modified TEAM protocol. Within each hectare, five 20 × 20 m subplots were systematically located to assess trees and shrubs with DBH between 10 and 15 cm. Trees with a DBH ≥ 15 cm were inventoried across the entire hectare. The parameters recorded for each individual included species identity, DBH, total height, height to first branch, crown height and diameter, and spatial location within the plot. In the reduced fragments, we established linear transects (100 m long each) subdivided into ten contiguous 50 × 2 m sampling units (total area sampled per transect = 0.1 ha). Three transects were surveyed across three reduced fragments (CAL02, CAL03, YAN02; combined 0.3 ha), with all stems ≥ 2.5 cm DBH recorded for species, DBH, height, and structural attributes. All individuals with DBH ≥ 2.5 cm were measured and recorded with data on species, DBH, total and trunk height, and growth form.

Taxonomic Identification

Voucher specimens were collected for morphospecies, typically three per taxon, and processed using standard herbarium protocols. Species identification was performed using regional taxonomic keys (Gentry & Vásquez Martínez, 1993;

Pennington et al., 2004; Reynel et al., 2003) complemented by virtual herbaria, such as the Neotropical Herbarium, Kew, JSTOR Plant Science, and The New York Botanical Garden. Taxonomic names were standardized to the Angiosperm Phylogeny Group III classification and verified using Tropicos and The Plant List. Morphospecies codes were assigned to taxa that were not identified as species.

Diversity and Richness Analyses

Alpha diversity metrics, including Shannon-Wiener (H'), Simpson's index (1-D), Pielou's evenness, and Fisher's alpha, were calculated for each fragment and across DBH classes using bootstrap resampling (1,000 iterations) to address any sampling biases. Species richness was estimated using the Chao-2 and second-order Jackknife estimators. Beta diversity was assessed using Jaccard and Morisita-Horn similarity indices to evaluate species turnover among sites. The dominant species were identified based on their basal area.

Ordination Analysis

Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities was used to analyze spatial variation in floristic composition between fragments. Model fit and stress values were evaluated to determine the appropriate dimensionality for interpreting community differences.

Vegetation Structure

Horizontal structure was characterized by diameter class distributions, basal area, and canopy cover based on the DBH and crown diameter. Basal area calculations followed the forestry guidelines for cross-sectional stem area per hectare. Vertical structure assessments incorporated measurements of total tree height, crown height, and trunk height, with distributions analyzed for statistical differences between the fragments.

Statistical Analysis

Statistical tests included Student's t-tests for comparing diversity indices and species richness, chi-square tests for diameter distributions, and Kruskal-Wallis tests for non-parametric comparisons of structural variables. The analysis was conducted using R statistical software (R Core Team, 2021) with relevant packages (e.g., vegan for ecological analyses). Statistical significance was set at $p < 0.05$.

Ethical Compliance

Research was performed under permits from the Peruvian authorities, complying with legal resolutions (e.g., Directoral Resolution Nº 329-2016 SERFOR) that regulate biological collection and research in forested environments. Ethical guidelines aimed at minimizing ecological disturbance were strictly adhered to.

RESULTS

Floristic Composition

A total of 237 morphospecies belonging to 53 families were recorded in the areas evaluated for *P. oenanthe* coverage. Of these, 161 were identified at the species level, while the remaining 77 morphospecies were assigned numerical codes for analysis. The families with greatest species diversity included Lauraceae (27 species), Moraceae (24), Leguminosae (21), Melastomataceae (19), Euphorbiaceae (15), Salicaceae (12), Anacardiaceae (9), Rubiaceae (8), Araliaceae (7), and Sapindaceae (7). A complete species list with their respective localities is provided in appendix. Together, pioneer dominance and low intersite similarity indicate mosaics of mid-successional stands under heterogeneous disturbance, framing the structural contrasts below.

Alpha diversity

All sites showed medium–high alpha diversity; YAN02 had the highest Shannon and Simpson indices, reflecting the high evenness typical of intermediate stages of succession (Table 1). In extensive fragments, no significant differences were found in the Shannon-Wiener diversity index between diameter classes (Student's t-test; $p > 0.05$). In the reduced fragments, significant differences were observed between CAL02 and YAN02 ($t = -9.73$, $p < 0.001$) and between CAL03 and YAN02 ($t = -11.1$, $p < 0.001$), but not between CAL02 and CAL03 ($t = 1.46$, $p = 0.14$). Similarly, the Simpson's diversity index was consistent across diameter classes in extensive fragments ($p > 0.05$), whereas reduced fragments showed significant differences between CAL02 and YAN02 ($t = 5.06$, $p < 0.001$) and between CAL03 and YAN02 ($t = 5.65$, $p < 0.001$), but not between CAL02 and CAL03 ($t = -1.37$, $p = 0.17$). Evenness and Fisher's alpha also varied significantly among the reduced fragments.

Table 1. Descriptive data and alpha diversity indices of the evaluated forest fragments. Individual counts included the number of trees, with lianas excluded from the diversity analyses.

	Large area				**Reduced area**		
	CAL01[a]	**YAN01**[a]	**CAL01**[b]	**YAN01**[b]	**CAL02**	**CAL03**	**YAN02**
Evaluated area (ha)	1	1	0.2	0.2	0.1	0.1	0.1
Species (S)	56	66	26	20	42	42	112

Families	23	26	17	16	20	20	35
Genera	35	41	21	17	28	25	61
Individuals (N)	302	302	48	35	228	236	414
Shannon y Wiener (H´)	4.22	4.55	4.26	3.89	4.29	4.07	5.78
Simpson (1-D)	0.89	0.90	0.93	0.90	0.91	0.89	0.98
Evenness (J)	0.73	0.75	0.91	0.90	0.79	0.76	0.89
Fisher's alpha (α)	20.23	26.68	23.17	19.39	15.12	14.86	50.46

Note: ^{a} refers to diameter class with DBH ≥ 15 cm; ^{b} to diameter class with DBH between 10 and 15 cm.

Species Richness Estimators

Chao2 and Jackknife2 suggest an underestimation of richness, especially in reduced fragments (e.g., YAN02 projects 118–126 spp.), which is consistent with many infrequent species in mosaics. According to the Chao-2 estimator, the extensive fragments showed between 57 ± 18 and 68 ± 19 species with DBH ≥ 15 cm and between 24 ± 11 and 32 ± 19 species with DBH of 10–15 cm. The reduced fragments exhibited estimated richness ranging from 44 ± 12 to 118 ± 36 species. The second-order Jackknife estimator predicted similar richness patterns, with extensive areas ranging from 62 ± 17 to 76 ± 17 species for DBH ≥ 15 cm and 24 ± 9 to 29 ± 12 species for DBH 10–15 cm, while the reduced areas ranged from 27 ± 6 to 126 ± 30 species (Table 2).

Table 2. Species richness was estimated using two non-parametric methods: Chao-2 and second-order Jackknife.

Estimator	Large area				Reduced area		
	CAL01[a]	YAN01[a]	CAL01[b]	YAN01[b]	CAL02	CAL03	YAN02
Observed	56	65	26	20	42	42	112
Chao-2	57 ± 18	68 ± 19	32 ± 19	24 ± 11	44 ± 12	45 ± 18	118 ± 36
Jackknife-2	62 ± 17	76 ± 17	29 ± 12	24 ± 9	48 ± 12	27 ± 6	126 ± 30

Observed species counts are provided alongside estimated values with standard errors. Values are rounded up to the nearest whole number.

Beta Diversity

Beta diversity analyses revealed low floristic similarity among the fragments. For example, the Jaccard similarity coefficient between CAL01 and YAN01 for species with DBH ≥ 15 cm was 0.21, whereas the Morisita-Horn index was 0.26. The values for species with a DBH of 10–15 cm were 0.12 (Jaccard) and 0.24 (Morisita). In the reduced fragments, the Jaccard coefficients ranged between 0.08 and 0.18, with Morisita-Horn indices from 0.03 to 0.43, the highest similarity noted between CAL02 and CAL03.

Abundance y relative frequency

The extensive areas evaluated exhibited distinct patterns of abundance and relative frequencies among localities. In CAL01, the most abundant species with

DBH ≥ 15 cm were *Cecropia concolor*, *Jacaranda macrocarpa*, and *Miconia aff. bailloniana*, which collectively accounted for more than half of all individuals recorded. These species also had the highest relative frequencies, indicating their consistent presence throughout the area. In contrast, YAN01 was dominated by *Vochysia ferruginea*, which had relative abundance and frequency of 28.8% and 12.2%, respectively, making it the most abundant and frequent species. *Jacaranda macrocarpa* and *Miconia elata* were the next most abundant species (Table 3A). In the reduced areas, floristic heterogeneity increased with different dominant species at each site. CAL02 was dominated by *Alchornea glandulosa*, *Pourouma guianensis*, and *Miconia myriantha*, whereas CAL03 was mainly characterized by *Miconia myriantha*, *Jacaranda macrocarpa*, and *Cecropia concolor*. YAN02's relative abundance was led by *Miconia elata*, *Vochysia ferruginea*, and *Chrysochlamys dependens*, although no species exceeded a 5% relative frequency (Table 3B).

Table 3. Relative abundance (Ab%) and relative frequency (Fr%) by site and size class of ten dominant species. Large areas (CAL01a, YAN01a) reported DBH ≥ 15 cm; subunits (CAL01b, YAN01b) reported 10 < DBH < 15 cm; and reduced areas (CAL02, CAL03, YAN02) were per the methods. Species shown are those contributing the most per site; the last row reports the cumulative percentage explained. Ab% is the proportion of individuals per species, and Fr% is the proportion of sampling units with presence.

Species	**(A) Large areas**								**(B) Reduced areas**					
	CAL01[a]		**YAN01[a]**		**CAL01[b]**		**YAN01[b]**		**CAL02**		**CAL03**		**YAN02**	
	Ab %	**Fr%**	**Ab %**	**Fr%**	**Ab %**	**Fr%**	**Ab %**	**Fr%**	**Ab %**	**Fr%**	**Ab %**	**Fr%**	**Ab %**	**Fr%**
Achatocarpus praecox							2.9	3.7						
Alchornea glandulosa									20.6	8.9	3.4	3.5		
Alchornea triplinervia					8.3	7.9					3.0	4.7		
Alchorneopsis floribunda					4.2	2.6								
Aniba sp.							2.9	3.7						
Banara guianensis			3.3	2.4										
Bellucia pentamera											2.5	4.7		
Calophyllum brasiliense			3.0	3.7			8.6	7.4					1.9	2.5
Calyptranthes bipennis							2.9	3.7						
Cecropia concolor	18.5	11.5			14.6	10.5	8.6	7.4			5.5	10.5		
Chrysochlamys dependens													5.8	4.2
Chrysophyllum argenteum									7.5	3.3				
Citrus sp.											5.1	3.5		
Clarisia biflora													1.9	2.5
Couepia ulei									0.4	1.1				
Cupania cinerea	2.7	3.6			2.1	2.6								
Cybianthus cf. *flavovirens*	4.6	2.4												
Ficus gomelleira													0.7	0.4
Ficus insipida			2.0	2.4			2.9	3.7						

Inga heterophylla	2.3	1.8												
Jacaranda macrocarpa	18.2	12.7	7.6	5.5	12.5	10.5					10.2	9.3	0.7	0.9
Ladenbergia oblongifolia			3.6	3.7										
Mangifera indica									0.9	1.1				
Maprounea guianensis									4.4	3.3				
Miconia aff. *bailloniana*	17.2	11.5			10.4	7.9			2.6	4.4	9.8	4.7		
Miconia aff. *ternatifolia*							5.7	3.7						
Miconia elata			5.6	5.5			11.4	11.1					10.4	4.2
Miconia myriantha					4.2	5.3			10.1	7.8	26.3	10.5		
Miconia tomentosa									4.0	4.4				
Oenocarpus mapora	2.0	3.0	5.0	6.1									3.6	2.5
Parinari aff. *romeroi*									0.9	1.1				
Persea sp.2					2.1	2.6								
Pourouma guianensis									13.2	6.7			4.6	4.2
Schefflera aff. *sprucei*	2.7	3.0												
Schefflera morototonii	2.3	3.6												
Schizocalyx multiflorus													2.9	0.9
Socratea exorrhiza					2.1	2.6								
Talisia japurensis							2.9	3.7						
Tetrorchidium macrophyllum	3.0	4.8	3.6	5.5	6.3	5.3								
Tetrorchidium rubrivenium											4.7	1.2		
Vernonanthura phosphorica											8.5	7.0		
Virola sebifera			2.7	4.3										
Vochysia ferruginea			28.8	12.2			22.9	14.8					8.5	3.4
Total percentage explained	**73.5**	**57.8**	**65.2**	**51.2**	**66.7**	**57.9**	**71.4**	**62.9**	**64.5**	**42.2**	**78.8**	**59.3**	**41.1**	**25.9**

The NMDS analysis based on Bray-Curtis dissimilarity revealed spatial heterogeneity in the floristic composition of the evaluated areas. Extensive fragments from both localities were clearly separated in multidimensional space, with Calzada sites positioned in the upper central quadrant and Yantaló sites in the lower left quadrant. The reduced fragments showed greater dispersion in ordination space, notably with CAL02 located in the upper right quadrant and YAN02 in the upper left quadrant (Figure 2).

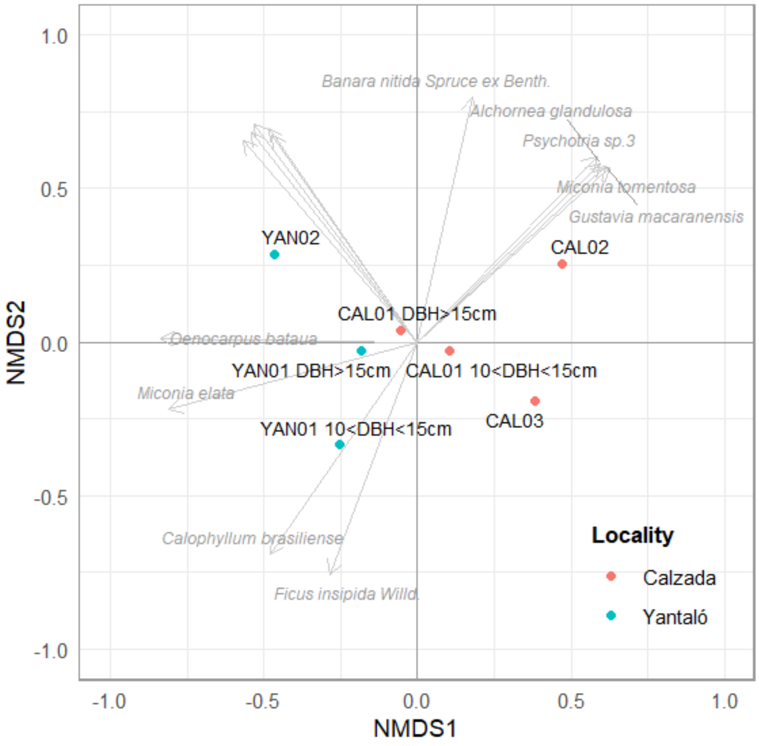

Figure 2. Non-metric multidimensional scaling (NMDS) ordination plot showing the spatial separation of forest fragments and diameter classes based on species relative abundance using Bray-Curtis dissimilarity (Stress = 0.0522).

Horizontal Structure

Extensive areas showed an inverted J-shaped diameter distribution, indicating active forest regeneration (Figure 3A). In CAL01, the 10–15 cm diameter class comprised 44.28% of individuals, followed by the 15–25 cm class with 41.88%, together making up 86.16% of all trees. YAN01 exhibited a similar pattern, with the

15–25 cm class prevailing at 46.96% and 10–15 cm at 36.69%. The frequency of individuals decreased steadily with increasing diameter at both sites. CAL01 had higher counts in the 25–35 cm and 45–55 cm classes than YAN01. Statistical tests showed no significant differences in mean DBH between the equivalent diameter classes (10–15 cm: chi-square = 1.44, df = 1, $p = 0.23$; >15 cm classes: chi-square = 2.4, df = 1, $p = 0.12$).

The reduced areas displayed markedly different diameter distributions, dominated by smaller trees (Figure 3B). In CAL02, 71.49% of individuals were in the 2.5–10 cm class and 21.05% were in the 10–20 cm class. CAL03 had an even stronger dominance of the smallest class (88.14%) with no individuals above a 30 cm DBH. YAN02 showed 78.99% in the smallest class and 14.01% in the next class. A significant difference in median DBH was detected among the reduced fragments (chi-square = 15.41, df = 2, $p < 0.001$), with CAL03 (5.94 ± 3.8 cm) having a significantly smaller median DBH than CAL02 (8.76 ± 7.9 cm) and YAN02 (7.67 ± 7.3 cm).

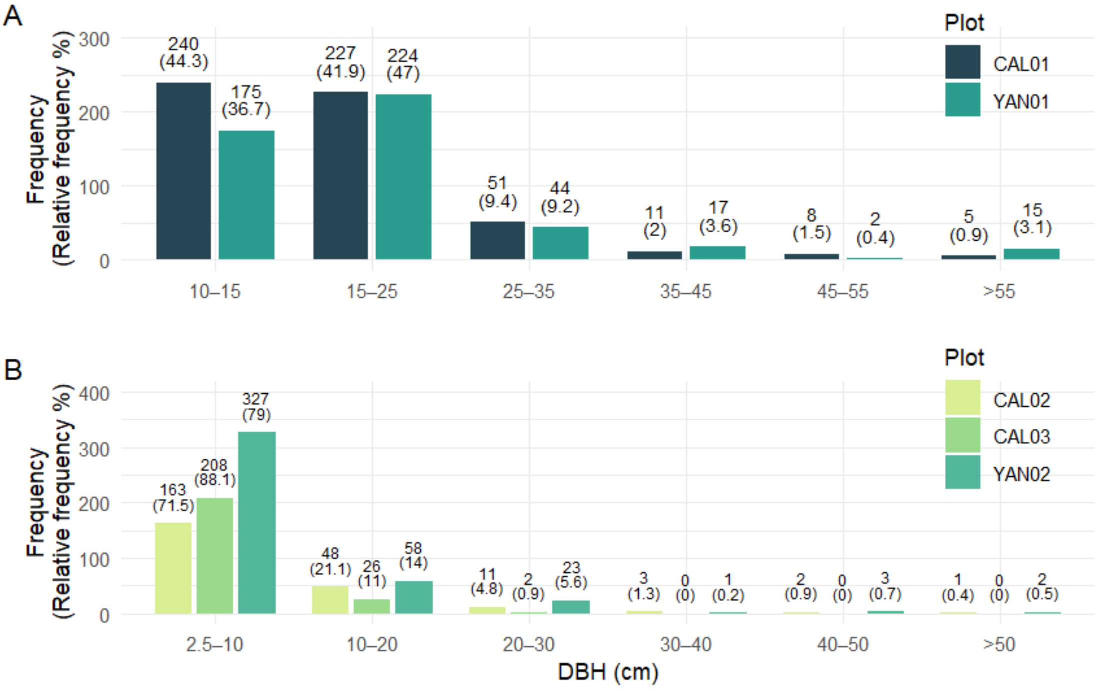

Figure 3. Diameter distribution in large (A) and reduced (B) areas; bars show absolute frequency, with relative frequency (%) indicated in parentheses. The first diametric category in the large areas was projected to match the surface evaluated for other diametric categories.

For the extensive fragments, horizontal occupancy differentiated the plots (Figure 4). In CAL01, individuals with DBH ≥ 15 cm contributed 16.69 m^2/ha of basal area, with over half attributed to three species: *Oenocarpus mapora* (25.81%), *Jacaranda macrocarpa* (13.69%), and *Miconia aff. bailloniana* (11.39%). In YAN01, the basal area for trees with DBH ≥ 15 cm was higher at 27.28 m^2/ha, mainly due to the greater abundance and basal area contribution of *Oenocarpus mapora*. Crown cover measured 14,271 m^2/ha in CAL01 compared to 8,319.48 m^2/ha in YAN01. For the 10–15 cm DBH class, absolute dominance was 2.77 m^2/ha in CAL01 and 0.42

m^2/ha in YAN01; crown cover was 5,266.60 m^2/ha and 2,481.54 m^2/ha, respectively.

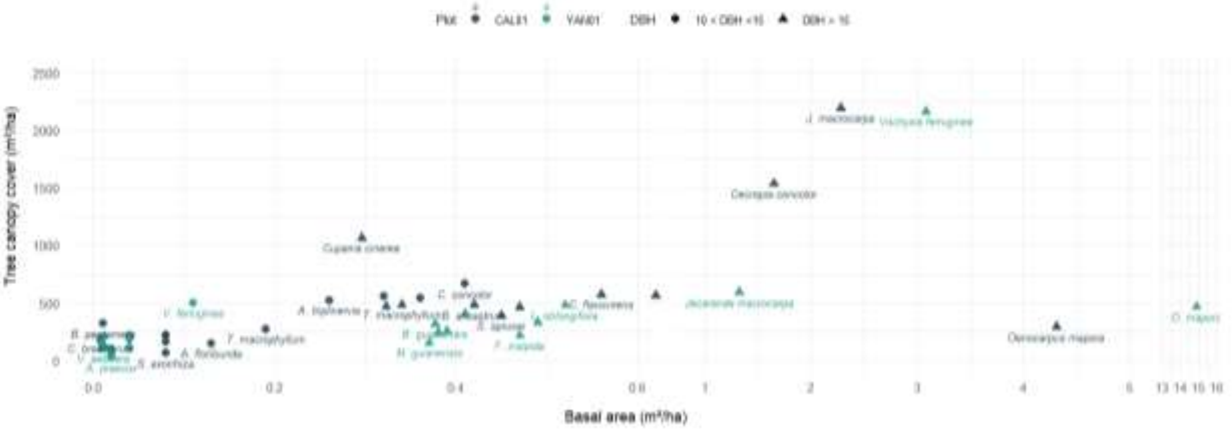

Figure 4. Relationship between basal area (m^2/ha) and tree canopy cover (m^2/ha) by species in large plots CAL01 and YAN01. Circles indicate species with 10 < DBH < 15 cm, and triangles indicate species with a DBH ≥ 15 cm. The labels identify the species with the highest relative contributions in either plot.

In the reduced areas, the total basal area measured 24.80 m^2/ha in CAL02, 9.17 m^2/ha in CAL03, and 36.48 m^2/ha in YAN02, with the highest value in YAN02 due to a greater number of individuals across diameter classes. In CAL02, the dominant contributors to the basal area included *Alchornea glandulosa* (6.42 m^2/ha; over 25%), *Couepia ulei* (3.12 m^2/ha; 13%), and *Mangifera indica* (2.23 m^2/ha; 9%). CAL03's basal area was mainly influenced by *Jacaranda macrocarpa* (1.71 m^2/ha; 18.7%), *Miconia myriantha* (1.40 m^2/ha; 15.3%), *Cecropia concolor* (1.16 m^2/ha; 12.7%), and *Alchornea glandulosa* (0.95 m^2/ha; 10.4%). In YAN02, the greatest basal area contributions came from *Vochysia ferruginea* (5.86 m^2/ha; 16.1%), *Jacaranda macrocarpa* (3.55 m^2/ha; 9.7%), *Ficus gomelleira* (3.10 m^2/ha; 8.5%), and *Clarisia biflora* (2.95 m^2/ha; 8.1%). Across the three sites, four to five dominant species accounted for approximately half of the total basal area.

Vertical Structure

Consistent with these successional floras, canopy metrics diverged by fragment class, with extensive plots retaining taller, more continuous crowns and reduced plots showing truncated, discontinuous strata. Trees with a DBH ≥ 15 cm in both CAL01 and YAN01 predominantly occupied the upper forest strata (>10 m). CAL01 had proportionally more individuals above 20 m, whereas YAN01 had more individuals in the 10–15 m range. In both areas, individuals in the lowest stratum (5–10 m) were rare. The median height differed significantly between the sites (CAL01:17.5 ± 4.7 m; YAN01:15.5 ± 3.7 m; $\chi^2 = 14.03$, df = 1, $p < 0.001$) (Figure 5A). For trees with a DBH of 10–15 cm, most individuals were found in the 10–15 m class. CAL01 presented slightly higher counts in the 15–20 m category than YAN01, and no individuals in YAN01 exceeded 20 m (Figure 5B). The median height did not differ significantly between the sites (CAL01:12.6 ± 3.3 m; YAN01:12 ± 2.9 m; $\chi^2 = 0.01$, df = 1, $p = 0.91$).

In the reduced areas (CAL02, CAL03, and YAN02), most individuals were found in the lower canopy strata (≤10 m). CAL02 showed a concentration of trees between 10 and 15 m, whereas CAL03 had most individuals in the 5–10 m range, and none exceeded 15 m. YAN02 also presented most trees in the 5–10 m range, with a small proportion reaching 15–20 m. No individual exceeded 20 m at any of these sites. Across all reduced areas, the highest density of trees occurred between 5 and 10 m, with frequencies declining in the adjacent strata (Figure 5C). Canopy height was significantly lower in CAL03 than in CAL02 and YAN02 (Kruskal–Wallis: $\chi^2 = 20.85$, df = 2, $p < 0.001$).

Figure 5. Tree height distributions by plot and size class. A: For DBH ≥ 15 cm, both CAL01 and YAN01 concentrated above 10 m, with CAL01 showing relatively more trees >20 m and YAN01 peaking at 10–15 m. B: For DBH 10–15 cm, most stems are 10–15 m; CAL01 has slightly more at 15–20 m, and YAN01 has none >20 m. C: Reduced areas are largely ≤10 m: CAL02 centers were at 10–15 m, CAL03 at 5–10 m with none >15 m, and YAN02 mostly 5–10 m with a few 15–20 m; no trees exceeded 20 m.

The ten dominant species by absolute dominance with DBH ≥ 15 cm in CAL01 had a mean height of 17 ± 2.6 m, with the tallest species reaching 20.4 m and the shortest species reaching 11.9 m. The mean crown height was 5.8 ± 1.4 m, which was slightly less than one-third of the mean total height. In YAN01, the mean height among the ten dominant species was 15.7 ± 2.2 m, with values ranging from 18.1 m to 11.4 m; crown height averaged 5.3 ± 1.5 m, just over one-third of the mean total height. The difference in the mean height between CAL01 and YAN01 was 1.3 m. The median crown height for all species with DBH ≥ 15 cm differed between areas, with values of 5.8 ± 3.3 m in CAL01 and 4.9 ± 2.6 m in YAN01 ($\chi^2 = 8.08$, df = 1, p = 0.005) (Figure 6A).

For trees with DBH between 10 and 15 cm, the mean height of the ten dominant species in CAL01 was 12.6 ± 2.0 m, ranging from 16.5 m to 10.0 m, and the mean crown height was 3.7 ± 1.1 m, just under one-quarter of the total height. In YAN01, the dominant species averaged 12.3 ± 2.5 m in height, with a range of 16.0 m to 7.5 m, and a mean crown height of 3.9 ± 1.2 m, which is approximately one-third of the mean total (Figure 6B). The differences in the mean heights between the areas were minimal. There was no significant difference in median crown height among all species in this diameter class, with means of 3.8 ± 2.1 m for CAL01 and 3.7 ± 1.7 m for YAN01 ($\chi^2 = 0.05$, df = 1, p = 0.83).

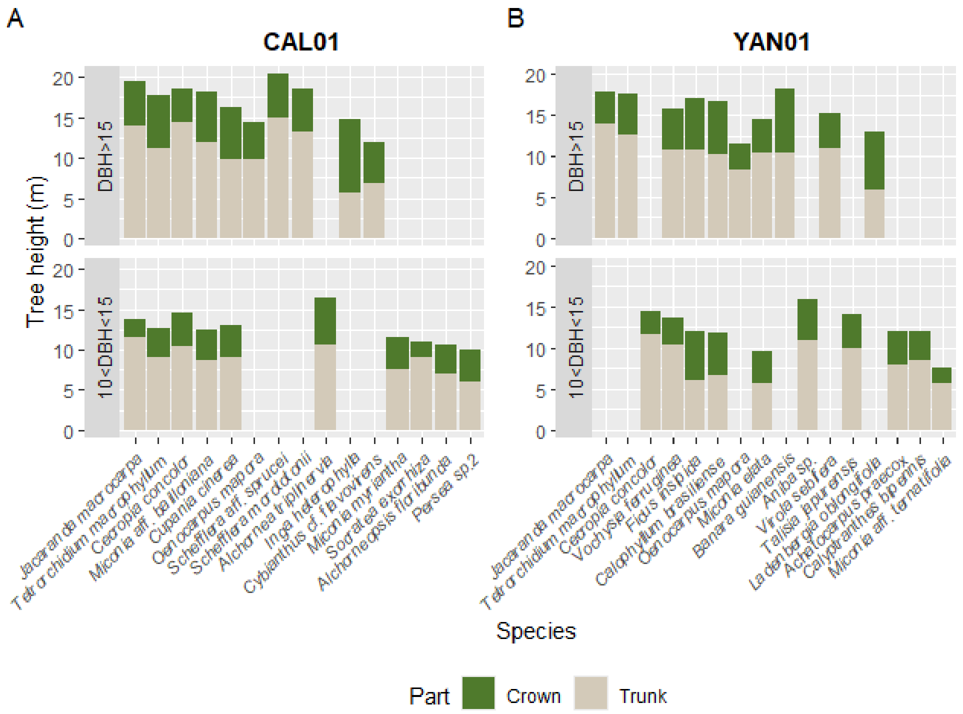

Figure 6. Crown and trunk heights of dominant species by plot and size class. A: CAL01—ten dominant species shown for DBH ≥ 15 cm (top) and 10–15 cm (bottom). B: YAN01—analogous panels for the ten dominant species. The legend indicates the stacked components (trunk and crown).

In the reduced areas, the ten dominant species in CAL02 averaged 9.4 ± 4.1 m in height, with maximum and minimum values of 17.0 and 4.4 m, respectively. The mean crown height was 4.1 ± 3.2 m, which is nearly half of the mean height. CAL03 showed a lower mean height among dominant species at 6.6 ± 1.3 m, with the tallest species at 7.9 m and shortest at 3.8 m. The mean crown height was 2.3 ± 0.7 m, which was slightly more than one-third of the total. YAN02 had a mean height for the dominant species of 9.4 ± 4.2 m, ranging from 17.0 m to 4.8 m, and a mean crown height of 3.5 ± 1.4 m, representing more than one-third of the mean. CAL03 displayed the lowest mean height of all the reduced areas, whereas CAL02 and YAN02 were similar in structure but differed in species composition (Figure 7). The median crown height differed significantly among the reduced areas, with CAL03 at 2.1 ± 1.3 m, compared to 2.7 ± 4.0 m in CAL02 and 2.8 ± 2.0 m in YAN02 (χ^2 = 25.84, df = 2, $p < 0.001$).

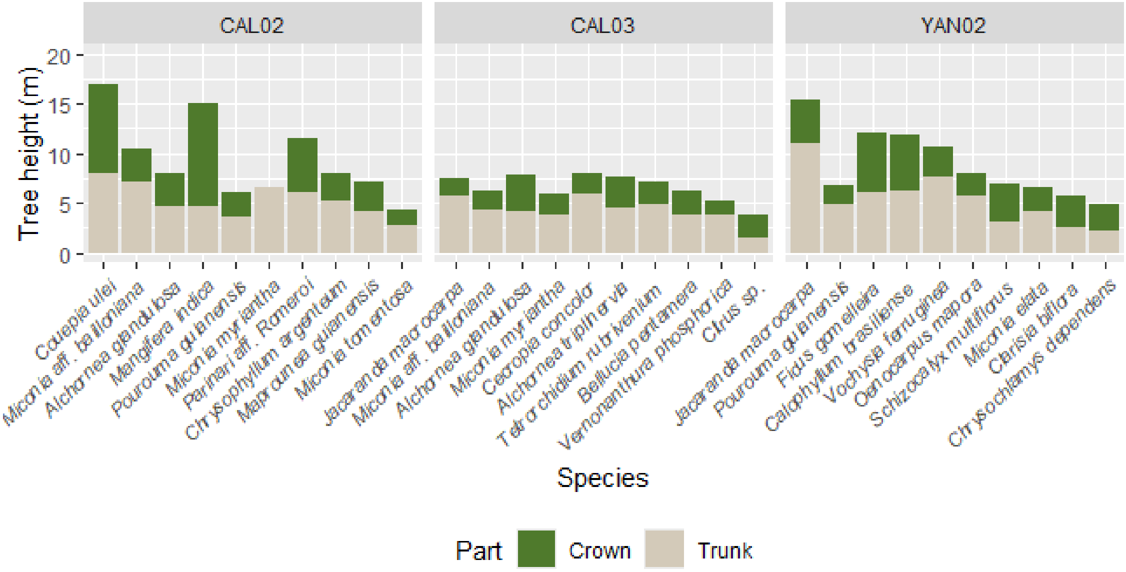

Figure 7. Crown and trunk heights of the ten dominant species in the reduced areas. CAL02 shows intermediate stature, with several species reaching 15–17 m and crowns comprising roughly half of the total height. CAL03 exhibited the shortest canopy profile, with species mostly under 8 m and comparatively small crowns. YAN02 resembles CAL02 in overall height but has a different dominant species; crowns represent over one-third of the total height.

DISCUSSION

The floristic and structural characteristics of *Plecturocebus oenanthe* habitats documented in this study reveal a landscape in which ecological flexibility and adaptability intersect with acute fragmentation pressures. Floristic patterns indicated pioneer-rich mid-successional assemblages with low intersite similarity, suggesting that *P. oenanthe* occupies habitats undergoing continuous ecological turnover. Structural metrics varied markedly by fragment class, with larger fragments maintaining taller and more continuous canopies, whereas smaller fragments showed truncated and lower vegetation profiles. The NMDS ordination clearly separated the sites along these structural and compositional gradients. Together, these results provide a critical baseline for understanding how this threatened primate persists in rapidly degrading tropical forest. They also highlighted the link between dietary flexibility and habitat structure, showing that persistence appears to depend on maintaining crown continuity, sufficient canopy height, and basal area within regional ranges.

Implications of floristic heterogeneity

The evaluated *P. oenanthe* habitats are composed of widely distributed premontane humid forest species, with dominant families including Lauraceae, Moraceae, Leguminosae, and Melastomataceae, consistent with regional floristic patterns (Gentry, 1995; Marcelo-Peña & Reynel, 2014). Pioneer species abundance (*Cecropia*, *Jacaranda*, *Miconia*) reflects successional dynamics and disturbance regimes (DeLuycker, 2007). The absence of commercially valuable timber species and the low density of palms indicate anthropogenic extraction pressures. Beta diversity analyses revealed low species overlap (Jaccard = 8–21%) among fragments, reflecting microclimatic variation, physiography and differential disturbance. This heterogeneity necessitates the interpretation of floristic composition within successional contexts rather than as a pristine deviation, particularly given the extreme fragmentation history of San Martín (Shanee et al., 2013).

Alpha diversity indices indicated medium-to-high biodiversity, with species richness estimates (Chao-2 and Jackknife) suggesting an underestimation typical of transitional forests with rare species (Chiarucci et al., 2010). A comparison with Amazonian premontane forests reveals approximately 30 fewer species, supporting the transitional forest classification (De Aledo et al., 2023; Quinteros-Gómez et al., 2021). The high evenness and low dominance suggest mid-successional recovery, which is typical of repeatedly disturbed landscapes (Yuan et al., 2024).

Canopy structure and habitat suitability

Vertical stratification and canopy connectivity are fundamental determinants of primate habitats. Canopy structure is a critical driver of arboreal primate richness, often exceeding productivity or precipitation in terms of predictive importance (Davies & Asner, 2014). *P. oenanthe*, with home ranges of 0.3–5 ha and obligate arboreality, requires a continuous canopy for secure movement and predator avoidance (DeLuycker, 2006; Schaffer-Smith et al., 2016). Extensive fragments with inverted J- diameter distributions sustain taller, closed, and more continuous canopies that arboreal primates select for safe, efficient movement, whereas reduced fragments with low, discontinuous crowns (e.g., CAL03:2.3 m mean crown height) elevate exposure and locomotor costs by interrupting crown-to-crown-- routes (Davies & Asner, 2014; McLean et al., 2016). The three-dimensional- movement space (crown cover × crown height) differed substantially between sites: 102,650 m^3 (CAL01) vs. 53,429 m^3 (YAN01), reflecting differential primate habitat suitability. Arboreal primates select for canopy closure, tall trees, and uniform height while avoiding gaps; therefore, these metrics directly predict habitat quality and should guide management priorities (McLean et al., 2016). In P. oenanthe, field studies have reported regular use of secondary and edge forests with foraging on pioneer plants (Cecropia, Pourouma, Miconia) and insect prey from mid-upper-- crowns when canopy continuity reduces exposure, linking structure to movement and diet in disturbed mosaics (DeLuycker, 2006, 2007; Deluycker, 2012; DeLuycker, 2021). A convergent case in titi monkeys shows *Callicebus nigrifrons* concentrating activity and feeding in secondary forest sectors with higher canopy closure and connected crowns while avoiding gap-rich-, low-crown- patches, which is evidence that canopy structure mediates space use even in fragmented landscapes (Trevelin et al., 2007).

Dietary flexibility in successional forests

Our floristic and structural profiles explain how habitat composition and canopy architecture enable dietary generalism in titi monkeys, and specifically, in *P. oenanthe*: pioneer-rich- fragments dominated by *Cecropia*, *Pourouma*, *Miconia*, and *Oenocarpus* supply small, fast-turnover- fruits and seasonal buffers, which *P. oenanthe* complements with arthropods from mid-to upper-- crowns when crown connectivity reduces exposure and travel costs (DeLuycker, 2006, 2007; Deluycker, 2012). Comparative evidence shows that this pattern is clade-wide- rather than idiosyncratic: in Brazil's Atlantic Forest, *Callicebus nigrifrons* concentrates feeding on secondary forest- taxa such as *Alchornea triplinervia*, *Tetrorchidium rubrivenium*, and *Inga* spp., and during bamboo masting years pivots toward seeds to sustain intake in disturbed habitats (Dos Santos et al., 2012; Trevelin et al., 2007). Syntheses for Callicebinae indicate that fruits contribute roughly 36–86% of intake across sites, with seasonal increases in seeds, flowers, young leaves, and invertebrates when fleshy fruits decline, and with plant genera consumed tracking regional floras typical of successional mosaics (Bicca-Marques & Heymann, 2013). Beyond floristics, fine-scale- structure mediates whether dietary flexibility is realized in practice: pair-living- titis with small ranges require closed, sufficiently tall, and connected canopies to move efficiently among patchy, fast-renewing- fruit sources; thus, persistence in fragmented premontane systems depends on aligning pioneer availability with vertical structure and crown connectivity (Fernandes et al., 2025). This structural linkage is reflected across fragmented landscapes, where titi presence and density correlate more strongly with vegetation structure (tree density, trunk diameter, and understory density) than with coarse landscape cover, linking successional diet breadth to safe arboreal access and reliable resource acquisition (Hilário et al., 2024; Souza-Alves et al., 2023).

Anthropogenic disturbance and dynamics

Selective logging and smallholder clearing in San Martín have simplified forest structure by lowering basal area, truncating diameter distributions, and increasing pioneer dominance, thereby locking many fragments into early–mid-successional states with low, discontinuous crowns that raise locomotion costs and exposure for small, pair-living- titis (Benitez-Malvido & Arroyo-Rodríguez, 2008). Deforestation rates in Peru are among the highest, driven by agriculture and timber extraction, which have transformed continuous forests into isolated patches embedded in farmland, impeding recolonization and weakening source–sink dynamics (Shanee et al., 2013). Consistent with this, the basal area in reduced fragments (e.g., CAL03:9.17 m^2/ha) falls well below premontane references (≈19–32 m^2/ha), indicating stands in recovery with insufficient vertical complexity and crown connectivity for efficient arboreal movement. Comparative cases across Callicebinae indicate that persistence under disturbance hinges on retained structure rather than forest area alone. In the Atlantic Forest, *C. nigrifrons* preferentially uses selectively logged fragments that still maintain crown continuity, whereas its use declines where height and connectivity are depressed (Trevelin et al., 2007). Similarly, *Callicebus coimbrai* occupancy and density align more with tree density, trunk diameter, and understory density than with coarse cover, demonstrating how depressed basal area cascades into vertical simplification that constrains site use (Hilário et al., 2024; Souza-Alves et al., 2023). In western Amazonia, *Plecturocebus cupreus* persists at edges and in secondary stands only where canopy connectivity is maintained; repeated selective logging that reduces basal area and lowers crown height compromises the realizability of this persistence strategy (Bicca-Marques & Heymann, 2013). Similarly, *Plecturocebus ornatus* in fragmented Colombian Llanos exhibit elevated foraging time and reduced social activity in highly fragmented landscapes with lower plant richness, suggesting that while titis can exploit edges and secondary succession when canopy continuity remains, intensive fragmentation coupled with structural simplification elevates behavioral and energetic costs (Quintero-Tapia & Carretero-Pinzón, 2024). These patterns underscore that small-scale- primates, such as titis, require closed, tall, and structurally uniform canopies with safe arboreal routes to move efficiently among patchy resources. Restoration efforts directed toward the recovery of canopy closure, height, and uniformity, accompanied by management targeting basal area recovery toward regional reference ranges, are thus essential for long-term- viability in fragmented systems (Barnett et al., 2024; DeLuycker, 2021).

Conservation implications and management

Current populations compressed into small, isolated fragments exist at extremely high densities (26.9–38 individuals/km^2), suggesting that contemporary persistence may reflect a transient demographic buffer rather than a stable equilibrium. This crowding elevates disease transmission, inbreeding, and reproductive costs, which are unsustainable without active recovery (Shanee et al., 2025).

A critical gap compounds these extinction risks: insufficient space for forest structural recovery. Although *P. oenanthe* exploits early successional flora, its persistence depends on canopy closure, height uniformity, and vertical complexity, which develop only through extended succession (DeLuycker, 2007). Current fragments remain trapped in low structural states owing to the ongoing extraction pressures. Mid- and late-successional forests that provide primate habitats and ecosystem services require decades to centuries to develop and are largely absent from protected areas. Small-bodied arboreal primates are thus intrinsically vulnerable to structural degradation, not solely to habitat loss (Rozendaal et al., 2019; Tito et al., 2022).

P. oenanthe remains absent from all government-protected areas. Shanee et al. (2013) identified a strategic priority: four new protected areas and one wildlife corridor would increase protected coverage from 14.6% to 66.7%, a transformation critical for species survival. Equally critical is strict protection from extractive uses to enable succession and allow fragments in early to-mid succession to transition toward structurally complex secondary forests. Secondary forests aged 30–50 years harbor 80–100% of the bird, mammal, and reptile species found in adjacent mature forests and are especially important for large-bodied primates (Tito et al., 2022). Such recovery requires protection from disturbance; forest attributes, including structure and species diversity, recover to 90% of old-growth values over 2.5–6 decades in naturally regenerating forests, provided extraction pressures cease (Poorter et al., 2021).

Limitations and future work

Immediate conservation priorities include integrating local communities into adaptive monitoring frameworks (Shanee et al., 2013) and recognizing secondary forests as viable conservation solutions (Esteves et al., 2024; Galán-Acedo et al., 2019). NGO-led reforestation initiatives using native species are critical for restoring degraded areas and establishing succession spaces. Proyecto Mono

Tocón, alongside Neotropical Primate Conservation and Amazónicos para la Amazonia, has spearheaded habitat restoration and protection efforts in the Morro de Calzada region, working to extend forest corridors that connect secondary growth areas to primary forest patches. Active restoration through strategic native tree planting, combined with protection from ongoing disturbance, can establish sufficient canopy complexity for primate habitat use within 5–15 years (Crouzeilles et al., 2017).

Future research should employ multi-year monitoring to link vegetation dynamics to P. oenanthe demographics to determine whether current high-density populations represent stable equilibria or transient states. Behavioral and movement ecology studies quantifying primate responses to forest structure, combined with LiDAR-derived canopy assessments and population genetics, would strengthen habitat suitability models (Chapman & Peres, 2001; Estrada & Garber, 2022). Community-based monitoring systems with government and NGO support have demonstrated effectiveness in maintaining stable primate populations over multi-year periods in sustainable-use Amazonian reserves (Sampaio dos Reis & Benchimol, 2024). The prevention of further habitat loss and the maintenance of connectivity between fragments remain critical conservation priorities (Rubio Vargas et al., 2024; Shanee et al., 2025), and local authorities in Moyobamba and San Martín should support these initiatives through capacity building, financial resources, and formalized coordination mechanisms with conservation organizations.

Conclusions

This study provides the first systematic characterization of the floristic composition and structural attributes of *P. oenanthe* habitats, identifying key botanical species supporting primate persistence and filling a critical knowledge gap. The presence of this species in secondary forests demonstrates its ecological flexibility. However, baseline data reveal that specific forest structures and botanical diversity, particularly the density and diversity of large-crowned trees and native species characteristic of advancing succession, are essential drivers of habitat suitability for this species However, baseline data reveal that specific forest structures and botanical diversity, particularly the density and diversity of large-crowned trees and native species characteristic of advancing succession, are essential drivers of habitat suitability for this species. Tropical forest restoration must become a central conservation strategy for primate persistence; effective implementation requires the restoration of the botanical communities and forest architecture identified in this study while restricting further disturbance (Chapman et al., 2020). Without the immediate implementation of habitat protection prioritizing forests with identified key species, successional recovery, and inter-patch connectivity across the fragmented landscape, P. oenanthe will remain trapped in a transient demographic state, vulnerable to stochastic extinction. The integration of this baseline habitat knowledge with ongoing population monitoring and community-based management offers the most promising pathway for securing the long-term viability of this species in San Martín.

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Conflicts of interest

The authors declare that they have no conflict of interest.

Author contributions

All authors conceived the study. JRH performed wrote the manuscript and analyzed data, CA reviewed and supervised the development of the manuscript.

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