



## Tree Structure and Turnover in a Peruvian Premontane Amazon Forest

Nikie Yessica Barboza Decada, Edilberto Díaz Quintana, Alberto Franco Cerna-Cueva<sup>\*</sup>, Casiano Aguirre Escalante, Jenri Ruiz Gonzales

Universidad Nacional Agraria de la Selva, Carretera Central Km. 1.21, Tingo María, Huánuco, Peru 10131

Received January 26, 2026/Accepted July 20, 2026

### Abstract

*Humid tropical forests are increasingly exposed to fire, yet local diversity, stand structure, and species composition may respond differently. We compared tree communities in lower and upper sectors of a university reserve near Tingo María, Peru, using 27 rectangular 500 m<sup>2</sup> sampling units (13 lower, 14 upper). The upper sector showed field evidence of fire, although fire history was confounded with elevation and no pre-fire inventory was available. We assessed alpha and beta diversity, diameter and height structure, and species and family importance values at the sampling-unit level. Species composition differed robustly between sectors for presence-absence and abundance data (PERMANOVA,  $p$ -value < 0.001), whereas multivariate dispersion did not. After false-discovery-rate correction, alpha-diversity and structural variables showed no confirmed differences. Nevertheless, medium-to-large effect sizes indicated trends toward lower mean height and emergent-tree representation, and larger crown diameter and understory representation, in the upper sector; these trends were not confirmed at this sample size. Dominance shifted: upper-sector importance was density-driven for *Senefeldera inclinata*, whereas lower-sector importance was basal-area-driven for *Cedrelinga cateniformis*. The data therefore demonstrate taxonomic turnover but cannot attribute sector differences specifically to fire rather than elevation-associated conditions. Repeated integrated monitoring is needed to distinguish these effects.*

**Keywords:** beta diversity, fire evidence, importance value index, species composition, BRUNAS

**\*Correspondence author, email:** alberto.cerna@unas.edu.pe

### Introduction

Premontane tropical forests sustain high biological diversity, protect slopes and water sources, and provide ecological functions that are central to forest management. In the humid tropics, these forests are increasingly exposed to disturbance from fire, land-use pressure, drought, forest edges, and local human activities, and recent Amazon-wide syntheses show that degradation by fire, drought, logging, and edge effects can affect forest structure and carbon dynamics at scales comparable to deforestation (Alencar et al., 2015; Aragão et al., 2018; Matricardi et al., 2020; Lapola et al., 2023). Fire is especially relevant because many humid-forest tree species are not adapted to recurrent burning, and even surface fires can alter tree mortality, recruitment, canopy openness, microclimate, and successional pathways (Nepstad et al., 1999; Cochrane, 2003; Barlow et al., 2016; Prestes et al., 2020; Berenguer et al., 2021).

Forest recovery after disturbance is not a single process. Structural attributes such as stem density or basal area may recover faster than floristic composition, functional traits, or dominance patterns. This decoupling is important for forest management because a stand can appear structurally resilient while still maintaining substantial taxonomic turnover. Neotropical syntheses show that richness, biomass, functional traits, and species composition may recover along

different timelines, with species composition and floristic distinctiveness often recovering more slowly than local richness or structural indicators (Rozendaal et al., 2019; Poorter et al., 2021; Jakovac et al., 2022). Studies in Neotropical and Amazonian forests have also shown that post-disturbance recovery often involves strong recruitment in small-diameter classes, changes in species dominance, and shifts in functional composition (Barlow & Peres, 2008; Brando et al., 2014; Chazdon, 2014; Poorter et al., 2016).

In Peru, the Bosque Reservado de la Universidad Nacional Agraria de la Selva (BRUNAS), located near Tingo María, represents an important remnant of premontane Amazon forest for education, research, conservation, and local forest management. Regional studies from Andean forests show that tree structure, carbon stock, and species composition vary strongly along elevation gradients and with natural or human disturbance (Miyamoto et al., 2018; Malizia et al., 2020). However, comparative information on how tree structure and composition vary between contrasting sectors within BRUNAS remains limited. The field campaign documented a lower sector and an upper sector with visible signs of fire disturbance, including charred surface material and scorched vegetation. Because the upper sector also occupies higher terrain, fire evidence and elevation-associated environmental conditions are con-

founded in this design. We therefore interpret all outcomes as differences between sectors, not as effects attributable specifically to fire.

This study asked whether tree community structure and taxonomic composition differ between the two contrasting BRUNAS sectors. Specifically, we evaluated alpha diversity, beta diversity, horizontal and vertical stand structure, species importance value, and family importance value. We expected local richness to be relatively similar between sectors, whereas species composition and structural attributes linked to vertical development and dominance might differ. These expectations were evaluated as sector-level contrasts because the design cannot isolate fire from elevation-associated conditions. The results are intended to support practical monitoring and management of premontane forests.

## Methods

**Study area** The study was conducted in BRUNAS, Tingo María, district of Rupa Rupa, province of Leoncio Prado, Huánuco, Peru. The reserve covers 217.22 ha (Puerta & Cárdenas, 2012). The analyzed area comprised two contrasting sectors within a premontane Amazon forest. The lower sector was treated as the comparison sector, whereas the upper sector was classified as showing field evidence of fire based on photographs from the October 2024 campaign, which documented charred litter and soil, scorched herbaceous and shrub vegetation, blackened rocky slopes, and a continuous burned patch on the ridge and upper slope. This classification describes observed field conditions but does not isolate fire effects from elevation or other environmental differences.

Sampling design and field measurements. The original field design followed a systematic stratified sampling scheme by sector, with a random starting point and a 90 m grid distance following the approach used for reconnaissance forest inventories (Dauber, 1995). Twenty-seven rectangular sampling units of 500 m<sup>2</sup> were established (14 in the upper sector and 13 in the lower sector), yielding a total sampled area of 13,500 m<sup>2</sup> (1.35 ha), equivalent to 0.62% of BRUNAS. Trees with diameter at breast height (DBH) ≥ 10 cm were inventoried and measured at 1.30 m above ground. For each tree, DBH, total height, merchantable height, crown diameter, species, and family were recorded. Wood density was not measured in the field; values were assigned from species- or genus-level trait databases when available (Chave et al., 2009; Zanne et al., 2009).

**Data preparation** Field data from the two Excel workbooks were imported, merged, and checked in Python. Column names were standardized, blank rows were removed, taxonomic spelling was harmonized, and basal area was recalculated from DBH. The sampling unit was the unit of statistical inference for all stand-level comparisons, including vertical strata. Individual-tree summaries were retained only as descriptive information because trees were nested within sampling units.

**Diversity and composition** For each sampling unit, abundance, richness, Shannon diversity, Simpson diversity, Pielou's evenness, and Hill numbers were calculated

(Shannon, 1948; Simpson, 1949; Pielou, 1966; Hill, 1973). Sector differences were tested using two-sided Mann-Whitney tests, 9,999-permutation tests of the median difference, and Cliff's delta effect sizes with 95% confidence intervals from 10,000 bootstrap resamples (Mann & Whitney, 1947; Cliff, 1993). False discovery rate correction was applied within each related family of tests (Benjamini & Hochberg, 1995). Beta diversity was evaluated from a sampling-unit-by-species matrix using Jaccard and Bray-Curtis dissimilarities (Jaccard, 1901; Bray & Curtis, 1957). Principal coordinates analysis was used for ordination, and sector differences were tested using PERMANOVA and PERMDISP with 9,999 permutations (Anderson, 2001; 2006; Legendre & Legendre, 2012).

**Forest structure and ecological importance** Horizontal structure was described with diameter-class histograms. Vertical structure was classified into understory (< 10 m), canopy (10 to < 25 m), and emergent strata (≥ 25 m); stratum percentages were calculated separately for each sampling unit before comparing sectors. At the sampling-unit level, we compared stem density, basal area per hectare, mean DBH, mean total height, mean merchantable height, and mean crown diameter. Assigned wood density was excluded as an independent structural response because it was derived from taxonomic databases and therefore mainly reflected species composition; it is reported only as a composition-linked trait in Supplementary Data S1. Species importance value index (IVI) was calculated as relative density + relative dominance + relative frequency. Family importance value (FIV) was calculated as relative abundance + relative dominance + relative diversity (Mueller-Dombois & Ellenberg, 1974). All analyses were conducted in Python.

## Results

The final screened database contained 615 trees distributed across 27 rectangular sampling units and 1.35 ha (0.62% of BRUNAS). The upper sector contained 344 trees in 14 sampling units, whereas the lower sector contained 271 trees in 13 sampling units. After taxonomic harmonization, the community matrix included 59 species and 25 families. Field photographs from the upper sector documented charred surface material, scorched vegetation, and blackened rocky substrates (Figure 1). These observations support the description of fire evidence in that sector but do not establish that fire caused the measured sector differences.

No alpha-diversity comparison remained significant after FDR correction (Table 1; Figure 2). Richness, Shannon diversity, Simpson diversity, and Hill numbers showed overlapping distributions. Pielou's evenness showed the strongest directional trend, with a lower median in the upper sector (Cliff's  $\delta = -0.593$ , 95% CI [-0.879, -0.220]), but it did not cross the adjusted significance threshold (qFDR = 0.0566). Thus, alpha diversity was broadly comparable, with an evenness trend that was not statistically confirmed after correction at this sample size.

Species composition showed robust sector differentiation (Table 2; Figure 3). PCoA ordination based on Jaccard and Bray-Curtis dissimilarities separated upper- and lower-sector sampling units. PERMANOVA confirmed differences for

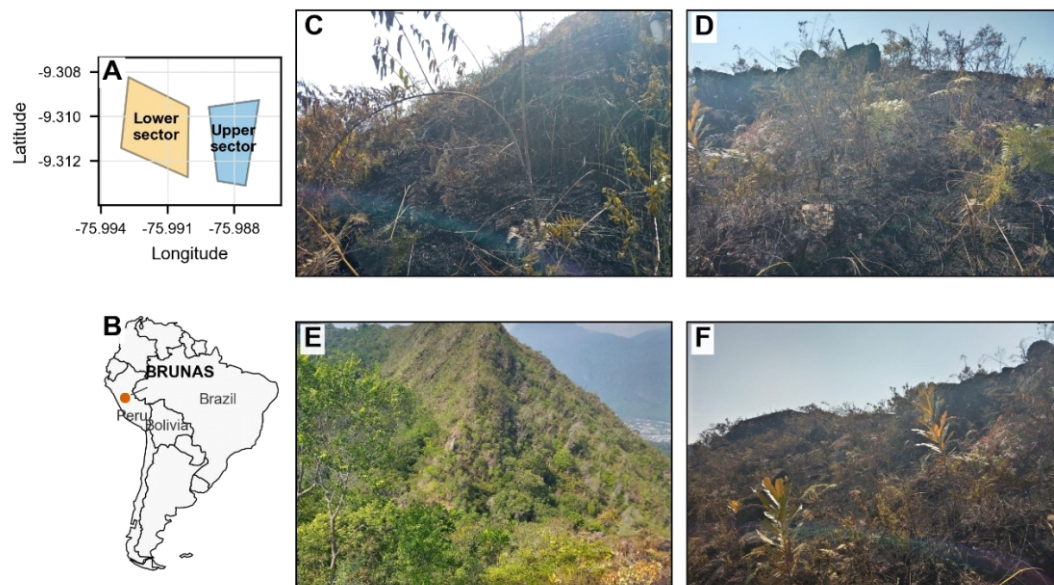


Figure 1 Study-area location and field photographic evidence from the upper sector of BRUNAS, Tingo María, Peru. (A) lower and upper study-sector polygons; (B) regional location; (C-F) charred ground, scorched vegetation, and burned ridge conditions. The photographs document fire evidence but do not isolate fire effects from elevation-associated conditions.

Table 1 Alpha diversity per sampling unit and non-parametric comparison between the lower and upper sectors

| Metric                     | Lower median<br>[IQR] | Upper median<br>[IQR] | $\Delta$<br>median | $p$ -value | qFDR   | Cliff's $\delta$ [95% CI] |
|----------------------------|-----------------------|-----------------------|--------------------|------------|--------|---------------------------|
| Richness (S)               | 10.000 [3.000]        | 12.000 [4.750]        | 2.000              | 0.4768     | 0.4768 | 0.165 [-0.280, 0.599]     |
| Shannon (H')               | 2.133 [0.317]         | 2.052 [0.507]         | -0.081             | 0.4520     | 0.4768 | -0.176 [-0.615, 0.275]    |
| Simpson (1-D)              | 0.867 [0.044]         | 0.819 [0.083]         | -0.048             | 0.1523     | 0.3046 | -0.330 [-0.736, 0.121]    |
| Pielou's evenness (J')     | 0.951 [0.040]         | 0.900 [0.115]         | -0.051             | 0.0094     | 0.0566 | -0.593 [-0.879, -0.220]   |
| Hill number <sup>1</sup> D | 8.442 [2.977]         | 7.786 [4.201]         | -0.656             | 0.4520     | 0.4768 | -0.176 [-0.604, 0.286]    |
| Hill number <sup>2</sup> D | 7.538 [2.978]         | 5.544 [3.595]         | -1.994             | 0.1523     | 0.3046 | -0.330 [-0.736, 0.121]    |

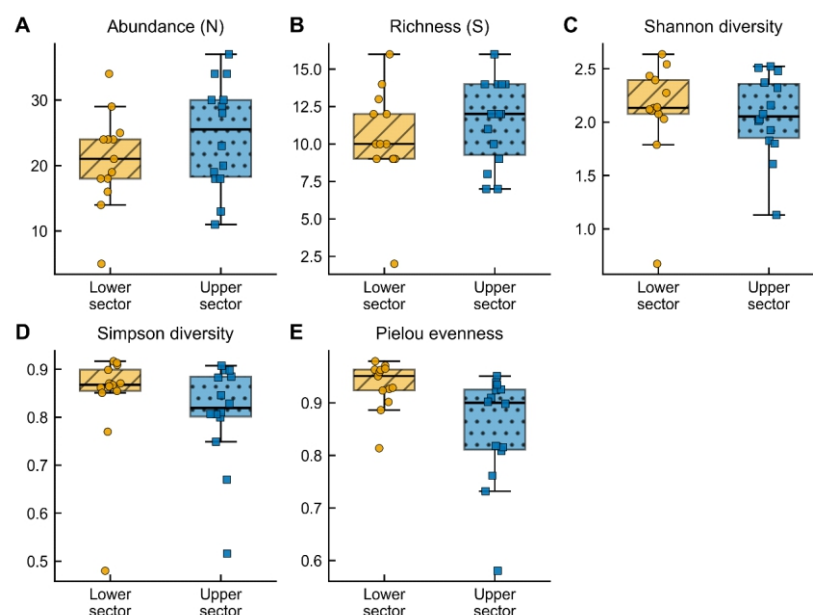


Figure 2 Alpha diversity per sampling unit in the lower ( $n = 13$ ) and upper ( $n = 14$ ) sectors for (A) abundance, (B) richness, (C) Shannon diversity, (D) Simpson diversity, and (E) Pielou's evenness.

Table 2 Distance-based beta-diversity tests comparing upper- and lower-sector sampling units

| Dissimilarity | PERMANOVA F | R <sup>2</sup> | p-value | PERMDISP F | p-value | Mean distance<br>upper | Mean distance<br>lower |
|---------------|-------------|----------------|---------|------------|---------|------------------------|------------------------|
| Jaccard       | 2.946       | 0.105          | <0.001  | 0.064      | 0.8131  | 0.516                  | 0.523                  |
| Bray-Curtis   | 3.804       | 0.132          | <0.001  | 0.911      | 0.3772  | 0.467                  | 0.496                  |

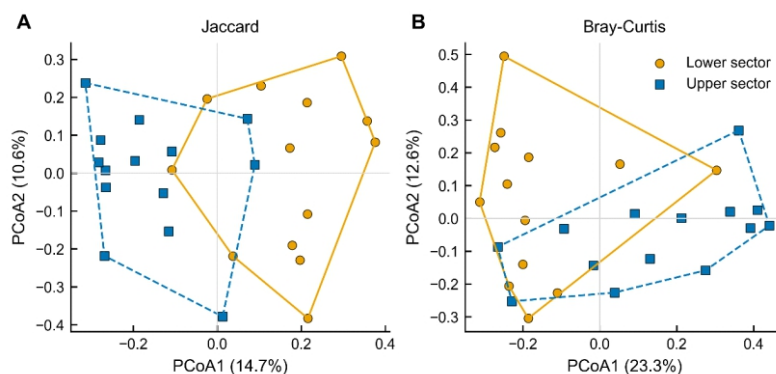


Figure 3 Beta-diversity ordination based on (A) Jaccard and (B) Bray-Curtis dissimilarities. Points are sampling units and polygons are sector convex hulls.

presence-absence composition (pseudo- $F = 2.946$ ,  $R^2 = 0.105$ ,  $p$ -value < 0.001) and abundance-based composition (pseudo- $F = 3.804$ ,  $R^2 = 0.132$ ,  $p$ -value < 0.001). PERMDISP was not significant for Jaccard ( $p$ -value = 0.813) or Bray-Curtis ( $p$ -value = 0.377), indicating that the sector separation was not explained by unequal multivariate dispersion.

Diameter distributions showed an inverted-J pattern in both sectors, with more individuals in small-diameter classes and progressively fewer in larger classes (Figure 4). Vertical structure was dominated by the canopy stratum in both sectors (Table 3; Figure 5). Sampling-unit comparisons indicated trends toward a larger understory fraction in the upper sector (Cliff's  $\delta = 0.390$ , qFDR = 0.108) and a smaller emergent fraction (Cliff's  $\delta = -0.412$ , qFDR = 0.108). Neither vertical-stratum trend was statistically confirmed after FDR correction at this sample size.

None of the six field-measured structural variables differed significantly after FDR correction (Table 4; Figure 6). Nevertheless, effect sizes indicated directional trends toward lower mean total height (Cliff's  $\delta = -0.527$ , qFDR = 0.072), lower mean merchantable height (Cliff's  $\delta = -0.440$ , qFDR = 0.103), and lower mean DBH (Cliff's  $\delta = -0.418$ , qFDR = 0.103) in the upper sector, together with a larger mean crown diameter (Cliff's  $\delta = 0.516$ , qFDR = 0.072). Stem density and basal area showed smaller or less precise effects. These are trends rather than confirmed differences at the available sample size. Assigned wood density was not interpreted as a separate structural result.

Species importance differed between sectors (Table 5; Figure 7). In the upper sector, *Senefeldera inclinata* had the highest IVI (49.801), driven primarily by relative density (29.070%) rather than relative dominance (13.856%) or relative frequency (6.875%). In the lower sector, *Cedrelinga cateniformis* had the highest IVI (41.727), driven primarily by relative dominance (31.748%) rather than relative density (5.535%) or relative frequency (4.444%). At the family level, Euphorbiaceae had the highest FIV in the upper sector, whereas Fabaceae had the highest FIV in the lower sector

(Table 6; Figure 8). These components identify how dominance differed but not whether fire, elevation-associated soil, or topography, or all of them, produced the pattern.

## Discussion

The clearest result was the robust difference in species composition between sectors, whereas no alpha-diversity metric was confirmed after FDR correction. The directional evenness trend nevertheless had a large effect size, indicating that the absence of adjusted significance should not be interpreted as evidence of identical communities. Similar local richness can coexist with marked taxonomic turnover, as reported during Neotropical forest recovery (Barlow & Peres, 2008; Chazdon, 2014; Rozendaal et al., 2019; Jakovac et al., 2022).

The inverted-J diameter pattern in both sectors is consistent with continuing recruitment and a multi-aged stand structure, although a single inventory cannot establish recruitment rates. The upper sector also exhibited medium-to-large directional effects, resulting in lower tree height and emergent representation, as well as larger crown diameter and understory representation. Because these comparisons did not remain significant after FDR correction, they indicate trends that require more replication rather than confirmed structural differences. This cautious interpretation is consistent with evidence that forest attributes recover at different rates and that composition and vertical development may lag behind local diversity (Rozendaal et al., 2019; Poorter et al., 2021).

The compositional differentiation has practical implications. PERMANOVA showed that sectors differed in both species occurrence and abundance structure, and nonsignificant PERMDISP results indicate that this separation was not driven by greater heterogeneity in one sector. Beta diversity is therefore the strongest current monitoring indicator for BRUNAS; stem density or basal area alone would miss this taxonomic differentiation.

Species and family importance values clarify the basis of

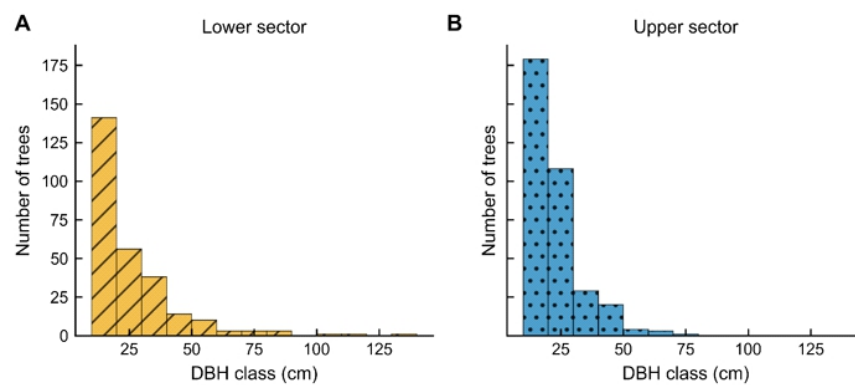


Figure 4 Diameter-class distributions using 10 cm DBH classes for (A) the lower and (B) upper sectors.

Table 3 Plot-level vertical-stratum percentages compared between the lower and upper sectors

| Stratum                    | Lower median<br>[IQR] (%) | Upper median<br>[IQR] (%) | $\Delta$ median | $p$ -value | qFDR   | Cliff's $\delta$ [95% CI] |
|----------------------------|---------------------------|---------------------------|-----------------|------------|--------|---------------------------|
| Understory<br>( $<10$ m)   | 0.000<br>[0.000]          | 2.703<br>[14.048]         | 2.703           | 0.0430     | 0.1080 | 0.390<br>[0.060, 0.709]   |
| Canopy<br>(10 to $<25$ m)  | 75.000<br>[12.000]        | 74.902<br>[13.033]        | -0.098          | 0.9806     | 0.9806 | -0.011<br>[-0.467, 0.429] |
| Emergent<br>( $\geq 25$ m) | 22.222<br>[5.000]         | 12.698<br>[19.241]        | -9.524          | 0.0720     | 0.1080 | -0.412<br>[-0.791, 0.011] |

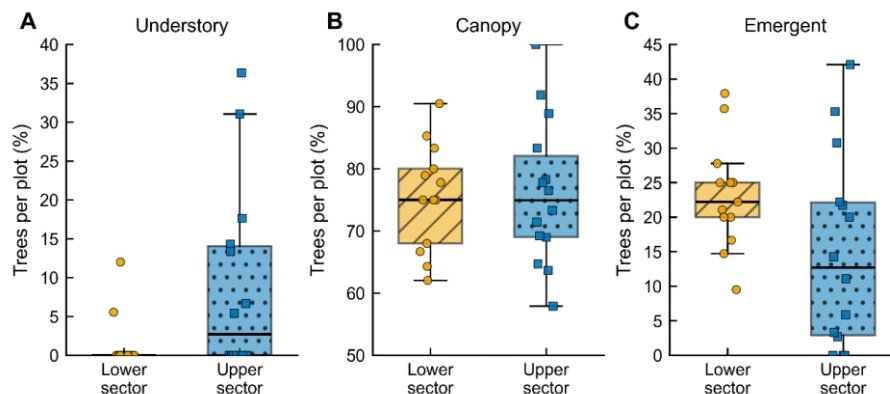


Figure 5 Plot-level percentages of trees in (A) understory, (B) canopy, and (C) emergent height strata for the lower ( $n = 13$ ) and upper ( $n = 14$ ) sectors. Panels use stratum-specific y-axis ranges for legibility.

Table 4 Field-measured structural variables compared at the sampling-unit level between the lower and upper sectors

| Metric                                           | Lower median<br>[IQR] | Upper median<br>[IQR] | $\Delta$ median | $p$ -value | qFDR   | Cliff's $\delta$ [95% CI]  |
|--------------------------------------------------|-----------------------|-----------------------|-----------------|------------|--------|----------------------------|
| Stem density<br>(trees ha <sup>-1</sup> )        | 420.000<br>[120.000]  | 510.000<br>[235.000]  | 90.000          | 0.2953     | 0.2953 | 0.242<br>[-0.214, 0.654]   |
| Basal area<br>(m <sup>2</sup> ha <sup>-1</sup> ) | 26.717<br>[14.667]    | 24.731<br>[10.745]    | -1.987          | 0.1523     | 0.1827 | -0.330<br>[-0.703, 0.110]  |
| Mean DBH<br>(cm)                                 | 25.533<br>[5.764]     | 22.509<br>[1.963]     | -3.025          | 0.0688     | 0.1032 | -0.418<br>[-0.791, 0.022]  |
| Mean total height<br>(m)                         | 19.579<br>[1.033]     | 17.245<br>[4.236]     | -2.334          | 0.0212     | 0.0721 | -0.527<br>[-0.857, -0.121] |
| Mean<br>merchantable<br>height (m)               | 11.362<br>[1.824]     | 9.250<br>[2.376]      | -2.112          | 0.0553     | 0.1032 | -0.440<br>[-0.824, -0.011] |
| Mean crown<br>diameter (m)                       | 3.446<br>[0.698]      | 4.262<br>[1.041]      | 0.817           | 0.0240     | 0.0721 | 0.516<br>[0.110, 0.868]    |

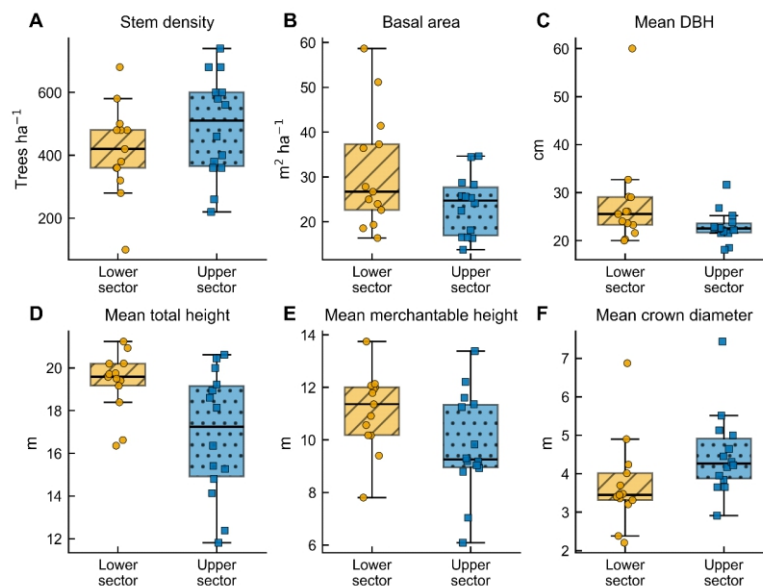


Figure 6 Sampling-unit-level field-measured structural variables in the lower ( $n = 13$ ) and upper ( $n = 14$ ) sectors. Assigned wood density is excluded because it is a database-derived, composition-linked trait.

Table 5 Components of importance value index for the top five species in each sector

| Sector       | Species                                       | Relative density (%) | Relative dominance (%) | Relative frequency (%) | IVI    |
|--------------|-----------------------------------------------|----------------------|------------------------|------------------------|--------|
| Upper sector | <i>Senefeldera inclinata</i> Müll. Arg.       | 29.070               | 13.856                 | 6.875                  | 49.801 |
| Upper sector | <i>Virola decorticans</i> Ducke               | 12.209               | 10.519                 | 8.750                  | 31.479 |
| Upper sector | <i>Cecropia sciadophylla</i> Mart.            | 6.686                | 7.470                  | 5.000                  | 19.156 |
| Upper sector | <i>Trattinnickia boliviana</i> (Swart) Daly   | 4.942                | 4.894                  | 5.625                  | 15.460 |
| Upper sector | <i>Parkia panurensis</i> Benth. ex HC Hopkins | 2.326                | 7.978                  | 3.750                  | 14.053 |
| Lower sector | <i>Cedrelinga cateniformis</i> (Ducke) Ducke  | 5.535                | 31.748                 | 4.444                  | 41.727 |
| Lower sector | <i>Virola decorticans</i> Ducke               | 13.653               | 7.605                  | 8.148                  | 29.406 |
| Lower sector | <i>Pourouma bicolor</i> Mart.                 | 7.749                | 5.246                  | 6.667                  | 19.662 |
| Lower sector | <i>Jacaranda copaia</i> (Aubl.) D. Don        | 4.428                | 6.294                  | 5.185                  | 15.907 |
| Lower sector | <i>Inga alba</i> (Sw.) Willd.                 | 4.428                | 4.845                  | 5.185                  | 14.458 |

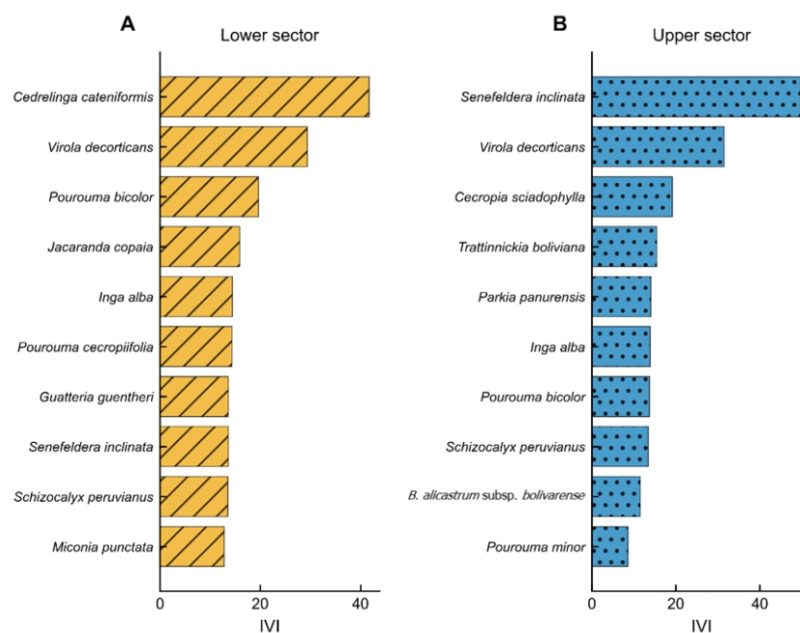


Figure 7 Top 10 species ranked by importance value index (IVI = relative density + relative dominance + relative frequency) in the lower and upper sectors. Full taxonomic authorities are provided in Table 5.

Table 6 Components of family importance value for the top five families in each sector

| Sector       | Family        | Relative abundance (%) | Relative dominance (%) | Relative diversity (%) | FIV    |
|--------------|---------------|------------------------|------------------------|------------------------|--------|
| Upper sector | Euphorbiaceae | 31.977                 | 18.597                 | 8.163                  | 58.737 |
| Upper sector | Myristicaceae | 14.826                 | 15.326                 | 8.163                  | 38.315 |
| Upper sector | Fabaceae      | 8.721                  | 16.496                 | 12.245                 | 37.462 |
| Upper sector | Urticaceae    | 13.663                 | 15.612                 | 8.163                  | 37.438 |
| Upper sector | Moraceae      | 7.267                  | 10.074                 | 12.245                 | 29.586 |
| Lower sector | Fabaceae      | 18.081                 | 47.429                 | 18.919                 | 84.429 |
| Lower sector | Myristicaceae | 15.867                 | 9.251                  | 8.108                  | 33.226 |
| Lower sector | Urticaceae    | 13.284                 | 8.901                  | 5.405                  | 27.591 |
| Lower sector | Rubiaceae     | 9.963                  | 6.233                  | 5.405                  | 21.601 |
| Lower sector | Moraceae      | 5.535                  | 3.306                  | 10.811                 | 19.652 |

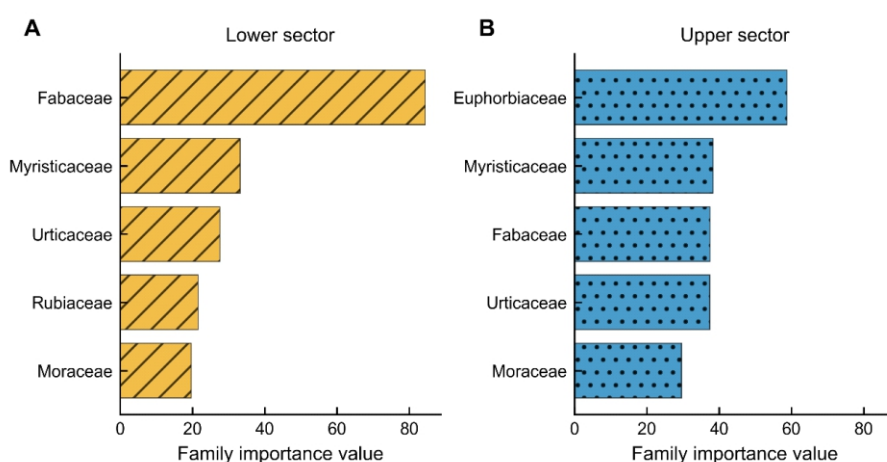


Figure 8 Top five families ranked by family importance value (FIV = relative abundance + relative dominance + relative diversity) in the lower and upper sectors.

sector dominance. The leading upper-sector species, *Senefeldera inclinata*, was important mainly because of its relative density, whereas lower-sector *Cedrelinga cateniformis* was important mainly because of basal-area dominance. The greater upper-sector importance of Euphorbiaceae and lower-sector importance of Fabaceae likewise describe different abundance, dominance, and diversity components. However, these patterns cannot determine whether fire, elevation-associated soil, or topography, or a combination of these factors, shaped the observed dominance.

Fire evidence and elevation were confounded because the sector showing burned conditions was also the upper sector. No pre-fire inventory was available, and the design included only one upper and one lower sector within a single reserve. The 27 sampling units were subsamples within those sectors rather than independent site-level replicates. Consequently, the data support a between-sector comparison but cannot determine whether the observed patterns arose from fire, elevation-associated soil and topography, or both. Repeated pre- and post-disturbance inventories across multiple independent sites are needed to separate these effects.

For management, the findings support fire prevention and repeated monitoring of species composition and vertical structure rather than intervention based on the present sector

contrast alone. Repeated surveys of the same rectangular sampling units can show whether current trends persist, while additional independent sectors spanning elevation and fire histories are needed before attributing differences to a particular driver. This design would provide a stronger basis for restoration planning, ignition control, and conservation of premontane forest remnants.

## Conclusion

Species composition differed robustly between the two BRUNAS sectors for both presence-absence and abundance data. Alpha-diversity and field-measured structural comparisons were not confirmed after FDR correction, although medium-to-large effect sizes indicated directional trends in evenness, height, crown diameter, and vertical-stratum representation. IVI components showed density-driven dominance by *Senefeldera inclinata* in the upper sector and basal-area-driven dominance by *Cedrelinga cateniformis* in the lower sector. Because the sector showing fire evidence was also the upper sector, no pre-fire inventory was available, and only one upper and one lower sector were studied, the data cannot attribute these patterns specifically to fire rather than elevation-associated conditions. Repeated, replicated monitoring is required to distinguish these effects.

## Recommendation

Forest managers should maintain fire prevention and repeat inventories in the same rectangular sampling units to track species composition, vertical structure, and dominance. Future monitoring should include independent sectors across comparable elevations and, where possible, pre- and post-disturbance measurements. Restoration actions such as enrichment planting should be considered only if repeated evidence shows persistent regeneration or compositional deficits.

## Disclosure Statement

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this manuscript.

## Data and Code Availability Statement

The raw and cleaned inventory data, analysis code, derived tables, and source data for Figure 2 until Figure 8 are provided in Supplementary Data S1. Field photographs used in Figure 1 are provided in Supplementary Data S2.

## References

- Alencar, A. A., Brando, P. M., Asner, G. P., & Putz, F. E. (2015). Landscape fragmentation, severe drought, and the new Amazon forest fire regime. *Ecological Applications*, 25(6), 1493–1505. <https://doi.org/10.1890/14-1528.1>
- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26(1), 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, 62(1), 245–253. <https://doi.org/10.1111/j.1541-0420.2005.00440.x>
- Aragão, L. E. O. C., Anderson, L. O., Fonseca, M. G., Rosan, T. M., Vedovato, L. B., Wagner, F. H., Silva, C. V. J., Silva Junior, C. H. L., Arai, E., Aguiar, A. P., Barlow, J., Berenguer, E., Deeter, M. N., Domingues, L. G., Gatti, L., Gloor, M., Malhi, Y., Marengo, J. A., Miller, J. B., ..., & Saatchi, S. (2018). 21st Century drought-related fires counteract the decline of Amazon deforestation carbon emissions. *Nature Communications*, 9, Article 536. <https://doi.org/10.1038/s41467-017-02771-y>
- Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Mac Nally, R., Thomson, J. R., Ferraz, S. F. B., Louzada, J., Oliveira, V. H. F., Parry, L., Solar, R. R. C., Vieira, I. C. G., Aragão, L. E. O. C., Begotti, R. A., Braga, R. F., Cardoso, T. M., de Oliveira Jr, R. C., Souza Jr, C. M., ..., & Gardner, T. A. (2016). Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature*, 535(7610), 144–147. <https://doi.org/10.1038/nature18326>
- Barlow, J., & Peres, C. A. (2008). Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1498), 1787–1794. <https://doi.org/10.1098/rstb.2007.0013>
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, 57(1), 289–300. <https://doi.org/10.1111/j.2517-6161.1995.tb02031.x>
- Berenguer, E., Lennox, G. D., Ferreira, J., Malhi, Y., Aragão, L. E. O. C., Barreto, J. R., Espírito-Santo, F. D. B., Figueiredo, A. E. S., França, F., Gardner, T. A., Joly, C. A., Palmeira, A. F., Quesada, C. A., Rossi, L. C., de Seixas, M. M. M., Smith, C. C., Withey, K., & Barlow, J. (2021). Tracking the impacts of El Niño drought and fire in human-modified Amazonian forests. *Proceedings of the National Academy of Sciences*, 118(30), Article e2019377118. <https://doi.org/10.1073/pnas.2019377118>
- Brando, P. M., Balch, J. K., Nepstad, D. C., Morton, D. C., Putz, F. E., Coe, M. T., Silvério, D., Macedo, M. N., Nóbrega, C. C., Alencar, A., & Soares-Filho, B. S. (2014). Abrupt increases in Amazonian tree mortality due to drought-fire interactions. *Proceedings of the National Academy of Sciences*, 111, 6347–6352. <https://doi.org/10.1073/pnas.1305499111>
- Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, 27(4), 325–349. <https://doi.org/10.2307/1942268>
- Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., & Zanne, A. E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12(4), 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>
- Chazdon, R. L. (2014). *Second growth: The promise of tropical forest regeneration in an age of deforestation*. University of Chicago Press.
- Cliff, N. (1993). Dominance statistics: Ordinal analyses to answer ordinal questions. *Psychological Bulletin*, 114(3), 494–509. <https://doi.org/10.1037/0033-2909.114.3.494>
- Cochrane, M. A. (2003). Fire science for rainforests. *Nature*, 421, 913–919. <https://doi.org/10.1038/nature01437>
- Dauber, E. (1995). *Guía práctica y teórica para el diseño de un inventario forestal de reconocimiento*. Proyecto de Manejo Forestal Sostenible, BOLFOR.

- Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, 54(2), 427–432. <https://doi.org/10.2307/1934352>
- Jaccard, P. (1901). Étude comparative de la distribution florale dans une portion des Alpes et des Jura. *Bulletin de la Société Vaudoise des Sciences Naturelles*, 37, 547–579.
- Jakovac, C. C., Meave, J. A., Bongers, F., Letcher, S. G., Dupuy, J. M., Piotto, D., Rozendaal, D. M. A., Peña-Claros, M., Craven, D., Santos, B. A., Siminski, A., Fantini, A. C., Rodrigues, A. C., Hernández-Jaramillo, A., Idárraga, A., Junqueira, A. B., Zambrano, A. M. A., de Jong, B. H. J., Pinho, B. X., ..., & Poorter, L. (2022). Strong floristic distinctiveness across Neotropical successional forests. *Science Advances*, 8(26), Article eabn1767. <https://doi.org/10.1126/sciadv.abn1767>
- Lapola, D. M., Pinho, P., Barlow, J., Aragão, L. E. O. C., Berenguer, E., Carmenta, R., Liddy, H. M., Seixas, H., Silva, C. V. J., Silva-Junior, C. H. L., Alencar, A. A. C., Anderson, L. O., Armenteras, D., Brovkin, V., Calders, K., Chambers, J., Chini, L., Costa, M. H., Faria, B. L., ..., & Walker, W. S. (2023). The drivers and impacts of Amazon forest degradation. *Science*, 379(6630), Article eabp8622. <https://doi.org/10.1126/science.abp8622>
- Legendre, P., & Legendre, L. (2012). *Numerical ecology* (3rd ed.). Elsevier.
- Malizia, A., Blundo, C., Carilla, J., Osinaga Acosta, O., Cuesta, F., Duque, A., Aguirre, N., Aguirre, Z., Ataroff, M., Baez, S., Calderón-Loor, M., Cayola, L., Cayuela, L., Ceballos, S., Cedillo, H., Ríos, W. F., Feeley, K. J., Fuentes, A. F., Álvarez, L. E. G., ..., & Young, K. R. (2020). Elevation and latitude drives structure and tree species composition in Andean forests: Results from a large-scale plot network. *PLOS ONE*, 15(4), Article e0231553. <https://doi.org/10.1371/journal.pone.0231553>
- Mann, H. B., & Whitney, D. R. (1947). On a test of whether one of two random variables is stochastically larger than the other. *The Annals of Mathematical Statistics*, 18(1), 50–60. <https://doi.org/10.1214/aoms/1177730491>
- Matricardi, E. A. T., Skole, D. L., Costa, O. B., Pedlowski, M. A., Samek, J. H., & Miguel, E. P. (2020). Long-term forest degradation surpasses deforestation in the Brazilian Amazon. *Science*, 369(6509), 1378–1382. <https://doi.org/10.1126/science.abb3021>
- Miyamoto, K., Sato, T., Arana Olivos, E. A., Clostre Orellana, G., & Rohner Stornaiuolo, C. M. (2018). Variation in tree community composition and carbon stock under natural and human disturbances in Andean forests, Peru. *Forests*, 9(7), Article 390. <https://doi.org/10.3390/f9070390>
- Mueller-Dombois, D., & Ellenberg, H. (1974). *Aims and methods of vegetation ecology*. Wiley.
- Nepstad, D. C., Verissimo, A., Alencar, A., Nobre, C., Lima, E., Lefebvre, P., Schlesinger, P., Potter, C., Moutinho, P., Mendoza, E., Cochrane, M., & Brooks, V. (1999). Large-scale impoverishment of Amazonian forests by logging and fire. *Nature*, 398, 505–508. <https://doi.org/10.1038/19066>
- Pielou, E. C. (1966). The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology*, 13, 131–144. [https://doi.org/10.1016/0022-5193\(66\)90013-0](https://doi.org/10.1016/0022-5193(66)90013-0)
- Poorter, L., Bongers, F., Aide, T. M., Almeyda Zambrano, A. M., Balvanera, P., Becknell, J. M., Boukili, V., Brancalion, P. H. S., Broadbent, E. N., Chazdon, R. L., Craven, D., De Almeida-Cortez, J. S., Cabral, G. A. L., de Jong, B. H. J., Denslow, J. S., Dent, D. H., DeWalt, S. J., Dupuy, J. M., Durán, S. M., ..., & Rozendaal, D. M. A. (2016). Biomass resilience of Neotropical secondary forests. *Nature*, 530(7589), 211–214. <https://doi.org/10.1038/nature16512>
- Poorter, L., Craven, D., Jakovac, C. C., van der Sande, M. T., Amissah, L., Bongers, F., Chazdon, R. L., Farrior, C. E., Kambach, S., Meave, J. A., Muñoz, R., Norden, N., Rüger, N., van Breugel, M., Zambrano, A. M. A., Amani, B., Andrade, J. L., Brancalion, P. H. S., Broadbent, E. N., ..., & Hérault, B. (2021). Multidimensional tropical forest recovery. *Science*, 374(6573), 1370–1376. <https://doi.org/10.1126/science.abh3629>
- Prestes, N. C. C. S., Massi, K. G., Silva, E. A., Nogueira, D. S., de Oliveira, E. A., Freitag, R., Marimon, B. S., Marimon-Junior, B. H., Keller, M., & Feldpausch, T. R. (2020). Fire effects on understory forest regeneration in southern Amazonia. *Frontiers in Forests and Global Change*, 3, Article 10. <https://doi.org/10.3389/ffgc.2020.00010>
- Puerta, R. H., & Cárdenas, P. J. (2012). El Bosque Reservado de la Universidad Nacional Agraria de la Selva (UNAS). *Xilema*, 25(1), 18–21.
- Rozendaal, D. M. A., Bongers, F., Aide, T. M., Álvarez-Dávila, E., Ascarrunz, N., Balvanera, P., Becknell, J. M., Bentos, T. V., Brancalion, P. H. S., Cabral, G. A. L., Calvo-Rodriguez, S., Chave, J., César, R. G., Chazdon, R. L., Condit, R., Dallinga, J. S., de Almeida-Cortez, J. S., de Jong, B., de Oliveira, A., ..., & Poorter, L. (2019). Biodiversity recovery of Neotropical secondary forests. *Science Advances*, 5(3), Article eaau3114. <https://doi.org/10.1126/sciadv.aau3114>
- Shannon, C. E. (1948). A mathematical theory of communication. *Bell System Technical Journal*, 27, 379–423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>

Simpson, E. H. (1949). Measurement of diversity. *Nature*, 163, Article 688. <https://doi.org/10.1038/163688a0>

Zanne, A. E., Lopez-Gonzalez, G., Coomes, D. A., Ilic, J.,

Jansen, S., Lewis, S. L., Miller, R. B., Swenson, N. G.,  
Wiemann, M. C., & Chave, J. (2009). Data from:  
Towards a worldwide wood economics spectrum  
[Dataset]. Dryad. <https://doi.org/10.5061/dryad.234>