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ARTICLE

RESEARCH ARTICLE

Tree composition and carbon turnover dynamics across 22 years in a Costa Rican premontane moist forest fragment

Recambio en la composición arbórea y la acumulación de carbono durante 22 años en un fragmento de bosque húmedo premontano en Costa Rica

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Abstract: *Aim of study:* Tropical forests are increasingly threatened by deforestation and fragmentation. In Costa Rica, extensive land-use change has left forest fragments whose long-term ecological dynamics remain poorly understood. This study assessed changes in tree diversity, composition, structure, and aboveground carbon stocks during a 22-year period (2000-2022) in a premontane moist forest fragment in Costa Rica. *Area of study:* Municipal Forest of Atenas (26.4-ha), Alajuela, Costa Rica. *Material and methods*: Tree inventories were conducted in 32 plots (10 m radius) in 2000 and 33 plots in 2022. We analysed diversity and composition using Bray-Curtis dissimilarity, Hill numbers, and Importance Value Index, while tree structure and carbon stocks were assessed using tree size distributions, PERMANOVA, and allometric models. *Main results:* We identified 71 species and 69 genera in 2000 (N = 535), and 62 species and 60 genera in 2022 (N = 534). We found high compositional stability, with a 76% similarity in genus abundance between years, and consistent dominance by the early successional species *Inga densiflora* Benth and the invasive *Syzygium jambos* (L.) Alston. A gradual shift toward intermediate and late-successional genera suggests ongoing successional processes. Carbon storage more than doubled, from 1,847.2 to 3,903.7 tC (70.0 tC/ha in 2000 and 147.9 tC/ha in 2022), approaching values reported for old-growth tropical forests. These changes may be driven by the presence of large individuals of *Ficus* and *Anacardium excelsum* (Bertero & Balb.) Skeels, supporting the mass-ratio hypothesis. *Research highlights:* These findings underscore the ecological importance of conserving secondary forest fragments in human-modified tropical landscapes, which can support long-term forest recovery and contribute to ecological resilience, carbon storage and climate change mitigation.

Keywords: aboveground biomass; forest structure; secondary forest succession; tree diversity; tropical forest regeneration.

Resumen: *Objetivo del estudio:* Los bosques tropicales están amenazados por la deforestación y la fragmentación. En Costa Rica, la dinámica ecológica en paisajes fragmentados es poco comprendida. Este estudio evaluó los cambios en la diversidad de árboles, composición, estructura y acumulación de carbono durante un período de

22 años (2000-2022) en un fragmento de bosque húmedo premontano en Costa Rica. *Área de estudio:* Bosque Municipal de Atenas (26.4 ha), Alajuela, Costa Rica. *Material y métodos:* Identificamos los árboles en 32 parcelas de 10 m de radio en el 2000, y 33 parcelas en el 2022. Analizamos la diversidad y composición utilizando el índice de disimilitud de Bray-Curtis, los números de Hill y el Índice de Valor de Importancia. Evaluamos la estructura forestal y el carbono usando histogramas, PERMANOVA y ecuaciones alométricas. *Resultados principales:* Identificamos 71 especies y 69 géneros en el 2000 (N = 535), y 62 especies y 60 géneros en 2022 (N = 534). Encontramos un 76% de similitud en la abundancia de géneros entre ambos años, y una dominancia de *Inga densiflora* Benth y la invasora *Syzygium jambos* (L.) Alston. El cambio hacia géneros de sucesión intermedia y tardía sugiere procesos sucesionales en curso. El carbono acumulado aumentó de 1.847,2 a 3.903,7 tC (70.0 tC/ha en 2000 y 147,9 tC/ha en 2022), acercándose a los valores reportados para bosques primarios. Estos cambios podrían estar influenciados por la presencia de individuos de gran tamaño como *Ficus* y *Anacardium excelsum* (Bertero & Balb.) Skeels. *Aspectos destacados de la investigación:* Estos hallazgos resaltan la importancia de conservar fragmentos de bosques en paisajes antropogénicos, los cuales pueden contribuir a la recuperación forestal, la resiliencia ecológica, la acumulación de carbono y la mitigación del cambio climático.

Palabras clave: biomasa aérea; diversidad de árboles; estructura forestal; regeneración natural; sucesión en bosques secundarios.

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Supplementary information ↓

1. INTRODUCTION

Tropical forests harbor the highest levels of biodiversity and provide critical ecosystem services, including climate regulation, water cycling, and carbon storage (Hunter et al., 2013; Artaxo et al., 2022). These ecosystems store nearly half of the global aboveground carbon and contribute to removing approximately 29% of annual CO_2 emissions, equating to 15.6 Gt per year (Friedlingstein et al., 2019). However, despite their importance, tropical forests are undergoing rapid degradation, including fragmentation and habitat loss. Since the 1990s, the global rate of tropical deforestation has remained at approximately 0.5% annually, leading to an annual carbon stock loss of roughly 10% (Achard et al., 2014; Brinck et al., 2017). Fragmentation alone contributes an additional 31% to forest carbon emissions (Brinck et al., 2017).

Forest fragmentation affects multiple ecological variables, including species composition, forest structure, and ecosystem functioning. Key factors such as patch size, isolation from seed sources, edge effects, and human disturbance influence tree community dynamics (Spletozer et al., 2023). The regeneration trajectory of fragments, whether passive (e.g. natural processes like seed dispersal and natural succession) or active (e.g. human-driven interventions like planting or habitat restoration), plays a critical role in determining successional trajectories and community composition (Hill & Curran, 2003; Groeneveld et al., 2009; Bechara et al., 2016). Furthermore, small forest patches in Neotropical lowlands may be dominated by pioneer and early secondary species, which can lead to rapid changes in forest structure and species composition over time (Laurance et al., 2006).

While primary old-growth forests are known for their role in long-term carbon storage, secondary forests also play a key role in rapid carbon sequestration (Chazdon, 2014). In some cases, young secondary forests accumulate carbon at rates up to 20 times higher than mature forests (Bongers

et al., 2015), highlighting their importance in mitigating carbon loss from fragmented landscapes. At fine spatial scales (e.g., 0.1 ha), forest attributes like species richness correlate strongly with aboveground biomass (AGB), likely due to mechanisms such as functional trait diversity and niche complementarity. Functional trait diversity refers to the variety of traits (e.g., leaf morphology, wood density) that influence species interactions and resource utilization (Laureto et al., 2015), whereas niche complementarity describes how species coexist by exploiting different resources or performing distinct ecological roles, thus enhancing ecosystem functioning (Amyntas et al., 2023). Additionally, at fine scales, a single species can disproportionately influence biomass, as suggested by the mass-ratio hypothesis, which posits that ecosystem functioning is primarily driven by dominant species rather than species richness or rare species (Grime, 1998).

In Costa Rica, despite long-standing conservation efforts, increasing agricultural demands and urban expansion have driven extensive deforestation, particularly in the Central Valley, where 60% of the country's population inhabits (Stan & Sanchez-Azofeifa, 2019; Montero et al., 2021). Historically, this region was covered by premontane moist forests, which occur at intermediate elevations between 800 and 1,500 masl. The ecological characteristics of these forests, including moderate temperatures, high humidity, and fertile volcanic soils, make them particularly suitable for the cultivation of coffee (*Coffea arabica* L.). The introduction of coffee in the 1800s marked a significant land-use transition, replacing native forest with coffee plantations, which have more recently been replaced by urban development, further fragmenting the landscape and altering ecosystem processes (Montero et al., 2021). The forest remnants that persist within this highly modified matrix provide critical opportunities to investigate the ecological consequences of land-use change. In particular, understanding how tree diversity, forest structure, and carbon stocks shift over time in these fragments is essential for improving carbon accounting and guiding conservation and restoration strategies in human-dominated tropical landscapes.

Despite increasing recognition of the role that secondary and fragmented forests play in carbon dynamics (Magnano et al., 2015; Broggio et al., 2024), long-term studies evaluating successional trends in highly modified landscapes remain scarce in Central America (Arroyo-Rodríguez et al., 2015). This study investigates changes in tree diversity, composition, structure, and aboveground carbon stocks over a 22-year period in a 26.4-ha premontane moist forest fragment in Atenas, Costa Rica. We hypothesize that the tree assemblage will undergo compositional and structural shifts over time, specifically a decrease in pioneer species and an increase in late-successional species. We also hypothesize that aboveground carbon stocks will increase, likely driven by a shift toward late-successional taxa, in accordance with the mass-ratio hypothesis. This research addresses a critical gap in understanding how forest dynamics in fragmented landscapes influence tree biodiversity and aboveground carbon storage over time in the Neotropics, offering insights to guide conservation and restoration efforts.

2. MATERIAL AND METHODS

2.1. Study site

This study was conducted in the Municipal Forest of Atenas (MFA) Anselmo Murillo Jiménez, a 26.4-ha premontane moist forest fragment located in Atenas (Alajuela, Costa Rica; 940-1,060 masl; Fig. 1). This area was used for coffee (*C. arabica*) plantations, sugar cane fields, and cattle ranching until the 1930s, when the Municipality of Atenas acquired it to protect water sources for the community of Plancillo. Since then, the forest has been under natural regeneration, holding around 119 tree species, being *Inga densiflora* Benth., and the invasive species *Syzygium jambos* (L.) Alston (known as rose apple) dominant in the canopy (Silva, 2008), and *S. jambos* and coffee seedlings the most abundant in the understory (Avalos et al., 2006). The MFA is co-managed by the Municipality of Atenas, the communal aqueduct of Plancillo, and the community development association of Alto del Monte, providing drinking water to about 2,500 people as well as serving as a recreational area.

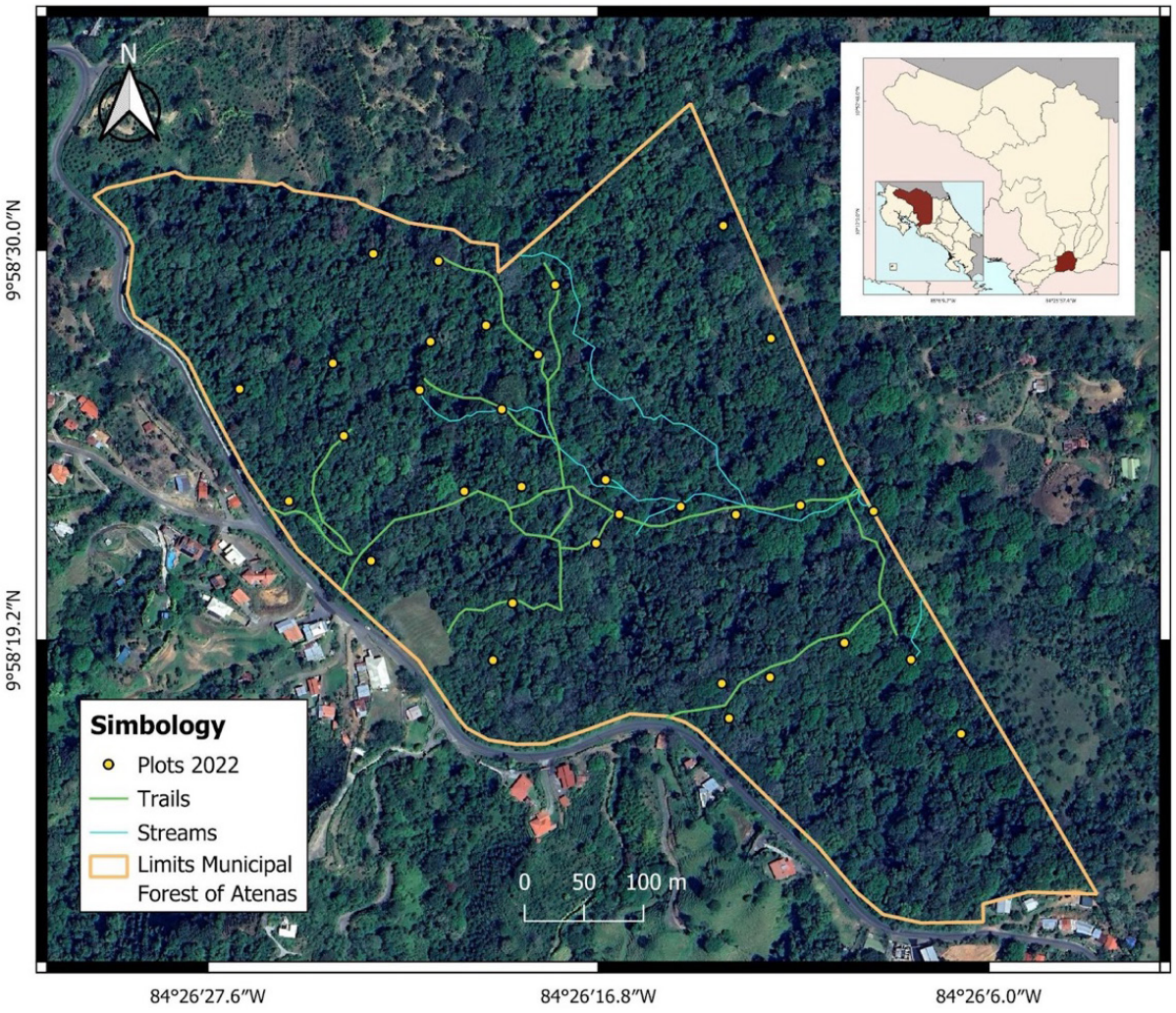

Figure 1. Location of 10-m radius plots in the Municipal Forest of Atenas (Alajuela, Costa Rica) sampled in 2022. Source: Municipality of Atenas, Google Satellite 2025.

2.2. Data collection

In 2000, 32 plots with a 10-m radius were established throughout the MFA, covering a total area of 1.01 ha. Plots were spaced at a minimum distance of 50 m from one another and were distributed across the study area to represent the spatial heterogeneity of the forest. Within each plot, all trees with a diameter at breast height (DBH) greater than 10 cm were identified to species when possible, and both DBH and total height were measured, using a Perfect Measuring Tape Co. 3.65-meter diameter tape and a Lufkin 50-meter measuring tape, respectively. DBH for buttressed trees was measured above the buttresses. The same methodology was applied in the 2021-2022 period (hereafter 2022), in which 33 plots of the same size were established, totaling 1.04 ha (Fig. 1). Although efforts were made to ensure comparable spatial distribution, the plots established in 2000 were not located at the same locations in 2022 due to the absence of permanent plot markers.

2.3. Taxonomic identification and plot comparability

In 2000, 535 trees were recorded in total, 409 were identified to species, 123 to genus, and 3 remained unidentified. In the 2022 survey, 534 trees were recorded, with 469 identified to species, 31 to genus, and 34 were unidentified. To ensure comparability between the 2000 and 2022 datasets, we reviewed all taxonomic names and standardized them using data bases "Tropicos" from the Missouri Botanical Garden (https://tropicos.org/), "Taxonomic Name Resolution Service" (https://tnrs.biendata.org/), and "Plants of the World Online" from the Royal Botanic Gardens, Kew (https://powo.science.kew.org/) as a reference. Synonymous names were consolidated under currently accepted names and outdated

or misspelled taxa were corrected. Analyses to evaluate potential differences in forest structure and composition between 2000 and 2022 samplings were conducted at the genus rather than the species level, in order to reduce the number of rare taxa that could confound statistical comparisons due to a potential lack of taxonomic consistency across both surveys.

2.4. Analysis of diversity and compositional metrics

A Bray-Curtis dissimilarity matrix was used to compare changes in forest structure and abundance of genera at the two surveys. We applied rarefaction and extrapolation curves based on Hill numbers, using individual-based abundance to evaluate differences in diversity (Chao et al., 2014; Hsieh et al., 2016). In this framework, q = 0 corresponds to the genera richness, q= 1 the effective number of equally common genera, and q = 2 emphasizes dominant genera. Analyses were performed in R (v4.4.3), using the vegan and iNEXT packages (Hsieh et al., 2016; Oksanen et al., 2022).

To assess changes in tree composition, we calculated the Importance Value Index (IVI), which is based on relative density (RD), relative frequency (RF), and relative dominance (RA), following Curtis and McIntosh (1951). The IVI was calculated as (Equation 1):

$$IVI = RD + RF + RA \quad (1)$$

where: RD = number of individuals of a genus / total number of individuals; RF = frequency of a genus / sum of frequencies for all genera; and RA = total basal area of a genus / total basal area of all individuals. IVI was calculated separately for genera and families.

2.5. Evaluation of changes in forest structure

To compare forest structure between 2000 and 2022, we analyzed size class distributions for DBH, tree height and wood density (WD). We used the Kolmogorov–Smirnov test to assess differences in their distributions between years. Additionally, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA) using DBH, height, WD and carbon storage to explore structural variation across genera. A Euclidean distance matrix was constructed using these variables, and significance was tested using 999 permutations. WD was obtained using the getWoodDensity function from the Biomass package in R (Réjou-Méchain et al., 2017). In addition, Non-metric Multidimensional Scaling (NMDS) was used to explore patterns of community composition in 2000 and 2022. A Bray-Curtis dissimilarity matrix was computed based on the variables of DBH, height WD, and carbon stock. Two-dimensional NMDS (k = 2) was performed to visualize the patterns of variation across these years. Analyses were performed in R (v4.4.3), using the factoextra (Kassambara & Mundt, 2016) and vegan packages (Oksanen et al., 2022).

2.6. Carbon Storage

Above-ground biomass (AGB) was estimated using the computeAGB function from the Biomass package in R (Réjou-Méchain et al., 2017). When tree height data were available, AGB was calculated using the model from Chave et al. (2014; Equation 2):

$$AGB= (0.0673 \times WD \times H \times D^2)^{0.976} \quad (2)$$

Where: WD = wood density (g/cm3), H = tree height (m), and D = DBH (cm). When height data were unavailable, AGB was estimated using a height-independent model (Equation 3):

$$AGB= \exp(-2.024 - 0.896 \times E + 0.920 \times \log(WD) + 2.795 \times \log(D) - 0.0461 \times (\log(D)^2)) \quad (3)$$

Where the bioclimatic compound parameter E is the same as the one given in Chave et al. (2014). Carbon storage for each year was calculated by multiplying AGB by 0.5 and extrapolated to the total area sampled. To assess the relationship between carbon storage and IVI, we performed a Spearman's rank correlation separately for each year and visualized the data using linear regression models.

3. RESULTS

3.1. Changes in genera diversity and composition

A total of 535 trees were recorded in 2000 and 534 trees in 2022. In 2000, we identified 71 species, 69 genera and 37 families, whereas in 2022, we identified 62 species, 60 genera and 33 families (Supplementary material Table S1). The most commonly found trees in 2000 were *Inga* sp., *S. jambos*, and *Allophylus racemosus* Sw. (96, 64, and 67 individuals, respectively), accounting for 42.4% of the trees recorded. In 2022, the most common species were *I. densiflora*, *S. jambos*, and *Cupania guatemalensis* (Turcz.) Radlk., with 79, 71, and 48 individuals, respectively, representing 37% of the total observations (Suppl. Table S1). In 2000, the genera with the highest IVI were *Inga*, *Syzygium*, and *Allophylus* (Fig. 2), while the families with the highest IVI were Fabaceae, Myrtaceae, and Malvaceae (Fig. 3). In 2022, the genera with the highest IVI were *Inga*, *Syzygium*, and *Cupania* (Fig. 2), and the families with the highest IVI were Fabaceae, Myrtaceae, and Anacardiaceae (Fig. 3).

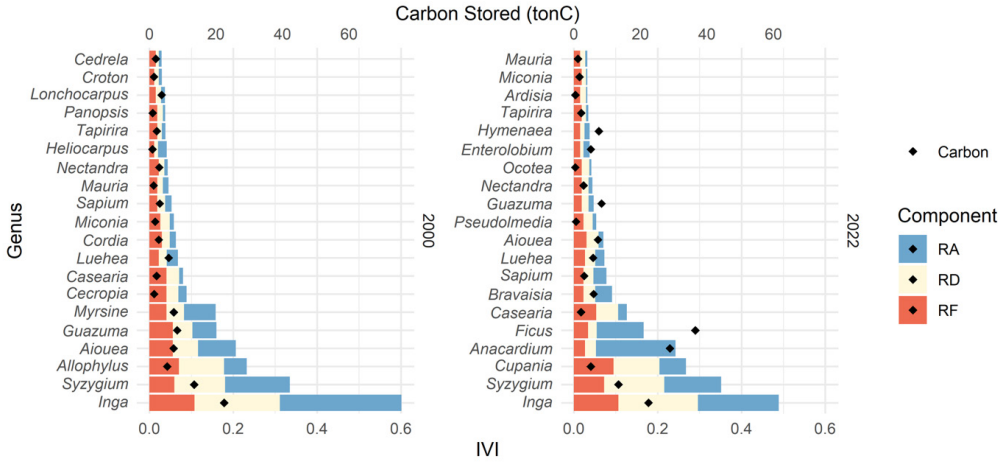

Figure 2. Importance Value Index (IVI) per genus in 2000 and 2022. Data include only the top 20 commonly found genera. Data were collected from 10 m-radius plots in the Municipal Forest of Atenas (Alajuela, Costa Rica). RA = Relative Dominance, RD = Relative Density, RF = Relative Frequency. N (2000) = 535; N (2022) = 534. Carbon stored (tC) is shown for each genus.

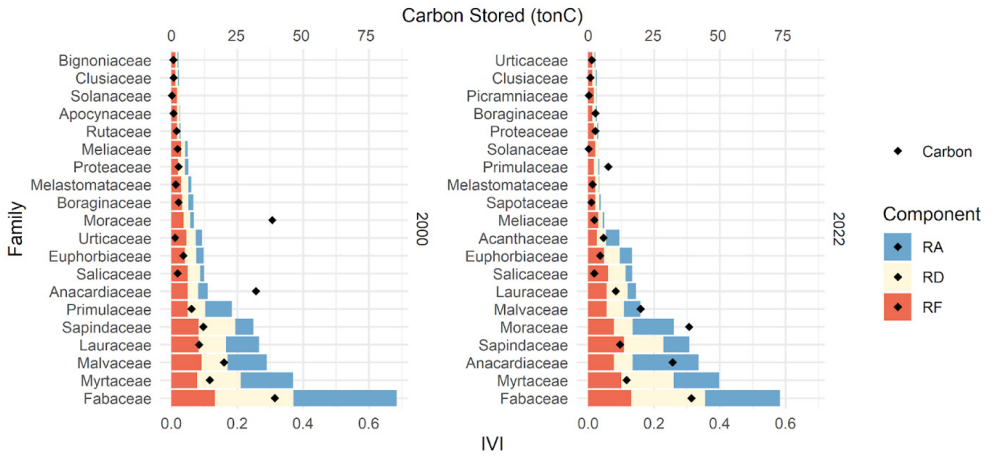

Figure 3. Importance Value Index (IVI) per family in 2000 and 2022. Data includes only the top 20 commonly found families. Data were collected from 10 m-radius plots in the Municipal Forest of Atenas (Alajuela, Costa Rica). RA = Relative Dominance, RD = Relative Density, RF = Relative Frequency. N (2000) = 535; N (2022) = 534. Carbon stored (tC) is shown for each family.

The Bray-Curtis dissimilarity index indicated a 76% similarity in terms of abundance and genera composition, suggesting a very similar structure between the years 2000 and 2022. This is supported by the rarefaction and extrapolation curves, which showed that the effective number of common and dominant genera was identical for both sampling periods (q1 = 10 and q2 = 4, respectively). The remaining dissimilarity can be attributed to genus richness, which was slightly higher in 2000 (q0 = 72) compared to 2022 (q0 = 61; Fig. 4). In both periods, the asymptote was not reached, indicating that genus richness could have been higher with further sampling efforts.

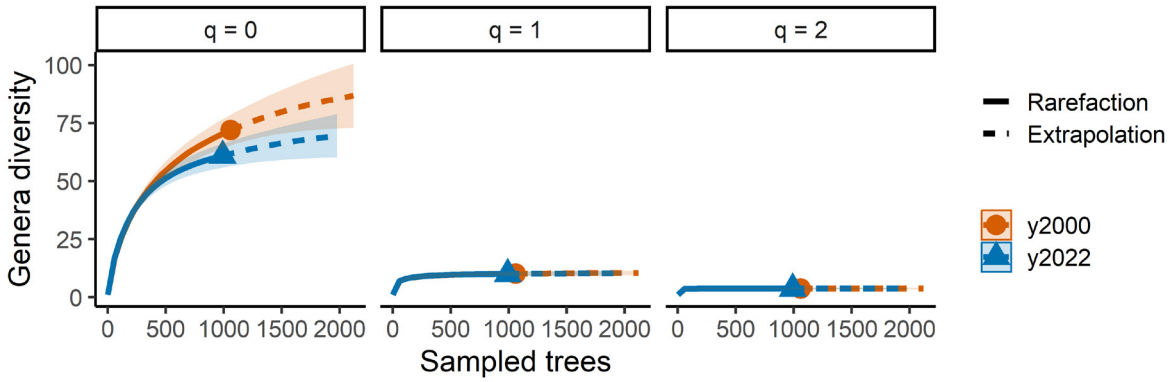

Figure 4. Rarefaction and extrapolation curves for tree genera recorded in the Municipal Forest of Atenas (Alajuela, Costa Rica) in 2000 and 2022. q = 0 represents genera richness, q = 1 the effective number of equally common genera, and q = 2 the dominant genera.

3.2. Tree structure comparison

Tree structure, measured by DBH, height, wood density (WD), and carbon storage, differed between the two years (PERMANOVA: $F_{1,1031} = 6.71$, $p = 0.01$; $R^2 = 0.007$). However, the ordination using NMDS (stress = 0.06) showed considerable overlap, indicating that the differences between years are not strong in the ordination space, and that the ecological differences may be subtle (Fig. 5). Tree height distributions were different between years (Kolmogorov-Smirnov test: $D = 0.16$, $p < 0.0001$), with the highest frequency of trees falling within the 10-20-meter height range (Fig. 6). Trees exceeding 30 m in height were observed exclusively in 2022. For DBH, most of the trees in both years were within the 10–20 cm range, while a few trees with DBH greater than 80 cm were recorded only in 2022. Despite the presence of larger DBH values in 2022, no significant difference was found in the DBH distribution between the years (Kolmogorov-Smirnov test: $D = 0.06$, $p = 0.23$). The distribution of WD classes also differed between the years (Kolmogorov-Smirnov test: $D=0.18$, $p < 0.0001$), with a higher frequency of trees in 2022 exhibiting wood densities higher than 0.6 g/cm3 (Fig. 6).

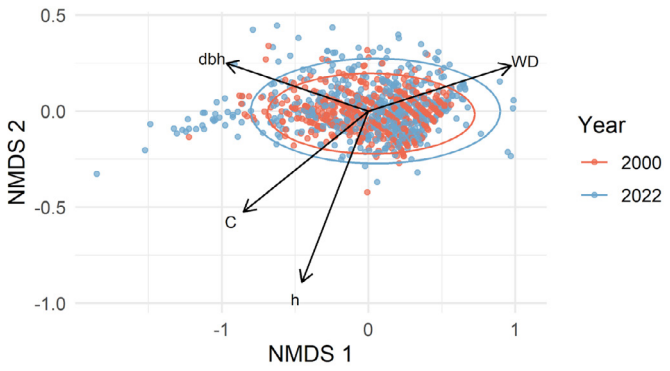

Figure 5. Non-metric Multidimensional Scaling ordination of tree structure for 535 trees measured in 2000 and 534 trees measured in 2022 in the Municipal Forest of Atenas (Alajuela, Costa Rica). WD = wood density (g/cm3), dbh = diameter at breast height (m), C = carbon stock (tC), h = height (m).

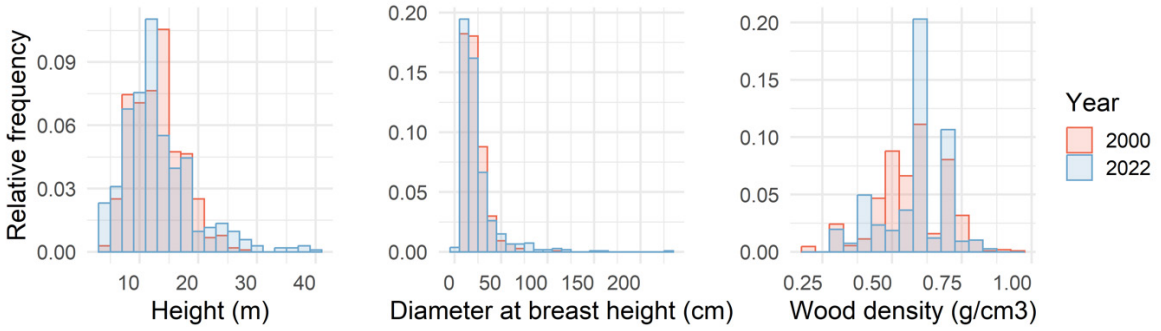

Figure 6. Size class distribution of trees recorded in the Municipal Forest of Atenas (Alajuela, Costa Rica) in 2000 and 2022. N (2000) = 535 trees; N (2022) = 534 trees.

3.3. Aboveground carbon storage

Aboveground carbon storage estimates more than doubled over 22 years, increasing from 1,847.2 tons of carbon (tC) in 2000 to 3,903.7 tC in 2022. Carbon storage rates also increased, from 70.0 tC/ha in 2000 to 147.9 tC/ha in 2022. The genera contributing the most carbon in 2000 were *Inga* and *Syzygium* (12.14 tC/ha and 4.41 tC/ha, respectively; Fig. 3), while in 2022, *Ficus* and *Anacardium* were the largest contributors (26.57 tC/ha and 34.8 tC/ha, respectively; Fig. 3), followed by *Inga* and *Syzygium* with 9.63 tC/ha and 8.69 tC/ha, respectively. A strong positive correlation between IVI and carbon storage was observed for both years (2000: Spearman correlation = 0.833, $p < 0.0001$; 2022: Spearman correlation = 0.829, $p < 0.0001$; Table 1, Fig. 7).

Table 1. Linear model coefficients describing the relationship between the Importance Value Index (IVI) and aboveground carbon (tC) by genus, for trees recorded in the Municipal Forest of Atenas (Alajuela, Costa Rica) in 2000 and 2022

Year		Estimate	Std. Error	t value	p
2000	(Intercept)	2.912	1.740	1.674	0.0995
	IVI	148.346	24.358	6.090	< 0.0001
2022	(Intercept)	0.3599	1.2525	0.287	0.775
	IVI	205.32	17.95	11.44	< 0.0001

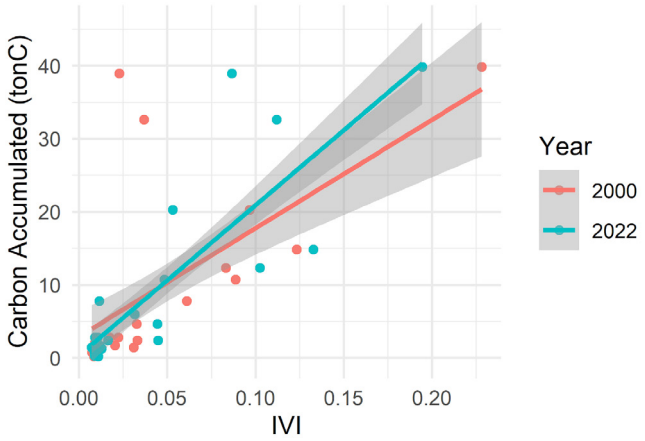

Figure 7. Relationship between the Importance Value Index (IVI) and aboveground carbon (tC) by genus, for trees recorded in the Municipal Forest of Atenas (Alajuela, Costa Rica) in 2000 and 2022. N (2000) = 535 trees; N (2022) = 534 trees.

4. DISCUSSION

4.1. Tree diversity and composition

Tree diversity and composition in the MFA was similar over the two-decade study period. The consistent dominance of *Inga* and *Syzygium* across both census years indicate compositional stability over 22 years. The MFA has been undergoing natural regeneration since the 1930s, following a history of land use dominated by coffee plantations, sugar cane fields, and cattle pastures. *Inga densiflora* and *S. jambos* are commonly found in agroforestry systems, particularly coffee plantations, due to their multiple benefits to farmers, including nitrogen fixation and provision of firewood, and edible fruit production (Aide et al., 2000; Siles et al., 2010; Baruch & Nozawa, 2014). *Syzygium jambos*, native to Southeast Asia, is considered invasive in many tropical regions (Rejmánek & Richardson, 1996; Ávalos et al., 2006; Aide et al., 2000) and can disrupt natural regeneration by forming monospecific stands (Di Stéfano et al., 1998). It is known that in the absence of effective control, abandonment of coffee plantations often promotes fast-growing non-native species (Baruch & Nozawa, 2014). Given the MFA's unmanaged regeneration, the continued dominance of *I. densiflora* and *S. jambos* may reflect prior land use and its competitive advantage in early successional stages (Aide et al., 2000; Baruch & Nozawa, 2014).

A 2006 study at the MFA reported that *S. jambos* comprised 51% of the understory seedlings, suggesting a strong influence on regeneration dynamics (Ávalos et al., 2006). Our data show that the IVI, which integrates relative abundance, dominance, and frequency, has remained nearly unchanged for this species over the 22-year period. Additionally, rarefaction and extrapolation curves confirm this stability, particularly for common and dominant genera (q1 and q2), despite a slight reduction in richness (q0). This relative stability can be partially explained by the influence of *S. jambos*, which although has not increased its dominance in the forest, as a fast-growing species that thrives in disturbed habitats, it may limit the establishment and growth of native species by occupying ecological niches that would otherwise be available for early-successional or native trees (Aide et al, 2000). Invasive species are particularly problematic in fragmented landscapes, where limited dispersal and increased isolation may slow down or prevent the establishment of native species, potentially delaying or inhibiting the natural regeneration process (Rejmánek & Richardson, 1996; Baruch & Nozawa, 2014).

In spite of the composition stability, our findings indicate some trends in community dynamics at the MFA. Excluding *Inga* and *Syzygium*, other pioneer genera, such as *Allophylus*, *Aiouea*, *Guazuma*, *Myrsine*, and *Cecropia*, which were relatively common in 2000, declined in frequency by 2022. In contrast, in 2022 there was a dominance of early-successional genera such as *Cupania*, *Anacardium*, and *Ficus* (Oliveira-Neto et al., 2017). There was also an increase in the presence of intermediate-successional genera, including *Ardisia*, *Bravaisia*, *Mauria*, *Pseudolmedia* and *Ocotea*, which are typically associated with more mature secondary forests (Cascante & Estrada, 2001), indicating that natural regeneration processes are proceeding towards late-successional stages. It is important to note that this regeneration may have been influenced by anthropogenic activities, such as the maintenance of recreational trails, as well as natural disturbances like treefalls, which occur with more frequency during the rainy season in the steepest areas of the forest. Although the MFA cannot yet be classified as a mature forest, the observed changes indicate that it is transitioning toward greater structural complexity.

4.2. Tree structure and aboveground carbon storage

Tree height and WD distributions showed minor differences between 2000 and 2022. The 2022 survey recorded some taller and larger-diameter trees, particularly for *Ficus* and *Anacardium*. Species of *Ficus* are well known for their high IVI in tropical forests, contributing to both abundance and basal area, as well as enhancing functional diversity (García-Cox et al., 2023). Although the presence of these genera could suggest sampling variability, potentially due to minor differences in plot relocation, it is worth noting that *Anacardium excelsum* (Bertero & Balb.) Skeels., a species typically characterized by medium to slow growth rates, can attain a DBH of approximately 40 cm in around 20 years (Lozano et al., 2012), which may explain a lower abundance in the 2000 dataset.

Estimates of aboveground carbon storage at the MFA increased from 70.0 tC/ha in 2000 to 147.9 tC/ha in 2022, approaching values reported for old-growth tropical forests (e.g., 99.6 tC/ha in semi-evergreen tropical forest, Aryal et al., 2014; 108.9 tC/ha in tropical wet forest, Rozendaal & Chazdon, 2015; 161 tC/ha in lowland tropical rainforest, Oberleitner et al., 2021). These changes may be partly explained by the presence of large trees of *Ficus* and *Anacardium* in the 2022 survey, which may have contributed disproportionately to total biomass and carbon stocks. Supporting this pattern, Moraceae and Anacardiaceae were the only families in the 2000 survey whose carbon storage exceeded their IVI, indicating that these taxa contribute more to carbon storage than their relative abundance or frequency would suggest.

These findings are consistent with the mass-ratio hypothesis, which posits that ecosystem functions such as carbon storage are driven primarily by the traits of dominant species (Grime, 1998). At smaller spatial scales (e.g., 20 × 20 m plots), tree species richness has been found to correlate strongly with AGB, largely due to the presence of mature individuals of large-statured species such as *Ficus* (Poorter et al., 2015; García-Cox et al., 2023). Furthermore, the presence of long-lived, high-density species tends to support greater carbon storage than short-lived, low-density, fast-growing taxa. However, this relationship tends to weaken or disappear at larger spatial scales (e.g., 100 × 100 m plots), likely due to species saturation effects (Poorter et al., 2015). Consequently, in a relatively small forest fragment such as the MFA (26.4 ha), the presence of large trees may exert a strong influence on carbon dynamics, allowing carbon storage levels to approach those of old-growth tropical forests.

We acknowledge that estimating aboveground carbon storage involves inherent uncertainties, particularly when multiple methods are used. Since models provide estimates rather than direct measurements, it is essential to account for model error and properly propagate uncertainties through to final carbon values (Chave et al., 2014). Future studies should include comprehensive error propagation analyses to enhance the reliability of carbon assessments. To better understand carbon dynamics in regenerating forest fragments, permanent plots should be established and include indicators such as crown dimensions, biomass turnover, and below-ground carbon storage. Remote sensing technologies can further enhance these efforts by providing more accurate and spatially comprehensive assessments of forest structure and function.

4.3. Ecological implications and management considerations

In highly degraded and fragmented landscapes, secondary forest patches play a crucial role in carbon recovery and biodiversity conservation, significantly contributing to species persistance and climate change mitigation (Borma et al., 2022). In human-dominated regions, like Costa Rica's Central Valley, these patches not only support carbon sequestration but also enhance landscape connectivity. They act as seed sources for nearby regenerating areas and provide essential ecosystem services, including climate regulation, water protection, pollination, and recreation (Chazdon, 2014; Bongers et al., 2015).

The MFA exemplifies these ecological functions by maintaining tree diversity and composition, while also contributing to regional carbon storage and enhancing ecological resilience. For instance, the presence of mature, large trees, such as *Ficus* and *Anacardium* in the MFA play a disproportional role in carbon storage and are considered keystone species due to their structural ecological importance. *Ficus* species belong to the Moraceae family, which is one of the most rich and conspicuous families in tropical lowland forests, providing critical food and refuge for wildlife, thus supporting natural forest regeneration even in young secondary forests (DeWalt et al., 2003; Ter Steege et al., 2013). Despite its small size, the MFA supports a variety of medium and large-sized mammals (Cambronero et al., 2023), highlighting the importance of these trees for both carbon storage and mammal conservation.

However, the MFA currently lacks formal management, with efforts limited to trail maintenance. This absence of a structured management strategy limits its long-term ecological potential. A key concern is the presence of the invasive species *S. jambos*, which restricts native plant regeneration and threatens local biodiversity (Di Stéfano et al., 1998; Avalos et al., 2006). To enhance plant diversity and forest resilience, it is recommended to reduce the abundance of this species. However, given the forest's role

in water protection, complete removal is discouraged as it may negatively impact water infiltration and soil stability. Chemical control should also be avoided to prevent contamination of water sources. Instead, a more appropriate strategy could involve the gradual mechanical removal of seedlings and young plants, coupled with selective cutting of mature trees (Ávalos, 2006). Active reforestation with native species should be prioritized to outcompete *S. jambos* and foster natural regeneration, focusing on species that provide habitat and food for wildlife, stabilize soil, and improve water quality.

Maintaining ecological connectivity with nearby forest fragments and riparian zones is also critical to maintain the MFA's ecological functions. Therefore, management actions should be integrated into broader regional conservation initiatives such as the Montes del Aguacate Biological Corridor or the General Integral Commission of the Grande Tárcoles River Basin. These initiatives can facilitate the active involving of local communities in land use planning and promote agroecological practices and alternative land uses that support the conservation of forest fragments at a landscape scale (Montero et al., 2021). Implementing these integrated management strategies is essential to safeguard the long-term ecological integrity and resilience of the MFA and ensure the continued provision of critical ecosystem services in an increasingly changing landscape.

5. CONCLUSIONS

1. The tree community in the MFA forest fragment showed compositional stability over the 22-year period, largely due to the continued dominance of *I. densiflora* and the invasive *S. jambos*. While diversity remained stable overall, the proliferation of *S. jambos* may be limiting the recruitment of native species, potentially slowing natural regeneration.
2. Between 2000 and 2022, aboveground carbon storage in the MFA forest more than doubled, from 70.0 to 147.9 tC/ha. This increase is linked to the presence and growth of large, mature trees such as *Ficus* and *Anacardium excelsum*, which have a disproportionately high impact on carbon storage.
3. Despite its small size, the MFA forest provides important ecological services in a fragmented, human-modified landscape, contributing to carbon sequestration, and supporting natural regeneration processes.
4. This study highlights the critical role of secondary forest fragments in forest recovery and climate change mitigation in human-modified landscapes, emphasizing the need for a formal management plan in the MFA to strengthen conservation and sustain of ecosystem services.

Supplementary information ↑

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Supplementary material

Table S1**:** accompanies the paper on *Forest Systems*' website.

Data availability

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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Authorship contribution statement

Milena Cambronero: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Fabián Araya-Yannarella: Investigation, Validation, Writing – original draft, Writing – review & editing.

Lauren Holmes: Investigation, Writing – original draft, Writing – review & editing.

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Competing interests

The authors have declared that no competing interests exist.

Statement on the use of Artificial Intelligence

Not applicable.

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