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SPECIES DIVERSITY IN TROPICAL DRY FORESTS OF ECUADOR: HOW EFFECTIVE ARE REGENERATED ECOSYSTEMS?

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RESUMEN

Los bosques secos tropicales son ecosistemas altamente vulnerables a la degradación, cuya restauración requiere estrategias efectivas de conservación. Este estudio evaluó la biodiversidad de un bosque seco tropical en estado natural y un bosque en regeneración asistida, comparando riqueza de especies, equidad y estructura comunitaria. Se establecieron cuatro parcelas de muestreo, de 20 x 50 metros cada una, en ambos ecosistemas y se analizaron índices de diversidad utilizando iNEXT.4steps y el software PAST. Los resultados muestran que el bosque natural presenta una mayor riqueza de especies (54) en comparación con el bosque regenerado (28), así como una distribución más equitativa de las abundancias. La dominancia de especies pioneras en el bosque regenerado indica que aún se encuentra en una etapa temprana de sucesión ecológica. La extrapolación de diversidad sugiere que el ecosistema restaurado difícilmente alcanzará la complejidad del bosque natural en el mediano plazo. Estos hallazgos resaltan la importancia de estrategias de restauración complementarias, como la introducción de especies tardío-sucesionales, para acelerar la convergencia estructural y funcional. El estudio subraya la necesidad de monitoreos a largo plazo para evaluar la efectividad de la regeneración asistida en bosques secos tropicales y sugiere que enfoques de restauración más integrales podrían mejorar la resiliencia y estabilidad de estos ecosistemas.

Palabras clave: Bosque seco tropical, regeneración asistida, biodiversidad, sucesión ecológica, restauración ecológica

DIVERSIDAD DE ESPECIES EN BOSQUES SECOS TROPICALES DEL ECUADOR: ¿QUÉ TAN EFECTIVOS SON LOS ECOSISTEMAS REGENERADOS?

ABSTRACT

Tropical dry forests are ecosystems highly vulnerable to degradation, whose restoration requires effective conservation strategies. This study assessed the biodiversity of a tropical dry forest in its natural state and a forest under assisted regeneration, comparing species richness, equity, and community structure. Four sample plots of 20 x 50 meters each were established in ecosystems, and diversity indices were analyzed using iNEXT.4steps and PAST software. The results show that the natural forest has a higher species richness (54) than the regenerated forest (28) and a more even abundance distribution. The predominance of fast-growing, light-demanding pioneer species in the regenerating forest indicates an early-to-mid successional stage, while the balanced distribution of functional groups in the natural forest reflects greater ecological complexity and resilience. These findings highlight the importance of complementary restoration strategies. The study underscores the need for long-term monitoring to assess the effectiveness of assisted regeneration in tropical dry forests. More holistic restoration approaches could improve the resilience and stability of these ecosystems.

Keywords: Tropical dry forest, assisted regeneration, biodiversity, ecological succession, ecological restoration.

1. INTRODUCTION

Tropical dry forests harbor high biological diversity and play a crucial role in ecological stability (Miles et al., 2006; Murphy & Lugo, 2012). However, these ecosystems have experienced accelerated degradation due to human activities such as agricultural expansion, deforestation, and the effects of climate change (Blackie et al., 2014). Faced with this problem, assisted regeneration has emerged as a key strategy for ecological restoration, facilitating the recovery of biodiversity and ecosystem functionality through interventions such as planting native species, controlling invasive species, and protecting recovering areas. (Oluwajuwon et al., 2024; Holl & Aide, 2011; Chazdon et al., 2020)

Knowledge about the differences in biodiversity between natural dry forests and those undergoing assisted regeneration remains limited (Mesa-Sierra et al., 2024; Oliveira et al., 2024; Reid et al., 2015). In particular, few studies evaluate the effectiveness of assisted regeneration over the medium term, which hinders understanding the ecological processes that determine the recovery of these ecosystems (Elliott et al., 2013). Assessing biodiversity in this context allows for identifying patterns of convergence or divergence in the composition and structure of biological communities compared to natural forests, providing fundamental information for improving restoration strategies. (Letcher & Chazdon, 2009; Meli et al., 2017)

Likewise, understanding these differences is essential for designing effective conservation and restoration strategies to optimize natural area management. This improved management takes on greater relevance, as the composition and structure of biological communities directly influence the capacity of ecosystems to provide services such as hydrological cycle regulation, carbon sequestration, pollination, and erosion control (Poorter et al., 2016). Thus, the restoration of these services represents a tangible benefit to local communities by improving their food security, access to water, and sustainable economic opportunities (Kumi et al., 2024; Gao et al., 2024; Aryee et al., 2024; Rath et al., 2024). Additionally, it strengthens the socioecological resilience of these communities to extreme climate events. (Cantarello et al., 2024; Mahjoubi et al., 2022; Hong & Chongjian, 2024)

The main objective of this study is to compare biodiversity indicators between a natural dry forest and one undergoing assisted regeneration. To this end, species richness and abundance were assessed in both ecosystems and species composition and distribution within the community. Furthermore, differences in dominance, evenness, and functional diversity in forest structure were analyzed to determine the recovery status of the regenerated ecosystem relative to the natural forest. It is hypothesized that the regenerated forest will have lower species richness and composition than the natural dry forest but with a tendency toward convergence in structure and ecological functionality.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted in two nature reserves located in northwestern Ecuador: the Lalo Loor Dry Forest Reserve, which houses the dry forest plots (TDF), and the

Jama-Coaque Nature Reserve, where the forest regenerated 10 years ago is located (ESF). The Jama-Coaque Reserve, managed by the nonprofit Third Millennium Alliance (TMA), protects 850 hectares of forest in the coastal mountain range of the same name and is part of the Tumbes-Chocó-Magdalena biodiversity hotspot. Located less than 8 kilometers from the Pacific Ocean, it presents an altitudinal gradient in which the tropical moist evergreen forest of the lowlands transforms into cloud forest at higher altitudes. Its climate is tropical monsoon, with a rainy season from December to May, recording between 1,000 and 1,500 mm of annual precipitation, while the cloud forest zone can exceed 2,000 mm.

The Lalo Loor Dry Forest Reserve is located less than 2 kilometers west of the Jama-Coaque Reserve, to which it is connected via the Three Forest Trail ecotourism trail. This reserve protects 201 hectares of lowland forest and is managed by its owner and the Ceiba Foundation for Tropical Conservation. Its altitude ranges from 41 to 414 meters above sea level, less than 1.4 kilometers from the Pacific Ocean. The lowland areas are dominated by tropical dry deciduous forests, transforming into semi-deciduous forests with increasing altitude. The reserve's climate is tropical monsoon, with an average annual rainfall of 1,000 mm or less. The field sampling was conducted in October and November of 2022.

2.2. *Sampling Design*

Four sampling plots were established for each vegetation type to capture the structural and compositional variability of the studied ecosystems. Each plot was 20 x 50 meters in size. Within these plots, all individuals of tree species with a diameter at breast height (DBH) equal to or greater than 5 cm were recorded. The location of the plots was randomly determined within each forest, ensuring a representative spatial distribution that would capture the environmental and ecological heterogeneity present in both ecosystems. Additionally, the plots were georeferenced using a high-precision GPS to facilitate their location in future monitoring.

2.3. Species Identification

Each species was identified with the support of experts from the Botanical Garden of the Technical University of Manabí, who provided specialized taxonomic advice. The initial identification was made in situ, based on key morphological characteristics such as the shape of the leaves, bark, flowers, and fruits. To ensure the accuracy of the determinations, records were cross-referenced with recognized international taxonomic databases, such as The World Flora Online (WFO), the International Plant Names Index (IPNI), and Tropicos (Missouri Botanical

Garden). In cases where identification could not be confirmed in the field due to the lack of reproductive structures or similarity between species, botanical samples (leaves, flowers, or fruits) were collected following standardized protocols. These samples were pressed, dried, and transported to the laboratory for detailed analysis under controlled conditions using specialized taxonomic keys and comparisons with herbarium specimens.

2.4. Biodiversity Analysis

To comprehensively assess biological diversity, the Shannon (H'), Simpson dominance (D), and Pielou evenness (J) indices were calculated using PAST version 5.1 software (Hammer et al., 2001). These indices allowed for the analysis of different dimensions of biodiversity: species richness, defined as the total number of species recorded in the community; evenness, which measures how evenly individuals are distributed among species; and dominance, which indicates the degree to which one or a few species predominate in abundance within the ecosystem (Table 1).

Table 1. *Indices and equations used to estimate biodiversity at each study site.*

Index	Equation	Description	Abr.
Shannon	$H' = \sum_{i=1}^{S} p_i log_b p_i$	Measures the unpredictability in identifying a randomly chosen individual's species. It is particularly responsive to changes in the abundance of uncommon species.	H'
Simpson	$D = \frac{\sum_{i=1}^{S} n_i(n_i - 1)}{N(N-1)}$	Assesses the likelihood that two randomly selected individuals belong to the same species. It is particularly sensitive to changes in the abundance of common species.	D
Pielou	$J = \frac{H'}{\log(S)}$	The equivalence among species in a community	J

Source: Shannon 1948, Simpson 1949, Pielou 1966.

Additionally, to ensure a more accurate and representative assessment of biodiversity, the iNEXT.4steps software (Chao & Hu, 2023; Chao et al., 2020) was used. This tool is based on Hill numbers and integrates a four-step approach to biological diversity analysis.

This software allowed for estimating sample completeness, assessing whether the sampling effort was sufficient to capture the true diversity of the analyzed system. Furthermore, it facilitated the interpolation and extrapolation of observed diversity, allowing for standardized comparisons between the studied ecosystems, even in situations where sample size or sampling effort varied between sites.

3. RESULTS AND DISCUSSIONS

A total of 72 species were recorded, comprising 39 families and 63 genera; 54 of these were found in the natural forest and 28 in the regenerated forest (Table 2). The observed richness indicates that the natural ecosystem hosts a greater diversity of tree species, suggesting that, despite restoration efforts, the regenerated forest assemblage still differs significantly from the reference ecosystem.

Table 2. Species and abundance information recorded at each of the sampling sites

Species	Family	Abundance	
		ESF	TDF
Acnistus arborescens (L.) Schltdl.	Solanaceae	6	0
Agonandra silvatica Ducke	Opiliaceae	0	1
Alseis eggersii Standl.	Rubiaceae	3	27
Ambelania occidentalis Zarucchi	Apocynaceae	0	8
Annona manabiensis Saff. ex R.E. Fr.	Annonaceae	0	1
Arbutus unedo L.	Ericaceae	6	1
Baccharis latifolia (Ruiz & Pav.) Pers.	Asteraceae	4	0
Bauhinia aculeata L.	Fabaceae	17	44
Brosimum alicastrum Sw.	Moraceae	0	2
Brownea multijuga Britton & Killip	Fabaceae	0	18
Caesalpinia glabrata Kunth	Fabaceae	0	4

Calophyllum brasiliense Cambess.	Calophyllaceae	1	0
Calycolpus surinamensis McVaugh	Myrtaceae	0	2
Carapa grandiflora Sprague	Meliaceae	0	28
Caryocar glabrum (Aubl.) Pers.	Caryocaraceae	0	4
Cassia moschata Kunth	Fabaceae	17	0
Castilla elastica Sessé ex Cerv.	Moraceae	0	2
Celtis iguanaea (Jacq.) Sarg.	Cannabaceae	0	4
Centrolobium ochroxylum Rose ex Rudd	Fabaceae	69	1
Chromolucuma baehniana Monach.	Sapotaceae	0	21
Chrysochlamys dependens Planch. & Triana	Clusiaceae	0	1
Clusia stenophylla Standl.	Clusiaceae	0	2
Cochlospermum vitifolium (Willd.) Spreng.	Bixaceae	1	12
Cordia alliodora (Ruiz & Pav.) Oken	Cordiaceae	79	2
Cordia hebeclada I.M. Johnst.	Cordiaceae	0	2
Cordia macrantha Chodat	Cordiaceae	1	0
Croton eggersii Pax	Euphorbiaceae	0	4
Cupania vernalis Cambess.	Sapindaceae	7	0
Faramea occidentalis (L.) A. Rich.	Rubiaceae	1	0
Ficus insipida Willd.	Moraceae	0	3
Ficus obtusifolia Kunth	Moraceae	2	0
Ficus trigonata L.	Moraceae	0	1
Grias peruviana Miers	Lecythidaceae	0	2
Guazuma ulmifolia Lam.	Malvaceae	97	0
Guettarda acreana K. Krause	Rubiaceae	0	1
Humiriastrum procerum (Little) Cuatrec.	Humiriaceae	0	3
Inga chocoensis Killip ex T.S. Elias	Fabaceae	0	1
Inga jaunechensis A.H. Gentry	Fabaceae	25	0
Inga sapindoides Willd.	Fabaceae	2	0

Ladenbergia pavonii (Lamb.) Standl.	Rubiaceae	0	43
Leucaena trichodes (Jacq.) Benth.	Fabaceae	2	1
Machaerium millei Standl.	Fabaceae	0	15
Malouetia albiflora Miq.	Apocynaceae	0	1
Mora oleifera (Triana ex Hemsl.) Ducke	Fabaceae	0	1
Myrcia fallax (Rich.) DC.	Myrtaceae	0	1
Nectandra obtusata Rohwer	Lauraceae	0	3
Neoptychocarpus chocoensis A.H. Gentry & Forero	Salicaceae	0	6
Phyllanthus juglandifolius Willd.	Phyllanthaceae	1	0
Piper corrugatum Kuntze	Piperaceae	2	0
Piper eriopodon (Miq.) C. DC.	Piperaceae	0	1
Pisonia aculeata L.	Nyctaginaceae	0	1
Pisonia floribunda Hook. f.	Nyctaginaceae	0	5
Pseudobombax millei (Standl.) A. Robyns	Malvaceae	0	6
Pseudolmedia eggersii Standl.	Moraceae	0	9
Pseudosamanea guachapele (Kunth) Harms	Fabaceae	19	0
Psidium guajava L.	Myrtaceae	1	0
Rauvolfia littoralis Rusby	Apocynaceae	1	0
Siparuna muricata (Ruiz & Pav.) A. DC.	iparunaceae	0	1
Spondias mombin L.	Anacardiaceae	0	2
Stryphnodendron porcatum D.A. Neill & Occhioni f.	Fabaceae	9	0
Stryphnodendron pulcherrimum (Willd.) Hochr.	Fabaceae	0	4
Swartzia polita (R.S. Cowan) Torke	Fabaceae	0	2
Tabebuia sp.	Bignoniaceae	0	16
Tapura angulata Little	Dichapetalaceae	0	7
Trichillia sp.	Meliaceae	0	1
Triplaris cumingiana Fisch. & C.A. Mey.	Polygonaceae	2	1
Turpinia paniculata Vent.	Staphyleaceae	10	2

Vismia baccifera (L.) Triana & Planch.	Hypericaceae	5	1
Vitex gigantea Kunth	Lamiaceae	2	5
Vochysia guatemalensis Donn. Sm.	Vochysiaceae	0	60
Ximenia americana L.	Ximeniaceae	0	6
Zanthoxylum sp.	Rutaceae	0	1

TDF = Tropical dry forest, ESF = Early successional forest

The results of the calculated diversity indices are shown in Table 3. The Shannon index (H') showed higher values in the natural forest (H' = 3.25) compared to the regenerated forest (H' = 2.39), indicating higher species diversity and a more equitable distribution of abundances in the uninterrupted ecosystem.

Simpson's dominance (D) was higher in the regenerated forest (D = 0.1433), suggesting that some species dominate the community. In comparison, in the natural forest (D = 0.0639) the dominance was lower, reflecting a more diverse and equitable community. These results agree with previous studies indicating that regenerating forests may present a more homogeneous community structure in their first decades of recovery. (Arroyo-Rodríguez et al., 2017)

Table 3. Diversity indices calculated for each sampling site

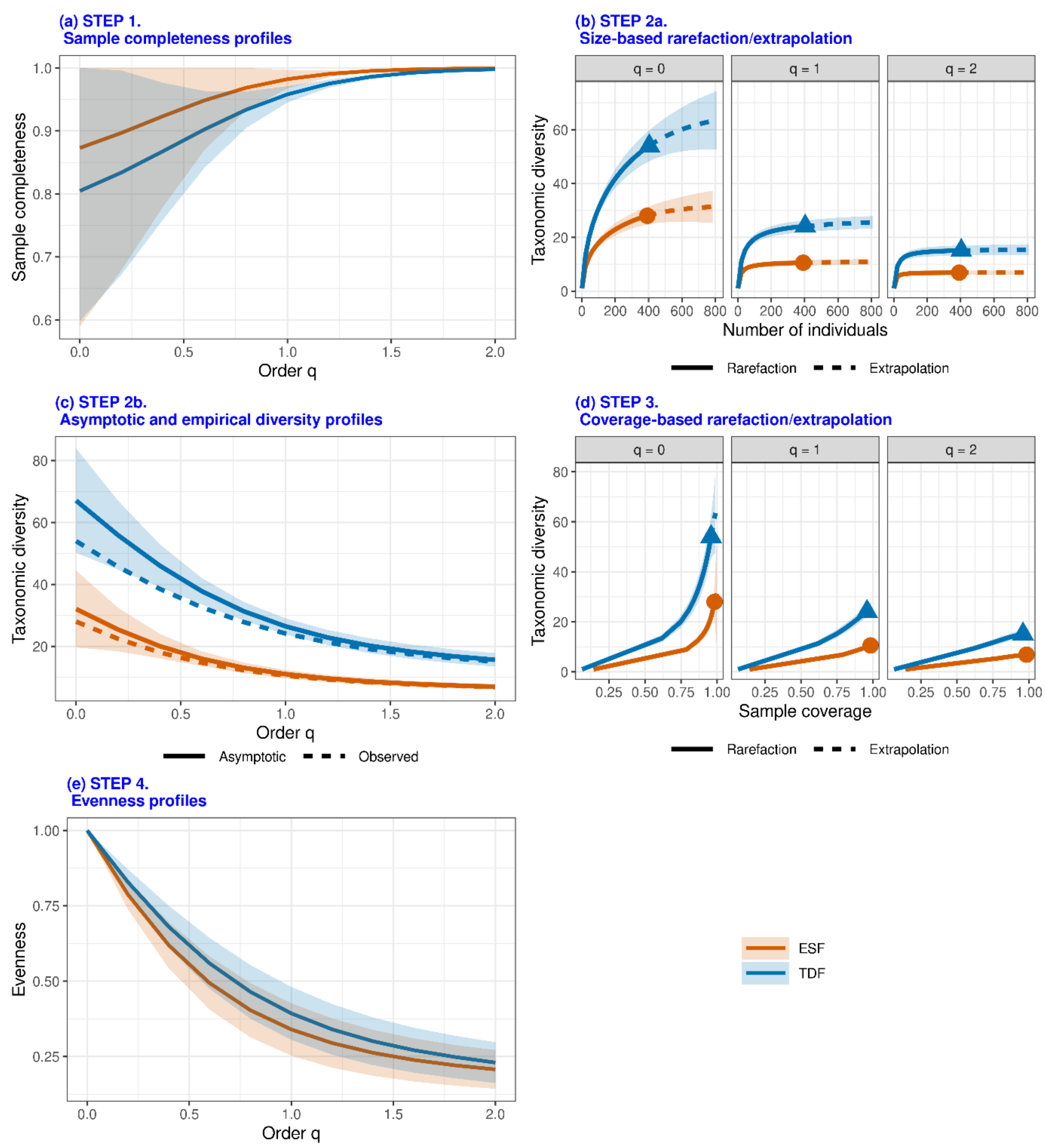
	ESF	TDF
Taxa_S	28	54
Individuals	392	404
Dominance_D	0,1433	0,0639
Shannon_H	2,391	3,25
Equitability_J	0,7072	0,7982

TDF = Tropical dry forest, ESF = Early successional forest

Pielou's evenness (J) was higher in the natural forest (J = 0.7982) than in the regenerated forest (J = 0.7072), indicating that species distribution in the restored ecosystem is less even. This could be because certain pioneer species dominate regeneration in the early stages of the successional process, while evenness increases as the ecosystem matures. (Ma et al., 2024)

The results of the sample completeness analysis with iNEXT.4steps showed a sampling coverage of 0.982 in the regenerated forest and 0.958 in the natural forest. The sample completeness profile (Figure 1a) showed that the proportion of diversity captured varied according to the q order. For q = 0 (species richness), completeness was lower, suggesting that not all species, especially rare ones, were detected.

Figure 1. Biodiversity analysis using iNEXT.4steps. a) Sample completeness profile. b) Size-based rarefaction and extrapolation curves. c) Asymptotic and empirical diversity profiles. d) Coverage-based rarefaction and extrapolation curves. e) Evenness profiles. TDF = Tropical dry forest, ESF = Early successional forest



This finding is consistent with previous studies that highlight the difficulty of sampling rare species in tropical ecosystems, where environmental heterogeneity and low density of individuals can limit their detection. (Chao et al., 2020; Hortal et al., 2015)

On the other hand, for q = 1 (Shannon diversity) and q = 2 (Simpson diversity), completeness was high, indicating that the most abundant or frequent species were well represented in the sample. This reflects that, although species richness may be underestimated, the functional and structural diversity of the ecosystem, based on dominant species, is adequately captured (Chao & Jost, 2015).

Size-based rarefaction and extrapolation curves (Figure 1b) confirmed these findings. For q = 0, the curve did not reach a plateau, suggesting that species richness was not fully captured, a typical result in biodiversity studies where sampling effort is limited (Gotelli & Colwell, 2011). In contrast, the curves stabilized for q = 1 and 2, reflecting a reasonable Shannon and Simpson diversity estimate. This indicates that the most common species contribute significantly to biomass and ecosystem processes and are well represented in the sample (Chao et al., 2014). Furthermore, asymptotic and empirical diversity profiles (Figure 1c) showed that, although species richness could be underestimated, diversity estimates for higher orders were accurate. This fact highlights the importance of using approaches that consider multiple dimensions of diversity, such as Hill numbers, to obtain a more complete view of community structure (Chao et al., 2020).

Coverage-based rarefaction and extrapolation curves (Figure 1d) allowed for standardized comparisons between samples, ensuring that differences in sampling effort did not bias the results. This approach is instrumental in comparative studies, where sampling effort can vary significantly between sites (Chao & Jost, 2012). Finally, the evenness profiles (Figure 1e) indicated a relatively balanced distribution of abundances among species, with high values for q = 1 and 2. This suggests that the studied communities have a lower dominance of a few species, which could be associated with greater resilience to environmental disturbances. (Chao & Ricotta, 2019)

The results underscore the importance of considering multiple dimensions of diversity (richness, diversity, and evenness) to understand biological communities' structure comprehensively. The lower sample completeness for q = 0 suggests that rare, yet ecologically important, species are challenging to detect with conventional sampling methods. This could affect conservation, as these species are often more vulnerable to environmental disturbances (Hortal et al., 2015). On the other hand, the high completeness for q = 1 and 2 reflects that the dominant

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species are well represented, which is relevant to maintaining the stability of the ecosystem and the associated ecosystem services. (Chao & Jost, 2015)

The stabilization of the rarefaction and extrapolation curves for higher orders (Figure 1b) confirms that the sampling effort was adequate to capture the diversity of the most common species but also highlights the need to increase the sampling effort or employ complementary techniques to improve the detection of rare species (Gotelli & Colwell, 2011). The observed evenness suggests that the studied communities have a relatively balanced distribution of abundance, which could indicate a lower dominance of a few species and, therefore, greater resilience to disturbances (Chao & Ricotta, 2019). However, it is important to consider that these patterns could vary depending on environmental factors, such as climate, resource availability, or land-use history, which opens new lines of research to explore the mechanisms underlying the structure of these communities. (Chao et al., 2020)

The results reinforce the importance of considering long-term ecological processes in restoring tropical dry forests. Although assisted regeneration has favored the establishment of a diverse tree community, the species composition and structure of the regenerated forest continue to differ from that of the natural forest. The lower evenness and greater dominance of certain species in the regenerated forest suggest that this ecosystem is still in its early recovery phase. Longer-term assessments are needed to determine whether the regenerated forest converges with the natural ecosystem in terms of biodiversity and community structure. Complementary restoration strategies, such as facilitating seed dispersal or enriching late-successional species, could accelerate this process and improve the resilience of the restored ecosystem. (Holl & Aide, 2011)

4. CONCLUSIONS

This study compared biodiversity between a natural tropical dry forest and one undergoing a 10-year assisted regeneration process, revealing significant differences in species richness, evenness, and community structure. Greater diversity was recorded in the natural forest. Furthermore, the Pielou index reflected a more equitable species distribution in the natural ecosystem, while the regenerated forest presented greater species dominance. The observed patterns indicate that assisted regeneration has facilitated the establishment of a tree community, but with less evenness and a structure dominated by few species, suggesting that the ecosystem is in an early stage of ecological succession. Extrapolation of diversity suggests that, even with a more significant sampling effort, the richness of the regenerated forest would not reach that of the natural forest in the medium term.

This study contributes to the knowledge of regeneration processes in tropical dry forests, providing empirical evidence on the differences in biodiversity between natural and restored ecosystems. The findings support theoretical models of ecological succession, highlighting that recovering forests can remain structurally distinct from mature ecosystems for decades. Furthermore, the information obtained can be used to refine theories about the resilience of these ecosystems and the factors that influence their recovery trajectories.

From an applied perspective, the results underscore the need for complementary restoration strategies to accelerate the convergence of regenerated forests toward a state more similar to the natural ecosystem. Actions such as introducing late-successional species and promoting seed dispersal can improve the resilience of the restored ecosystem. Furthermore, the findings can be used in designing conservation policies to restore tropical dry forests and mitigate biodiversity loss. The recovery of these ecosystems also has implications for local communities, given their role in providing essential ecosystem services, such as water regulation and carbon sequestration.

Our results strongly support the development of public policies that integrate a longer time horizon for tropical dry forest restoration projects. Specifically, policymakers should establish regulatory frameworks that require post-restoration monitoring for at least 15-20 years, implement financial incentives for landowners who maintain assisted regeneration areas beyond the typical 5-10 year funding cycles, and develop cross-sectoral coordination mechanisms between forestry, agriculture, and environmental departments. Such policies would recognize that ecological recovery requires sustained intervention and support, particularly in the crucial transition from early to late-successional stages, thereby enhancing biodiversity conservation and ecosystem service provision in these threatened ecosystems.

While this study provides valuable information, it has certain methodological limitations. The analysis's sample size and time scale may not fully capture the recovery dynamics of regenerated forests. Long-term monitoring studies assessing biodiversity evolution in these ecosystems are recommended. Future research could include the analysis of key ecological interactions, such as seed dispersal by fauna and competition among species. Furthermore, integrating ecological modeling tools would allow for predicting the recovery trajectory of regenerated forests under different management and climate change scenarios.

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