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KEYSTONE SPECIES AND CO-OCCURRENCE PATTERNS IN ECUADORIAN TROPICAL DRY FORESTS

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Tropical dry forests represent an important part of the world's natural capital. One of their most notable characteristics is the presence of species with seasonal foliage, which are adapted to extreme climatic conditions. This study explored tree species assemblages in Ecuadorian dry forests at three sites: Joa, Agua Blanca, and San Marcos. We used systematic sampling along transects and 10 × 10 m grids to record the presence and abundance of tree species. We used Jaccard's index to perform a similarity analysis that revealed high similarity between Joa and San Marcos (>0.8) but low similarity with Agua Blanca (≈0.3). Significant species for Joa included *Ceiba trischistandra*, *Erythrina velutina*, and *Acacia farnesiana*. Agua Blanca consisted of *Prosopis* sp., *Cynophylla sclerophylla* and *Mimosa pigra*, while San Marcos highlighted *Uncaria tomentosa*, *Caesalpinia glabrata*, and *Bursera graveolens* as key species. The analysis detected a high co-occurrence between species such as *Cordia lutea* and *B. graveolens* and between *Armatocereus cartwrightianus* and *C. glabrata*. However, we observed a low co-occurrence between *Acacia farnesiana* and *Leucaena trichodes*, or *Malva sylvestris*. These findings provide knowledge to guide conservation strategies, sustainable management, and future research on these unique and threatened ecosystems.

Keywords: co-occurrence, species interactions, indicator species, ecosystem dynamics, sustainable management

INTRODUCTION

Tropical dry forests represent a significant portion of the global natural heritage, constituting approximately 42% of the total tropical and subtropical forests (Hasnat & Hossain 2022, Guerra et al. 2021). These ecosystems, although less recognised than their humid counterparts (Moro et al. 2016), play a fundamental role in global biodiversity conservation. One of their most noTable characteristics is their seasonal foliage, adapted to extreme climatic conditions, with annual rainfall of 250 to 600 mm and average annual temperatures close to 24.9 °C, especially between February and April (Aguirre-Padilla et al. 2018). This adaptation allows them to survive and host an exceptional biodiversity of approximately 75% of plant species adapted to seasonality (López 2004).

These ecosystems› ecological function in preserving unique habitats is indispuTable (Aguirre-Padilla et al. 2018). However, the deciduous characteristic of their foliage, which accumulates on the ground, allows them to solve nutritional aspects and simultaneously be vulnerable to forest fires, representing a significant threat to their conservation. In this context, Ewel (1999) and Rivas et al. (2020, 2024) warn that the conditions of dry forests are frequently intervened by anthropogenic activities, which contribute to the establishment of fragile systems that are not very resilient and are constantly threatened (Folke et al. 2004).

Tropical and subtropical dry forests of the Tumbesino-Andean Valleys in Ecuador are classified as «endangered» (Janzen 1988, Olson et al. 2000). The importance of these ecosystems transcends biodiversity conservation, as they act as important carbon sinks, contributing to climate change mitigation (Ren et al. 2017), play a crucial role in watershed conservation by regulating water and preventing soil erosion, and have economic importance by providing timber and other forest products, as well as food interest by harboring a variety of edible plants. In the coastal region of Ecuador, these forests are also critical for mitigating the impacts of extreme weather events such as El Niḥo and La Niḥa by maintaining soil stability and providing shelter for wildlife during adverse weather conditions. These implications demonstrate these forests› vital importance for maintaining ecological balance in coastal zones, which can exhibit high levels of vulnerability to environmental changes and human activities (Rivas et al. 2024).

The threats faced by these ecosystems and the species that inhabit them are diverse; they include agricultural expansion, urbanization, irrational extractivism, and the effects of climate change (Janzen 1988, Cueva-Ortiz et al. 2019). These threats translate into negative impacts on the functioning and ecosystem services generated in forests. In addition, scientists know that tropical dry forests exist in 25 of the 36 biodiversity hotspots worldwide. Additionally, this forest type experienced high deforestation rates (11%) between 2000 and 2020, aggravating its vulnerability (Ocón et al. 2021).

Research by Aguirre and Geada (2017) reveals that, historically, dry forests covered approximately one-third of western Ecuador. However, recent estimates indicate that 70% of the area of these ecosystems has very high levels of fragility (Rivas et al. 2020). This situation is particularly worrisome in unprotected areas, where the risk of loss of diversity is significant, and therefore, the conservation status of the ecosystem is also compromised (Fremout et al. 2020, Rivas et al. 2024).

In the face of these challenges, the Ecuadorian state has taken decisive steps to ensure the protection and care of these valuable ecosystems. Rodríguez et al. (2015) highlight the creation of conservation areas designed to protect representative samples of ecosystems and promote the participation of local communities in conservation efforts. In this regard, the Ministerio de Ambiente, Agua y Transición Ecológica (MAATE), has implemented some national strategies to promote forest management that prioritize the preservation and restoration of ecosystem services (Ministry of Environment of Ecuador 2016).

However, as indicated by Loto et al. (2018), more research in this area is needed to acquire detailed information on the composition and development of dry forests and assess the impacts of human activity and climate change on these ecosystems. In this regard, Hasnat & Hossain (2022) mention that despite the considerable diversity of tree species (30–90% compared to tropical rainforests) and their primary productivity (50–70% compared to tropical rainforests), research and studies on these ecosystems are significantly lower, representing only one-fifth of those conducted on tropical rainforests. Furthermore, the literature on the restoration of tropical dry forests is scarce, reaching barely 3% compared to the restoration of tropical rainforests (Stan & Sanchez-Azofeifa 2019).

The knowledge gap highlights the urgent need for research on ecological interactions and coexisting species to gain a structured and functional understanding of ecosystems. This approach is crucial for the conservation of individual species and for developing sustainable forest management practices and effective conservation and preservation strategies. Studying the assemblage of tree species and their distributions and variabilities provides a more complete view of forest dynamics. This approach allows us to understand how species interact and respond to environmental changes and disturbances. This analysis helps to identify biogeographic patterns, understand colonization and dispersal processes, and anticipate potential impacts of climate change. This in-depth understanding is fundamental for the design of policies and actions that promote the long-term health and resilience of forest ecosystems (Ibarra et al. 2004, Manrique-Ascencio et al. 2024, Cupertino-Eisenlohr & Simon 2023, Grant et al. 2023, Sabogal 2023).

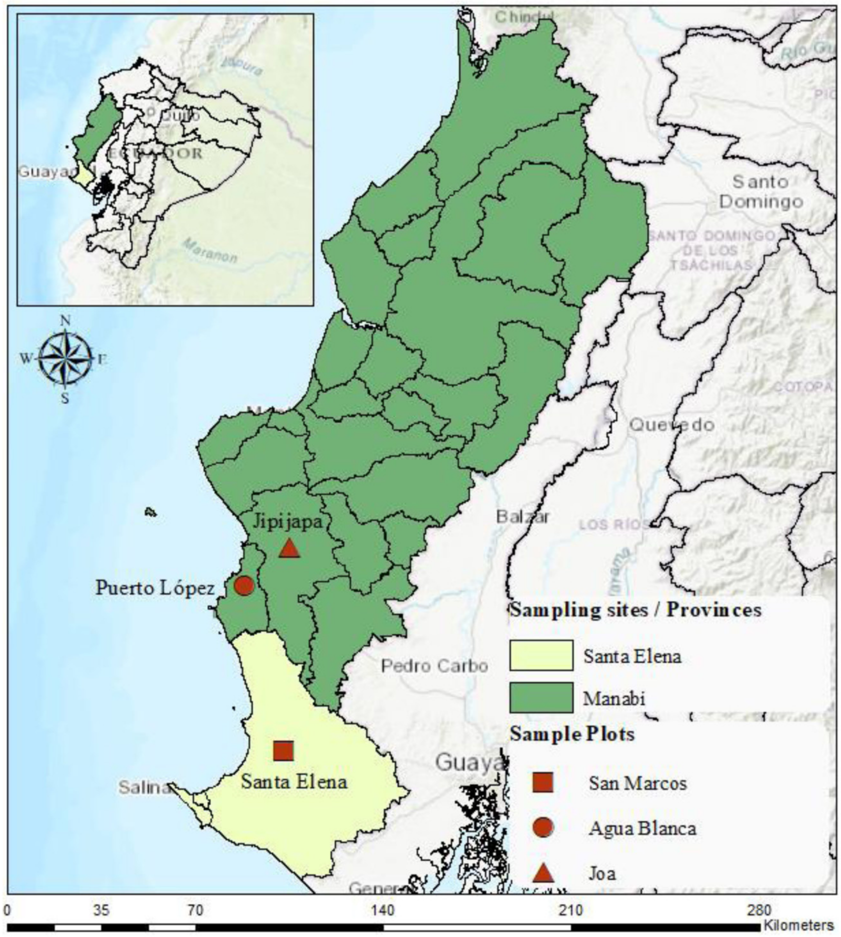

Figure 1 Location of study sites

MATERIALS AND METHODS

Characterisation of the study areas.

This study was carried out in three different dry forests located in the Province of Manabí, (Joa commune of Jipijapa, Agua Blanca commune of Puerto López); and in the Province of Santa Elena (San Marcos commune) (Figure 1).

The community of Joa is located 6 km south of the city of Jipijapa, marking the boundary between the Tiján plain, which extends from south to north from Piḥas de Julcuy, and the foothills of the Cordillera Costanera de Chongón - Colonche (Salas et al. 2020). It has a mean annual temperature of 26 ˚C and a mean annual precipitation of 300 mm (Álvarez & Álvarez 2018). This community routinely engages in activities such as charcoal and brick production. In addition, it has carried out mining for more than 25 years by exploiting limestone, a mineral used to improve the canton›s roads. However, these activities have considerably reduced the native forest and limited its regeneration. MAATE classifies the surrounding ecosystem as deciduous forest of the equatorial Pacific coastal range. Two sampling plots were used at this location.

The San Marcos commune belongs to the Colonche parish in the province of Santa Elena. It has a dry climate with wind speeds varying from 50.25 m s^{-1} to 53.4 m s^{-1}, with October being the month when it records higher speeds. Rainfall ranges around 300 mm minimum and 800 mm maximum. The months with rainfall are January, February, March, and April. The average annual temperature is 24.5 ˚C. Clayey soils characterise the soils. This area has a great diversity of endemic flora and fauna species because it is within the Colonche parish, which proportionally has the most significant number of forests in a good state of conservation (GADPSE 2021). MAATE classifies the surrounding ecosystem as Jama-Zapotillo lowland deciduous forest and lowland scrub. Three sampling plots were used in this location.

The Agua Blanca Commune is an ancestral community located in the Machalilla National Park, 12 kilometers north of Puerto Lopez, in a valley surrounded by mountains. The climate is warm and humid, with an average temperature of 26 °C. The vegetation resembles a tropical dry forest (Jiménez et al. 2019). The minimum rainfall is 2 mm, and the maximum is 79 mm, with February being the month with the highest precipitation (Garcia & Moran 2023). MAATE classifies the surrounding ecosystem as Jama-Zapotillo lowland deciduous forest and lowland scrub. One sampling plot was used in this location.

Experimental design & tree sampling

Systematic sampling on a transect defined in combination of analysis points and study plots for flora were used as proposed by GITEC-IGIP in cooperation with the World Wildlife Fund and implemented by Deutsche Gesellschaft für Internationale Zusammenarbeit (GIZ) GmbH in the framework of the Program "Conservation and sustainable use of natural heritage - Bioeconomy". As a result, we established 540 × 20 m (10,400 m^2) plots at each study site to collect field data (Figure 2a). Subsequently, we could adapt these plots to site conditions, giving them an L-shaped layout (Figure 2b). Subsequently, four 20 × 20 m quadrats were established within each plot to characterise the plant communities (Figure 2C). Each quadrat was subdivided into four sections to facilitate internal comparisons. The quadrats were evenly distributed, spaced 35 meters apart, starting 30 meters from the center of the plot. We designed this sampling strategy to ensure a balanced and representative sample distribution, thus optimizing the validity of subsequent analyses.

Species diversity and abundance

Fieldwork was conducted between March and May 2021, identifying and counting individuals of each species in every quadrant (Figure 2C).

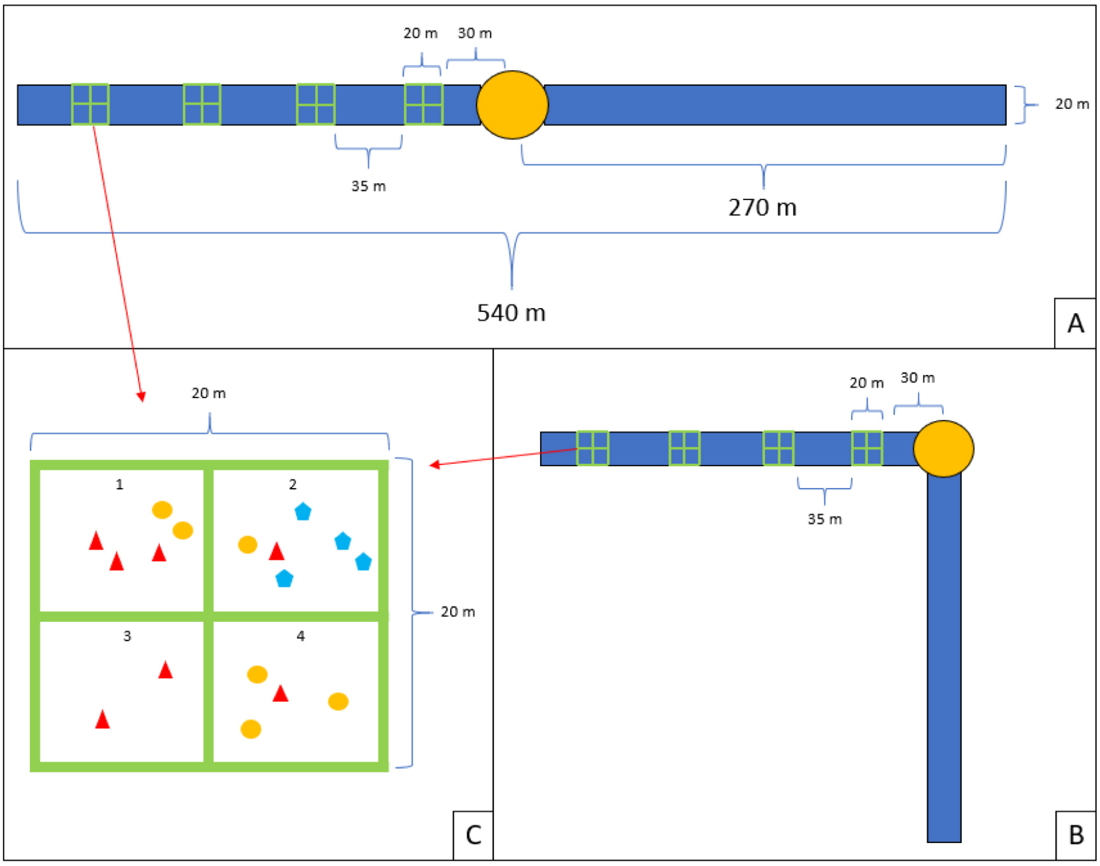

Figure 2 Sampling plot to identify tree diversity at sampling sites. (A) initial design, (B) design adapted to site conditions, (C) scheme of quadrats for tree monitoring (shapes inside the quadrants represent the trees of different species)

The absolute abundance data was converted into a presence/absence binary matrix to evaluate the similarity between pairs of sampling sites, as required for applying the Jaccard index (Snijders et al. 1990). This index measures the proportion of shared species or characteristics between sites (Hao et al. 2019, Yue & Clayton 2005, Jaccard 1900). Subsequently, based on this index, a similarity or distance matrix was created for a hierarchical clustering analysis. The result of this analysis is a dendrogram, which reflects the similarity in species composition among the different study sites.

Simpson's diversity index (D), Shannon's diversity index (H'), and Pielou's evenness index (J) were calculated for each locality (Table 1). The absolute abundance matrix was utilised to derive the Indicator Value Index (IndVal%) and corresponding *p*-values for all species within each plot group using PAST 4.15 software (Hammer et al. 2001). By analysing the IndVal%, the relationship between each species and a particular group, and the *p*-values provided insight into the statistical significance of these relationships were assessed. Species considered typical (indicative) of a habitat condition will be those with InVal≥50% (González et al. 2011).

Co-occurrence of tree species

A presence/absence matrix was constructed, where each row represented a specific plot and each column, a species. This matrix was used to generate a co-occurrence matrix by multiplying the data matrix by its transpose. That is, if the original matrix is M, the co-occurrence matrix C is calculated as C = MT × M. In this multiplication, each element of the resulting matrix (co-occurrence matrix C) represents the number of times a pair of species (one from the row and one from the column) co-occur in the same plots. Finally, the co-occurrence matrix was analysed to identify patterns of interaction between species (Arita et al. 2012).

Table 1 Species diversity indices and equations used to estimate indices in each study site

Diversity Index	Equation	Description	Abbr.
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	$\mathrm{J} = \frac{\mathrm{H'}}{\log(\mathrm{S})}$	The equivalence among species in a community	J

Sources: Shannon (1948), Simpson (1949) & Pielou (1966)

Table 2 Taxa, number of individuals, and calculated indices for each sampling site

	Joa	Agua Blanca	San Marcos
Taxa_S	17	12	22
Individuals	244	157	499
D	0.137	0.343	0.130
H'	2.303	1.607	2.365
J	0.813	0,647	0.765

RESULTS AND DISCUSSIONS

Tree species identification and diversity

The analysis of the ecological parameters of Joa, Agua Blanca, and San Marcos's localities revealed differences in species richness, abundance of individuals, dominance, Shannon diversity, and equity (Table 2). San Marcos stood out as the locality with the highest species richness, counting 22 taxa, and the highest abundance of individuals, with a count of 499. In terms of dominance, the lowest values obtained in San Marcos (0.1299) and Joa (0.1367), compared to Agua Blanca (0.3428), indicate a more equitable distribution of individuals among the species present in the first two localities.

Additionally, the Shannon diversity index revealed that San Marcos has the highest diversity (2.365), closely followed by Joa (2.303), while Agua Blanca presented a significantly lower diversity (1.607). Finally, in terms of equity, measured by the Equitability J index, Joa showed the highest equity (0.8128), followed by San Marcos (0.7652) and Agua Blanca (0.6466). In this regard, Aguirre-Mendoza et al. (2013) reported similar values for forests classified as "Jama-Zapotillo Lowland Deciduous Lowland Forest and Shrub" in Loja, southern Ecuador. Their findings showed an H' index between 2.38 and 2.7, a D index between 0.85 and 0.91, and a J index between 0.64 and 0.80. These results are consistent with the values estimated in the present study for San Marcos and Agua Blanca towns.

This variability between the study locations highlights the complex interactions between species and their environment and the impact of environmental and anthropogenic factors on biodiversity. The high species richness and abundance of individuals at San Marcos suggests that this locality could benefit from potentially more favorable environmental conditions or conservation practices for a wide range of species than the other two localities. According to Chase & Leibold (2003), habitat diversity is a critical factor influencing species richness and abundance, which could explain the more extraordinary biodiversity observed in San Marcos. Furthermore, vegetation structure and resource availability can be crucial in species distribution and abundance (Tilman 1982), reflected in the observed Shannon dominance and diversity indices.

The lower dominance in San Marcos and Joa, compared to Agua Blanca, indicates a more equitable distribution of individuals among the species, which could result from more significant heterogeneity of habitats or less human intervention, thus limiting the dominance of a few species (Connell 1978). This fact is consistent with intermediate disturbance theory, which postulates that moderate levels of disturbance can increase species diversity by preventing the dominance of competitive species (Roxburgh et al. 2004, Wilkinson 1999).

Shannon's diversity, higher in San Marcos, signals not only a rich species composition but also a more balanced community in terms of the distribution of individuals among different species. This balance is fundamental for ecosystems' resilience and ability to respond to environmental changes (Hooper et al. 2005). Equity, particularly at Joa, suggests that land management and conservation practices may promote balanced species coexistence, which is crucial for long-term ecological stability (Loreau 2010).

Hierarchical clustering analysis

The grouping patterns of tree species across the three study sites were determined using the Jaccard index (Figure 3). This analysis enabled us to generate a dendrogram visually representing the collected data's affinities and divergences.

San Marcos and Joa share a high proportion of species with an index that exceeds 0.8, indicating a significant similarity in their tree composition. In contrast, Agua Blanca demonstrates a relatively reduced similarity with an index close to 0.3, suggesting a distinctively different species composition from the other two sites, thus underlining the uniqueness of Agua Blanca's biodiversity compared to San Marcos and Joa. In this context, Lebron & Guerrero (2023) and Soler et al. (2012) maintain that low Jaccard similarity values show that species identified in one environment will not necessarily reproduce in another.

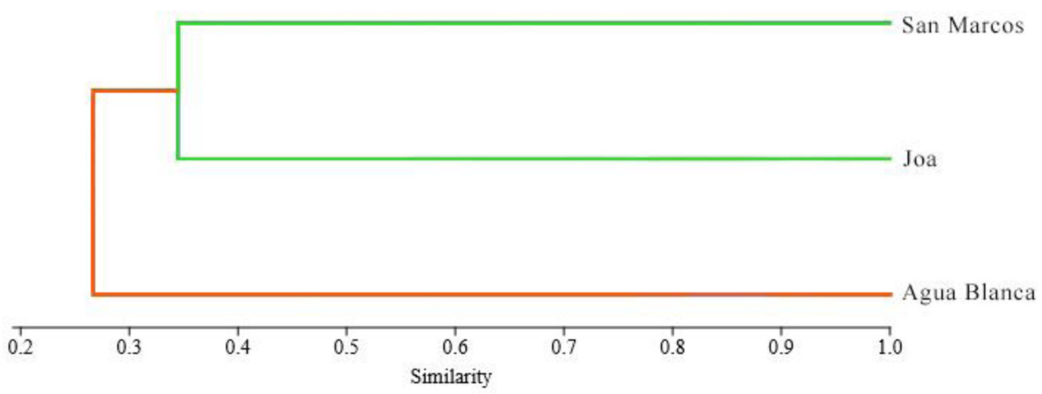

Figure 3 Hierarchical clustering with Jaccard similarity index for the forests located at the three study sites

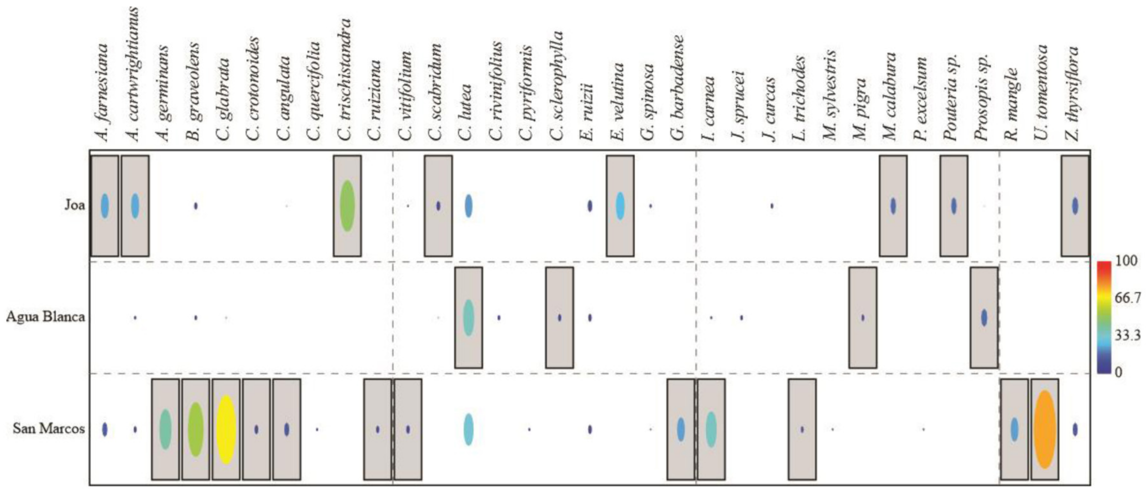

Figure 4 Indicator value (IndVal%) and statistical significance for tree species in three sampling sites in Manabí (n = 33)

Indicator values of coastal tree species (IndVal%)

Figure 4 shows circles of different sizes and colors representing the statistical significance and species indicator values (IndVal%) for various species in six forest types. Larger circles indicate a lower p-value, which implies greater statistical significance of the species as an indicator of the forest type in question. As for colors, the blue circles represent low IndVal% values, increasing towards turquoise, green, yellow, and red as the IndVal% values increase. The boxes surrounding some circles indicate those species with a statistically significant association ($p<0.05$) with their respective forest type.

This analysis revealed considerable variability in Indicator Value (IndVal%) percentages between different species and locations, pointing to notable differences in their ecological relevance depending on the site. In Joa, for example, the species *C. trischistandra*, *E. velutina*, *A. cartwrightianus*, and *A. farnesiana* stood out for their high IndVal% of 50.0, 27.1, 25.1 and 23.5, respectively. High IndVal% values of a species population are synonymous with the fidelity and specificity of each species in a sample pattern (Dufrêne & Legendre 1997, Antonelli et al. 2016). This fact means these species can be determined with other rare species in the environment. These high values, accompanied by low levels of statistical significance (Table 3), highlight its strong ecological presence and statistical robustness. On the other hand, *C. lutea* showed a moderate IndVal% but without statistical significance for this site.

In Agua Blanca, *Prosopis* sp., *C. sclerophylla*, and

Table 3 Indicator value (IndVal%) and p-values associated with the species recorded in the study sites

No	Species	Joa		Agua Blanca		San Marcos	
		IndVal%	*p* - value	IndVal%	*p* - value	IndVal%	*p* - value
1	*Acacia farnesiana* (L.) Willd.	23.50	0.0003	0.00	1.0000	13.62	0.0977
2	*Armatocereus cartwrightianus* (Britton & Rose) Backeb. ex A.W. Hill	25.13	0.0007	2.48	0.9914	5.32	0.8508
3	*Avicennia germinans* (L.) L.	0.00	1.0000	0.00	1.0000	39.58	0.0001
4	*Bursera graveolens* (Kunth) Triana & Planch.	3.53	0.9999	2.96	1.0000	64.06	0.0001
5	*Caesalpinia glabrata* Kunth	0.03	1.0000	0.29	1.0000	70.38	0.0001
6	*Capparicordis crotonoides* (Kunth)	0.00	1.0000	0.00	1.0000	8.33	0.0108
7	*Capparis angulata* Ruiz & Pav. ex DC.	0.26	0.9642	0.00	1.0000	12.76	0.0020
8	*Carica quercifolia* (A. St.-Hil.) Hieron.	0.00	1.0000	0.00	1.0000	2.08	0.3285
9	*Ceiba trischistandra* (A. Gray) Bakh.	50.00	0.0001	0.00	1.0000	0.00	1.0000
10	*Coccoloba ruiziana* Lindau	0.00	1.0000	0.00	1.0000	6.25	0.0366
11	*Cochlospermum vitifolium* (Willd.) Spreng	1.39	0.5797	0.00	1.0000	6.94	0.0415
12	*Colicodendron scabridum* (Kunth) Seem.	8.68	0.0149	0.35	0.9189	0.00	1.0000
13	*Cordia lutea* Lam.	19.76	0.9998	31.56	0.2641	38.61	0.0012
14	*Croton rivinifolius* Kunth.	0.00	1.0000	4.17	0.1130	0.00	1.0000
15	*Cryptocarpus pyriformis* Kunth	0.00	1.0000	0.00	1.0000	2.08	0.3339
16	*Cynophylla sclerophylla* (H.H. Iltis & X. Cornejo) (H.H. Iltis & X. Cornejo)	0.00	1.0000	6.25	0.0366	0.00	1.0000
17	*Eriotheca ruizii* (K. Schum.) A. Robyns	12.96	0.1420	6.62	0.7338	6.67	0.6958

continued

Table 3 Continued

No	Species	Joa		Agua Blanca		San Marcos	
		IndVal%	*p* - value	IndVal%	*p* - value	IndVal%	*p* - value
18	*Erythrina velutina* Willd.	27.08	0.0001	0.00	1.0000	0.00	1.0000
19	*Geoffroea spinosa* Jacq.	2.78	0.2601	0.00	1.0000	0.69	0.7046
20	*Gossypium barbadense* L.	0.00	1.0000	0.00	1.0000	22.92	0.0001
21	*Ipomoea carnea* Jacq.	0.00	1.0000	1.69	0.9717	36.66	0.0001
22	*Jacquinia sprucei* Mez.	0.00	1.0000	4.17	0.1101	0.00	1.0000
23	*Jatropha curcas* L.	4.17	0.1099	0.00	1.0000	0.00	1.0000
24	*Leucaena trichodes* (Jacq.) Benth.	0.00	1.0000	0.00	1.0000	6.25	0.0368
25	*Malva sylvestris* L.	0.00	1.0000	0.00	1.0000	2.08	0.3380
26	*Mimosa pigra* L.	0.00	1.0000	6.25	0.0335	0.00	1.0000
27	*Muntingia calabura* L.	16.67	0.0002	0.00	1.0000	0.00	1.0000
28	*Pithecellobium excelsum* (Kunth) Mart.	0.00	1.0000	0.00	1.0000	2.08	0.3300
29	*Pouteria* sp.	16.67	0.0001	0.00	1.0000	0.00	1.0000
30	*Prosopis* sp.	0.16	0.9822	17.31	0.0006	0.00	1.0000
31	*Rhizophora mangle* L.	0.00	1.0000	0.00	1.0000	22.92	0.0001
32	*Uncaria tomentosa* (Willd.) DC.	0.00	1.0000	0.00	1.0000	77.08	0.0001
33	*Ziziphus thyrsiflora* Benth.	15.63	0.0127	0.00	1.0000	13.54	0.0371

M. pigra were identified as significant ecological indicators, with IndVal% of 17.3, 6.3, and 6.3, respectively, and p values less than 0.05 (Table 3), indicating an essential ecological presence. San Marcos, for its part, exhibited a broader diversity of species with significant ecological and statistical relevance. Species such as *U. tomentosa*, *C. glabrata*, and *B. graveolens* showed IndVal% greater than 50%. Likewise, *A. germinans*, *C. lutea*, *I. carnea*, *G. barbadense*, *R. mangle*, *Z. thyrsiflora*, and *C. angulata* recorded IndVal% in the range of 10 to 40%, all with significantly low p values, reaffirming its ecological importance in the dry forest. Studies conducted by Carmona et al. (2016) show that IndVal% values between 25% and 50% indicate detector species. These researchers emphasise that such species adapt well to environmental changes and provide more information about their habitat.

The resulting visualization (Figure 5) displayed the co-occurrence matrix of tree species in the sampled plots. Each cell of the matrix reflects the number of times two species, represented in the rows and columns, coexist in the same quadrants. In this matrix, lighter shades indicated more significant co-occurrence (i.e., a higher frequency of co-occurrence), while darker shades signaled less frequent co-occurrence.

In order to facilitate the interpretation of these patterns, a heat map was generated in which different colors indicated various levels of co-occurrence frequency: warmer colors denoted higher frequency, while cooler colors denoted lower frequency. This approach provides a detailed and comprehensive insight into the ecological relationships and dynamics among species in the studied ecosystem.

The analysis of tree species co-occurrence revealed intriguing patterns of interaction between species. Among the cases of high co-occurrence, the species *C. lutea* and *B. graveolens* stand out, which cooccurred 58 times, suggesting a possible shared habitat preference or ecological compatibility. Other examples include *A. cartwrightianus* and *C. glabrata*, as well as *E. ruizii* and *A. cartwrightianus*, both showing high levels of co-occurrence. These patterns could indicate joint adaptation to specific environmental conditions or symbiotic interactions. However, for Giraldo (2018), the levels of co-occurrence also enter in dependence on the design of the

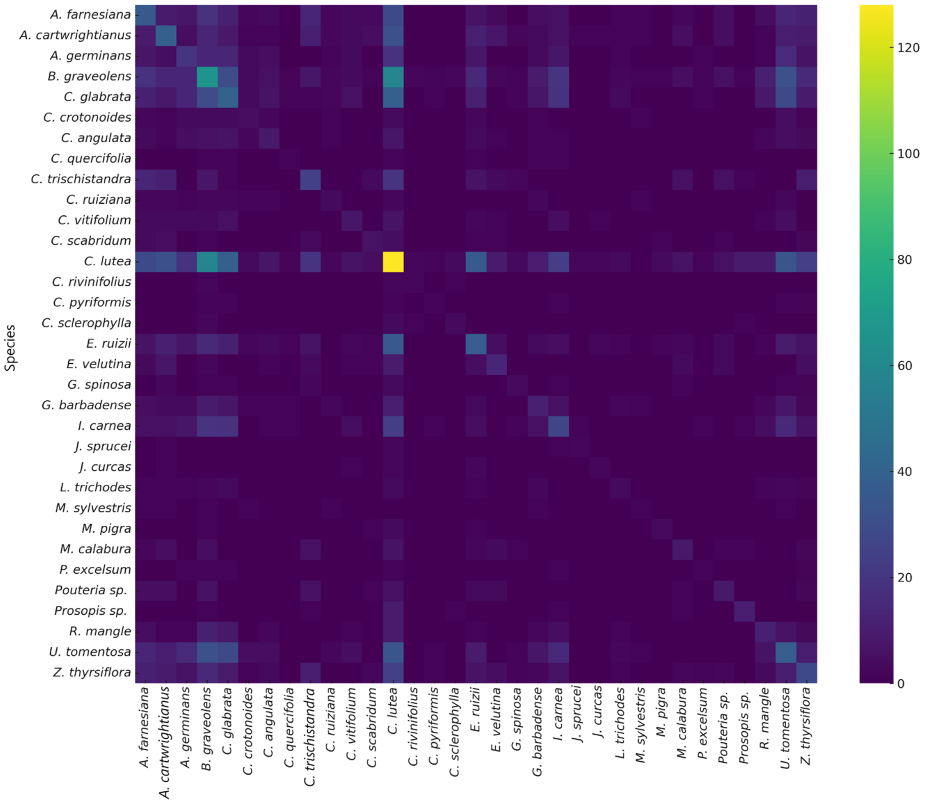

Figure 5 Co-occurrence matrix of tree species in three sampling sites in dry forest in Manabí

plots due to the probability of occurrence of species in pairs.

In this context, it is relevant to note that most of the observed coexistences involve species from different botanical families, which supports the observations made by Souza et al. (2021). This pattern indicates the presence of niche adaptation mechanisms that facilitate the occupation of different ecological spaces (Wright 2002, Chen et al. 2020). Thus, diverse species in seasonal forests coexist due to variations in ecological needs and species-specific survival strategies (Cirne-Silva et al. 2020). This coexistence significantly impacts ecosystem dynamics and functioning (Wright 2002, Barraclough 2015, Neves et al. 2017).

Besides the already mentioned high level of co-occurrence of *B. graveolens* with *C. lutea*, it also showed a strong co-occurrence with *U. tomentosa*, with a frequency of 31, and with *C. glabrata*, with a frequency of 29. These data suggest that *B. graveolens* tends to share its habitat with various other species and, in turn, sustains uniform distribution patterns (Aguirre & Cabrera 2021). This fact could indicate remarkable ecological adaptability or a preference for specific environmental conditions favorable for these other species. Meanwhile, more moderate co-occurrences of *I. carnea* and *A. farnesiana* were observed, with frequencies of 19 and 18, respectively, which adds to the understanding of how this species interacts and distributes about other members of its ecosystem.

On the other hand, we observe exceptionally low co-occurrence, which sheds light on a different aspect. Co-occurrence of *A. farnesiana* with *L. trichodes*, as well as with *M. sylvestris*, was remarkably low. This finding suggests that it is uncommon for these species pairs to share the same space, which may be due to differences in their ecological preferences. We could interpret this pattern of low co-occurrence among species in more limiting contexts through the stress gradient hypothesis (Huston 1979, Holmgren & Scheffer 2010). From this perspective, inter-species relationships play a somewhat secondary role in the structuring and functionality of deciduous forests. Instead, these assemblages would be primarily influenced by facilitative mechanisms, as suggested by Holmgren and Scheffer (2010), Hart and Marshall (2013), and Carrión et al. (2017).

We should note that typical species of these ecosystems co-occur in the dry forests under study. Historical evolutionary processes of colonization could explain their joint presence (Pennington et al. 2009). In this sense, Souza et al. (2021) point out that random sampling in these regions is highly likely to identify similar co-occurrences.

CONCLUSIONS

The hierarchical grouping of the Jaccard index allows us to determine the affinities and divergences between the data obtained from the samples. San Marcos and Joa obtained an index exceeding 0.8. However, Agua Blanca obtained a reduced similarity. The IndVald% made it possible to establish the species named as significant ecological indicators in each of the sites chosen for the study; in the case of Joa, the tree species *C. trischistandra*, *E. velutina*, *A. cartwrightianus*, and *A. farnesiana* stood out. In Agua Blanca, the representative species were *Prosopis* sp., *C. sclerophylla*, and *M. pigra*. Finally, the species *U. tomentosa*, *C. glabrata*, and *B. graveolens* were outstanding in San Marcos.

The species *C. lutea* and *B. graveolens*, *A. cartwrightianus* and *C. glabrata*, *E. ruizii*, and *A. cartwrightianus* had the highest co-occurrence, while *A. farnesiana* and *L. trichodes*, *A. farnesiana*, and *M. sylvestris*, resulted in low co-occurrence. The interpretation of these relationships should be done cautiously and, if possible, complemented with additional information on the species and their habitats. In this regard, it is essential to note that co-occurrence patterns do not necessarily imply causal relationships between species but could derive from various ecological and environmental factors. These results highlight the importance of considering species interactions in ecological studies for a deeper understanding of ecosystem dynamics.

The findings of this study offer crucial guidance for shaping public policies geared towards the preservation of tropical dry forests, bolstering biodiversity, ecosystem services, and the well-being of society. By elucidating the intricate relationships between species and their interactions, this research underscores the necessity of incorporating such dynamics into ecological studies to grasp the complexities of ecosystem functioning fully. However, interpreting these patterns demands careful consideration, coupled with the supplementation of comprehensive data on species and habitats. Ultimately, these results highlight the imperative of integrating ecological insights into policymaking frameworks to foster the efficient conservation and management of tropical dry forest ecosystems.

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