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Original article

Relationship between environmental variables and tree flora in two fragments of submontane rainforest, Alejandro de Humboldt National Park, Cuba

Relación entre variables ambientales y la flora arbórea en dos fragmentos de bosque pluvisilva submontano, Parque Nacional Alejandro de Humboldt, Cuba

Relação entre variáveis ambientais e flora arbórea em dois fragmentos de floresta submontana, Parque Nacional Alejandro de Humboldt, Cuba

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ABSTRACT

The submontane rainforests of the Alejandro de Humboldt National Park in Cuba harbor extraordinary biodiversity and endemism, but few studies have documented the variables that condition the distribution of its floristic diversity. The relationship between topographic, structural, edaphic, and anthropogenic environmental variables, such as logging and accessibility, and the tree flora was evaluated in two fragments: Mola, on ophiolite substrate, and Monte Fresco, on metamorphic rocks. Thirty-two 400 m² plots were established, 21 in Mola and 11 in Monte Fresco, where all tree individuals with a diameter at breast height (DBH) ≥ 1 m were recorded. Shannon and Simpson diversity indices and beta diversity (based on Whittaker's index) were calculated. Canonical correlation analysis was applied to determine the relationships between environmental variables, species, and plots; cluster analysis was used to reveal similarities between plots; and an IndVal was used to identify indicator species. Mola exhibited lower species richness (36 species) but high evenness, dominated by *Calophyllum utile* and serpentinite-tolerant species. Monte Fresco showed twice the richness with 64 species, including numerous climax species such as *Carapa guianensis* and *Manilkara zapota* . Canonical correlation analysis explained 35.9 % of the variability and identified altitude, accessibility, canopy density, and topography as significant predictors. IndVal analysis revealed nine indicator species for Mola and 33 for Monte Fresco. The results confirmed that high floristic complementarity between the two fragments underscores the need to conserve the environmental heterogeneity of the National Park.

Keywords: alpha and beta diversity, endemism, ophiolites, serpentinites, rainforest, conservation.

RESUMEN

Los bosques pluvisilvas submontanos del Parque Nacional Alejandro de Humboldt en Cuba albergan una extraordinaria biodiversidad y endemismo, pero pocos estudios han documentado las variables que condicionan la distribución de su diversidad florística. Se evaluó la relación entre variables ambientales topográficas, estructurales, edáficas y antrópicas como tala y accesibilidad con la flora arbórea en dos fragmentos, Mola sobre sustrato de ofiolitas y Monte Fresco sobre rocas metamórficas. Se establecieron 32 parcelas de 400 m², 21 en Mola y 11 en Monte Fresco, donde se registraron todos los individuos arbóreos con DAP ≥ 1 m. Se calcularon los índices de diversidad de Shannon y Simpson, diversidad beta según el índice de Whittaker. Se aplicó un análisis de correlación canónica para determinar las relaciones en las variables ambientales, las especies y parcelas, un análisis de clúster para revelar las similitudes entre parcelas y un IndVal para identificar especies indicadoras. Mola presentó menor riqueza, 36 especies, pero alta equidad, dominada por *Calophyllum utile* y especies tolerantes a serpentinitas. Monte Fresco mostró el doble de riqueza con 64 especies, y numerosas especies clímax como *Carapa guianensis* y *Manilkara zapota*. El análisis de correlación canónica explicó el 35,9 % de la variabilidad, e identificó la altitud, la accesibilidad, la densidad de dosel y el relieve como predictores significativos. El análisis IndVal reveló nueve especies indicadoras para Mola y 33 para Monte Fresco. Los resultados confirman que alta complementariedad florística entre ambos fragmentos subraya la necesidad de conservar la heterogeneidad ambiental del Parque Nacional.

Palabras clave: diversidad alfa, beta, sucesión, ofiolitas, bosque pluvisilva, *Calophyllum utile*.

RESUMO

As florestas tropicais submontanas do Parque Nacional Alejandro de Humboldt, em Cuba, abrigam biodiversidade e endemismo extraordinários, mas poucos estudos documentaram as variáveis que influenciam a distribuição de sua diversidade florística. A relação entre variáveis ambientais topográficas, estruturais, edáficas e antropogênicas (como exploração madeireira e acessibilidade) e a flora arbórea foi avaliada em dois fragmentos: Mola, em substrato ofiolítico, e Monte Fresco, em rochas metamórficas. Trinta e duas parcelas de 400 m² foram estabelecidas, 21 em Mola e 11 em Monte Fresco, onde todos os indivíduos arbóreos com diâmetro à altura do peito (DAP) ≥ 1 m foram registrados. Os índices de diversidade de Shannon e Simpson e a diversidade beta (baseada no índice de Whittaker) foram calculados. A análise de correlação canônica foi aplicada para determinar as relações entre variáveis ambientais, espécies e parcelas; a análise de agrupamento foi usada para revelar similaridades entre as parcelas; e o IndVal foi usado para identificar espécies indicadoras. Mola apresentou menor riqueza de espécies (36 espécies), mas alta equitabilidade, dominada por *Calophyllum utile* e espécies tolerantes à serpentinita. Monte Fresco apresentou o dobro da riqueza, com 64 espécies, e numerosas espécies clímax, como *Carapa guianensis* e *Manilkara zapota*. A análise de correlação canônica explicou 35,9% da variabilidade e identificou altitude, acessibilidade, densidade do dossel e topografia como preditores significativos. A análise IndVal revelou nove espécies indicadoras para Mola e 33 para Monte Fresco. Os resultados confirmam que a alta complementaridade florística entre os dois fragmentos ressalta a necessidade de conservar a heterogeneidade ambiental do Parque Nacional.

Palavras-chave: diversidade alfa e beta, endemismo, ofiolitos, serpentinitos, floresta tropical, conservação.

INTRODUCTION

Alejandro de Humboldt National Park, a Category II protected area by the International Union for Conservation of Nature (IUCN), is considered one of Cuba's most important sites in terms of biodiversity and endemism. It constitutes the largest remaining area of preserved mountain ecosystems in the country, harboring 595 endemic species, representing 55.5% of the recorded species and 18.7% of all endemic vascular plants in Cuba. This richness positions it as a key area within the Caribbean biodiversity hotspot (Myers *et al.*, 2000). The park's complex geology, which includes ophiolitic (serpentinite) and metamorphic rocks, combined with varied topography, has generated a diversity of ecosystems unparalleled in the insular Caribbean.

Of the 28 plant formations described for Cuba (Capote and Berazaín, 2025), 16 are found in the park, among which the submontane rainforests stand out. These forests contain a tree flora with high endemism and various threats. They function as reservoirs of biological diversity and constitute priority sites for conservation. Currently, according to Reyes and Acosta-Cantillo (2018 and 2017), they are the best developed, extensive, and best- preserved rainforests in eastern Cuba and the Cuban archipelago. These rainforests occur on substrates of ophiolites and metamorphic rocks.

Multiple studies have shown that variables such as altitude, slope, or forest density act as environmental filters that condition the distribution of tree species (Gonmadje *et al.*, 2019). However, in regions with ultramafic (serpentine) soils, the geological substrate can exert even stronger control than climate or topography over the plant community (Geada-López *et al.*, 2021). These soils are known for their high toxicity from heavy metals such as nickel, chromium, and magnesium, and for their deficiency of essential nutrients (Reyes and Acosta-Cantillo 2017), which creates extreme conditions for plant development and promotes high endemism (López-Almirall 2013).

Given this background, the objective of this study was to explain the relationship between environmental factors: edaphic, topographic and structural, with the arboreal flora in two fragments of submontane rainforest in Cupeyal del Norte, Alejandro de Humboldt National Park.

MATERIALS AND METHODS

Study area

The study was conducted in two fragments of submontane rainforest located in Cupeyal del Norte of Alejandro de Humboldt National Park, Cuba. Two fragments were selected. The first, Mola (MO): 20°28'12.59'' N and 75°34'5.64'' W with an average altitude of 689 m asl, on soils derived from ophiolites; and the second, Monte Fresco (MF): 20°26'57.21'' N and 75°0'42.15'' W with an average altitude of 615 m asl, on soils derived from red ferralitic metamorphic rocks.

Sampling design and data collection

In each fragment, 32 plots were established randomly, plots of 20 m × 20 m (400 m^2); of these, 21 plots correspond to Mola and 11 plots to Monte Fresco.

Within each plot, all individuals of tree species with a total height ≥ 1 m were measured. For each individual, the following was recorded:

- Taxonomic identification: Identification in the field or by means of herbarium preparation for subsequent determination in the herbarium. The species were classified by botanical family.
- Diameter (DBH): Measured with a diameter tape at 1.30 m from the ground.

Environmental variables

The following variables were measured in each plot:

Topographic:

- Slope (%), measured with clinometer.
- Altitude (MSMN): expressed in m asl .
- Relief (R): qualitative classification (1=flat, 2=undulating, 3=abrupt).

Forest structures:

- Density (D, N ha $^{-1}$): $D = \frac{n}{a} \times 10\,000$, where n = number of individuals in the plot, a = area (400 m^2).
- Basal area (G): sum of the basal area of all individuals per hectare, expressed in m^2 ha^{-1} .
- Mortality (Ma): count of dead trees standing or fallen within the plot.

Anthropogenic:

- Felling (T): count of stumps or felled trees within the plot.
- Accessibility (Acc): composite semi-quantitative index (Table 1), sum of scores for road type, road condition and distance to main road (range: 1=Difficult to 9=Easy).

Table 1. *- Criteria for the evaluation of the accessibility index*

Road type	Points	Road conditions	Points	Distance to main road	Points
Pavement	3	Optimal (accessible all year round)	3	< 1 km	3
Soil/gravel	2	Moderate (passable in dry seasons)	2	1-5 km	2
Nature trail	1	Critical (inaccessible without equipment)	1	> 5 km	1

Note: Final classification: Easy access = 7-9 points; medium access = 4-6 points; difficult access = 1-3 points.

Data analysis

Composition and alpha diversity: Species richness (S) and abundance were compared. The Shannon-Wiener (H', base log 10) and Simpson ($\frac{1}{D}$) indices (Magurran, 2004) were calculated, and evenness was calculated as $J' = \frac{H'}{\ln(S)}$

Beta diversity: It was estimated using the Whittaker index.

Cluster analysis was performed using Ward's method and the Bray-Curtis distance. The goodness of fit was assessed using the cophenetic correlation coefficient with the InfoStat program (Di Rienzo, 2020).

Species-environmental variable relationship: A canonical correspondence analysis (CCA) was performed with the evaluated environmental variables. Statistical significance was estimated using a Monte Carlo permutation test (499 permutations) (ter Braak, 1986).

Effective number of occurrences (Hill's N2): Calculated for each species following Hill (1973); low values (N2 < 5) indicate specialists or restricted distribution species and high values (N2 > 5), generalist species.

Indicator species: This was performed using the Dufrêne and Legendre method implemented in PAST version 4.0 software (Hammer *et al*., 2001). Indicator species were considered to be those with IndVal ≥ 0.7 and P < 0.05; the evaluation was performed with 9999 permutations, and p-values were corrected for multiple comparisons using the Bonferroni correction method to reduce the false positive rate. Multivariate analyses such as ACC and Hill's N2 were performed in CANOCO version 4.5 (ter Braak and Šmilauer, 2002).

RESULTS

Alpha composition and diversity

Table 2 shows that both fragments differ in species richness and abundance, particularly in Monte Fresco. However, they exhibited high evenness and low dominance. The families with the greatest richness were: in Mola, Sapotaceae (three species); in Monte Fresco, Bignoniaceae and Sapotaceae, with four species each. 91.7% of the Mola species, or 33 out of 36, were present in Monte Fresco.

Table 2. *Diversity indices by location*

Indexes	Cool	Monte Fresco
Wealth (S)	36	63
Individuals	1,419	991
Common species	33	33
Shannon H' (log10)	1,318	1,494
Equity J'	0.847	0.827
Simpson ($\frac{1}{D}$)	16,239	17,977

Beta diversity and similarity

The Whittaker index was βw = 3.64, indicating a high species turnover among locations. The dendrogram (Figure 1) showed four main groups, clearly separating most of the plots from Mola (group 1) from those from Monte Fresco (group 4). An intermediate group (group 3) mixed plots from both sites dominated by Miconia elata, and a second group (plots MO 19, 20, and 21) adjacent to group 1 (Mola) but differing in the absence of *Calophyllum. useful*.

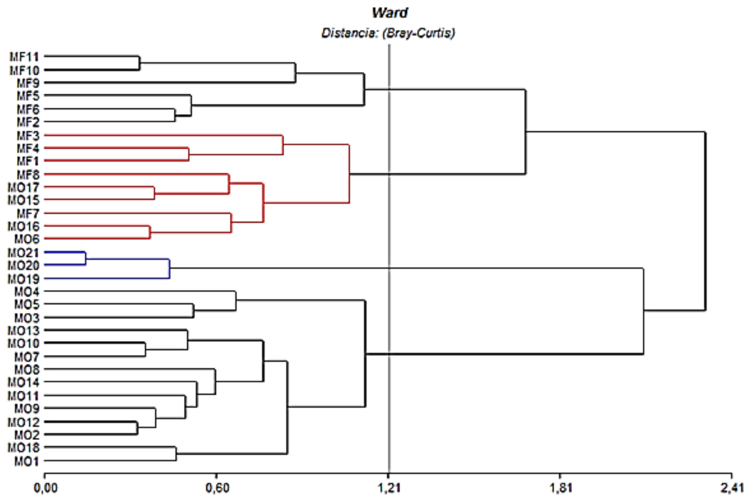

***Figure 1.** - Dendrogram of Mola and Monte Fresco plot grouping, with cophenetic correlation coefficient = 0.622*

Relationship with environmental variables (ACC)

Canonical correlation analysis explained 35.9% of the total variability in species composition with a total inertia = 3.76. The first four canonical axes accumulated 74.3% of the species-environment relationship (Table 3).

***Table 3. -** Results of the canonical correspondence analysis*

Axes	1	2	3	4
Self-values:	0.416	0.25	0.198	0.138
Correlation of species - environmental variables	0.932	0.852	0.856	0.827
Cumulative variance percentage				
species data:	11.1	17.7	23	26.7
of the relationship between species and environmental variables:	30.8	49.4	64.1	74.3
Correlation of environmental variables with the axes				
P	**-0.3892**	0.172	-0.0013	0
MSNM	**-0.685**	0.3879	0.395	0
Acc	**-0.6814**	0.4256	-0.1364	0.0959
Ma	-0.4238	0.1984	**0.4808**	0.1602
T	**-0.4023**	0.3506	0.1634	0.1946
D	**0.7321**	0.3147	0.0352	-0.3383
G	-0.1441	-0.3555	**0.4221**	-0.0321
R	-0.339	**-0.5553**	-0.0418	-0.4895

The forward selection procedure identified MSNM (p=0.002), D (p=0.002), Acc (p=0.026), and R (p=0.022) as significant variables. The ordination (Figure 2) showed that Axis 1 fundamentally separates the two locations: Monte Fresco projects towards the positive side (associated with greater canopy density D, r=0.732), while Mola projects towards the negative side (associated with greater altitude MSNM, r=-0.685, and accessibility Acc , r=-0.681).

Furthermore, Figure 3 shows the ordering of species with respect to environmental variables, where the species closer to the center of the ordering plane show less influence with environmental variables and can be considered as generalists.

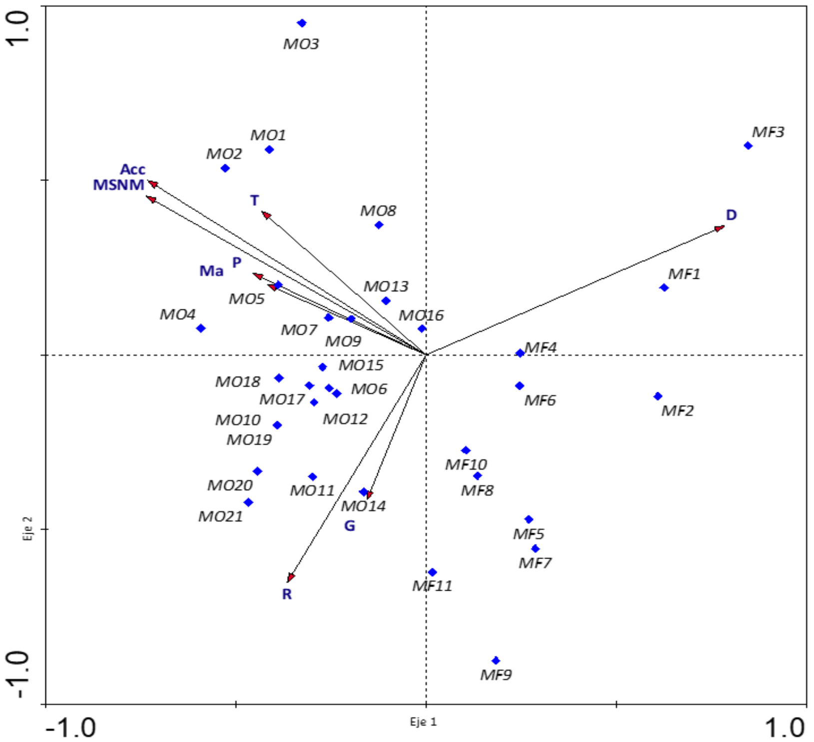

***Figure 2. -** Projection of environmental variables, of census units according to the first two canonical axes*

Legend: MO – Mola, MF – Monte Fresco

(T-Deforestation); (P-Slope); (ACC-Accessibility); (D-Density); (G-Basal Area); (MSNM-Altitude above sea level); (MA - Mortality); (R – Relief)

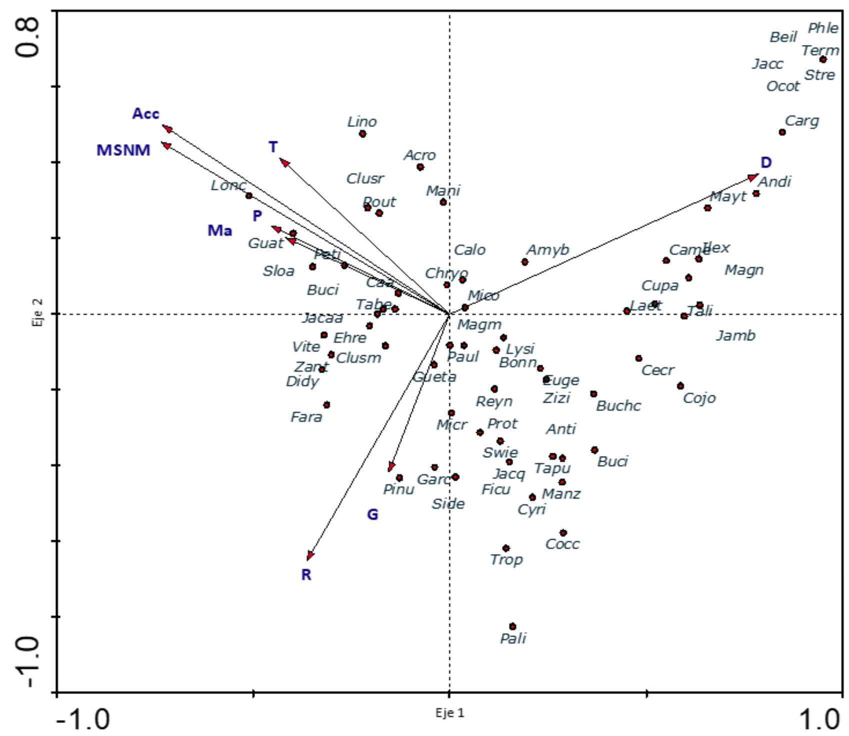

Figure 3 *- Projection of environmental variables and species according to the first two canonical axes*

Legend*: MO – Mola, MF – Monte Fresco*

(T-Deforestation); (P-Slope); (ACC-Accessibility); (D-Density); (G-Basal Area); (MSNM-Altitude above sea level); (MA-Mortality); (R-Relief)

Species and their acronyms

Acrosynanthus trachyphyllus -Acro, Amyris balsamifera - Amyb ; Andira inermis - Andi; Antirhea lucida -Anti; Beilschmiedia pendula - Beil; Bonnetia cubensis - Bonn; Buchenavia capitata - Buchc; Bucida buceras - Buci; Byrsonima crassifolia - Buci; Calophyllum useful -Calo; Cameraria latifolia - Came; Carapa guianensis - Carg; Casearia arborea - Caa ; Cecropia peltata - Cecr; Chrysophyllum olive-shaped - Chryo; Clusia minor - Clusm; Clusia rosea - Clusr; Coccoloba rufescens - Cocc; Cojoba arborea -Lame; American cupania - Cupa;Cyrilla Cuban - Cyri; Didymopanax morototoni - Didy; Ehretia tinifolia - Ehre; Eugenia glabrata - Euge; Faramea occidentalis -Fara; Ficus citrifolia - Ficu; Garcinia aristata - Garc ; Guatteria moralesii - Guat; Guettarda calyptrata - Gueta; Ilex nannophylla - Ilex; Jacaranda arborea - Jacaa; Jacaranda cowellii - Jacc; Jacquinia aculeata - Jacq; Jambosa vulgaris - Jamb; Laetia ternstroemioides - Laet; Linociera bakeri - Flax; Lonchocarpus sericeus - Lonc; Lysiloma sabicu - Lysi; Magnolia cristalensis - Magn; Magnolia minor - Magm; Manilkara albescens - Mani; Manilkara zapota - Manz; Maytenus elaeodendroids - Mayt; Miconia elata -Mico; Micropholis polita - Micr; Ocotea *leucoxylon - Ocot; Palicourea alpina -Pali; Paullinia fuscescens -Paul; Petitia domingensis - Peti; Phlebotaenia cuneata - Phle; Pinus cubensis - Pinu; Pouteria aristata - Pout; Protium fragrans - Prot; Reynosia wrightii - Reyn; Sideroxylon jubilla - Side; Sloanea curatellifolia - Sloa; Strempeliopsis strempelioides - Stre; Swietenia mahagoni - Swie; Tabebuia shaferi - Tabe; Taliparitis elatus - Tali; Tapura cubensis - Tapu; Terminalia nipensis - Term; Trophis racemosa - Trop; Vitex heptaphylla -Vite; Zanthoxylum duplicipunctatum -Zant; Ziziphus rhodoxylon - Zizi*

Species analysis

Analysis of the effective number of occurrences (Hill's N2) reveals that 45 of the 66 species, 68%, have an N2 < 5, indicating that they are infrequent and appear in a small number of plots. Eight of these species were exclusive to a single plot (unique), seven of them in Monte Fresco: Ficus citrifolia, Jacquinia aculeata, Beilschmiedia pendula, Jacaranda cowellii, Ocotea leucoxylon, Phlebotaenia cuneata, Strempeliopsis Strempelioides and Terminalia nipensis, which contributes to the high uniqueness of this fragment, especially in plot MF3 which contains six of these species.

On the other hand, a group of ten species with N2 > 5 was identified that act as the most common and generalist in the study area, with N2 values between 10 and 15 (e.g., *Calophyllum utile*, *Miconia elata, Clusia rosea*). These generalist species are projected towards the center of the ordination diagram in Figure 3, while the species with low N2, called specialists or rare species, are located at the ends of the axes, defining the more particular habitats of Mola or Monte Fresco.

Indicator species

The indicator species analysis (IndVal) identified nine indicator species for Mola (P<0.05) and 33 for Monte Fresco (P<0.05). After Bonferroni correction, the most reliable species were:

Mola: Pouteria aristata (IndVal =9.5; P=0.0132)

Mount Fresco: *Antirhea lucida, Beilschmiedia pendula, Cameraria latifolia, Carapa guianensi, Cecropia peltata, Coccoloba rufescens, Eugenia glabrata, Ficus citrifolia, Jacaranda cowellii, Jacquinia aculeata, Jambosa vulgaris, Laetia ternstroemioides, Ocotea leucoxylon, Phlebotaenia* *cuneata, Strempeliopsis strempelioides, Swietenia mahagoni, Taliparitis elatus, Terminalia nipensis, Ziziphus rhodoxylon* (P=0.0132 in all cases).

DISCUSSION

Sapotaceae species in both fragments suggests that these are relatively mature and well-preserved forests, as this family is characteristic of undisturbed ecosystems (Finegan, 1996). Monte Fresco, with 64 species and high evenness (J' = 0.827), exhibits characteristics typical of a forest in an advanced stage of succession (Villa *et al.* , 2019; Finegan, 1996). The high diversity (Simpson ($\frac{1}{D}$) = 17.98) suggests a structured community with low dominance, typical of mature forests (Finegan, 1996; Odum, 1969), where late-emerging and climax secondary species have become established after more than six decades of recovery (Villa *et al.* , 2019; Dent *et al.* , 2013).

Mola exhibits lower species richness (36 species) but slightly higher evenness (J' = 0.847), suggesting a more homogeneous community (Reyes and Acosta-Cantillo, 2018). This pattern is consistent with mature forests dominated by closed-canopy climax species (Villa *et al.*, 2019; Dent *et al.*, 2013; Odum, 1969). The lower absolute richness reflects more restrictive environmental conditions associated with the ophiolite substrate (Jaffré *et al.*, 2024; Rivero-Gutiérrez *et al.*, 2018).

Recent studies in tropical forests on ultramafic substrates have reported similar patterns. In New Caledonia, Jaffré *et al.* (2024) found that adjacent forests on serpentinites and volcano -sedimentary rocks showed comparable richness but markedly different floristic composition, with only 35.8% of tree species shared. These authors attributed the differences to soil chemistry, particularly pH, aluminum, manganese, and nickel. In this study, altitude and topography emerged as significant variables, likely acting in conjunction with soil conditions (Castillo-Ávila *et al.*, 2025; Rivero-Gutiérrez *et al.*, 2018).

The ACC results and the analysis of indicator species support the idea that the geological substrate acts as the primary environmental filter (Jaffré *et al.*, 2024; Reyes and Acosta-Cantillo, 2017). For example, Mola on ophiolites exhibits characteristics that suggest serpentinite soils , widely distributed in the eastern region of Cuba (Reyes and Acosta-

Cantillo, 2017; López-Almirall, 2013). These soils are known for their high toxicity from heavy metals such as nickel, chromium, and cobalt, and for their deficiency in essential nutrients such as calcium, phosphorus, and potassium (Jaffré *et al.,* 2024; Adamidis). *et al.*, 2014; Berazaín *et al.*, 2007), which explains the lower richness (36 species) and the dominance of *Calophyllum utile* (186 individuals), a species with physiological adaptations to ultramafic soils.

Research in forests on serpentinites has documented that plants develop tolerance mechanisms that include the exclusion of heavy metals, accumulation in specific tissues, or hyperaccumulation (Jaffré *et al.,* 2024; Adamidis *et al.,* 2014; Berazaín *et al.,* 2007). In New Caledonia, Jaffré *et al.* (2024) demonstrated that foliar nickel concentrations are significantly higher in plants growing on ultramafic substrates, while manganese and aluminum are higher in volcano -sedimentary substrates. Future studies should evaluate foliar heavy metal concentrations in dominant Mola species to confirm these adaptations.

In contrast, Monte Fresco, on metamorphic rocks with deeper and more fertile red ferralitic soils (Reyes and Acosta-Cantillo, 2018), supports greater richness and climax species such as *Carapa guianensis* and *Manilkara zapota*. The presence of 19 reliable indicator species in Monte Fresco reflects the greater heterogeneity of microhabitats available in more fertile soils (Castillo-Avila *et al.*, 2025).

The high species turnover (βw=3.64) indicates that both sites represent different floristic assemblages within the landscape. This value is comparable to the turnover observed between forests on contrasting substrates in other tropical regions (Jaffré *et al.*, 2024; Villa *et al.*, 2019). The floristic complementarity between the two fragments has fundamental implications for conservation: neither location is redundant (IUCN, 2025).

The 33 shared species (91.7% of Mola's species richness) indicate a common core of species capable of tolerating a relatively wide range of soil conditions (Bisse, 1988). These generalist species (e.g., *Miconia elata, Clusia* rosea) *are* projected toward the center of the ordination diagram and exhibit high Hill N2 values (>5) (Hill, 1973; ter Braak, 1986). In contrast, the 31 species exclusive to Monte Fresco and the three exclusive to Mola represent floristic components associated with more specific environmental conditions (Reyes and Acosta-Cantillo, 2018).

The pattern of high beta diversity and presence of rare species (68% of species with N2 < 5) is consistent with what has been reported for mature tropical forests, where rare species predominate at the local scale and only a few common species dominate the community (Jaffré *et al.,* 2024; Villa *et al.,* 2019). This pattern has implications for ecosystem resilience to disturbances, as rare species can perform unique ecological functions and contribute to ecosystem stability (Castillo-Ávila *et al.* , 2025; Tasnim *et al.* , 2024).

Contrary to expectations, logging (T) was not statistically significant in the forward selection model (P>0.05), although its projection on the ordination diagram suggests an association with Mola plots. Accessibility (Acc) was significant (P=0.026), but was strongly correlated with the first canonical axis, mixed with altitude.

These results indicate that, although accessibility is greater in Mola, it is not the primary cause of the floristic differences. This finding aligns with the IUCN assessment (2025), which notes that selective logging in the park is localized and does not threaten the overall integrity of the ecosystem. Recent research in protected areas of Southeast Asia, such as Lineva, also supports this finding. *et al.* (2025) in Cat Tien National Park , have shown that the human disturbance index can vary significantly between core zones and buffer zones, with localized anthropogenic pressures that do not necessarily affect overall ecological integrity.

The absence of a significant effect from logging may be due to the fact that the studied forests are in advanced stages of succession, where seed banks, seed sources, and disperser communities are relatively intact, allowing succession to remain uninterrupted by repeated logging (Chazdon, 2003; Helmer *et al.* , 2008).

The high beta diversity (βw=3.64) and the presence of unique indicator species in both fragments demonstrate that neither location is redundant for the conservation of the park's tree flora. The observed habitat specificity, with species adapted to serpentinites in Mola and climax species of fertile soils in Monte Fresco, underscores the need to maintain the environmental heterogeneity of Alejandro de Humboldt National Park (IUCN, 2025; Reyes and Acosta-Cantillo, 2017).

Recent studies on tropical forest restoration have emphasized the importance of considering soil heterogeneity in the design of conservation strategies (Castillo-Ávila *et al.*, 2025; Tasnim *et al.*, 2024). In Indo- Burma Biodiversity Hotspot , Tasnim *et al.* (2024) demonstrated that mature forests sustain higher levels of nutrients than mixed and monospecific plantations, underscoring the importance of preserving primary and advanced secondary forests.

Conservation efforts should focus on preserving both fragments as complementary conservation units (IUCN, 2025), monitoring localized threats (logging, accessibility) which, although not currently determining, could become critical if they increase (IUCN, 2025), maintaining connectivity between fragments to allow gene flow and recolonization of species (Tasnim *et al.*, 2024), and deepening ecophysiological studies that allow understanding the adaptation mechanisms of species to oil-bearing substrates, including analysis of foliar concentrations of heavy metals and functional traits (Jaffré *et al.*, 2024; Adamidis *et al.*, 2014).

The complementary flora between the two fragments means that effective conservation of the park requires conservation efforts in both. Thus, Monte Fresco stands out for its greater richness (64 species) and the presence of numerous exclusive climax species, while Mola presents a more homogeneous and specialized community, dominated by *Calophyllum. useful* and tolerant to extreme conditions.

CONCLUSIONS

Altitude above sea level, relief, density, and accessibility were the variables with a significant effect on the distribution of tree flora in the two fragments of submontane rainforest in Cupeyal del Norte.

The two submontane rainforest fragments studied harbor mature, but floristically differentiated, tree communities with high beta diversity.

The floristic complementarity between both fragments implies that the effective conservation of the park requires differentiated conservation actions in both fragments.

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The authors have participated in the writing of the work and analysis of the documents.