

Article

Morphological Trait-Based Typology Captures Carbon Strategies but Not Drought Tolerance of Tree Species in Dry and Cloud Tropical Forest

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Abstract

Tropical forests host a remarkable diversity of tree species with contrasting functional strategies. Typologies based on easily measurable morphological traits (soft traits) are widely used to group species along the plant economics spectrum, yet their capacity to reflect drought tolerance remains heavily debated. This study evaluates whether a typological framework based on five soft traits (specific leaf area, leaf area, wood density, stomatal density, and leaf trichome density) can capture both carbon acquisition and drought response strategies. We examined 14 dominant canopy species from contrasting tropical ecosystems (cloud and dry forests) of the Lesser Antilles. A typology comprising three groups was proposed, which differed significantly along the acquisitive–conservative spectrum, demonstrating the utility of soft traits for characterizing carbon management and growth potential at the regional scale. However, critical hard traits such as xylem vulnerability (P50) and turgor loss point (ψ_{tlp}) were decoupled from this classification. Our findings confirm the value of soft-trait typologies for modeling local carbon dynamics but highlight their limitations in predicting complex physiological drought vulnerability. Integrating phenological and hydraulic proxies into functional classifications is essential to accurately represent species drought tolerance in an increasingly water-limited Caribbean archipelago.

Keywords: carbon acquisition; Caribbean forest; cavitation resistance; leaf economics spectrum; functional trait; growth; hard traits; soft traits; turgor loss point; forest management

1. Introduction

Tropical forests play a critical role in regulating the global climate, conserving terrestrial biodiversity, and maintaining essential ecosystem services [1–4]. However, anthropogenic climate change is profoundly altering their structural and physiological functioning through increasing drought frequency and intensity [5–8]. Recent data confirm that tropical biomes are experiencing unprecedented water stress, with severe repercussions for net primary productivity, carbon sequestration, and tree mortality [1,6,7]. Understanding the mechanisms underlying tree responses to water limitation has thus become crucial for predicting forest dynamics, guiding regional conservation strategies, and mitigating climate change [7,9,10]. From a sustainability perspective, identifying contrasting plant drought strategies directly supports the United Nations’ Sustainable Development Goals (SDG 13: Climate Action, and SDG 15: Life on Land), particularly in vulnerable small island systems, where forest ecosystems face accelerating climatic pressures.



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In seasonally dry forests (DF), drought stress is primarily driven by prolonged rainfall deficits and severe soil moisture depletion. Conversely, in tropical montane cloud forests (CF), critical water deficits can develop despite high annual precipitation. In these high-elevation ecosystems, shifting cloud cover and elevated solar radiation trigger rapid increases in temperature and atmospheric vapor pressure deficit (VPD) [11]. This high atmospheric evaporative demand, compounded by shallow rooting environments, can severely depress leaf water potentials and inhibit plant ecophysiological process [11–13]. Despite these distinct environmental drivers, the functional mechanisms governing tree responses to water deficit across these adjacent ecosystems remain poorly resolved and rarely compared.

Grouping taxa into a finite number of functional types represents a powerful approach for simplifying highly diverse tropical forest ecosystems into functional models [7,9,10]. Typological frameworks traditionally rely on morphological “soft traits”, such as specific leaf area (SLA), leaf area (LA), and wood density (WD), which are easily quantifiable across numerous species and environmental gradients. At the leaf scale, SLA (leaf area/leaf dry mass) is a key determinant of plant carbon economics [14] and is widely used as an indirect proxy for drought sensitivity [14–17]. Concurrently, LA directly influences leaf energy and water balances, as smaller leaves are generally more resistant to drought [17]. At the stem level, WD reflects growth rate and biomass allocation strategies [18]. It is generally negatively correlated with hydraulic conductivity [19–21] and can predict drought-induced mortality, although its relationship with plant hydraulic functioning often varies across forest types [22], suggesting a context-dependent predictive capacity. Additionally, epidermal traits like stomatal density regulate transpiration and gas exchange capacity [3,23,24], while trichome density can reduce cuticular water loss, enhance foliar water capture, and increase leaf albedo [25,26].

Despite their widespread use, the ability of soft traits to predict functional drought tolerance remains debated, particularly when contrasted with the direct mechanistic insights provided by physiological “hard traits” [3,6,10,27–31]. Key hydraulic hard-trait predictors include the stem water potential inducing a 50% loss of xylem conductivity (P50), and the leaf water potential at turgor loss point (Ψ_{tlp}) [6,32,33]. While a highly negative P50 reflects a species’ capacity to sustain high xylem tension without critical embolism formation [30,31], a lower Ψ_{tlp} extends the leaf water potential range over which cells maintain turgor and metabolic activity [6,34]. Conventionally, these traits support a global growth–drought trade-off, where fast-growing, acquisitive species (high SLA, low WD) maximize carbon gain under favorable conditions at the cost of increased drought vulnerability, whereas slow-growing, conservative species (low SLA, high WD) favor hydraulic safety and greater drought tolerance at reduced growth cost [22,35]. Integrating hydraulic traits into functional typologies of insular tropical forests remains rare due to methodologies that are technically demanding and time-consuming, severely limiting large-scale data acquisition. Moreover, global growth–drought trade-offs are not necessarily transferable to these ecosystems [14,36–38]. Indeed, these trade-offs are not universal and may be modulated by factors such as rooting depth, phenological strategies, and hydraulic safety mechanisms [21,39]. Consequently, empirical assessments of the coordination between soft and hard traits at a regional scale remain essential, particularly in high-diversity and highly vulnerable tropical ecosystems [3,21,33,35,40,41].

In this context, the islands of the Lesser Antilles offer a particularly relevant study site. They combine remarkable ecosystem diversity over short spatial scales with high levels of endemic biodiversity, making them an ideal setting for understanding functional responses to drought intensification. The Guadeloupe archipelago exhibits steep climatic gradients from coastal dry forests (~1300 mm annual rainfall) to montane cloud forests

(~4600 mm), generating strong and contrasting selective pressures for drought tolerance within a limited geographic area. This natural gradient offers a unique opportunity to evaluate functional trait relationships across extreme water availability conditions. Identifying the most drought resilient species and functional groups is therefore essential to optimize forest management and conservation strategies in the Caribbean [10,34,42].

The primary objective of this study is to evaluate the extent to which easily measurable morphological “soft” traits can effectively capture and predict underlying carbon-use strategies and drought tolerance, much like physiological “hard” traits do, across two contrasting tropical tree communities. Specifically, we aim to: (1) establish a multi-trait functional typology of 14 dominant Caribbean canopy tree species using both classical leaf and wood structural features (SLA, LA, WD) and less-studied epidermal traits (stomatal and trichome densities); and (2) quantify the statistical congruence between these emergent morphological groups and independent physiological traits, including hydraulic parameters (P_{50} , Ψ_{tlp}), carbon assimilation rates expressed by mass and area (A_m , A_a), leaf nitrogen content (N) and long-term radial trunk growth (ΔD). We test two central hypotheses: (H1) morphological soft traits will successfully segregate species into distinct functional groups aligned with the leaf economics spectrum (reflecting a continuum from acquisitive to conservative carbon investment), and (H2) the growth–drought trade-off can be decoupled, such that hydraulic traits (P_{50} , Ψ_{tlp}) will exhibit weak coordination with growth proxies, thereby restricting the universal predictive power of soft trait frameworks across highly contrasted environments.

2. Materials and Methods

2.1. Study Sites and Species Selection

Two contrasting forest ecosystems of the Caribbean Guadeloupe archipelago were selected for this study: the tropical montane cloud forest (CF) and the tropical dry forest (DF). These ecosystems represent distinct ends of an environmental gradient of water availability, allowing for a comparative analysis of the of traits coordination within two plant communities [43,44].

Cloud forests are regularly immersed in fog and receive more than 3500 mm of annual rainfall [44,45]. In Guadeloupe, the CF covers 5312 ha above 650 m elevation [46]. We selected seven native dominant tree species of local CF: *Charianthus alpinus* Howard, *Clusia major* L., *Ilex sideroxyloides* Griseb., *Rapanea trinitatis* Mez, *Richeria grandis* Vahl., *Schefflera attenuata* Swartz, and *Siphoneugena densiflora* Berg [46,47]. Samples and measurements were collected at the top of the mountain locally referred to as Mamelle Pigeon ($-61.38^\circ\text{W}/16.11^\circ\text{N}$) at an elevation of 786 m on Basse-Terre Island. The average annual rainfall at this site is 4644 mm, ensuring that vegetation does not experience soil water shortage (2010–2014 data, from Météo France, Morne Léger’s station at an elevation of 510 m, 1 km from the plot). The soil is a ferralitic (oxisol).

Tropical dry forest (DF) accounts for 42% of the forested tropical landscape [47,48], with annual rainfall typically below 2000 mm, and marked intra-annual variation [49]. In Guadeloupe, this ecosystem develops below 300 m elevation [46]. We selected seven dominant native species of local DF: *Bursera simaruba* (L.) Sarg., *Citharexylum fruticosum* L., *Ficus citrifolia* Mill., *Guaiacum officinale* L., *Guapira fragrans* Dum. Cours., *Sideroxylon salicifolium* L. and *Tabebuia heterophylla* Britt. [46,47]. Samples were collected below 20 m elevation in areas receiving 1330 mm of annual rainfall within the Petit-Canal Landscape Park and Petite-Terre Nature Reserve ($-61.48^\circ\text{W}/16.38^\circ\text{N}$ and $-61.12^\circ\text{W}/16.17^\circ\text{N}$). This vegetation may experience water shortages for up to 10 consecutive months. The soil is a shallow skeletal Leptosol (FAO-UNESCO classification) characterized by numerous calcareous outcrops of Pleistocene limestone bedrock.

Species selection was based on their ecological dominance within CF or DF communities. At each study site, species selection was guided by local floristic inventories documenting all individuals with a diameter at breast height (DBH > 10 cm). In the CF plot of Mamelle-Pigeon, the seven sampled canopy angiosperms represent 54% of the total community basal area, confirming their ecological dominance. In the DF of Petit-Canal, transect-based inventories identified six native canopy species accounting for 82% of the total basal area, which were complemented by the climactic, structurally important, and IUCN-listed *Guaiacum officinale*. Consequently, the selected experimental taxa capture the main structural and functional components of each forest community. For each of the 14 selected species, mature and healthy individuals were measured. The sample size ($n \geq 3$ per species) was constrained by the substantial logistical limitations inherent to accessing the canopy of protected or remote tropical ecosystems. However, this design still maintained sufficient analytical power to detect interspecific differences, in line with established sampling practices in numerous forest trait studies [6,17,41,47,50,51]. The phenology of these species has also been described (Table 1).

Table 1. Botanical name and family, author and years, habitat, phenology and number of individuals sampled of each species (n) included in the study (taxonomic and author information from the International Plant Names Index (<https://www.ipni.org/>)).

Species	Family	Author	Ecosystem	Phenology	n
<i>Bursera simaruba</i>	Burseraceae	Sargent and Forest (1890) [52]	Dry forest	deciduous	4
<i>Citharexylum fruticosum</i>	Verbenaceae	Linné (1759) [53]	Dry forest	deciduous	4
<i>Ficus citrifolia</i>	Moraceae	Miller (1768) [54]	Dry forest	deciduous	4
<i>Guaiacum officinale</i>	Zygophyllaceae	Linné (1753) [55]	Dry forest	Evergreen	4
<i>Guapira fragrans</i>	Nyctaginaceae	Dumont de Courset (1968) [56]	Dry forest	Evergreen	4
<i>Sideroxylon salicifolium</i>	Sapotaceae	Lamarck (1794) [57]	Dry forest	Evergreen	4
<i>Tabebuia heterophylla</i>	Bignoniaceae	Britton (1915) [58]	Dry forest	deciduous	3
<i>Chorizanthe alpinus</i>	Melastomataceae	Howard (1972) [59]	Cloud forest	Evergreen	4
<i>Clusia major</i>	Clusiaceae	Linné (1753) [55]	Cloud forest	Evergreen	4
<i>Ilex sideroxyloides</i>	Aquifoliaceae	Grisebach (1857) [60]	Cloud forest	Evergreen	4
<i>Rapanea trinitatis</i>	Myrsinaceae	Mez (1901) [61]	Cloud forest	Evergreen	4
<i>Richeria grandis</i>	Euphorbiaceae	Vahl (1797) [62]	Cloud forest	Evergreen	4
<i>Schefflera attenuata</i>	Araliaceae	Frodin (1989) [63]	Cloud forest	Evergreen	4
<i>Siphoneugena densiflora</i>	Myrtaceae	Berg (1893) [64]	Cloud forest	Evergreen	4

2.2. Selection and Quantification of Soft Traits

Traits were selected to capture multiple dimensions of plant resource acquisition and drought tolerance strategies, spanning the leaf economics spectrum and water management efficiency [65–68]. Three key soft traits are frequently identified in the literature as critical for both plant carbon use and drought response: leaf area (LA), specific leaf area (SLA) and wood density (WD). Additionally, we incorporated two less-studied epidermal traits, stomatal density (Ds) and trichome density (Dt), to improve our understanding of plant water-use response [26,27,42,69]. These traits are summarized in Table 2.

Table 2. Summary of the traits measured in the study, with their abbreviations, units and types.

Abbreviation	Name	Unit	Trait Type
Ds	Stomatal density	N mm ⁻²	soft
Dt	Leaf trichome density	N mm ⁻²	soft
LA	Leaf area	cm ²	soft
SLA	Specific leaf area	cm g ⁻¹	soft
WD	Wood density	g cm ⁻³	soft
Aa	Carbon assimilation rate per unit of area	μmolCO ₂ m ⁻² s ⁻¹	hard
Am	Carbon assimilation rate per unit of mass	μmolCO ₂ g ⁻¹ s ⁻¹	hard
N	Leaf nitrogen content	%	hard
P50	Leaf water potential at 50% loss of hydraulic conductivity	MPa	hard
ΔD	Diameter at breast increment	mm yr ⁻¹	hard
Ψ _{tlp}	Water potential at turgor loss point	MPa	hard

For every individual, all measurements were performed on recently fully expanded sun leaves and their associated branches. Field sampling was conducted in both ecosystems at the end of the wet season (January) to ensure conditions of maximum water availability. For each individual, LA was measured for 15 leaves using a leaf area meter (Licor3000C, Li-Cor, Lincoln, NE, USA). Dry weight of each component was determined after 48 h at 70 °C. SLA was calculated for each leaf as the ratio between leaf area and leaf dry weight. Stomatal and trichome densities (both abaxial and adaxial) were quantified using clear nail polish epidermal imprints of fresh leaf surfaces. Three leaves per individual were sampled and photographed using an optical microscope with a digital camera (Nikon Eclipse 80i and DXM 1200F, Nikon instrument Europe BV, Badhoevedorp, The Netherlands). Stomatal and trichome counts were performed using the Mesurim Pro 3.4 software (©J-F. Madre, Academy of Amiens, France). Because of the destructive nature of wood density measurements and the protected status of several species in the study, specific wood density values were obtained from Rollet [47]. To confirm the reliability of Rollet's values, we performed a validation using the extensive and independent geographical dataset from Fischer et al. [70], which includes more than 100,000 measurements for 16,829 species. Across the 14 studied species extracted from this database [70], intraspecific variability in WD remained below 20%, consistent with previous consensus on low within-species wood trait variation [47,71]. Our analysis revealed a high statistical congruence between Rollet's values and the independent American region dataset ($WD_{Fisher} = 0.79 \times WD_{Rollet} + 0.042$, $R^2 = 0.86$), confirming that Rollet WD values represent reliable and robust proxies for species means.

2.3. Selection and Quantification of Hard Traits

Physiological hard traits provide direct information regarding carbon assimilation and drought tolerance, together spanning the continuum from conservative to acquisitive water use strategies [31,33,66]. The six selected hard traits were: leaf nitrogen content (N), carbon assimilation (per unit mass, Am, and per unit area, Aa), the water potential inducing a 50% loss of xylem hydraulic conductivity (P50), the leaf water potential at turgor loss point (Ψ_{tlp}), and annual diameter increment (ΔD). Leaf N is directly coupled to photosynthetic activity (Am or Aa) [14,72], while ΔD represents an integrative proxy of whole-plant performance, as it depends on both carbon acquisition and drought tolerance. These traits are presented in Table 2.

To determine leaf N, one dry leaf blade per individual was crushed to 200 μm for total N analysis using a CHN elemental analyzer (NC 2100 Soil, CE Instruments, Milan, Italy).

Leaf gas exchange was measured on clear and sunny days on three sun-exposed leaves per individual. The maximal CO₂ assimilation rate per unit area (A_a) was recorded between 09:00 and 12:00 using a portable IRGA system (Ciras-2, PP Systems, UK) under ambient temperature and humidity, with a saturating photosynthetic photon flux density (PPFD) of 1600 µmol m⁻² s⁻¹ and a reference CO₂ concentration of 380 ppm. The maximum carbon dioxide assimilation rate per unit mass was calculated as: A_m = A_a × SLA.

Xylem vulnerability curves were constructed to determine the stem water potential at 50% loss of hydraulic conductivity (P₅₀). These curves describe the relationship between the percentage loss of hydraulic conductivity (PLC) and the xylem water potential (Ψ_{xylem}). For 4–8 individuals per species, cavitation resistance was assessed by monitoring xylem pressure during bench dehydration at 25 °C [73,74]. At each dehydration step, Ψ_{xylem} was estimated on three stems per branch using a dew point potentiometer (WP4 Decagon Devices, Pullman, WA, USA). Simultaneously, a minimum of five stem segments of the last growth unit were connected to a XYL'EM flow meter manifold (Bronkhorst, France) to measure native hydraulic conductance (K) and then maximum conductance (K_{max}) following flushing. The PLC was calculated following the Tyree and Sperry equation [74]:

$$PLC = 100 \times 1 - \frac{(K)}{K_{max}}$$

Paired PLC and mean Ψ_{xylem} values were plotted, and an exponential sigmoid function was fitted to the data:

$$PLC = \frac{100}{1 + \exp\left(s \times \frac{P - P_{50}}{25}\right)}$$

where P₅₀ is the xylem pressure causing a 50% loss of conductance (PLC) and s is a slope parameter. P₅₀ was estimated for each curve via non-linear regression using XLSTAT (Addinsoft SARL, France). Vulnerability curves could not be established for two latex-exuding species (*Ficus citrifolia* and *Clusia major*), as latex exudation occludes xylem vessels and invalidates standard hydraulic conductivity methods.

Leaf water potential at the turgor loss point (Ψ_{tlp}) was determined by constructing pressure-volume (P-V) curves. For each species, one leaf from three distinct individuals was excised and placed in deionized water at dawn; leaves were then wrapped in plastic bags and rehydrated overnight in the dark. P-V curves were generated by tracking leaf water potential and fresh leaf mass loss during controlled bench dehydration using a Scholander pressure chamber. Measurements continued until at least five data points were recorded beyond the turgor loss point. Leaves were then oven-dried at 70 °C for 48 h. Because it is impossible to distinguish xylem sap from latex when using a pressure chamber, P-V curves could not be generated for the two latex-exuding species (*F. citrifolia* and *C. major*).

Diameter at breast height (DBH) was monitored annually using dendrometer bands (UMS, Munich, Germany) over two years. The annual diameter increment (ΔD) was calculated as follows:

$$\Delta D = \frac{W2 - W1}{t2 - t1}$$

where W1 and W2 represent DBH values at times t1 and t2 (ΔD, mm yr⁻¹). For technical reasons, ΔD could not be quantified for *S. attenuata* and *G. officinale*. The trunks of *S. attenuata* were densely covered with lianas, whereas *G. officinale* sheds its bark in large chunks, invalidating incremental radial measurements.

2.4. Statistical Treatments and Classification

The functional typology was established using soft traits at the individual level. The statistical multivariate approach and its outputs are presented in Figure 1.

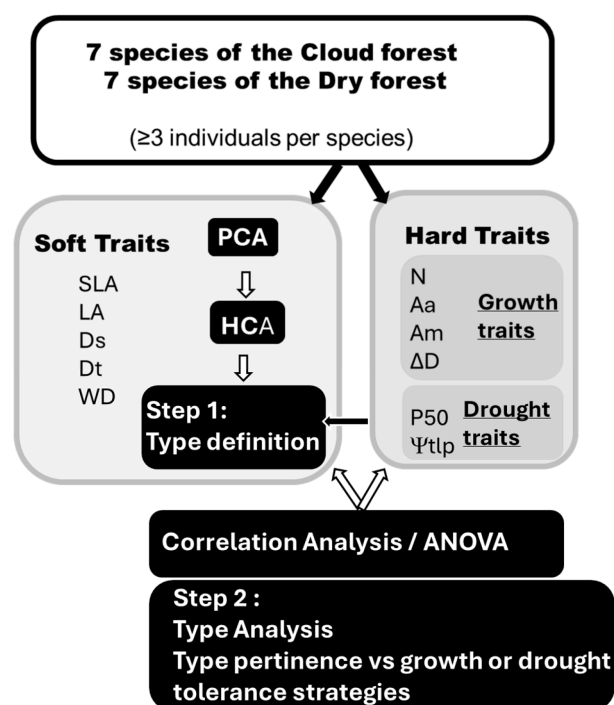


Figure 1. Simplified presentation of the key methodological steps and statistical analyses (black frame) to facilitate understanding of the analytical workflow, with trait definitions provided in Table 2. PCA (Principal Component Analysis) was used to summarize multivariate trait variation, and HCA (Hierarchical Cluster Analysis) was applied to identify groups of individuals based on their multivariate similarity.

To identify homogeneous functional groups of trees based on soft traits, a two-step multivariate framework was applied [9,75]. In the first step, a Principal Component Analysis (PCA) was performed to reduce dimensionality into orthogonal, uncorrelated synthetic axes. Following Kaiser's criterion [76], only principal components associated with an eigenvalue greater than one were retained. These components exhibit correlation structure of the initial variables and served as the basis for grouping individuals. In the second step, an Agglomerative Hierarchical Clustering (AHC) algorithm was applied to these principal components. Each component was weighted by its corresponding eigenvalue to reflect its contribution to the total variance. The AHC algorithm sequentially clustered individuals according to their similarity using an index of dissimilarity and Ward's minimum-variance method [77], which minimizes the increase in total intra-class inertia to optimize group homogeneity. Once the clusters were defined, group characteristics were assessed using mean trait values. To rigorously assess cluster stability and internal validity, a silhouette width analysis was performed to confirm partition strength. Additionally, multiscale bootstrap resampling (1000 iterations) was conducted using the pvclust package 2.2.0 in R to derive Approximately Unbiased (AU) p -values for each node, considering clusters well-supported when $AU \geq 95\%$. The discriminatory power of the resulting typology for both soft and hard traits was evaluated using a one-way analysis of variance (ANOVA) followed by Tukey's post hoc test, in order to quantify which individual traits differed significantly among the functional types identified by the multivariate analyses [78]. This step provides the necessary inferential support to validate the clusters derived from PCA and AHC, which are primarily descriptive, and to determine the specific traits driving the observed functional differentiation [38]. Finally, a Pearson correlation matrix was generated to assess pairwise associations among all functional traits. The statistical analysis was performed using RStudio (v. 4.5.1).

3. Results

3.1. Typology Based on Soft Traits

Significant relationships emerge among the five soft traits examined across 14 indigenous tree species of Caribbean tropical forests (Figure 2). SLA and LA are strongly positively correlated ($p < 0.001$), while both are negatively related to WD ($p < 0.001$) (Figure 2 and Supplementary Figure S1).

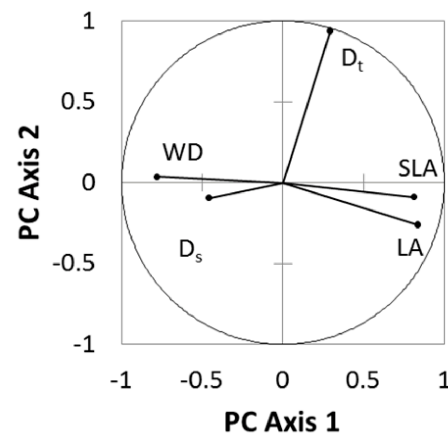


Figure 2. Correlation circle of the principal component analysis (PCA) performed on five soft traits from cloud forest and dry forest. Arrows represent trait loadings on PC1 (45% variance) and PC2 (19% variance). Trait abbreviations: SLA = specific leaf area ($\text{cm}^2 \text{g}^{-1}$), LA = leaf area (cm^2), WD = wood density (g cm^{-3}), Dt = trichome density (N mm^{-2}), Ds = stomatal density (N mm^{-2}). Sample sizes: cloud forest (7 species and 28 trees), dry forest (7 species and 27 trees).

The first two PCA axes capture 64% of the total variance, with PC1 explaining 45% and PC2 explaining 19% (Figure 3, Supplementary Table S1). The first axis ranks individuals along a gradient primarily defined by LA, SLA and WD. These results correspond to the global leaf economics spectrum axis, where acquisitive strategies (high SLA, large LA) trade off against conservative wood investment (high WD). Variation along the second axis was dominated by trichome density (Dt). Illustrations of trichomes and stomata are presented in Supplementary Figure S2.

Hierarchical clustering discriminates three distinct functional groups (Figure 3). The first group (Type 1) contains four dry forest species: *B. simaruba*, *C. fruticosum*, *F. citrifolia*, and *T. heterophylla*. The second group (Type 2) encompasses nine species occurring in both cloud and dry forest (*G. fragrans*, *S. salicifolium* and all seven CF species). The third group (Type 3) includes only one DF species, *G. officinale*. Silhouette analysis indicates an overall good clustering structure (average silhouette width = 0.51), indicating good overall separation among the three groups (Type 3: 0.63; Type 2: 0.42; Type 1: 0.53). Bootstrap resampling identifies several stable sub-clusters ($\text{AU} > 95\%$). Silhouette and bootstrap plots are provided in Supplementary Figure S3.

The functional typology derived from PCA and hierarchical clustering (Figure 3) is strongly associated with phenology, which exerts a stronger influence than forest type on the structuring of functional trait variation (Figure 4). Type 1 groups all deciduous dry forest species, whereas Types 2 and 3 comprise evergreen species occurring in both dry and cloud forests. Consequently, species from the two contrasting forest types can occur within the same functional group, as illustrated by Type 2.

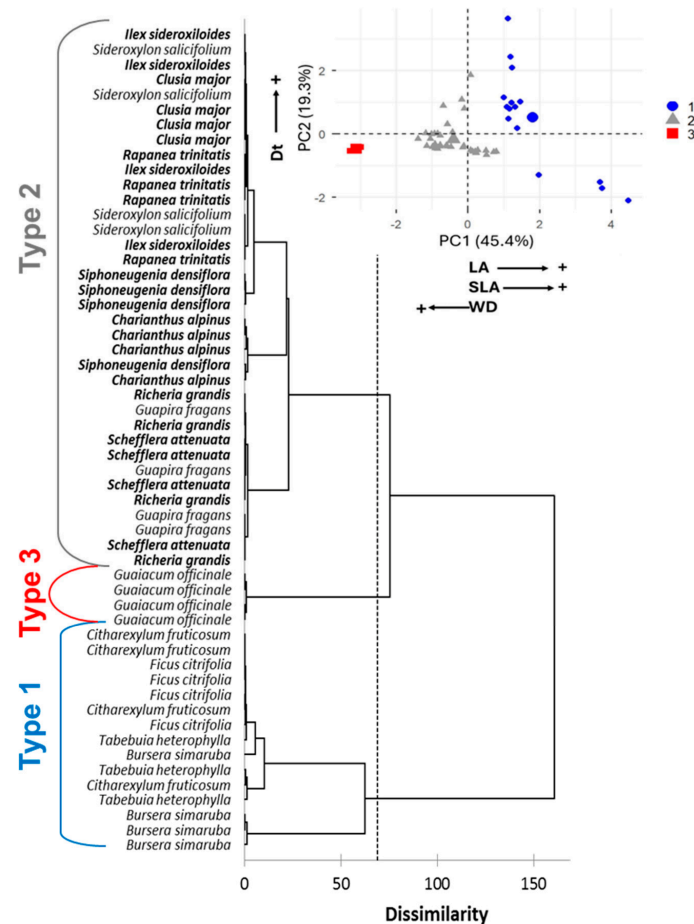


Figure 3. Agglomerative hierarchical classification (AHC) of 14 Caribbean tropical species (seven from cloud forest and seven from dry forest), based on five soft traits (SLA = specific leaf area, LA = leaf area, WD = wood density, Ds = stomatal density, Dt = trichome density). Three functional groups identified at optimal cut height ($h = 60$, dotted lines). Cloud forest species are shown in bold. Inset: PCA ordination of species along axes 1 and 2, with trait vectors positioned according to their highest loadings on each axis. Each functional type is represented by a distinct color: Type 1 in blue, Type 2 in grey, and Type 3 in red.

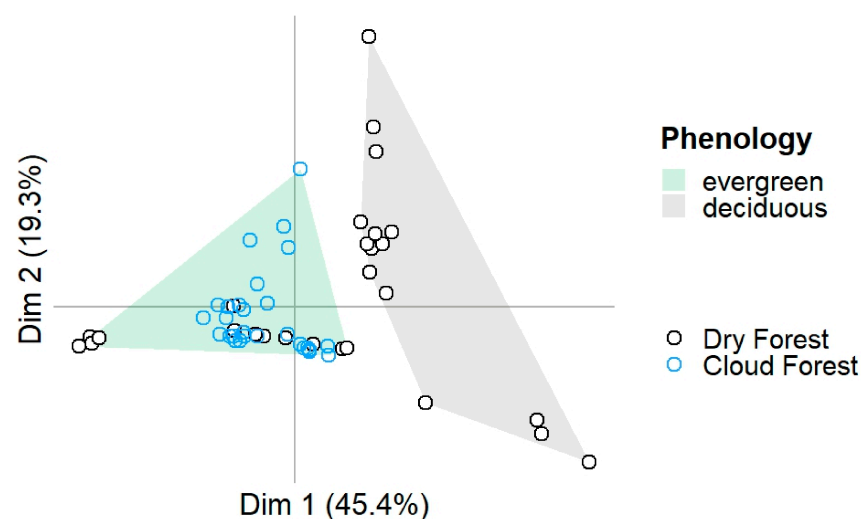


Figure 4. PCA ordination of 14 Caribbean tropical tree species from dry and cloud forest along the first two principal axes, based on five soft traits (SLA, LA, WD, Dt, Ds). Species are distinguished according to their phenology (deciduous vs. evergreen).

The soft traits of the three functional types are presented in Figure 5. ANOVA results reveal that Type 1 differs significantly from Types 2 and 3 regarding SLA, LA, WD and Dt. Together, these significant differences statistically validate the acquisitive strategy of Type 1, which is characterized by larger and thinner leaves (higher SLA and LA), lower wood density, and higher trichome density. In contrast, Types 2 and 3 exhibit more conservative trait values, consistent with slower resource-use strategies. Within these conservative groups, *G. officinale* (Type 3) stands out by its exceptionally high stomatal and wood density, distinguishing it from the species clustered in Type 2. The presence of dry forest species across all three functional types further highlights the substantial functional diversity characterizing Caribbean dry forests.

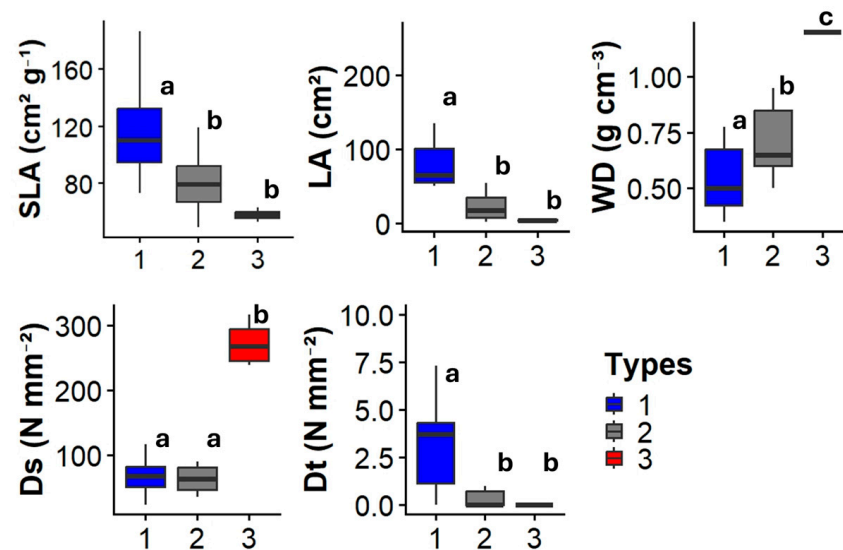


Figure 5. Boxplots of soft traits for the three functional types identified by the AHC. Different letters indicate significant differences among types (Tukey's post hoc test, $p < 0.05$). Trait abbreviations: SLA = specific leaf area, LA = leaf area, WD = wood density, Ds = stomatal density, Dt = trichome density.

3.2. Hard Traits and Typology

The typology of Caribbean trees from two contrasting forests, based on soft traits, is validated by hard traits related to carbon economics, but not by drought-tolerance traits (P50 and Ψ_{tlp}). As shown in Figure 6, hard traits reflecting carbon-acquisition capacity (photosynthesis capacity, leaf nitrogen content and growth rate) tend to decrease from Type 1 to Type 3. Consequently, Type 1 species have significantly higher leaf N, Am and ΔD than Type 2 and 3. These results confirm that the soft traits used in the typology successfully capture the carbon economics spectrum: Type 1 exhibits a carbon-acquisitive strategy (high values of SLA, LA, N, Am and ΔD) validated by higher physiological capacity, while Types 2 and 3 represent a conservative carbon strategy with opposite trait values.

This pattern reflects contrasting carbon-use strategies associated with opposite traits, consistent with species phenology. Deciduous species (Type 1) with shorter leaf lifespans maintain a higher potential for carbon fixation, as indicated by their elevated Am and N values. Their carbon allocation prioritizes rapid growth over costly wood investment, as evidenced by significantly faster growth rates and lower wood density (Figure 6). Conversely, evergreen species (Types 2 and 3) display more conservative traits characterized by greater carbon investment.

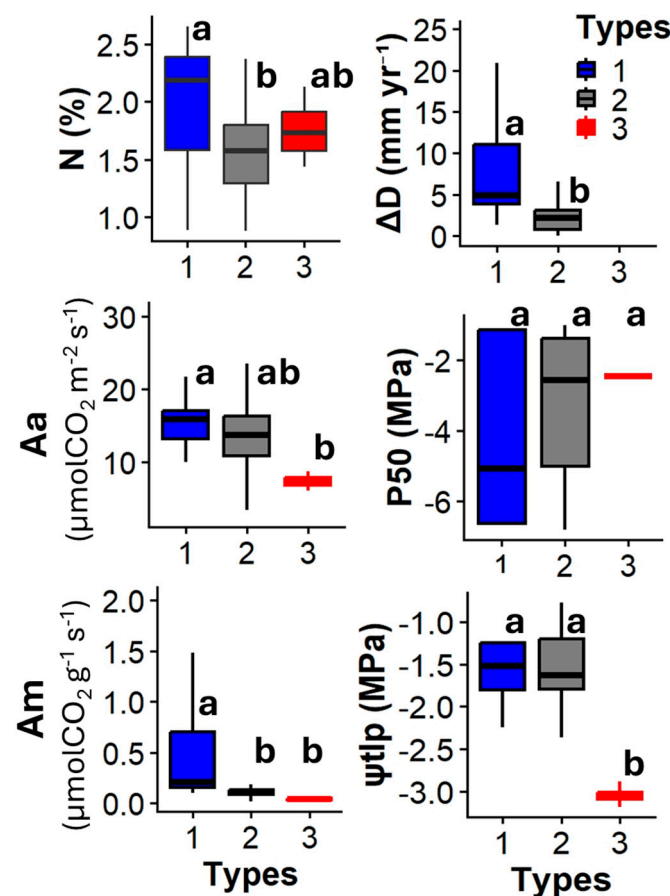


Figure 6. Boxplots of hard traits for the three functional types identified by the AHC. Different letters indicate significant differences among types (Tukey's post hoc test, $p < 0.05$). Trait abbreviations: N = leaf nitrogen content, Aa = net maximal carbon assimilation rate per unit leaf area, Am = net maximal carbon assimilation rate per unit leaf mass, ΔD = annual diameter increment at breast, P50 = water potential at 50% loss of hydraulic conductivity, Ψ_{tlp} = water potential at turgor loss point.

Regarding hydraulic traits, the distribution was largely homogeneous across the functional types, as neither P50 nor Ψ_{tlp} differed significantly between Type 1 and 2 ($p > 0.05$; Figure 6). However, a notable exception was observed for Type 3 (represented solely by *G. officinale*), which exhibited extreme resistance to leaf dehydration with a Ψ_{tlp} of -3.8 MPa, compared with -2.1 MPa in Type 1 and -2.3 MPa in Type 2. This species expresses an extreme combination of carbon-conservative and hydraulic-tolerant strategies.

These results directly support the conclusion that, in these insular forest ecosystems, conservative evergreen species are not systematically associated with higher drought tolerance, and carbon-acquisitive deciduous species are not associated with greater hydraulic vulnerability.

4. Discussion

4.1. Soft Trait Typology Reflects the Leaf Economics Spectrum in Tree Species from Dry and Cloud Forest in the Caribbean

The three functional types identified in this study are consistent with the global leaf economics spectrum [14,24,65,79], here extended to an underrepresented Caribbean context. While the first two axes of our principal component analysis capture approximately 64% of the total variance, this value remains consistent with large-scale macroecological analyses (e.g., [9,24,37,38,41,43,79]). This moderate variance highlights the multi-dimensional nature of plant functional strategies. Specifically, Type 1 (deciduous dry forest species) occupies the acquisitive end of the spectrum, characterized by high SLA, large LA, low WD, fast

growth, and high photosynthetic capacity. In contrast, Types 2 and 3 (evergreen species from both forest types) cluster at the conservative end, with low SLA, small LA, high WD, slow growth, and reduced photosynthetic rates. This pattern confirms that soft traits (SLA, LA and WD) effectively discriminate carbon functional strategies in Caribbean forests, extending findings from multi-biome analyses [14,18,24,38,43].

A particularly notable result is the convergence of dry (DF) and cloud (CF) forest evergreen species within Type 2. Despite contrasting water availability (1330 mm vs. 4644 mm annual rainfall), these species share similar conservative leaf traits. This convergence reflects distinct yet functionally overlapping ecological filters. While DF species are constrained by seasonal soil water deficits, CF species experience episodic atmospheric water deficits. Even in high-rainfall environments, CF trees frequently face cloud-clearing events that generate high VPD above the canopy, combined with shallow or poorly developed root systems that restrict water uptake. Both selective environmental constraints favor sclerophylly and conservative resource-use strategies [24,32,80–82]. Such patterns illustrate convergent trait syndromes arising under different environmental selective pressures [28,38].

Consequently, while this study highlights the importance of phenology (deciduous vs. evergreen) in structuring the carbon strategies of DF species, it also provides a critical baseline for understanding functional coordination in understudied Caribbean tropical ecosystems. This suggests that leaf habit must be carefully integrated into trait-based models of Caribbean forest dynamics, while functional diversity should be actively prioritized in species selection for restoration programs specific to the Caribbean, notably for DF, where high functional diversity exists.

4.2. Why Do Soft Traits Fail to Predict Drought Tolerance?

4.2.1. The Decoupling of Economic and Hydraulic Axes

Despite their widespread use as drought indicators, the failure of soft traits (Ds, Dt, SLA, WD) to predict drought tolerance in our study is consistent with growing evidence that morphological proxies are often insufficient to capture the complex physiological dimensions of drought resistance [1,3,28,43]. At the group level, the distribution of drought-related traits was largely homogeneous across the three functional types. Neither Ψ_{tlp} nor P50 differed significantly between Types 1 and 2, indicating that evergreen species with conservative carbon strategies are not systematically associated with higher drought tolerance, nor are acquisitive deciduous species consistently linked to greater vulnerability, as frequently suggested in the literature, e.g., [17–20]. This lack of differentiation at the group level suggests a decoupling between the carbon economics spectrum and plant hydraulic strategies. Recent modelling work further supports this independent evolution of carbon-use strategies and hydraulic traits. For instance, Langan et al. [7] demonstrated that tropical forest species are structured along two distinct axes: a productive–conservative axis and a whole-plant hydraulic strategy axis. Their simulations confirm that leaf habit explains only a fraction of hydraulic variance and does not fully predict drought tolerance. These findings reinforce that, although phenology strongly structures carbon-use strategies and is often associated with contrasting water-use behaviours (deciduous = avoidance, evergreen = tolerance), phenological and hydraulic traits remain related yet distinct dimensions of drought-response strategies. In particular, phenology does not predict hydraulic tolerance as quantified by P50 or Ψ_{tlp} , which vary widely within both leaf-habit groups [42].

4.2.2. Mechanistic Limitations of SLA, WD Ds and Dt as Drought Proxies

The relevance of SLA and WD as proxies for plant drought tolerance requires careful, context-specific evaluation [41,42]. While earlier research suggested that SLA could serve as a proxy for drought tolerance [15,16], our findings indicate that it fails to differenti-

ate water sensibility among Caribbean species, confirming that Ψ_{tlp} and P50 often vary independently of carbon economic investments [1,33–35,40,42].

Similarly, although high WD is often associated with embolism resistance [3,6,17,30,71], its lack of differentiation across our functional types may stem from its inherent multifunctionality. Because WD integrates mechanical support, pathogen defense, and water storage [18,19], it can be decoupled from xylem embolism resistance. Indeed, xylem vulnerability is more directly influenced by microscopic properties, such as pit membrane structure and vessel diameter, rather than bulk wood density [20,21,40–42]. Instead of relying on soft traits, actual drought responses are likely mediated by complex trade-offs involving unmeasured key traits, including rooting depth, cuticle thickness, and dynamic physiological responses during the dry season [21,39,41,83,84].

This decoupling is coherent with the results of epidermal morphological traits, Ds and Dt, which showed weak discriminatory power among the three functional types (accounting for less than 20% of the variance). These traits were characterized by high intra-type variability and limited inter-type contrast. Consequently, the pattern where stomatal traits provide stronger mechanistic insight into drought response than SLA and WD is not supported in this Caribbean tree typology. Instead, our results suggests that Ds captures fine-scale, physiological adjustments rather than broad functional strategies. In this sense, several studies report a strong link between stomatal density and plant water regulation capacity, particularly through its effects on transpiration rates and drought sensitivity [3,23–28,37,42]. A higher Ds may primarily enable faster and more precise transpiration regulation rather than defining a fixed group-level tolerance strategy.

4.2.3. Phenological Traps in Dry Forest: Avoidance vs. Tolerance

A closer look at these patterns highlights that while phenology (deciduous vs. evergreen) is traditionally associated in the literature with two distinct water-use schemes, drought avoidance versus drought tolerance [6], this framework can be misleading if oversimplified. In DF, our results reflect a clear distinction deciduous species (via leaf shedding characterizes a drought avoidance strategy) and evergreens (which rely on the physiological ability to maintain function at low water availability characterizes a drought tolerance strategy) [6]. However, within this ecosystem, there is no straightforward hydraulic gradient based on P50 and Ψ_{tlp} . Instead, drought avoidance and tolerance represent multi-trait syndromes that are difficult to characterize using only two drought traits, as exemplified by the overlapping interspecific hierarchy observed in this study: *Citharexylum fruticosum* ~ *Bursera simaruba* ~ *Ficus citrifolia* ~ *Tabebuia heterophylla* > *Sideroxylon salicifolium* > *Guapira fragrans* > *Guaiacum officinale*. To refine the characterization of these overlapping strategies, future research should integrate complementary dynamic hydraulic measurements, such as leaf capacitance, minimum leaf water potential, and the speed of stomatal closure under seasonal drought conditions.

4.2.4. *Guaiacum officinale* as a Functional Outlier and Restoration Key Species

Within this framework, Type 3 (*G. officinale*) illustrates a highly distinct functional group with an extreme conservative strategy not captured by the main conservative typology of DF. This species displays exceptionally high wood and stomatal densities coupled with the strongest physiological resistance to leaf dehydration documented in our sample (Ψ_{tlp} of -3.8 MPa, compared to -2.1 Mpa in Type 1 and -2.3 Mpa in Type 2). Combined with some of the highest WD values recorded in tropical trees and extremely slow growth rates [43], the distinctiveness of this species demonstrates that interspecific functional differences among DF evergreens can far exceed the differences found between evergreen species of different biomes, such as dry and cloud forests [32,42,85].

Caribbean dry forests were historically overexploited during 17th-century colonization, leading to a drastic reduction of primary dry forest in favor of agricultural landscapes. Given its unique functional specificity, extreme drought tolerance, and current rarity, *G. officinale* should be prioritized in Caribbean forest restoration programs. It represents a potential keystone species for maintaining ecosystem resilience under projected increases in tropical drought intensity.

4.3. Implications for Trait-Based Modeling and Forest Management

Our results confirm H1 (soft traits identify distinct carbon-use strategies), and H2 (weak context-dependent correlations between soft and hard traits limit the use of morphological proxies for drought tolerance). These findings underline the need for caution when using soft traits to predict drought responses in tropical plant communities [3,42] and highlight the importance of integrating hydraulic and cellular traits such as P50 and Ψ_{t1p} into management strategies. This has implications both for the use of functional traits to characterize tree drought response strategies and for the sustainable management of tropical Caribbean forests [29]. The functional diversity observed within dry forest may help buffer ecosystem functioning against drought intensification. Integrating multiple trait dimensions is therefore essential for maintaining forest resilience, safeguarding Caribbean biodiversity, and developing more robust predictive frameworks for forest management in an increasingly water-limited world [7,35,42,85,86]. Within this regional approach and exploratory framework, our results provide an initial functional baseline for guiding forest restoration and management in Caribbean (SIDS). To align with the objectives of Caribbean SIDS national forest management strategies, specific forest restoration programs should prioritize the maintenance of functional diversity within dry forest communities. This includes incorporating species from all functional types, protecting and restoring *G. officinale* populations as an extreme drought-tolerant species, and identifying zones where the vulnerability of acquisitive deciduous species (Type 1) could be monitored in the context of drought intensification.

5. Conclusions

By integrating a wide array of morphological traits linked to carbon economy and drought response across two contrasting insular ecosystems, this study successfully distinguished three functional groups of Caribbean tree species reflecting a clear gradient along the fast–slow carbon economics spectrum. This unique and understudied biogeographic context, characterized by distinct climate regimes and species pools compared with continental tropical forests, provided a robust framework to demonstrate that functional types defined solely by morphological soft traits fail to capture the drought tolerance of these species, highlighting that closer attention must be paid to plant phenology. One evergreen species, *G. officinale*, stands out by exhibiting an extreme conservative strategy, characterized by exceptionally high wood density and the strongest resistance to leaf dehydration.

For forest management and conservation under climate change, these results have critical implications for local species selection, highlighting the need to include species with high water resistance, while maintaining a gradient of functional diversity within insular communities. This approach can directly support regional conservation priorities in Caribbean ecosystems. Future research should expand this trait database to include additional water-related plant responses, a broader range of insular species and sites, in order to rigorously test the stability and generality of these functional types across the Caribbean archipelago and to strengthen predictive frameworks for ecosystem resilience in an increasingly water-limited future.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/su18146968/s1>. Figure S1. Pearson correlation matrix among soft and hard functional traits measured on 14 tree species from the Lesser Antilles. Correlation coefficients are represented by circles, where the color indicates the sign (blue: negative; red: positive) and the color intensity reflects its strength (more saturated colors indicate stronger correlation). Circle size is proportional to the absolute value of the correlation coefficient. White cells indicate non-significant correlations (Pearson test, $p \geq 0.05$). * Correspond to $p < 0.05$; ** to $p < 0.01$; and *** $p < 0.001$. Trait abbreviations are provided in Table 2. Table S1. Eigenvector scores of plant traits on the first three axes of a standardized PCA, obtained from a matrix of 5 traits $\times$ 55 individuals from 14 species. The table also reports the eigenvalues for each axis and the Kaiser–Meyer–Olkin (KMO) measure of sampling adequacy, reported per variable and globally (indicate by * in the table). Eigenvalues > 1 indicate components retained according to Kaiser’s criterion (1958). The KMO statistic (Kaiser 1974) [87] evaluates the proportion of shared variance among variables; values ≥ 0.60 are considered acceptable for component extraction. Trait abbreviations: LA = leaf area (cm^2), SLA = specific leaf area ($\text{cm}^2 \text{g}^{-1}$), WD = wood density (g cm^{-3}), Ds = stomatal density (N mm^2), Dt = trichome density (N mm^{-2}). Figure S2. Leaf adaxial imprints of A: *Bursera simaruba*, B: *Citharexylum fruticosum*, C: *Ficus citrifolia*, D: *Guaiacum officinale*, E *Guapira fragrans*, F: *Sideroxylon salicifolium*, G: *Tabebuia heterophylla*, H: *Charianthus alpinus*, I: *Clusia major*, J: *Ilex sideroxyloides*, K: *Rapanea trinitatis*, L: *Richeria grandis*, M: *Schefflera attenuata*, N: *Siphoneugena densiflora*. Arrows show trichoms. Figure S3. A. Silhouette widths (si) quantify the cohesion and separation of the three clusters obtained from hierarchical clustering on PCA coordinates. Each bar represents one species, grouped by cluster. Positive values indicate consistent cluster assignment, while negative values would indicate misclassification. The average silhouette width (0.51) reflects an overall good clustering structure, with type 3 showing the highest cohesion (0.63), followed by Type 1 (0.53) and Type 2 (0.42). B. Bootstrap dendrogram showing the stability of hierarchical clustering. The dendrogram displays the hierarchical relationships among species based on Euclidean distances and Ward.D2 linkage. Red numbers indicate AU p -values (Approximately Unbiased), derived from multiscale bootstrap resampling; values above 95% denote statistically stable clusters. Green numbers indicate BP p -values (Bootstrap Probability), corresponding to classical bootstrap support, generally more conservative. Red rectangles highlight branches with AU $\geq 95\%$, representing highly stable sub-clusters. Note that pvclust evaluates the stability of individual hierarchical splits independently of the chosen number of clusters, so stable sub-clusters do not necessarily correspond to the three functional groups defined from PCA. Figure S4. Mean P50 and Ψ_{tlp} values for each species of the study in two Caribbean ecosystems, with dry forest species shown in black and cloud forest species shown in blue.

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