

Vegetation Structural Complexity across Tenerife's Zonal Vegetation Types, captured by Terrestrial Laser Scanning

Abstract

Questions: Vegetation structural complexity, defined as the density and distribution of plants in three-dimensional (3D) space, is a key ecological property of plant communities, influencing biodiversity and ecosystem functioning. Yet, how vegetation structural complexity varies across contrasting vegetation types, and which factors drive this variation remain poorly understood. This knowledge gap is particularly relevant on oceanic islands, where diverse vegetation types occur across steep environmental gradients and are often highly vulnerable to disturbance. Specifically, we asked: (1) how does vegetation structural complexity vary among and within vegetation types, (2) by which structural dimensions do the vegetation types most differ, and (3) which climatic factors explain this variation?

Location: Tenerife, Canary Islands.

Methods: With 140 scans in 28 plots covering 6 major zonal vegetation types, we derived the Stand Structural Complexity Index (SSCI), which measures the 3D arrangement of vegetation, and other metrics related to vertical stratification, vegetation density, and canopy openness, captured by terrestrial laser scanning (TLS) 3D point clouds. For each metric, mean values and coefficient of variation (CV) per plot were analysed with a permutation Analysis of Variance (ANOVA) and a Principal Component Analysis (PCA). Relationship with long-term climatic plot data was analysed using robust linear models.

Results: The SSCI differed significantly among zonal vegetation types (permutation ANOVA, $p < 0.001$). The SSCI ranged from a high mean value and low variability in laurel forests (mean = 7.00, CV = 10.1%) to the lowest mean value in the summit scrub (mean = 2.65, CV = 65.6%) but highest variability in the tabaibal coastal scrub (mean = 4.93, CV = 91.0%). PCA indicates that vegetation structural complexity in forests was characterised by high vertical stratification and closed canopy. In contrast, scrub types displayed greater canopy openness and a high variation in 3D vegetation density. Greater annual precipitation were associated with linear increased SSCI across zonal vegetation types, positively related to increased vertical stratification and canopy height and negatively related to canopy openness and 3D vegetation density.

Conclusions: Our results suggest that TLS-derived metrics of vegetation structural complexity captures within and across vegetation type variation. The SSCI can provide meaningful information beyond forests when interpreted alongside other structural metrics. Our results suggest that differences across vegetation types are associated with climatic gradients. This study provides a basis for future studies and applications of TLS beyond forests, that can aid biodiversity monitoring and conservation of environmentally-distinct and disturbance-prone island vegetation.

Keywords: Vegetation Structural Complexity, Oceanic Islands, Habitat Heterogeneity, Terrestrial Laser Scanning, Plant Architecture, Climatic Gradients, Vegetation Organisation, Stand Structural Complexity Index

1. Introduction

Vegetation structural complexity is broadly defined by the density and distribution of plants in three-dimensional (3D) space (Seidel *et al.*, 2016; Ehbrecht *et al.*, 2017). As an emergent property of vegetation, it influences food web dynamics, species diversity, and primary productivity (Castaño-Villa *et al.*, 2014; Saint-Béat *et al.*, 2015; Fotis *et al.*, 2018; Ray *et al.*, 2024), and so helps biodiversity patterns and ecosystem functioning (Braunisch *et al.*, 2019; Atkins *et al.*, 2023). Modifications to vegetation structural complexity, whether through natural succession or anthropogenic disturbance, can therefore alter ecosystem processes and habitat suitability. Quantifying vegetation structural complexity and tracking its change over time is thus increasingly important for biodiversity monitoring and conservation.

This quantification is particularly important in locations experiencing land-use change and climate-induced shifts, such as oceanic islands (Otto *et al.*, 2007; Grimm *et al.*, 2013; Otto *et al.*, 2017; Fernández-Palacios *et al.*, 2021). On Tenerife and Gran Canaria (Canary Islands), for instance, over 98% of thermophilous woodland and 99% of laurel forest have been lost, respectively, (Otto *et al.*, 2012; Fernández-Palacios *et al.*, 2021). Such habitat degradation can alter community composition, vegetation density, and canopy cover, potentially simplifying vegetation structure (Caviedes and Ibarra, 2017). This simplification can affect ecosystem stability and species habitat suitability, ultimately driving species extinctions or extinction debts (Caviedes and Ibarra, 2017; Otto *et al.*, 2017; Fernández-Palacios *et al.*, 2025). Characterising the vegetation structural complexity of vulnerable ecosystems may therefore help assess future disturbance, restoration success, and climate-driven vegetation

change (Shugart *et al.*, 2010; Godbold *et al.*, 2011; Fischer *et al.*, 2019; Fernández-Palacios *et al.*, 2025).

Although vegetation structural complexity is often treated as a single property, it is inherently multidimensional. Vertical stratification, vegetation height, canopy layering, vegetation density, and architectural variation all contribute to the 3D arrangement of plant material (Ehbrecht *et al.*, 2017; Coverdale and Davies, 2023). New remote sensing approaches have become useful in the rapid quantification of multiple structural metrics, particularly in forests (Camarretta *et al.*, 2020). For example, Ehbrecht *et al.* (2016, 2017) developed the Stand Structural Complexity Index (SSCI) and the Effective Number of Layers (ENL) – a measure of vertical stratification – to capture the heterogeneity of plant material distribution in 3D space using terrestrial laser scanning (TLS). The SSCI has deepened our understanding of the relationships between vegetation structural complexity, species diversity, and forest management outcomes (Zemp *et al.*, 2019; Perles-Garcia *et al.*, 2021). Unlike conventional field measurements that quantify individual structural attributes (e.g., canopy height or total vegetation cover), TLS captures the 3D distribution of vegetation and allows multiple structural dimensions to be measured simultaneously (Cimmins *et al.*, 2026). This gives a detailed reconstruction of vegetation space occupation that is difficult to quantify with traditional methods. Furthermore, it allows rapid and more systematic surveying and monitoring of vegetation (Frey *et al.*, 2019). However, methods to quantifying vegetation structural complexity have been developed and tested primarily in forest systems, where vertical stratification is usually a dominant axis of structural variation.

Low-stature, open vegetation such as shrublands can express structural complexity differently from forests. In these vegetation types, density, patchiness, and fine-scale architectural variation contribute more to overall vegetation structural complexity than canopy height alone (Burrell, 2024). Horizontal structural attributes or 3D structural heterogeneity are known to matter for biodiversity, likely creating more niche space for a wider range of taxa by altering light availability and microclimate (Tuolalibieke *et al.*, 2026). Even in tall vegetation, horizontal heterogeneity has a larger influence on bird species richness than vertical structure (Carrasco *et al.*, 2019). This contribution suggests the horizontal dimension is ecologically significant regardless of the habitat type (Bhatta *et al.*, 2025).

These contrasting structural characteristics suggest that overall vegetation structural complexity can vary across vegetation types depending on the relative importance of vertical

and horizontal dimensions. These structural components can also vary within vegetation types, creating gradients of structural complexity (Figure 1). Such variation may arise from unique combinations of abiotic and biotic drivers (Ehbrecht *et al.*, 2021). Accordingly, the relative contribution of structural components to overall vegetation structural complexity in low-stature and open vegetation may differ fundamentally both from and between forest-types. Understanding how structural dimensions vary among and within vegetation types is critical to treating vegetation structural complexity as a general ecological property rather than a forest-specific metric. Whether integrated indices such as the SSCI can capture this variability remains poorly understood. Establishing this would strengthen the application of these metrics in conservation and restoration, enabling ecosystem-specific baselines, degradation detection, and recovery tracking following restoration to be quantified. This is essential if we are to adequately conserve the structural integrity in contrasting ecosystems threatened by disturbance and climate change.

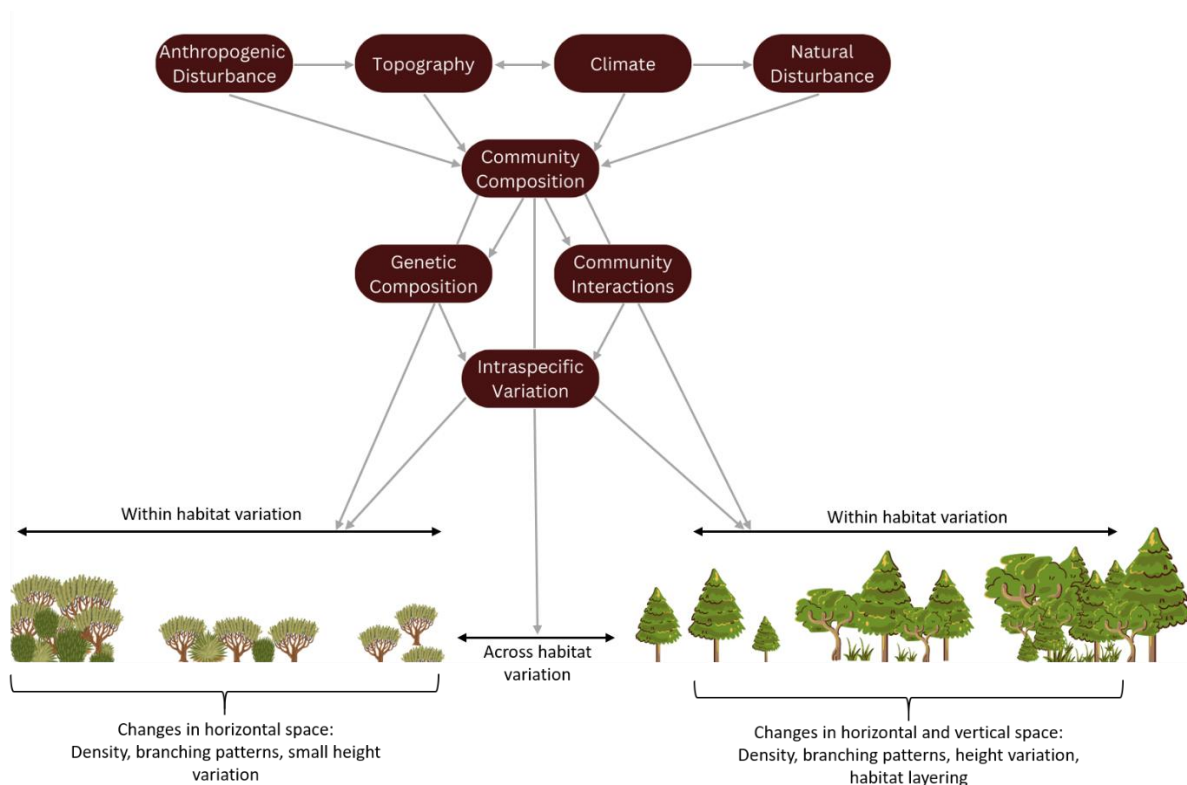


Figure 1. Cascading effects of abiotic and biotic drivers of vegetation structural complexity leading to across and within vegetation type variation in vegetation structural complexity.

Figure adapted from Ehbrecht *et al.*, 2021. Figure created in Canva: ©Media elements designed by Jea Gaviña and Ianna Rallonza via Canva.com.

Oceanic islands provide an ideal opportunity to study vegetation structural complexity across contrasting vegetation types, given their environmental gradients over relatively small spatial extents. The volcanic origin, complex topography, and often high precipitation variation (Weigelt *et al.*, 2013; Barajas-Barbosa *et al.*, 2020) may drive high vegetation heterogeneity at fine spatial scales, producing distinct zonal vegetation types (Mallet *et al.*, 2014). These conditions provide an opportunity to examine how vegetation structural complexity metrics vary across contrasting vegetation types within a common biogeographic setting. Quantifying this structural variation can also provide baseline data for detecting future changes in island vegetation and supporting biodiversity monitoring and ecosystem restoration (Borges *et al.*, 2018).

Here, we quantified vegetation structural complexity across the major zonal vegetation types, whose distribution is largely determined by climatic gradients (del Arco *et al.*, 2018), across the oceanic island of Tenerife. Using TLS, we derived several metrics of vegetation structural complexity across these contrasting vegetation types, including SSCI, ENL, and other metrics related to vegetation density, and canopy openness. Although numerous structural complexity indices exist (Seidel, 2018; Reich *et al.*, 2021; Batchelor *et al.*, 2022), we used the SSCI (Ehbrecht *et al.*, 2017), as it is a well-established indicator of structure linked to management, micro- and macroclimate, and species diversity (Knuff *et al.*, 2020; Zemp *et al.*, 2023; Ehbrecht *et al.*, 2026; Pierick *et al.*, 2026).

Specifically, we asked (i) to what extent does the SSCI and other metrics vary within and across vegetation types?, (ii) based on which structural dimensions do the vegetation types most differ?, and (iii) what is the relationship between the SSCI and its components with climatic variables across zonal vegetation? We predicted that (H1) forest vegetation would show greater structural complexity through increased vertical stratification and height whereas shrub-dominated vegetation would achieve structural complexity primarily through denser branching architecture and horizontal organisation. We expected (H2) that metrics related to these vertical and horizontal dimensions would differentiate forests and shrub-related vegetation types. We further predicted (H3) that SSCI would be positively associated with wetter environments through increased development of vertical structure, reflecting greater vegetation structural complexity under favourable climatic conditions.

By exploring vegetation structural complexity patterns, along with the climatic associations in Tenerife, we aimed to determine how vegetation architecture is organised across a steep

island environmental gradient and advance our understanding of vegetation structural complexity as a multidimensional ecological property. Further, this is a novel application of the SSCI and ENL outside forests, and exploration of its capacity to detect variability within and across vegetation types along environmental gradients. Our quantification provides baseline data of vegetation structural complexity in primary habitats and builds a foundation for future conservation applications and biodiversity monitoring of island zonal vegetation types, utilising TLS LiDAR data.

2. Methods

2.1 Study Site and Island Habitats

Tenerife (28°35'15'' - 27°59'59'' N and 16°5'27'' – 16°55'4'' W) is a 2038 km² large island located within the Canary archipelago off the northwest coast of Africa. Due to its volcanic origin, Tenerife has high topographical variation, with a maximum elevation of 3718 m above sea level (Blanco-Montenegro *et al.*, 2011). Five major zonal vegetation types (Figure 2) occur on Tenerife because of environmental gradients across the island (del Arco *et al.*, 2018):

1. Coastal scrub – a habitat with lower-lying shrub vegetation dominated by endemic *Euphorbia* species, made up of two communities: tabaibal and cardonal. Dominant species include *Euphorbia balsamifera* and *Euphorbia canariensis* respectively. The vegetation type is adapted to lowland semi-arid environment between 200 – 300 m (windward slope) and up to 600 m (leeward slope) above sea level (Otto *et al.*, 2001).
2. Thermophilous woodland – open woodland, typically found at mid-elevations of 200 – 800 m on steep windward and leeward slopes, dominated by juniper (*Juniperus turbinata* subsp. *canariensis*), wild olives (*Olea cerasiformis*) or mastic (*Pistacia atlantica*) trees (Otto *et al.*, 2012; Fernández-Palacios *et al.*, 2024).
3. Laurel forest – a neogene relic broadleaved forest, characterised by high humidity and dominated by different trees species, including four Lauraceae species, on windward slopes of elevations between 600 – 1200 m (Fernández-Palacios *et al.*, 2017).
4. Canarian pine forest – coniferous forest dominated by *Pinus canariensis*, found between 1200 – 2000 m on the windward slope and 800 – 2200 m at the leeward slope (Parsons, 1997).

5. Summit scrub – restricted to the peak of El Teide surroundings (i.e. summit, highlands, high elevation above 2000 m), largely consisting of shrub leguminous vegetation, dominated by *Cytisus supranubius* and *Pterocephalus lasiospermus* (Renner *et al.*, 2023).



Figure 2. The main zonal vegetation types found on Tenerife: A) tabaibal coastal scrub, B) cardonal coastal scrub, C) thermophilous woodland, D) laurel forest, E) pine forest, and F) summit scrub. Image credits: Samantha Suter (A, B, C, D, E) and José María Fernández-Palacios (F).

2.2 Sampling Design

Between June and November 2024, we surveyed the major zonal vegetation types of Tenerife, including two distinct coastal scrub types: one dominated by the cactus-like *Euphorbia canariensis* (cardonal) and the other by the hemispherical, highly branched cushion-like *Euphorbia balsamifera* (tabaibal). The surveyed plots belong to a network established in previous studies (Otto *et al.*, 2001; de Nascimento *et al.*, 2015; Borges *et al.*, 2018), selected to cover the most mature stands with low disturbance levels of each vegetation type. We surveyed three to five plots within each zonal vegetation type (Figure 3), each 20 x 20 m for shrubby communities or 50 x 50 m in size for forested communities, determined by the vegetation type accessibility and extent in these previous studies (Table 1). As the SSCI and its components are scale-independent, i.e., they do not increase with area, differing plot sizes do not influence the computed indices values.

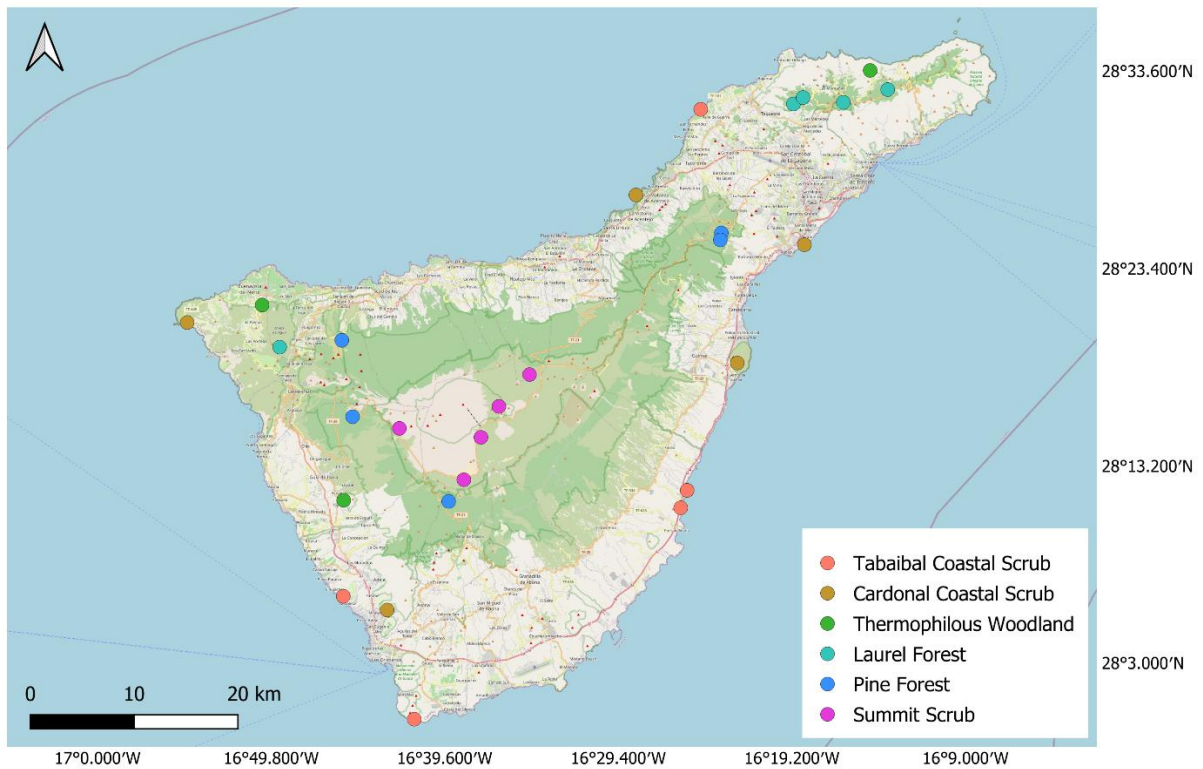


Figure 3. Plot locations of terrestrial laser scans taken in the major zonal vegetation types across Tenerife: coastal scrub (tabaibal and cardonal), thermophilous woodland, laurel forest, pine forest, and summit scrub.

A FARO Focus M70 terrestrial laser scanner (Faro Technologies Inc., Lake Mary, USA) was used to scan the plots in each vegetation type. Five single scans in each plot were performed, one in the centre of the plot and one in each corner. A tripod was used to set the scanner height at approximately 1.3 m, scanning a field of view of 360° horizontally, 300° vertically, and a step width of ~0.035° (Soto *et al.*, 2024; Onyiriagwu *et al.*, 2025; Ehbrecht *et al.*, 2026). A total of 140 scans were performed.

2.3 Vegetation Structural Complexity Computation

The scans were imported into the software FARO SCENE to handle the point cloud data from the TLS. This enables the exportation of scans into an .xyz format, using the export function to convert individual points into coordinates and angular information. The .xyz files were then analysed in R version 4.3.3 (R Core Development Team, 2024). The SSCI is constructed through two other underlying variables: the mean fractal dimension index (MeanFRAC) and the effective number of layers (ENL).

The MeanFRAC index incorporates the geometric complexity of vegetation arrangement, influenced by vegetation packing and architecture, and increases with vegetation density. Higher MeanFRAC values imply higher vegetation density (*sensu* Ehbrecht *et al.*, 2026). It is calculated through the creation of polygons at cross-sections within the 3D point cloud and averaging the fractal dimensions across these (Ehbrecht *et al.*, 2017). The ENL captures the vertical distribution of plant material and increases with increasing stand height and a more even occupation of vertical layers by plant material. The ENL is based on the diversity of vertical layers weighted by the vegetation relative space occupation derived from a Simpson's Index calculation (Ehbrecht *et al.*, 2016). Canopy openness and canopy height were also computed, following the description in Ehbrecht *et al.* (2021).

Each metric was aggregated from the five scans per plot to calculate plot means, standard deviations, and coefficient of variation. Distribution of the data at plot level can be visualised in Figure S1.

Modifications to the script to compute vegetation structural complexity occurred when errors were encountered in post-processing of the point cloud data. No values of SSCI were considered as outliers after inspection of 3D point clouds to ensure no artifacts were present. These points are discussed further in Supplementary Note 1.

2.4 Climate Data

We extracted climatic data from the CanaryClim v1.0 dataset in our analyses (Patiño *et al.*, 2023), that incorporates downscaled climatic data for the period 1979–2013 at a 100 m spatial resolution, to provide long-term climatic averages. We originally extracted all available climatic variables from the dataset to explore the relationship between vegetation structural complexity metrics and climate. The full list of variables can be found in Table S2, further descriptions can be found in Patiño *et al.* (2023). We subsequently conducted variable selection outlined in section 2.5.

2.5 Statistical Analysis

We tested differences in vegetation structural complexity metrics across vegetation types using permutation analysis of variance (ANOVA) (5000 permutations, suitable for small sample sizes, using the R package “lmPerm” (Wheeler *et al.*, 2016)). We report effect size (ω^2), as the proportion of variance in the response variable attributable to vegetation type, while accounting for sampling error. Pairwise comparisons used permutation tests, reporting adjusted-p values with the false discovery rate (FDR), which controls for multiple testing. Given the small number of plots, we ran a linear mixed-effects model (scan ID as random effect) as a sensitivity analysis to investigate explained variance in SSCI from vegetation type (Table S1). Within-vegetation type variability in vegetation structural complexity was quantified using the coefficient of variation (CV: SD of per-scan SSCI, ENL, and MeanFRAC divided by plot-mean values). Permutation ANOVAs and FDR-corrected pairwise comparisons similarly investigated differences in within-vegetation type variability.

A principal component analysis (PCA) was used to investigate the organisation of structural components across vegetation types in reduced (two) dimensions. We used the “prcomp” function in the “stats” package to compute the PCA (R Core Development Team, 2024). The variables were scaled for computation of the PCAs. We looked at the variable loadings to understand how each structural metric was differentiating vegetation types and defining structural gradients.

To explore how climate is associated with vegetation structural complexity, we initially used multiple linear regression analysis. A linear mixed-effects model including vegetation type as a random intercept was initially fitted; however, the random-effect variance was estimated to be negligible, and the model fit was improved with a linear model ($\Delta\text{AIC} = 34$). Therefore,

subsequent analyses were conducted using a robust linear model (package “MASS” (Ripley, 2022)) to account for a moderately influential observation identified during model diagnostics (Cook's Distance = 0.49).

To identify climatic variables most consistently associated with vegetation structure, we fitted separate single-predictor robust linear regression models for each of the five structural metrics and each climatic predictor. We used Akaike's Information Criterion corrected (AICc) for small sample size to evaluate model performance, with models having $\Delta\text{AICc} \leq 2$ considered to have substantial support (Figure S2). We identified and retained the climatic predictor that showed the most consistent support across structural metrics (weighted across the five structural metrics), as the common climatic predictor in the final analyses: mean annual precipitation (Table S2). Visual model diagnostic checks indicated no severe violation of regression assumptions. Effects were considered indicative of an association when the robust regression t-statistic was either greater than 2 or less than -2 (i.e., $|t| > 2$). This was supported with uncertainty in regression coefficients, quantified using 5000 bootstrap resamples to obtain percentile-based 95% confidence intervals. Effects were considered supported when confidence intervals did not cross zero. Model fit was quantified using pseudo R^2 values calculated using the residual sum of squares and total sum of squares from the robust regression models. All analysis was conducted in R version 4.3.3 (R Core Development Team, 2024) with significance values set to 0.05 where applicable.

3. Results

3.1 Vegetation Structural Complexity across Zonal Vegetation Types

The SSCI ranged from the lowest mean values per plot exhibited by the summit scrub (average across plots: 2.65; 95% CI: 0.33 – 4.98) to the highest by the laurel forest (average across plots: 7.00; 95% CI: 4.67 – 9.33). These differences in the SSCI mean values per plot were overall significant across vegetation types (permutation ANOVA, $p < 0.001$, 5000 permutations) (Figure 4a), where habitat had a moderate effect size on SSCI ($\omega^2 = 0.23$). Pairwise permutation comparisons indicated significant differences in the SSCI mean values per plot specifically between cardonal coastal scrub and laurel forest ($F = 75.77$, $R^2 = 0.904$, adjusted- $p = 0.039$), and pine forest and laurel forest ($F = 44.04$, $R^2 = 0.85$, adjusted- $p =$

0.039), and laurel forest and summit scrub ($F = 20.59$, $R^2 = 0.72$, adjusted- $p = 0.039$). The full summary of the pairwise comparisons can be found in Table S3.

The other metrics also differed amongst vegetation types (Table 1). Vertical stratification as calculated by mean ENL values per plot was lowest in tabaibal coastal scrub (average across plots: 2.38; 95% CI: 0.51 – 4.29), and highest in pine forest (average across plots: 20.80; 95% CI: 18.91 – 22.69). We found that these differences in ENL mean values per plot were significant across vegetation types (permutation ANOVA $p < 0.001$, 5000 permutations) with a large effect size $\omega^2 = 0.92$. Pairwise comparisons showed that most vegetation type pairs (12 of 15) differed significantly after FDR correction (Figure 4b; Table S3), with particularly large effects involving laurel forest and pine forest ($R^2 = 0.57 – 0.92$; Table S3). However, cardonal coastal scrub did not significantly differ from summit scrub or tabaibal coastal scrub, and summit scrub did not differ from tabaibal coastal scrub.

Vegetation density as measured by MeanFRAC mean values per plot was lowest in pine forest (average across plots: 1.57; 95% CI: 0.51 – 2.63) and highest in tabaibal coastal scrub (average across plots: 6.63; 95% CI: 5.76 – 7.87). The MeanFRAC mean values per plot significantly differed across vegetation types (permutation ANOVA $p < 0.001$, 5000 permutations, $\omega^2 = 0.69$) (Figure 4c). Pairwise permutation comparisons revealed significant differences in MeanFRAC mean values per plot among seven of the 15 vegetation type pairs (Table S3). The strongest differences were seen between the pine forest and the tabaibal coastal scrub ($F = 81.715$, $R^2 = 0.91$, adjusted- $p = 0.031$) as well as the laurel forest ($F = 65.329$, $R^2 = 0.89$, adjusted- $p = 0.031$), and the laurel forest and tabaibal coastal scrub ($F = 57.097$, $R^2 = 0.88$, adjusted- $p = 0.031$).

Canopy openness was on average 100% (95% CI: 90.00 – 110.00) for scrubs. For the forests and woodlands, the lowest canopy openness was observed in laurel forest (average across plots: 5.01%, 95% CI: 5.00 – 15.00) and the highest in thermophilous woodland (average across plots: 73.26%, 95% CI: 60.30 – 86.20). The highest canopy height was recorded in the pine forest at 31.40 m on average across plots (95% CI: 28.33 – 34.47) and the lowest in the tabaibal coastal scrub of 4.08 m on average across plots (95% CI: 1.01 – 7.15) (Table 1).

Table 1. Plot information and vegetation type averages (+ 95% confidence intervals (CIs)) of computed structural measures: Stand Structural Complexity Index (SSCI), Effective Number of Layers (ENL), Mean Fractal Dimension (MF), canopy openness (CO), and canopy height (CH) derived from terrestrial laser scanning across Tenerife.

	Vegetation Type					
	Tabaibal Coastal Scrub	Cardonal Coastal Scrub	Thermo-philous Woodland	Laurel Forest	Pine Forest	Summit Scrub
Processed Scans (n)	24	25	15	25	25	25
Plot Size (m)	50 x 50; (1 plot 20 x 20)	50 x 50	20 x 20	50 x 50	50 x 50	50 x 50
SSCI	4.93 CI 2.45 – 8.96	3.31 CI 2.96 – 3.81	5.77 CI 4.01 – 7.76	7.00 CI 6.54 – 7.63	3.92 CI 3.4 – 4.38	2.65 CI 1.83 – 4.22
ENL	2.33 CI 1.66 – 3.30	3.44 CI 2.71 – 4.1	6.89 CI 4.23 – 8.59	14.60 CI 13.16 – 16.24	20.80 CI 17.66 – 22.86	3.28 CI 2.62 – 4.27
MF	6.79 CI 5.33 – 8.25	2.93 CI 2.31 – 3.59	2.82 CI 1.99 – 4.22	2.09 CI 2.01 – 2.19	1.57 CI 1.50 – 1.62	2.40 CI 1.61 – 3.68
CO	100 CI 100 – 100	100 CI 100 – 100	73.26 CI 8.92 – 137.60	5.01 CI -1.79 – 11.80	40.21 CI 19.65 – 60.77	100 CI 100 – 100
CH	3.91 CI -0.66 – 8.478	6.04 CI 3.64 – 8.44	16.13 CI 2.71 – 29.56	22.56 CI 19.20 - 25.91	31.40 CI 26.67 - 36.13	4.92 CI 2.55 - 7.29

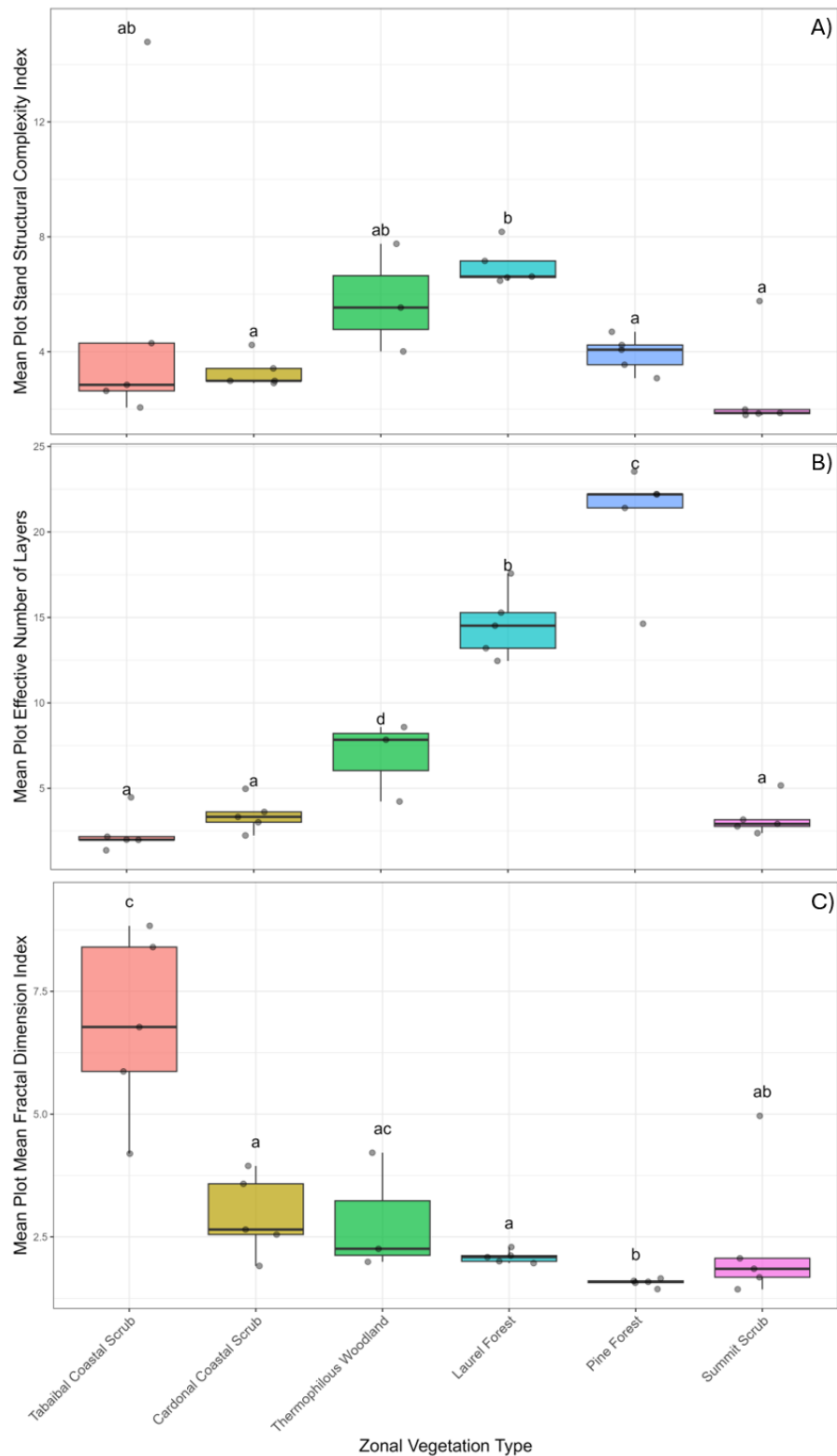


Figure 4. Distribution of mean plot (A) Stand Structural Complexity Index, (B) Effective Number of Layers, and (C) Mean Fractal Dimension Index by zonal vegetation type across Tenerife. Permutation analysis of variance (5000 permutations) shows a significant difference in all variables across vegetation types ($p < 0.001$). Pairwise permutation comparisons are indicated by the letters above the boxes, where vegetation types that share the same letter are not significantly different. Pairwise associations can be found in Supplementary Tables S3.

Relative within-vegetation type variability in SSCI differed significantly among vegetation types (permutation ANOVA $p < 0.001$, 5000 permutations, $\omega^2 = 0.54$), with CV values per plot ranging from 10.1% (95% CI: 0.9 – 12.4) on average across plots in laurel forest to 91.0% (95% CI: 12.4 – 104.2) on average across plots in tabaibal coastal scrub (Table S4). Specifically, significant differences in CV values per plot for SSCI were found between cardonal coastal scrub and pine forest, laurel forest and tabaibal coastal scrub, thermophilous woodland and pine forest, pine forest and tabaibal coastal scrub and summit scrub, and between laurel forest and tabaibal coastal scrub and summit scrub (all adjusted- p values ≤ 0.050 ; Figure 5a; Table S5).

The tabaibal coastal scrub also exhibited the greatest relative within-type variation in ENL (CV = 44.7% on average across plots). The smallest within-vegetation type variation in ENL was found in the laurel forest, resulting in an ENL CV of 13.6% on average across plots (Figure 5b). Relative within-vegetation type variability in MeanFrac was highest in the summit scrub (60.6%) and lowest in the pine forest (5.1%) (Figure 5c). Significant differences in CV values per plot of the ENL and MeanFRAC across vegetation types were also found (permutation ANOVAs $p < 0.001$, 5000 permutations, $\omega^2 = 0.29$ and 0.65 respectively). Full pairwise comparisons can be visualised in Figure 5 and found in Table S5.

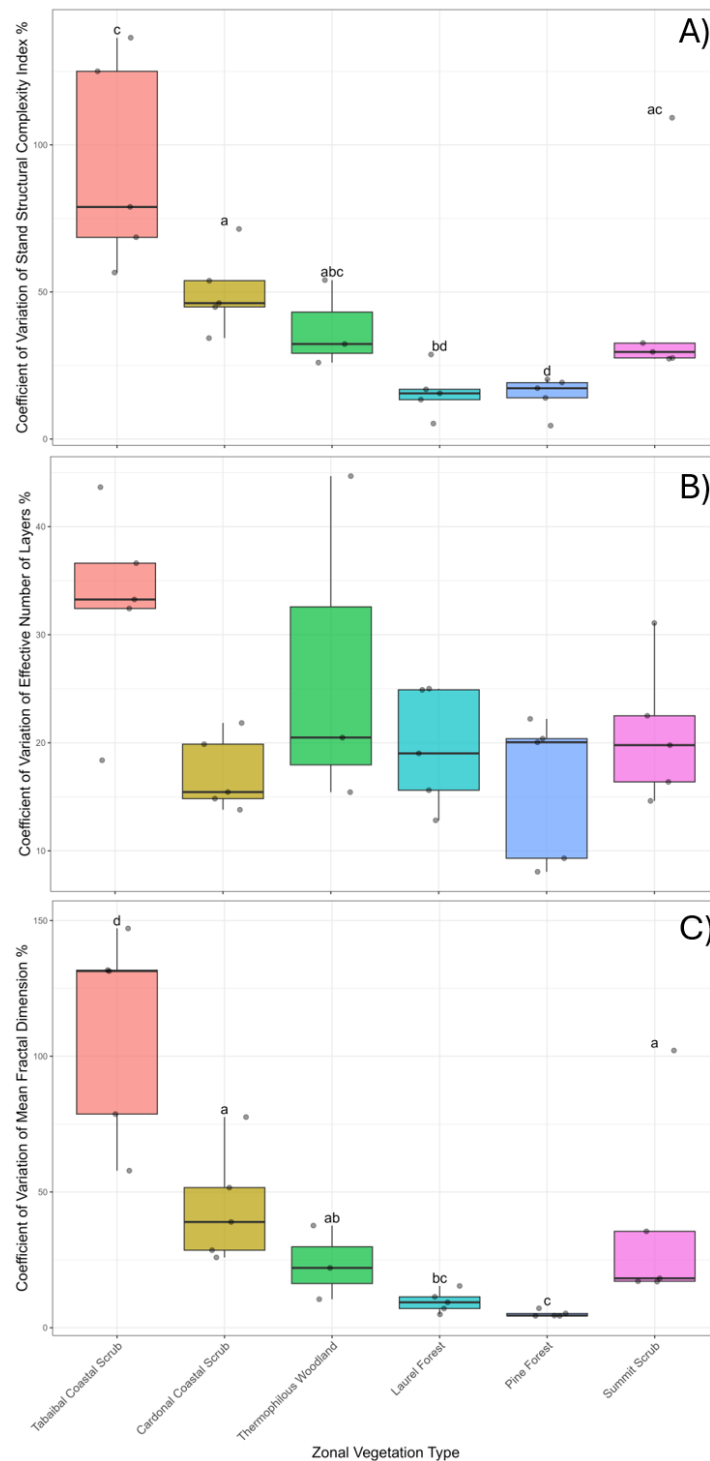


Figure 5. Within-vegetation type variation represented by the coefficient of variation of the Stand Structural Complexity Index (A), Effective Number of Layers (B), and Mean Fractal Dimension (C) across vegetation types. Within-vegetation type variation of structural metrics significantly differed across vegetation types for all three metrics (permutation ANOVAs $p < 0.001$, 5000 permutations). Pairwise permutation comparisons are indicated by the letters above the boxes, where vegetation types that share the same letter are not significantly different. Full summaries of pairwise comparisons can be found in Table S5.

3.2 A multi-dimensional perspective of Vegetation Structural Complexity and its components

The PCA revealed a distinct separation between forest and scrub vegetation types, demonstrating contrasting structural arrangement in 3D space (Figure 6). The first two principal components explained 86.5% of the total variation in vegetation structure (PC1 = 64.3%, PC2 = 22.2%) (Figure 6; Table S6). The first principal component was positively associated with canopy openness (loading = 0.51) and negatively associated with vertical stratification (represented by ENL, loading = -0.53), and canopy height (loading = -0.54). Differences between forest and scrub vegetation were mainly associated with PC1, which represented a structural gradient from open scrub vegetation to vertically stratified and tall forest vegetation. Specifically, pine and laurel forests have, overall, higher ENL and lower canopy openness, showing higher variation in components related to both vertical and horizontal structure. In contrast, scrub habitats had overall lower ENL, higher MeanFRAC, and canopy openness. For cardonal and summit scrubs, most of the within-vegetation type variation was related to the PC2, with larger within-vegetation type variation in both PCA components associated with tabaibal coastal scrub.

PC2 was negatively associated with the 3D structure including the SSCI (loading = -0.84) together with MeanFRAC (loading = -0.51), distinguishing the sites within the scrub communities with greater vegetation density. Regarding forest communities, the thermophilous woodland, although represented by the structural components in both dimensions, is associated more strongly with MeanFRAC compared to the laurel or pine forest, suggesting greater horizontal density of vegetation. Contrastingly, the cardonal coastal and summit scrubs have higher canopy openness. The tabaibal coastal scrub displayed the greatest variation in MeanFRAC.

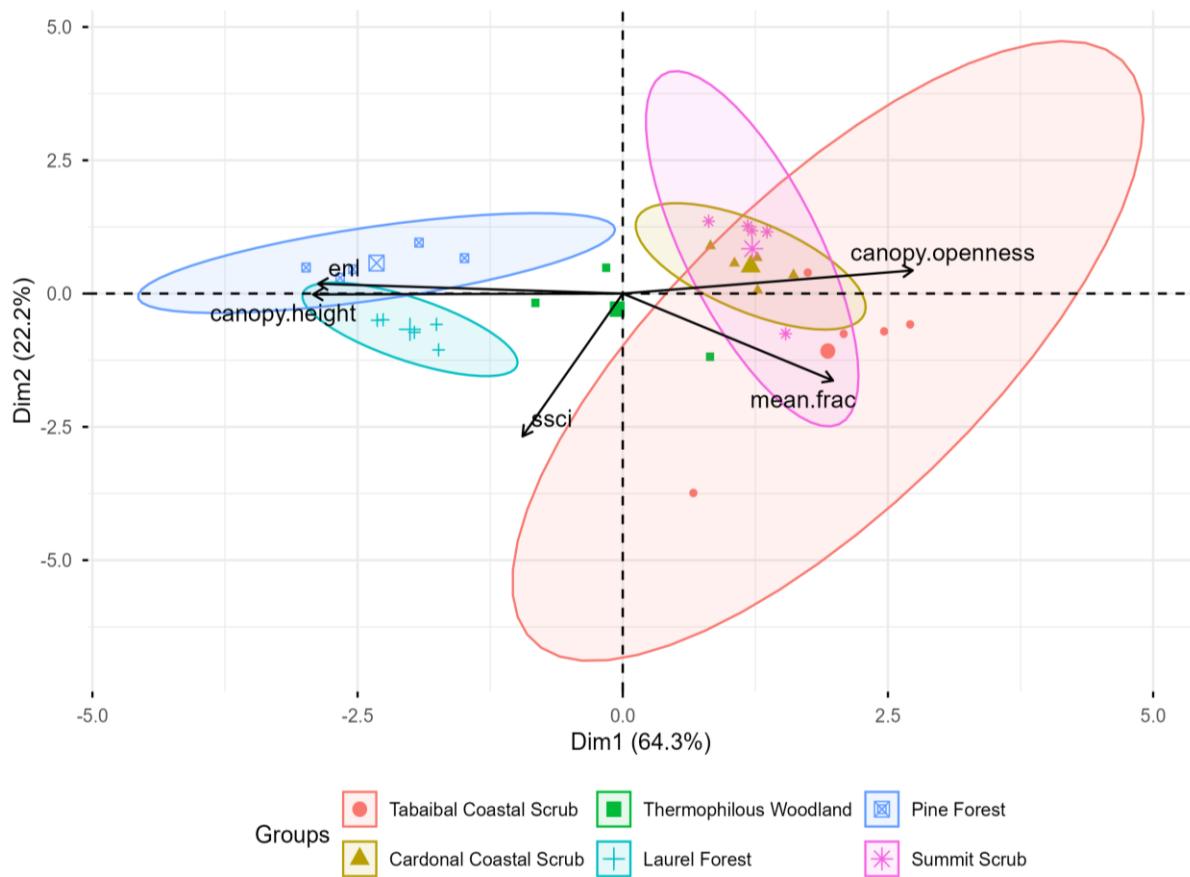


Figure 6. Representation of terrestrial laser scanning variables for vegetation structural complexity by the first two principal components (PC1 = 64.3%, PC2 = 22.2%) derived from principal component analyses in vegetation types across Tenerife. The variables include Effective Number of Layers (enl), Stand Structural Complexity Index (ssci), Mean Fractal Dimension (mean.frac), canopy height, and canopy openness. Coloured shapes represent the mean plot values per vegetation type, with ellipses representing the vegetation type clusters. Each vegetation type centralisation is represented by a larger coloured shape within the plot distributions.

3.3 Climate drivers of Vegetation Structural Complexity

Robust linear regression identified significant relationships between climate and all metrics of vegetation structural complexity (Table 2). The robust linear model revealed a positive relationship between annual precipitation and SSCI (estimate = 0.005, $t = 2.545$, 95% bootstrap CI = 0.002 – 0.009) (Figure 7a). Similar patterns were observed with other structural metrics. There was a significant positive relationship between annual precipitation and the ENL (estimate = 0.029, $t = 6.192$, 95% bootstrap CI = 0.021 – 0.035) (Figure 7b). Conversely, MeanFRAC showed a significant negative relationship with annual precipitation (estimate = -0.003, $t = -2.231$, 95% bootstrap CI = -0.009 – -0.001) (Figure 7c).

Table 2. Results of robust general linear models investigating the relationship between climate annual precipitation (pmed) and vegetation structural complexity: Stand Structural Complexity Index (SSCI), Effective Number of Layers (ENL), Mean Fractal Dimension (MeanFRAC), canopy openness, and canopy height. Significant associations are highlighted in bold.

Response	Predictor	Estimate	SE	t	CI_lower	CI_upper	Pseudo R ²
SSCI	(Intercept)	2.346	0.832	2.819	1.269	3.389	0.11
	pmed	0.005	0.002	2.545	0.002	0.009	
ENL	(Intercept)	-3.267	2.079	-1.572	-5.909	-0.660	0.57
	pmed	0.029	0.005	6.192	0.021	0.035	
MeanFRAC	(Intercept)	3.388	0.492	6.889	2.196	7.060	0.09
	pmed	-0.003	0.001	-2.231	-0.009	-0.001	
Canopy Height	(Intercept)	-3.408	3.656	-0.932	-7.313	1.171	0.54
	pmed	0.043	0.008	5.134	0.032	0.052	
Canopy Openness	(Intercept)	130.689	10.917	11.971	117.845	146.443	0.58
	pmed	-0.153	0.025	-6.144	-0.197	-0.110	

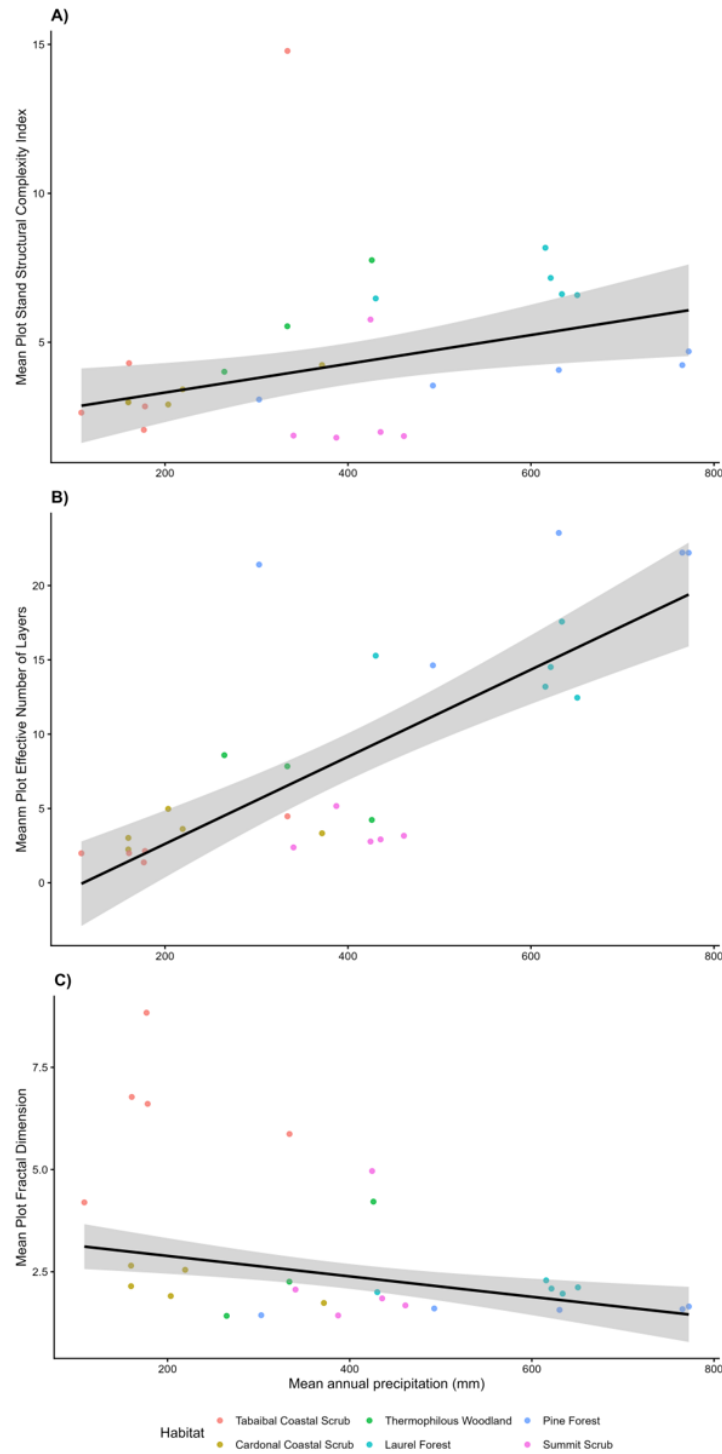


Figure 7. Significant associations between mean annual precipitation (mm) (calculated between 1979 – 2013 at 100 m spatial resolution) and mean plot A) Stand Structural Complexity Index ($t = 2.55$, 95% CI 0.002 – 0.009), B) Effective Number of Layers ($t = 6.20$, 95% CI 0.021 – 0.035), and C) Mean Fractal Dimension Index ($t = -2.23$, 95% CI -0.008 – -0.001) across zonal vegetation types in Tenerife. The black lines show the robust linear regression fit with the 95% confidence interval (shaded area). Each point represents a sampled site, coloured by vegetation type.

4. Discussion

We present the first evidence of how vegetation structural complexity varies across and within native zonal vegetation on Tenerife along a steep environmental gradient. There was clear differentiation in structural metrics, dependent on the vegetation type. Forest types achieved the greatest structural complexity through pronounced vertical stratification and canopy height. In contrast, variation in vegetation 3D density (described by the MeanFRAC) and greater canopy openness characterise the scrub communities, contributing to lower overall structural complexity. These differences were associated with increased precipitation, promoting higher vertical structure development (ENL) and lower 3D density (MeanFRAC). Overall, this contributed to greater SSCI values in the forested vegetations. Our findings demonstrate that TLS is a useful tool for differentiating structural complexity within and across contrasting ecosystems.

4.1 Organisation and Development of Vegetation Structural Complexity in Zonal Vegetation Types

The higher vegetation structural complexity we observed in pine and laurel forests align with previous studies and global predictions of the SSCI. Consistent with Juchheim et al. (2020) and Ehbrecht et al. (2021), vegetation structural complexity was higher in broad-leaved than coniferous forests. In contrast, scrub communities generally exhibited lower overall vegetation structural complexity, which varied through changes in vegetation density and branching architecture, contrasting with the forests and woodlands of Tenerife. Our PCA results demonstrate that the dominant axis of structural variation among vegetation types (PC1, 64.3%) represented a gradient from open scrub vegetation to taller and stratified forest vegetation. In taller habitat stands, such as forests, vertical structure, such as stratification (ENL) and height, was the main axis of differentiation, consistent with De Conto et al. (2024), who found positive relationships between forest structural complexity and canopy height. In scrub, MeanFRAC and canopy openness were more influential. Koller et al. (2025) underscore the importance of tree branching architecture for vegetation structural complexity, particularly its contribution to MeanFRAC. This metric captures branching and vegetation density, as well as fine-scale architectural irregularity – traits that become more important where vertical stratification is reduced.

Numerous vegetation traits contribute to vegetation structural complexity. Seidel *et al.* (2019a) show that crown size from individual trees has a positive relationship to forest plot stand structural complexity, whilst tree branching patterns (direction, density, etc.) produce unique tree morphologies (Seidel *et al.*, 2019b), strongly influencing overall complexity (Koller *et al.*, 2025). Community traits such as species abundance and average basal area (Peck *et al.*, 2014) and canopy height (Atkins *et al.*, 2022) are also influential. Although these studies are forest based, similar traits likely operate at different scales in our scrub vegetation, contributing to vegetation structural complexity in these vegetation types.

Various aspects of vegetation structural complexity are closely linked to habitat availability and niche diversity (Knuff *et al.*, 2020; Tuolalibieke *et al.*, 2026). For example, tall canopies and high vegetation volume and cover increase avian species diversity (Brahmia *et al.*, 2025), whilst shrub branching density impacts arthropod abundance (Alfeus *et al.*, 2026). Structural components beyond vertical stratification may therefore have impacts on biodiversity and ecosystem functioning.

Notably, we observed high SSCI in one *Euphorbia balsamifera*-dominated plot (Figure S4), where dense branching architecture and near-complete canopy cover was present. This is confirmed by the high cover (100%) of the tabaibal habitat at the northern coast of Tenerife (Otto *et al.*, 2001), compared to the sparser canopies of the southern coastal and summit scrubs. Compact branching architecture is similarly seen in *Cytisus supranubius* in the summit scrub. These cases emphasise how vegetation density and branching morphology can generate higher overall structural complexity in a vegetation type independent of vertical structure.

Assessments of vegetation structural complexity in island scrub and woodland are scarce, limited to a few characterisations such as shrub height and canopy cover in sagebrush steppe (Vierling *et al.*, 2013) and biomass and leaf area in Arctic shrub (Greaves *et al.*, 2015). While TLS can be used for the quantification of shrub biomass, canopy height, and rugosity (for example, Muumbe *et al.*, 2021; Bhatta *et al.*, 2025) assessments of structural complexity with an integrated index such as the SSCI are lacking. Further work is needed to establish links between vegetation structural complexity, biodiversity patterns, and ecosystem functioning in these vegetation types.

Our results suggest that structural metrics differentiating zonal vegetation types were associated with climate, where wetter environments increased vegetation structural

complexity. Increased precipitation was consistently associated with greater canopy height, increased vertical stratification (ENL) and higher SSCI, whilst canopy openness and MeanFRAC declined. This aligns with regional (Soto *et al.*, 2024) and global (Ehbrecht *et al.*, 2021) analyses that similarly demonstrate how precipitation drives vegetation structural complexity, particularly through vertical structure development.

Interestingly, the pseudo- R^2 value for SSCI-climate model was much lower than the pseudo- R^2 values for the other structural metrics (Table 2). This suggests that other factors also explain variation in the SSCI. Building on evidence that seasonality is important for SSCI development (Ehbrecht *et al.*, 2021), stable climatic environments can lead to higher vegetation structural complexity. This is consistent with evidence of higher stem turnover in forests experiencing longer dry periods, higher temperatures, and greater water deficits (Vilanova *et al.*, 2018): sustained rainfall likely extends growing periods and allows structural complexity to develop, probably via vertical growth. This is a critical consideration under current climate change, which is likely to alter patterns of vegetation structural complexity and, in turn, how ecosystems function.

The climatic conditions that were associated with increased vegetation structural complexity across zonal vegetation may similarly influence within-vegetation type variation. Although we could not explicitly test this, the high intra-vegetation type variation in vegetation structural complexity in the tabaibal coastal scrub is consistent with documented precipitation gradients on cover, vegetation height, and biomass of well-conserved coastal scrub from the arid southern to the semi-arid northern coast of Tenerife (Otto *et al.*, 2001).

4.2 Future Considerations

Further research is needed to understand the environmental drivers of the branching architecture or other structural features in scrubs, where vertical structure is limited. Soil conditions are also known to influence vegetation growth and structural complexity (Rodrigues *et al.*, 2018; Ehbrecht *et al.*, 2021; Yang *et al.*, 2025). On volcanic oceanic islands, spatial shifts in substrate age and composition, driven by recurring natural disturbances (such as fire and volcanic eruptions (Shatto *et al.*, 2024)), make soil development a potential driver of vegetation structure. We excluded plots on very young volcanic substrate and did not test this directly, but edaphic factors likely play a key role in shaping distinct vegetation types.

Our study spans vegetation that differs fundamentally in structural composition. In such systems, climatic drivers likely interact with local disturbance and management regimes, which we did not test here since plots were selected in areas with minimal human disturbance. Such interactions likely reduce the dominance of one driver, offering scope for future research. Fire, logging, and livestock presence are known to alter vegetation structural complexity (Caviedes and Ibarra, 2017), whilst management practices can either reduce (e.g. plantations; Ehbrecht *et al.*, 2017; Zemp *et al.*, 2019; Perles-Garcia *et al.*, 2021) or increase (Saarinen *et al.*, 2021) it.

Successional stage may also determine vegetation structural complexity; for example, cover and height of coastal scrub increased during secondary succession on abandoned fields on Tenerife (Otto *et al.*, 2006). While mature, less disturbed habitats accumulate species richness, vegetation layering, and deadwood presence (Casas *et al.*, 2016; Perles-Garcia *et al.*, 2021; Coverdale and Davies, 2023), vegetation structural complexity may peak prior to maturity, before dominant species eliminate space for greater species richness (Sferra *et al.*, 2017; Qianwen *et al.*, 2022). The dense, twisted architecture of *Morella-Erica* heath on Tenerife, in disturbed or transitional zones, may exhibit high vegetation structural complexity, illustrating how disturbance-mediated systems could exceed the structural complexity of mature forests (Bermúdez *et al.*, 2007).

All major vegetation zones of Tenerife have experienced significant human disturbance (Otto *et al.*, 2007; Otto *et al.*, 2012; Fernández-Palacios *et al.*, 2019, Fernández-Palacios *et al.*, 2024). This underscores the value of quantifying vegetation structural complexity, as we have started to do in our study, to enable future monitoring of these influences, particularly relevant on islands. While we modelled only climatic drivers, vegetation structural complexity likely emerges from interacting abiotic and biotic processes across multiple scales (Figure 1).

We highlight that the SSCI remains an informative measure of vegetation structural complexity and its components, within and beyond forest ecosystems. TLS enables this rapid quantification of vegetation structural complexity by combining multiple structural components that are difficult to capture without fine-detailed scanning. While other remote sensing approaches exist, such as aerial LiDAR and optical remote sensing (Camarretta *et al.*, 2020), TLS provides an under-canopy perspective that allows the quantification of 3D structural arrangement, as with the MeanFRAC and the SSCI.

Baseline data of vegetation structure, combined with understanding of biodiversity patterns, can support conservation decisions (Caviedes and Ibarra, 2017) and help detect spatio-temporal changes linked to management practices or disturbance (Zemp *et al.*, 2019; Perles-Garcia *et al.*, 2021; Saarinen *et al.*, 2021; Penman *et al.*, 2023). Our results provide this baseline for future studies to explore how disturbance regimes further influence vegetation structural complexity and monitor climatic change in vegetation types that are defined by steep environmental gradients.

4.3 Conclusions

Our results suggest that vegetation structural complexity across Tenerife is expressed through different combinations of vertical and horizontal components depending on vegetation type. The SSCI and other metrics provides a practical approach to quantifying overall vegetation structural complexity, yet dominant structural axes differ across vegetation types. These differences appear to be associated with climatic factors of precipitation, while other factors that were not tested such as disturbance or soil may have influenced the development and alteration of vegetation structural complexity across these vegetation types. Oceanic islands provide ample opportunities for future research to disentangle the direct and indirect drivers of vegetation structural complexity. This necessitates sampling across environmental and disturbance gradients, accounting for inter- and intra- species trait variation. Here, we initiate a baseline quantification across Tenerife and expand our knowledge of vegetation structural complexity across a steep island gradient, calling for future research in disturbed ecosystems.

References

- Alfeus, Martha, Robert Hering, Benjamin Schnerch, Simon Angombe, and Klaus Birkhofer. "Moderately thinning encroaching shrub species is key to balancing rangeland restoration and arthropod biodiversity conservation in Namibia." *Journal of Applied Ecology* 63, no. 6 (2026): e70454.
- Atkins, Jeff W., Alexey Shiklomanov, Kayla C. Mathes, Ben Bond-Lamberty, and Christopher M. Gough. "Effects of forest structural and compositional change on forest microclimates across a gradient of disturbance severity." *Agricultural and Forest Meteorology* 339 (2023): 109566.
- Atkins, Jeff W., Jonathan A. Walter, Atticus EL Stovall, Robert T. Fahey, and Christopher M. Gough. "Power law scaling relationships link canopy structural complexity and height across forest types." *Functional Ecology* 36, no. 3 (2022): 713-726.
- Barajas Barbosa, Martha Paola, Dylan Craven, Patrick Weigelt, Pierre Denelle, Rüdiger Otto, Sandra Díaz, Jonathan Price, José María Fernández-Palacios, and Holger Kreft. "Assembly of functional diversity in an oceanic island flora." *Nature* 619, no. 7970 (2023): 545-550.
- Barajas-Barbosa, Martha Paola, Patrick Weigelt, Michael Krabbe Borregaard, Gunnar Keppel, and Holger Kreft. "Environmental heterogeneity dynamics drive plant diversity on oceanic islands." *Journal of Biogeography* 47, no. 10 (2020): 2248-2260.
- Batchelor, Jonathan L., Todd M. Wilson, Michael J. Olsen, and William J. Ripple. "New structural complexity metrics for forests from single terrestrial LiDAR scans." *Remote Sensing* 15, no. 1 (2022): 145.
- Bermúdez, Alfredo Manuel, José María Fernández-Palacios, Juana María González-Mancebo, Jairo Patiño, José Ramón Arévalo, Rüdiger Otto, and Juan Domingo Delgado. "Floristic and structural recovery of a laurel forest community after clear-cutting: A 60 years chronosequence on La Palma (Canary Islands)." *Annals of Forest Science* 64, no. 1 (2007): 109-119.
- Bhatta, Ramesh, Manisha Das Chaity, Robert Ormal Chancia, Jasper Slingsby, Glenn Moncrieff, and Jan Van Aardt. "Assessment of Structural Differences in a Low-

- Stature Mediterranean-Type Shrubland Using Structure-From-Motion (SfM)." *Remote Sensing* 17, no. 16 (2025): 2784.
- Blanco-Montenegro, Isabel, Iacopo Nicolosi, Alessandro Pignatelli, Alicia García, and Massimo Chiappini. "New evidence about the structure and growth of ocean island volcanoes from aeromagnetic data: The case of Tenerife, Canary Islands." *Journal of Geophysical Research: Solid Earth* 116, no. B3 (2011).
- Borges, Paulo AV, Pedro Cardoso, Simone Fattorini, François Rigal, Thomas J. Matthews, Letizia Di Biase, Isabel R. Amorim et al. "Community structure of woody plants on islands along a bioclimatic gradient." *Frontiers of Biogeography* 10, no. 3-4 (2018).
- Brahmia, Z., Machtoub, R., Benyacoub, S., Ziane, N. and Rouag, R., 2025. Effects of forest composition and structure on breeding bird communities in Mount Edough (north-eastern Algeria). *Biodiversity Data Journal*, 13, p.e172987.
- Braunisch, Veronika, Stefanie Roder, Joy Coppes, Jérémy SP Froidevaux, Raphael Arlettaz, and Kurt Bollmann. "Structural complexity in managed and strictly protected mountain forests: Effects on the habitat suitability for indicator bird species." *Forest Ecology and Management* 448 (2019): 139-149.
- Burrell, Nancy C., Katherine J. Willis, Marcus Spiegel, Jeff Kerby, and Marc Macias-Fauria. "Integrating Structure from Motion and 5-Band Imaging to Estimate Above-and Belowground Biomass in a Rewilded Scrubland Ecosystem." *What is the carbon storage potential of scrubland created by rewilding?*: 205.
- Camarretta, Nicolò, Peter A. Harrison, Tanya Bailey, Brad Potts, Arko Lucieer, Neil Davidson, and Mark Hunt. "Monitoring forest structure to guide adaptive management of forest restoration: a review of remote sensing approaches." *New forests* 51, no. 4 (2020): 573-596.
- Carrasco, Luis, Xingli Giam, Monica Papeş, and Kimberly S. Sheldon. "Metrics of lidar-derived 3D vegetation structure reveal contrasting effects of horizontal and vertical forest heterogeneity on bird species richness." *Remote Sensing* 11, no. 7 (2019): 743.
- Casas, Grasiela, Bianca Darski, Pedro MA Ferreira, Andreas Kindel, and Sandra C. Müller. "Habitat structure influences the diversity, richness and composition of bird

- assemblages in successional Atlantic rain forests." *Tropical Conservation Science* 9, no. 1 (2016): 503-524.
- Castaño-Villa, Gabriel J., Santiago A. Ramos-Valencia, and Francisco E. Fontúrbel. "Fine-scale habitat structure complexity determines insectivorous bird diversity in a tropical forest." *Acta Oecologica* 61 (2014): 19-23.
- Caviedes, Julian, and José Tomás Ibarra. "Influence of anthropogenic disturbances on stand structural complexity in Andean temperate forests: implications for managing key habitat for biodiversity." *PloS one* 12, no. 1 (2017): e0169450.
- Cimdins, Reinis, Tuomas Yrttimaa, Mikko Vastaranta, and Ville Kankare. "Assessing forest structural complexity: insights from alternative laser scanning approaches." *Scandinavian Journal of Forest Research* 41, no. 1 (2026): 40-53.
- Conry, P. J., and R. Cannarella. "Hawai'i Statewide Assessment of Forest Conditions and Resource Strategy". *Honolulu, HI: Hawai'i Department of Land and Natural Resources, Division of Forestry and Wildlife*. (2010). Available online at: [Hawaii Statewide Forest Assessment and Strategies 2010.Vol1 FULL](#). Accessed 01/04/2025.
- Coverdale, Tyler C., and Andrew B. Davies. "Unravelling the relationship between plant diversity and vegetation structural complexity: A review and theoretical framework." *Journal of Ecology* 111, no. 7 (2023): 1378-1395.
- de Conto, Tiago, John Armston, and Ralph Dubayah. "Characterizing the structural complexity of the Earth's forests with spaceborne lidar." *Nature Communications* 15, no. 1 (2024): 8116.
- de Nascimento, Lea, Sandra Nogué, Silvia Fernández-Lugo, Javier Méndez, Rüdiger Otto, Robert J. Whittaker, Kathy J. Willis, and José María Fernández-Palacios. "Modern pollen rain in Canary Island ecosystems and its implications for the interpretation of fossil records." *Review of Palaeobotany and Palynology* 214 (2015): 27-39.
- del Arco Aguilar, Marcelino J., Octavio Rodríguez Delgado, Marcelino J. del Arco Aguilar, and Octavio Rodríguez Delgado. *Vegetation of the canary islands*. Springer International Publishing, (2018).

- Ehbrecht, Martin, Dominik Seidel, Peter Annighöfer, Holger Kreft, Michael Köhler, Delphine Clara Zemp, Klaus Puettmann et al. "Global patterns and climatic controls of forest structural complexity." *Nature communications* 12, no. 1 (2021): 519.
- Ehbrecht, Martin, Peter Schall, Christian Ammer, and Dominik Seidel. "Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate." *Agricultural and Forest Meteorology* 242 (2017): 1-9.
- Ehbrecht, Martin, Peter Schall, Julia Juchheim, Christian Ammer, and Dominik Seidel. "Effective number of layers: A new measure for quantifying three-dimensional stand structure based on sampling with terrestrial LiDAR." *Forest Ecology and Management* 380 (2016): 212-223.
- Ehbrecht, Martin, Tim Lehmann, Sebastián Escobar, David A. Donoso, María-José Endara, Juan Ernesto Guevara-Andino, and Nico Blüthgen. "Recovery of forest structural complexity during secondary succession in a human-modified neotropical landscape." *Journal of Ecology* 114, no. 1 (2026): e70241.
- Faro Technologies Inc., Lake Mary, USA.
- Fernández-Palacios, José María, J. R. Arévalo, R. Barone, A. Castilla-Beltrán, L. De Nascimento, M. C. Duarte, E. Fernández-Palacios et al. "Los Bosques Termófilos. Canarias, Madeira y Cabo Verde." (2024).
- Fernández-Palacios, José María, Holger Kreft, Severin DH Irl, Sietze Norder, Claudine Ah-Peng, Paulo AV Borges, Kevin C. Burns et al. "Scientists' warning—The outstanding biodiversity of islands is in peril." *Global ecology and conservation* 31 (2021): e01847.
- Fernández-Palacios, José María, J. R. Arévalo, E. Balguerías, R. Barone, L. De Nascimento, R. B. Elias, J. D. Delgado et al. *La Laurisilva. Canarias, Madeira y Azores*. (2017).
- Fernández-Palacios, J. M., Fructuoso, M., Illera, J. C., Rando, J. C., de Nascimento, L., Fernández-Palacios, E., Patiño, J., Otto, R., Castilla-Beltrán, Á., Martín González, E., Orihuela-Rivero, R., Alcover, J. A., & Whittaker, R. J. (2025). A synthesis of terrestrial species extinctions in the Macaronesian Islands and their correspondence with human occupancy. *PNAS Nexus*, 4(8), Article pgaf215. <https://doi.org/10.1093/pnasnexus/pgaf215>

- Fischer, Rico, Nikolai Knapp, Friedrich Bohn, Herman H. Shugart, and Andreas Huth. "The relevance of forest structure for biomass and productivity in temperate forests: New perspectives for remote sensing." *Surveys in Geophysics* 40 (2019): 709-734.
- Fotis, Alex T., Timothy H. Morin, Robert T. Fahey, Brady S. Hardiman, Gil Bohrer, and Peter S. Curtis. "Forest structure in space and time: Biotic and abiotic determinants of canopy complexity and their effects on net primary productivity." *Agricultural and Forest Meteorology* 250 (2018): 181-191.
- Frey, Julian, Bettina Joa, Ulrich Schraml, and Barbara Koch. "Same viewpoint different perspectives—A comparison of expert ratings with a TLS derived forest stand structural complexity index." *Remote Sensing* 11, no. 9 (2019): 1137.
- Godbold, Jasmin A., Mark T. Bulling, and Martin Solan. "Habitat structure mediates biodiversity effects on ecosystem properties." *Proceedings of the Royal Society B: Biological Sciences* 278, no. 1717 (2011): 2510-2518.
- Greaves, Heather E., Lee A. Vierling, Jan UH Eitel, Natalie T. Boelman, Troy S. Magney, Case M. Prager, and Kevin L. Griffin. "Estimating aboveground biomass and leaf area of low-stature Arctic shrubs with terrestrial LiDAR." *Remote Sensing of Environment* 164 (2015): 26-35.
- Grimm, Nancy B., F. Stuart Chapin III, Britta Bierwagen, Patrick Gonzalez, Peter M. Groffman, Yiqi Luo, Forrest Melton et al. "The impacts of climate change on ecosystem structure and function." *Frontiers in Ecology and the Environment* 11, no. 9 (2013): 474-482.
- Juchheim, Julia, Martin Ehbrecht, Peter Schall, Christian Ammer, and Dominik Seidel. "Effect of tree species mixing on stand structural complexity." *Forestry: An International Journal of Forest Research* 93, no. 1 (2020): 75-83.
- Knuff, Anna Katharina, Michael Staab, Julian Frey, Carsten F. Dormann, Thomas Asbeck, and Alexandra-Maria Klein. "Insect abundance in managed forests benefits from multi-layered vegetation." *Basic and Applied Ecology* 48 (2020): 124-135.
- Koller, Alexandra, Matthias Kunz, Maria D. Perles-Garcia, and Goddert von Oheimb. "3D structural complexity of forest stands is determined by the magnitude of inner and outer crown structural attributes of individual trees." *Agricultural and Forest Meteorology* 363 (2025): 110424.

- Mallet, Bertrand, Florent Martos, Laury Blambert, Thierry Paillet, and Laurence Humeau. "Evidence for isolation-by-habitat among populations of an epiphytic orchid species on a small oceanic island." *PloS one* 9, no. 2 (2014): e87469.
- Muumbe, T.P., Baade, J., Singh, J., Schmulius, C. and Thau, C., 2021. Terrestrial laser scanning for vegetation analyses with a special focus on savannas. *Remote Sensing*, 13(3), p.507.
- Onyiriagwu, Magnus, Nereoh Leley, Caleb WT Ngaba, Anthony Macharia, Henry Muchiri, Abdalla Kisiwa, Martin Ehbrecht, and Delphine Clara Zemp. "On the compatibility of single-scan terrestrial LiDAR with digital photogrammetry and field inventory metrics of vegetation structure in forest and agroforestry landscapes." *Remote Sensing in Ecology and Conservation* (2025).
- Otto, Rüdiger, Bertil O. Krüsi, and F. Kienast. "Degradation of an arid coastal landscape in relation to land use changes in Southern Tenerife (Canary Islands)." *Journal of Arid Environments* 70, no. 3 (2007): 527-539.
- Otto, Rüdiger, Bertil O. Krüsi, C. A. Burga, and José María Fernández-Palacios. "Old-field succession along a precipitation gradient in the semi-arid coastal region of Tenerife." *Journal of Arid Environments* 65, no. 1 (2006): 156-178.
- Otto, Rüdiger, José María Fernández-Palacios, and Bertil O. Krüsi. "Variation in species composition and vegetation structure of succulent scrub on Tenerife in relation to environmental variation." *Journal of Vegetation Science* 12, no. 2 (2001): 237-248.
- Otto, Rüdiger, Rubén Barone, Juan-Domingo Delgado, José-Ramón Arévalo, Víctor Garzón-Machado, Francisco Cabrera-Rodríguez, and José-María Fernández-Palacios. "Diversity and distribution of the last remnants of endemic juniper woodlands on Tenerife, Canary Islands." *Biodiversity and Conservation* 21 (2012): 1811-1834.
- Otto, Rüdiger, Víctor Garzón-Machado, Marcelino del Arco, Silvia Fernández-Lugo, Lea de Nascimento, Pedro Oromí, Marcos Báez, Miguel Ibáñez, María R. Alonso, and José María Fernández-Palacios. "Unpaid extinction debts for endemic plants and invertebrates as a legacy of habitat loss on oceanic islands." *Diversity and Distributions* 23, no. 9 (2017): 1031-1041.

- Parsons, James J. "Human influences on the pine and laurel forests of the Canary Islands." In *Agriculture, Resource Exploitation, and Environmental Change*, pp. 169-187. Routledge, (1997).
- Patiño, Jairo, Flavien Collart, Alain Vanderpoorten, José Luis Martin-Esquivel, Agustín Naranjo-Cigala, Sébastien Mirolo, and Dirk N. Karger. "Spatial resolution impacts projected plant responses to climate change on topographically complex islands." *Diversity and Distributions* 29, no. 10 (2023): 1245-1262.
- Peck, JeriLynn E., Eric K. Zenner, Peter Brang, and Andreas Zingg. "Tree size distribution and abundance explain structural complexity differentially within stands of even-aged and uneven-aged structure types." *European journal of forest research* 133 (2014): 335-346.
- Penman, Sandra, Pia Lentini, Bradley Law, and Alan York. "An instructional workflow for using terrestrial laser scanning (TLS) to quantify vegetation structure for wildlife studies." *Forest Ecology and Management* 548 (2023): 121405.
- Pereira, Henrique Miguel, Simon Ferrier, Michele Walters, Gary N. Geller, Rob HG Jongman, Robert J. Scholes, Michael William Bruford et al. "Essential biodiversity variables." *Science* 339, no. 6117 (2013): 277-278.
- Perles-Garcia, Maria D., Matthias Kunz, Andreas Fichtner, Werner Härdtle, and Goddert von Oheimb. "Tree species richness promotes an early increase of stand structural complexity in young subtropical plantations." *Journal of Applied Ecology* 58, no. 10 (2021): 2305-2314.
- Pierick, Kerstin, Dominik Seidel, Pia Bradler, Simone Cesarz, Orsi Decker, Benjamin M. Delory, Sebastian Dittrich et al. "Spatial microclimatic heterogeneity is associated with forest structure and biodiversity." *Ecological Indicators* 187 (2026): 114874.
- Qianwen, Geng, Muhammad Arif, Yuan Zhongxun, Zheng Jie, He Xinrui, Ding Dongdong, Yin Fan, and Li Changxiao. "Plant species composition and diversity along successional gradients in arid and semi-arid regions of China." *Forest Ecology and Management* 524 (2022): 120542.
- R Core Development Team. "R: A language and environment for statistical computing." (2024).

- Ray, Tama, Benjamin M. Delory, Rémy Beugnon, Helge Bruelheide, Simone Cesarz, Nico Eisenhauer, Olga Ferlian, Julius Quosh, Goddert Von Oheimb, and Andreas Fichtner. "Tree diversity increases productivity through enhancing structural complexity across mycorrhizal types." *Science Advances* 9, no. 40 (2023): eadi2362.
- Reich, Karl Friedrich, Matthias Kunz, and Goddert von Oheimb. "A new index of forest structural heterogeneity using tree architectural attributes measured by terrestrial laser scanning." *Ecological Indicators* 133 (2021): 108412.
- Renner, Susanne S., Rüdiger Otto, José Luis Martín-Esquível, Manuel V. Marrero-Gómez, and José María Fernández-Palacios. "Vegetation change on Mt. Teide, the Atlantic's highest volcano, inferred by incorporating the data underlying Humboldt's Tableau Physique des Iles Canaries." *Journal of Biogeography* 50, no. 2 (2023): 251-261.
- Ripley, Brian. "MASS: support functions and datasets for Venables and Ripley's MASS. 2022." URL <https://CRAN.R-project.org/package=MASS>. *R package version* (2022): 7-3.
- Rodrigues, Priscyla Maria Silva, Carlos Ernesto Gonçalves Reynaud Schaefer, Jhonathan de Oliveira Silva, Walnir Gomes Ferreira Júnior, Rubens Manoel dos Santos, and Andreza Viana Neri. "The influence of soil on vegetation structure and plant diversity in different tropical savannic and forest habitats." *Journal of Plant Ecology* 11, no. 2 (2018): 226-236.
- Saarinen, Ninni, Kim Calders, Ville Kankare, Tuomas Yrttimaa, Samuli Junttila, Ville Luoma, Saija Huuskonen, Jari Hynynen, and Hans Verbeeck. "Understanding 3D structural complexity of individual Scots pine trees with different management history." *Ecology and Evolution* 11, no. 6 (2021): 2561-2572.
- Saint-Béat, Blanche, Dan Baird, Harald Asmus, Ragnhild Asmus, Cédric Bacher, Stephen R. Pacella, Galen A. Johnson, Valérie David, Alain F. Vézina, and Nathalie Niquil. "Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review." *Ecological indicators* 52 (2015): 458-471.
- Schrader, Julian, Patrick Weigelt, Lirong Cai, Mark Westoby, José María Fernández-Palacios, Francisco J. Cabezas, Gregory M. Plunkett et al. "Islands are key for protecting the world's plant endemism." *Nature* (2024): 1-7.

- Seidel, Dominik. "A holistic approach to determine tree structural complexity based on laser scanning data and fractal analysis." *Ecology and evolution* 8, no. 1 (2018): 128-134.
- Seidel, Dominik, Martin Ehbrecht, and Klaus Puettmann. "Assessing different components of three-dimensional forest structure with single-scan terrestrial laser scanning: A case study." *Forest Ecology and Management* 381 (2016): 196-208.
- Seidel, Dominik, Martin Ehbrecht, Peter Annighöfer, and Christian Ammer. "From tree to stand-level structural complexity—Which properties make a forest stand complex?." *Agricultural and Forest Meteorology* 278 (2019a): 107699.
- Seidel, Dominik, Martin Ehbrecht, Yonten Dorji, Jambay Jambay, Christian Ammer, and Peter Annighöfer. "Identifying architectural characteristics that determine tree structural complexity." *Trees* 33 (2019b): 911-919.
- Sferra, Christopher O., Justin L. Hart, and Jennifer G. Howeth. "Habitat age influences metacommunity assembly and species richness in successional pond ecosystems." *Ecosphere* 8, no. 6 (2017): e01871.
- Shatto, Christopher, Marvin Kiene, Peter Hofmann, Anna Walentowitz, Vincent Wilkens, Tobias Heuser, and Frank Weiser. "Assessing the recovery of *Pinus canariensis* stands after wildfires and volcanic eruption on La Palma, Canary Islands." *Forest Ecology and Management* 572 (2024): 122317.
- Shugart, H. H., S. Saatchi, and F. G. Hall. "Importance of structure and its measurement in quantifying function of forest ecosystems." *Journal of Geophysical Research: Biogeosciences* 115, no. G2 (2010).
- Soto, Daniel P., Dominik Seidel, Ángela Hernández-Moreno, Klaus J. Puettmann, and Pablo J. Donoso. "Increase in forest structural complexity along a precipitation gradient is mediated by partial harvests in temperate Patagonian forests." *Scientific Reports* 14, no. 1 (2024): 13656.
- Suter, S., Otto, R., Fernández-Palacios, J. M., de Nascimento, L., Rodriguez Arvelo, F., Sierra Cornejo, N., Guerrero-Ramirez, N., Ehbrecht, M., Kreft, H., & Zemp, D. C. (2025). Terrestrial laser scanning for measuring structural complexity across habitats on an oceanic island (V1.0) [Data set]. Zenodo.
<https://doi.org/10.5281/zenodo.16318411>

- Tuolalibieke, Jiadeera, Yujia Liu, Chunjing Zou, and Yanxia Li. "Branching Structure and Fractal Patterns of Urban Forest Plants in Shanghai, China." *Fractal and Fractional* 10, no. 7 (2026): 437.
- Vierling, Lee A., Yanyin Xu, Jan UH Eitel, and John S. Oldow. "Shrub characterization using terrestrial laser scanning and implications for airborne LiDAR assessment." *Canadian Journal of Remote Sensing* 38, no. 6 (2013): 709-722.
- Vilanova, Emilio, Hirma Ramirez-Angulo, Armando Torres-Lezama, Gerardo Aymard, Luis Gamez, Cristabel Duran, Lionel Hernandez et al. "Environmental drivers of forest structure and stem turnover across Venezuelan tropical forests." *PLoS One* 13, no. 6 (2018): e0198489.
- Weigelt, Patrick, Walter Jetz, and Holger Kreft. "Bioclimatic and physical characterization of the world's islands." *Proceedings of the National Academy of Sciences* 110, no. 38 (2013): 15307-15312.
- Westerband, A. C., J. L. Funk, and K. E. Barton. "Intraspecific trait variation in plants: a renewed focus on its role in ecological processes." *Annals of botany* 127, no. 4 (2021): 397-410.
- Wheeler, Bob, Marco Torchiano, and Maintainer Marco Torchiano. "Package 'Imperm'." *R package version 2*, no. 0 (2016).
- Worsham, McLean LD, Eric P. Julius, Chris C. Nice, Peter H. Diaz, and David G. Huffman. "Geographic isolation facilitates the evolution of reproductive isolation and morphological divergence." *Ecology and Evolution* 7, no. 23 (2017): 10278-10288.
- Yang, Chengfeng, Jingyan Zhao, Shengzhuo Huang, Shurong Zhou, and Yikang Cheng. "Distribution of different plant life forms on tropical islands: patterns and underlying mechanisms." *Frontiers in Plant Science* 16 (2025): 1566156.
- Zemp, Delphine Clara, Martin Ehbrecht, Dominik Seidel, Christian Ammer, Dylan Craven, Joshua Erkelenz, Bambang Irawan, Leti Sundawati, Dirk Hölscher, and Holger Kreft. "Mixed-species tree plantings enhance structural complexity in oil palm plantations." *Agriculture, Ecosystems & Environment* 283 (2019): 106564.

Zizka A, Onstein RE, Rozzi R, Weigelt P, Kreft H, Steinbauer MJ, Bruehlheide H, Lens F
(2022) *The evolution of insular woodiness*. *Proc. Natl. Acad. Sci.*
U.S.A. 119(37):e2208629119. <https://doi.org/10.1073/pnas.2208629119>.