Characterising the structural complexity across major habitats of Tenerife, Spain

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Abstract

Understanding biodiversity changes across ecosystems requires the consideration of various biodiversity dimensions, such as habitat structural complexity – the degree of heterogeneity in the distribution of plant material in three-dimensional space. Yet, its inclusion in long-term biodiversity monitoring on oceanic islands remains limited. Terrestrial laser scanning (TLS) can be used to quantify habitat structural complexity for ecosystem monitoring, management, and restoration purposes, but its applications are restricted to forests. This constrains our understanding of structural complexity across habitats and how best we can use this knowledge for biodiversity conservation. We characterised structural complexity with TLS using the stand structural complexity index and its components, quantified by three-dimensional point clouds, across and within key habitats on Tenerife: laurel and pine forests, thermophilous woodland, tabaibal and cardonal coastal scrub, and summit scrub. On average, the highest structural complexity index values were observed in the laurel forest (7.00), with lowest values recorded in the summit scrub (2.65), indicating a broad variation in habitat structural complexity across oceanic island habitats. The greatest within-habitat variation was found in the tabaibal coastal scrub (SD = 4.67) with lowest variation found within the pine forest (SD = 0.59). Laurel and pine forests were characterised by high vertical stratification and closed canopy, whereas scrub habitats were characterised by short and open vegetation. A significant positive relationship between annual precipitation and the stand structural complexity index was found across the island habitats ($p = 0.003$). We show that TLS can be extended to other habitats to characterise structural complexity and provide baseline data for long-term monitoring of changing habitats, useful in guiding ecosystem restoration and biodiversity conservation strategies. From this, habitat management protocols can be adapted beyond forests to utilise TLS in conservation management across diverse habitats.

Keywords: Biodiversity Monitoring; Essential Biodiversity Variable; Habitat Structural Complexity; Island Ecosystems; Terrestrial Laser Scanning; Vegetation Structure

1. Introduction

Terrestrial habitats on oceanic islands are subject to isolation, leading to unique evolutionary adaptations (Worsham *et al*., 2017). For instance, distinctive traits observed in island species often stem from limited dispersal ability and reduced gene flow (Schrader *et al.,* 2024). Additionally, volcanic origins, undulating topography, and high precipitation variation (Weigelt *et al.,* 2013) on many oceanic islands drive localised adaptations at fine spatial scales due to considerable differences in abiotic conditions, which ultimately influence species presence and functional traits (Mallet *et al*., 2014).

One consequence of these factors is distinctive habitat structural complexity, which can broadly be defined as the "three-dimensional distribution of plants within an ecosystem" (Coverdale and Davies, 2023). However, this structural complexity remains largely uncharacterised in many island habitats. Collecting such data is essential for understanding ecosystem functioning and biodiversity patterns, which are critical for effective conservation management amid rising anthropogenic pressures (Fischer *et al*., 2019; Godbold *et al*., 2011; Shugart *et al*., 2010).

Oceanic islands have experienced extensive habitat loss, both through conversion to agricultural land and urban expansion for tourism, with native habitats destroyed, highly fragmented, or severely degraded (Fernández-Palacios *et al*., 2021). For instance, in Tenerife and Gran Canaria, over 98% of thermophilous woodland and 99% of laurel forest have been reduced, respectively, whereas in Hawaii, over 60% of native vegetation has been lost (Conry and Cannarella, 2010; Fernández-Palacios *et al*., 2021). Such habitat modification leads to changes in community composition, vegetation density, and canopy cover, thereby affecting ecosystem stability and species habitat suitability (Caviedes and Ibarra, 2017). These threats, exacerbated by rising human populations (Russell and Kueffer, 2019) and climate change-induced shifts in vegetation growth and habitat structure (Grimm *et al*., 2013), pose severe risks to the resilience of unique island ecosystems. Consequently, long-term monitoring of habitat structure on islands has been identified as a critical conservation priority (Borges *et al*., 2018a).

Structural complexity, as an Essential Biodiversity Variable (EBV) under the “Ecosystem Structure” class, is a suitable indicator for monitoring biodiversity change and ecosystem integrity (Pereira *et al*., 2013). These EBVs are designed to harmonise biodiversity monitoring programmes and help meet the Kunming-Montreal Global Biodiversity Framework targets by halting and reversing global biodiversity loss and restoring ecosystems (CBD, 2022). Thus, in areas that are experiencing habitat structural complexity changes due to anthropogenic disturbances, it is important to 1) characterise the structural complexity of their native habitats, and 2) monitor changes in habitat structural complexity (or other aspects of biodiversity) over space and time. Monitoring shifts in habitat structural complexity can aid in early detection of drivers of change, while baseline data allow restoration projects to target natural ecosystem states and prevent irreversible biodiversity loss or changes to ecosystem functioning (Schmeller *et al*., 2018). However, island biodiversity monitoring has historically been underrepresented in global conservation efforts and only recently recognised as a priority (Borges *et al*., 2018a). To minimise and reverse the losses to island biodiversity, harmonised and comprehensive monitoring is required.

Presently, advanced and emerging technologies are sought to increase the spatial and temporal scale of this monitoring. Issues in complete biodiversity monitoring typically stem from limitations in time, funding, and site accessibility (Stephenson, 2020). Novel technologies, including camera trapping, satellite, aerial, and ground-based remote sensing, and the use of environmental DNA, allow us to target some of these challenges through upscaling monitoring methods, increasing data capture and efficiency. The use of these technologies, however, needs to be appropriately determined by the monitoring goal; remote sensing applications allow spectral and radar data to be used for the characterisation of vegetations structure, for example (Dalton *et al.,* 2021). The fusion of these datasets derived from multiple technologies, combined with field data, allow an all-encompassing overview of biodiversity within a system (Kerry *et al.,* 2022). Regarding the monitoring of EBVs, remote sensing technologies, specifically LiDAR, was determined the most suitable for assessing Ecosystem Structure (Mulatu *et al.,* 2017), with, for instance, Terrestrial Laser Scanning (TLS) enhancing the monitoring and management of forest ecosystems over the 21st century.

TLS involves the use of a LiDAR sensor that emits laser beams, which backscatter off the surface of an object, giving detailed information on the 3D structure of such object (Lemmens and Lemmens, 2011; Slob and Hack, 2004). TLS has many applications, including wide use in urban planning and mapping, and engineering (Aryan *et al.,* 2021). For environmental monitoring, TLS utilisation is primarily focused on studies of geomorphology and topographical mapping (Telling *et al*., 2017). However, in biodiversity monitoring TLS is largely employed for upscaling forestry inventorying (Liang *et al*., 2016). Within forests, detailed information on forest structure can be gathered, such as above-ground biomass, branching architecture, canopy height, and structural complexity (Calders *et al.,* 2020). This has had important implications for sustainable resource use in forest management both for conservation efforts and ecosystem service valuation (Krok *et al.,* 2020). We see few studies have implemented TLS in other habitats, such as wetlands and shrublands (Alonso-Rego *et al.,* 2020; Rouzbeh Kargar *et al*., 2020; Xie *et al.,* 2021). Beyond this, TLS has not been extended into many further habitats (Ashcroft *et al.,* 2014; Richardson *et al.,* 2014). Applying TLS to low lying and fine scale vegetation needs further exploration if we are to fully understand these habitats for sustainable management and conservation practices.

Here, we characterised the structural complexity of a range of habitats across an oceanic island (Tenerife). Furthermore, we employed the TLS in non-forested habitats to assess its potential applicability across multiple habitat types. Specifically, we explored (i) the patterns of structural complexity in forested and non-forested habitats, (ii) the contribution of different components of structural complexity (such as vertical stratification and horizontal packing) to habitat structural complexity across island habitats, and (iii) the extent climatic drivers (precipitation and temperature) explain habitat structural complexity.

We focus on Tenerife in the Canary Islands due to the number of habitat types found on the island. Furthermore, land-use changes, including urbanisation, agriculture, and tourism development, have significantly altered Tenerife's habitats (Betzin *et al*., 2016). Therefore, establishing long-term monitoring of structural complexity is crucial for conservation, management, and restoration efforts here.

We consider the structural complexity of a habitat to be composed by the vertical (vegetation height and stratification) and horizontal (density and architecture) elements, aligning with Coverdale and Davies' (2023) definition. From our knowledge, this definition does not differ across habitats and, as such, testing and expanding the use of the TLS beyond forestry for capturing structure across multiple habitat types is justifiable. We acknowledge that habitat complexity itself encapsulates more than habitat structural complexity, ranging from the organisation of the "parts" of a habitat, to its movement and change over time, and interactions within the components of a system and from external factors (Riva *et al.,* 2023). As such, habitat complexity is an emergent property moving beyond the structural components (Bullock *et al.,* 2022). However, comparisons, comprehension, and predictions of complexity, as a concept, within and across habitats, go beyond the scope of what is currently observable for biodiversity monitoring.

In forested ecosystems, a Stand Structural Complexity Index (SSCI) was developed by Ehbrecht et al. (2017) to capture the heterogeneity of plant material distribution in 3D space (that align with our definition of structural complexity) into one quantified index, indicating the intricacy of these 3D habitat features. The SSCI has consequently been used to investigate relationships with species diversity and the promotion of more natural habitat variation in plantations, for example (Perles-Garcia *et al.,* 2021; Zemp *et al.,* 2019). We can, therefore, use this information in further studies and long-term monitoring to understand biodiversity relationships, ecosystem functioning, and change over time in these underrepresented habitats. Additionally, this knowledge can help stakeholders to sustainably manage these habitats to reduce or reverse current biodiversity loss.

2. Methods

2.1 Study Sites

Between June and November 2024, we surveyed the five key habitats (Figure 1) of Tenerife (28.28° N, 16.15° W). Tenerife is an island located within the Canary archipelago off the west 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 ecosystems are established on Tenerife because of climatic gradients across the island (del Arco and Rodríguez *et al.,* 2018):

1. Coastal scrub – a habitat with lower-lying shrub vegetation dominated by endemic *Euphorbia* species, adapted to lowland semi-arid environment (Otto *et al.,* 2001).
2. Thermophilous woodland – open woodland, typically found at mid elevation on steep slopes, dominated by juniper (*Juniperus*), wild olives (*Olea*) or mastic (*Pistacia*) trees.Fernández-Palacios *et al.,* 2024).
3. Laurel forest – Neogene relic broadleaved forest, characterised by high humidity and dominated by Lauraceae trees (Fernández-Palacios *et al.,* 2019).
4. Canary pine forest – coniferous forest, found at higher elevations, between 1200 – 1800 m, dominated by the Canarian pine (Parsons, 2021).
5. Summit scrub – restricted to the peak of El Teide surroundings (i.e. summit, highlands, high elevation), largely consisting of shrub leguminous vegetation (Renner *et al.,* 2023).

We sampled two distinct coastal scrub types: one dominated by the larger *Euphorbia canariensis* (cardonal) and the other by the shorter *Euphorbia balsamifera* (tabaibal).

Figure 1. The main habitats found on Tenerife: A) Tabaibal coastal scrub, B) Cardonal coastal scrub, C) Thermophilous woodland, D) Summit scrub, E) Pine forest, and F) Laurel forest. Image credits: Samantha Suter (A, B, C, E, F) and José Maria Fernández-Palacios (D).

2.2 Sampling Design

A plot network exists on the island from previous studies establishing long-term monitoring of species richness, carbon stocks, above ground biomass and other vegetation dynamics, or characterising modern pollen rain (Borges *et al.,* 2018b; de Nascimento *et al.,* 2015; Grupo de Investigación de Ecología y Biogeografía Insular, Universidad de La Laguna, N.D; Otto *et al.,* 2001). We used five 50 x 50 m plots for all habitats except the thermophilous woodland where three 20 x 20 m plots were used. Differences in size and number of plots were related to the remaining thermophilous woodland located in inaccessible terrain (Figure 2). One site of tabaibal coastal scrub was measured at 20 x 20 m due to the density of vegetation. The SSCI by construction is scale-independent (i.e. it does not increase with area). Thus, plot size should be reflective of the environmental conditions such as vegetation density, where scan overlap can be avoided to capture true vegetation heterogeneity.

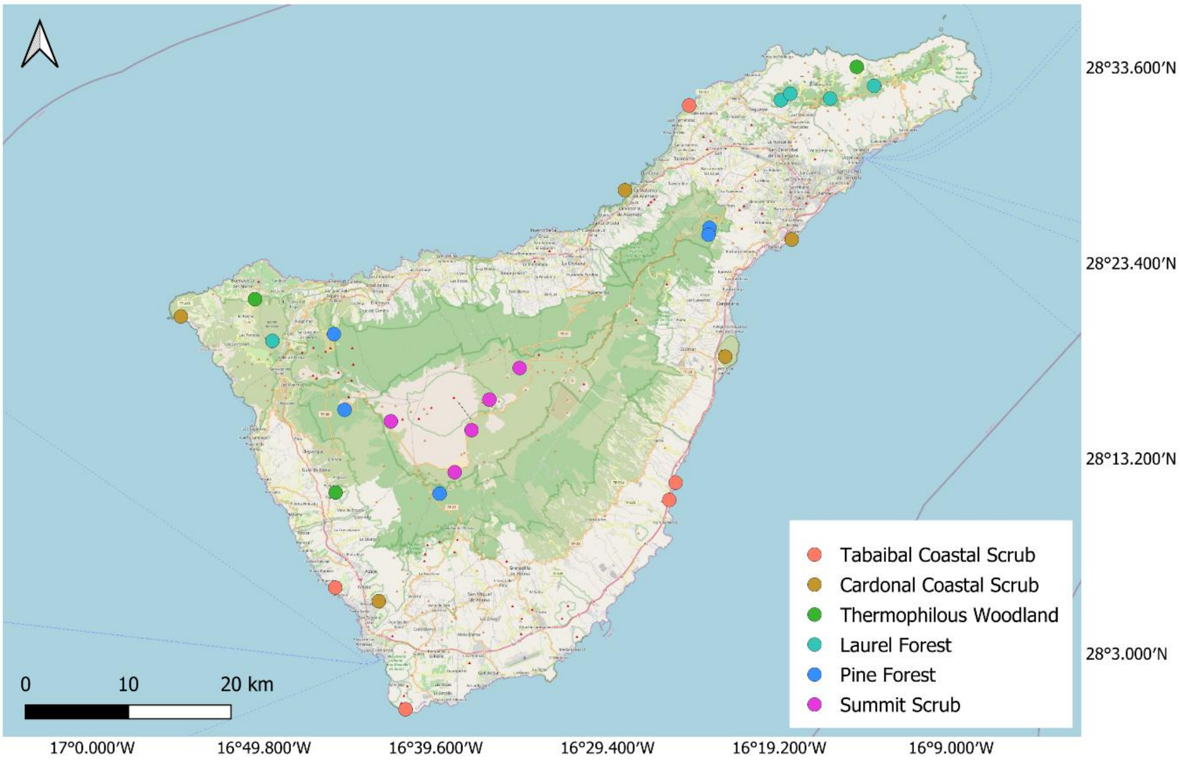

Figure 2. Plot locations of terrestrial laser scans taken in the five key habitats across Tenerife: coastal scrub (tabaibal and cardonal), thermophilous woodland, laurel forest, pine forest, and summit scrub.

A FARO Focus M70 terrestrial laser scanner (Faro Technologies Inc., Lake Mary, USA) was used to scan the plots in each habitat. Five single scans in each plot were performed, one in the centre of the plot and then 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°. A total of 140 scans were performed.

2.3 Structural Complexity Computation

The scans were imported into the software FARO SCENE to handle the point cloud data from the TLS. The scans were processed using standard filtering algorithms to remove noise from the data and were then converted into an. xyz format. The .xyz files were then inputted into R version 4.3.3 (R Development Core Team, 2019).

We made use of the SSCI index by Ehbrecht et al. (2017) to explore structural complexity across the habitats. The SSCI is constructed through two other derived variables: the mean fractal dimension index (MeanFRAC) and the effective number of layers (ENL). MeanFRAC 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 MeanFRAC index can be considered a proxy for vegetation density. The ENL captures the vertical stratification and 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). As such, ENL can be considered a proxy for the vertical distribution of plant material. Canopy openness and the mean distance from the stand were also computed, the latter as an average of the distance between the TLS and laser returns within the point cloud. We propose this as a useful indicator of structural complexity that further represents vegetation density.

The understory complexity index (UCI), the latter index developed by Willim et al. (2019), are also calculated. The UCI differs from the SSCI in that it is calculated between a restricted height (0.8 – 1.8 m across the habitat stand), where the understorey vegetation is typically distributed. The UCI does not incorporate the ENL and is calculated through one fractal dimension value (Willim *et al.,* 2019). Preliminary tests were performed to investigate the adaptation of the SSCI index for non-forested habitats, explore the applicability of utilising the UCI instead of the SSCI in our scrub habitats, and to try address errors encountered in post-processing of the data. These can be found in Supplementary Note 1 and Figure S1.

2.4 Climate and Topographical Data

We incorporated climatic data for Tenerife into the analysis. We used data from the CanaryClim v1.0 dataset that was generated as part of the study by Patiño et al. (2023). Mean annual precipitation and temperature for the plots were extracted from the CanaryClim v1.0 dataset that incorporated climatic data between 1979–2013 at a 100 m spatial resolution.

2.5 Statistical Analysis

We explored patterns of structural complexity across the habitats in Tenerife using descriptive statistics. Variation within habitat was described with standard deviation. A principal component analysis (PCA) was used to investigate variability across habitats in reduced (two) dimensions. We used the "prcmp" function in the "stats" package to compute the PCA (R Core Team, 2024). The variables were scaled for computation of the PCAs.

To test the relationship between structural complexity and climatic drivers (annual precipitation and annual temperature), a multiple linear regression analysis was conducted. A linear mixed effect model was used, including annual precipitation and mean annual temperature as fixed effects, and habitat as a random intercept to account for non-independence and baseline variation across habitat types. The model did not include random slopes, as the sample size per habitat was insufficient. Specifically, a robust linear mixed effect model (R package “robustlmm” (Koller, 2016)) was chosen as assumptions of normality could not be met and to account for high variance in SSCI in some habitats. Model residuals were checked, and deviating observations were down weighted to reduce the influence on the overall model fit. All analysis was conducted in R version 4.3.3 (R Core Team, 2024) with significance values set to 0.05 where applicable.

3. Results

3.1 Patterns of Habitat Structural Complexity

Across the habitats of Tenerife, SSCI varied between lowest mean value of 2.65 to the highest mean value of 7 for summit scrub and laurel forest respectively (Figure S2). Within habitat variation in SSCI was largest in the tabaibal coastal scrub with a mean plot SSCI standard deviation of 4.67. Whilst the smallest within habitat variation in SSCI was found in the pine forest, resulting in a mean plot SSCI standard deviation of 0.59 (Figure S3). In addition, differences amongst habitats were also observed for ENL, ranging from 2.36 in Tabaibal Coastal Scrub to 20.89 in Pine Forest. MeanFRAC ranged from -28.18 in the tabaibal coastal scrub to 2.63 in the thermophilous woodland. Canopy openness was 100 for scrub habitats. For the forests and woodland habitats, the lowest canopy openness was observed on Laurel Forest (5.0) and the highest on thermophilous woodland (73.2). We saw the greatest mean distance to the stand in the tabaibal coastal scrub at 22.08 and the lowest in the thermophilous woodland of 3.91 (Table 1).

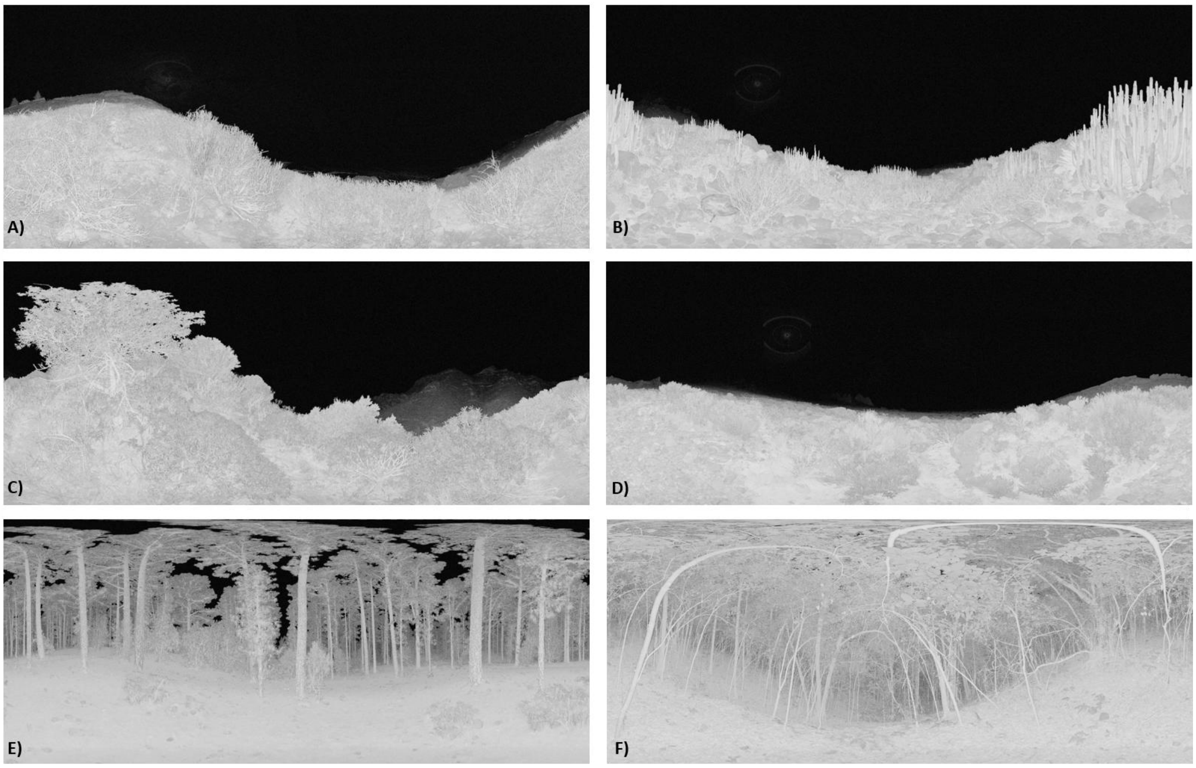

Figure 3. Example previews of terrestrial laser scans taken in habitats across Tenerife: A) tabaibal coastal scrub, B) cardonal coastal scrub, C) thermophilous woodland, D) summit scrub, E) pine forest, and F) laurel forest.

Table 1. Plot information and computed structural measures (means ± standard errors) from terrestrial laser scanning (underlined) across the studied habitats in Tenerife.

Habitat	*Processed Plots n*	Plot Size (m)	Dominant Species	SSCI	ENL	MeanFRAC	Canopy Openness	Mean Distance to the Stand
Summit Scrub	25	50 x 50	*Cytisus supranubius, Pterocephalus lasiospermus*	2.65 ± 0.61	3.28 ± 0.24	2.40 ± 0.50	100 ± 0.00	20.82 ± 1.52
Tabaibal Coastal Scrub	24	50 x 50; (1 plot 20 x 20)	*Euphorbia balsamifera*	5.06 ± 2.08	2.36 ± 0.25	-28.18 ± 22.89	100 ± 0.00	22.08 ± 3.69
Cardonal Coastal Scrub	25	50 x 50	*Euphorbia canariensis*	3.02 ± 0.25	3.44 ± 0.21	2.20 ± 0.41	100 ± 0.00	8.51 ± 0.89
Pine Forest	25	50 x 50	*Pinus canariensis*	3.92 ± 0.16	20.89 ± 0.91	1.57 ± 0.02	40.21 ± 3.84	16.05 ± 1.17
Thermophilous Woodland	15	20 x 20	*Phoenix canariensis, Juniperus turbinata* ssp. *canariensis*	5.79 ± 0.79	6.89 ± 0.76	2.63 ± 0.40	73.26 ± 9.51	3.98 ± 0.45
Laurel Forest	25	50 x 50	Many different trees, among them four Lauraceae species	7.00 ± 0.25	14.60 ± 0.66	2.09 ± 0.04	5.01 ± 2.24	6.91 ± 0.46

3.2 Components of Habitat Structural Complexity

The PCA showed that principal components one and two captured 72.4% of the variability (Figure 4). The first principal component was positively correlated with measures of horizontal structure (mean distance to the stand, canopy openness, mean fractal dimension). There is a negative relationship between the horizontal structural metrics (represented by mean distance to the stand and canopy openness) and the vertical structure (represented by ENL). Thus, differences between forest and scrub habitats were mainly associated with the PC1. 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 have overall lower ENL, higher mean distance to the stand, and canopy openness. For cardinal and summit scrub habitats, most of the intra-habitat variation was related to the PC2, with larger intra-habitat variation in both dimensions associated with tabaibal coastal scrub.

The second component shows a weak negative correlation to the MeanFRAC, distinguishing the sites within the scrub habitats with greater horizontal packing. For example, the thermophilous woodland, although represented by the structural components in both dimensions, is associated with greater MeanFRAC values, suggesting greater horizontal density of vegetation. Contrastingly, the cardonal coastal and summit scrubs appear to have higher mean distances from the stand with greater canopy openness. The tabaibal coastal scrub displayed the greatest variation in mean fractal dimensions, however.

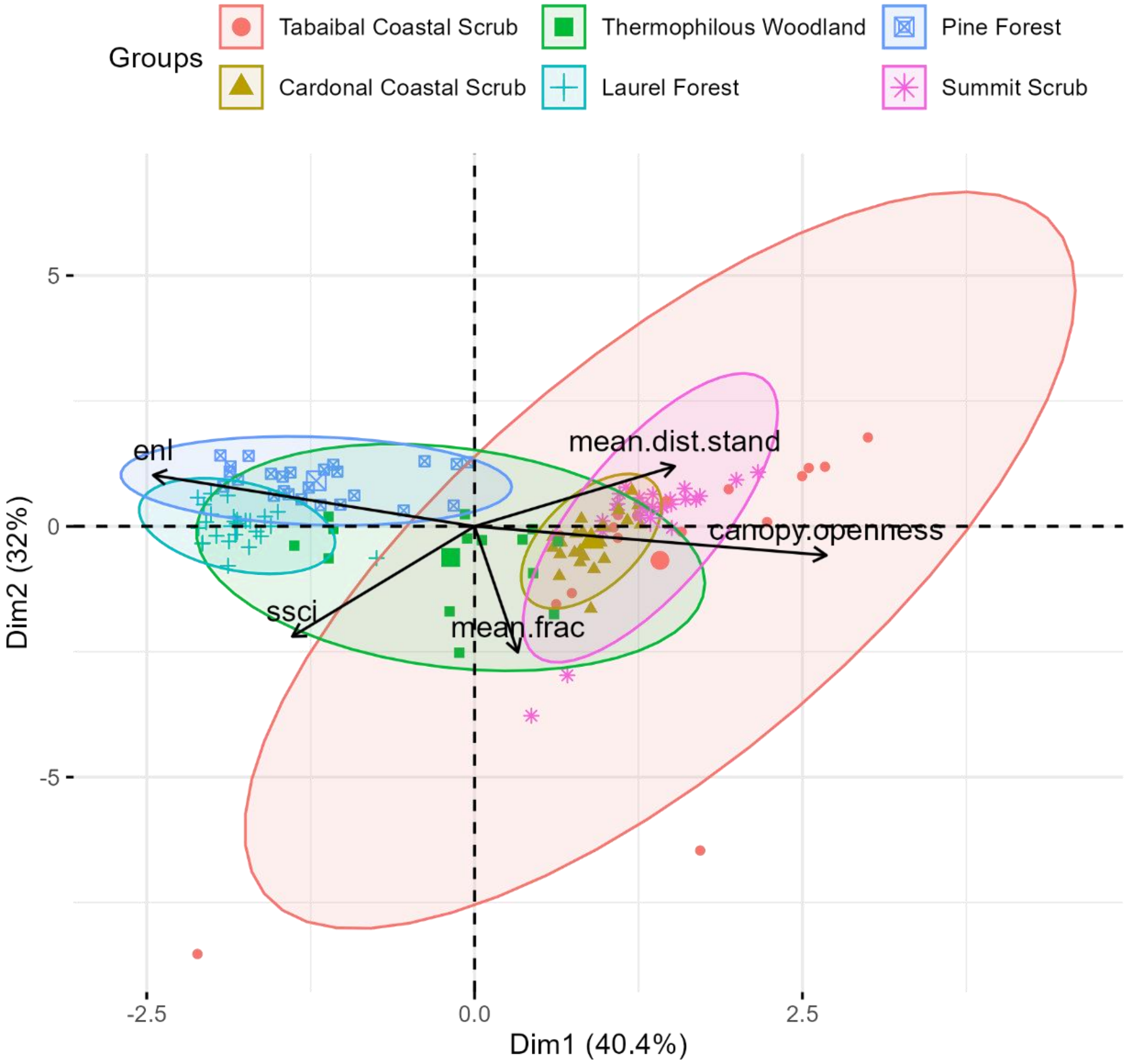

Figure 4. Representation of terrestrial laser scanning variables for stand structural complexity by the first two principal components derived from principal component analyses in habitat types across Tenerife.

3.3 Drivers of Structural Complexity

Climatic conditions explained variation in the SSCI when accounting for habitat type (Marginal $R^2 = 0.16$, conditional $R^2 = 0.84$; Table 2). Specifically, annual precipitation had a statistically significant positive effect on mean SSCI ($\beta = 0.004$, SE = 0.001, t = 3.21, p = 0.003) (Figure 5). In contrast, mean annual temperature had a non-significant effect on mean SSCI ($\beta = 0.124$, SE = 0.085, t = 1.45, p = 0.161). There was variability in the intercepts across habitat types, with a variance of 2.40, suggesting that baseline mean SSCI values differ between habitat types. The residual variance was 0.55, indicating within-group variability.

Table 2. Results of the robust linear mixed effect model investigating the relationship between fixed effects of climate (annual precipitation and mean annual temperature) and habitat stand structural complexity, controlling for random effects of habitat type. Model variation of fixed effects are represented by the marginal R^2, whilst the variation explained by the random effect is represented by the conditional R^2.

	Mean SSCI				
Predictors	**Estimate**	**Std. Error**	**t Value**	**p Value**	**Conf. Interval**
(Intercept)	-0.111	1.819	-0.061	0.951	[-3.804, 3.583]
Annual Precipitation	0.004	0.001	3.211	0.003	[0.002, 0.007]
Mean Annual Temperature	0.124	0.085	1.453	0.161	[-0.049, 0.300]
Random Effects					
Variance (Habitat)	2.401				
Residual Variance	0.551				
N_{Habitat}	6				
Observations	28				
Marginal R^2 / Conditional R^2	0.159 / 0.843				

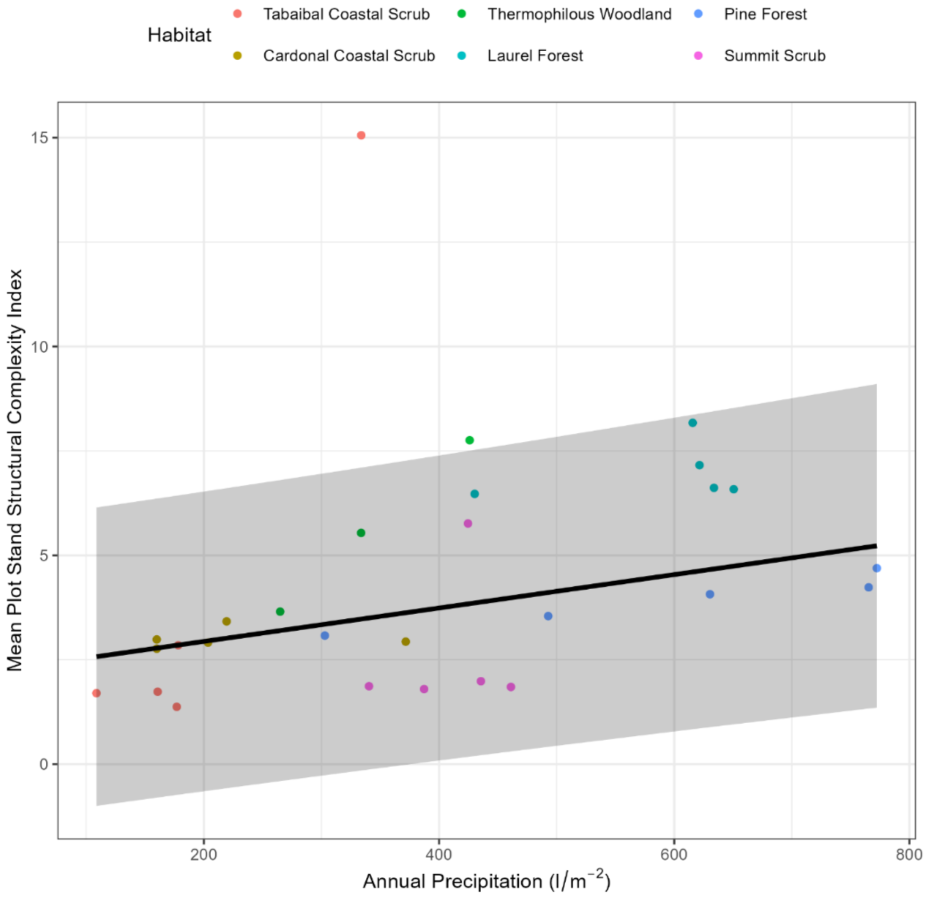

Figure 5. Relationship between mean annual precipitation (calculated between 1979 – 2013 at 100 m spatial resolution) and mean plot stand structural complexity across key habitats in Tenerife. The black line shows the fixed-effect prediction of precipitation with temperature held constant at its mean, with the 95% confidence interval (shaded area). Each point represents a sampled site, coloured by habitat.

4. Discussion

The results of this investigation provide the first insights into the structural complexity from TLS of major habitats found on Tenerife. The importance of characterising structural complexity on island habitats is unparalleled, with these areas representative of likely changes we can expect to see as defined by the Anthropocene (Russell and Kueffer, 2019). With habitat transformation of these habitats occurring more rapidly, collecting baseline data to monitor long-term changes remains a priority. We trialled TLS in endemic coastal and summit scrub, and thermophilous woodland habitats, where this method and structural complexity analysis has not been used before. Our results show clear patterns of structural complexity across island habitat types, and that it is possible to use TLS technology in other habitats (in addition to forests), highlighting the inclusion of metrics capturing horizontal structural complexity. This is because we see that components of structural complexity contribute differently dependent on the habitat type, with vertical stratification characteristic of the forest habitats compared to the varying vegetation density in horizontal space distinguishing the scrub habitats. Climatic conditions were able to explain only 16% of variation in structural complexity across habitat types, however, we saw as annual precipitation increased, habitat structural complexity increased across habitats on Tenerife.

Among the studied habitats, the laurel forest exhibited the highest stand-level structural complexity whereas the summit scrub showed the lowest. In comparison, the tabaibal coastal scrub showed the highest within-habitat structural variation. The observed patterns of structural complexity in forest habitats (pine and laurel forests) align with previous studies and global predictions of the SSCI. As reported by Ehbrecht et al. (2021), SSCI is typically higher in broad-leafed forest communities compared to coniferous forests, which is consistent with our findings. The relationship between precipitation and SSCI described by Ehbrecht et al. (2021) could explain our findings. In fact, our climate data similarly indicate that higher annual precipitation is associated with greater stand structural complexity across habitat types. Interestingly, we saw evidence of a similar positive relationship with the ENL (Figure S4) but not found with understorey complexity and less evident with the MeanFRAC (Supplementary Note 2), suggesting that precipitation is influencing more greatly the vertical rather than horizontal structural components.

The structural complexity of scrub and thermophilous woodland habitats cannot be directly compared to previous studies. Structural characterisation of components with TLS have occurred in sagebrush steppe (shrub height and canopy cover) (Vierling *et al.,* 2013) and arctic shrub (above ground biomass and leaf area) (Greaves *et al.,* 2015), however, the overall complexity of the habitats was not captured. This is a notable gap in the characterisation of habitat structural components, especially complexity, beyond forests using TLS (Greaves *et al.,* 2015; Muumbe *et al.,* 2021). Given the diversity of life forms and high intra- and interspecific variability we know of many scrub habitats, there is inherent structural complexity, informed by known ecological traits such as plant architecture, that can be captured. Therefore, further characterisations across scrub habitats are needed.

4.1 Within and Across Habitat Structural Complexity Variation

Although precipitation emerged as a significant driver of structural complexity, only 16% of variation in our model was explained, compared to 66% at global scale (Ehbrecht *et al.,* 2021). This variation may be reduced by the inclusion of multiple habitat types or additional factors might influence structural complexity more greatly (such as level of disturbance, management regimes, nutrient availability and competition, regeneration dynamics, succession, and species diversity) within and across habitat types.

All major altitudinal ecosystems of Tenerife, except the summit scrub, have experienced high levels of human disturbance (Otto *et al.,* 2007, Otto *et al*., 2012, Fernández-Palacios *et al*., 2019, Fernández-Palacios *et al*., 2024), limiting the availability of undisturbed plots. We endeavoured to select the least anthropogenically disturbed sites but, owing to the extent restriction, the plots are not uniform in their maturity, management, community, and level of disturbance. Previous studies demonstrate that management practices can either reduce (e.g. plantations; Ehbrecht *et al.,* 2017; Perles-Garcia *et al.,* 2021; Zemp *et al.,* 2019) or increase (Saarinen *et al.,* 2021) habitat structural complexity. Other disturbances, such as logging, fire, and livestock presence can simplify habitat structural complexity (Caviedes and Ibarra, 2017). For instance, three of five pine forest plots were subject to a large forest fire in 2023, whilst thermophilous woodland plots varied in dominance between juniper and palm species, thus contributing to within habitat variation of structural complexity.

The greatest habitat structural complexity variation was observed within the tabaibal coastal scrub, potentially indicating greater affects from disturbance or environmental conditions. In fact, Otto et al. (2001) showed that cover, vegetation height, and biomass of well-conserved coastal scrub increased strongly along a precipitation gradient from the arid southern to the semi-arid northern coast of Tenerife. Cover and height of coastal scrub also increases during secondary succession on abandoned fields on Tenerife (Otto *et al*., 2006). Furthermore, although we see that a more speciose habitat is likely to have higher structural complexity (such as in the laurel forests of Tenerife), other less species diverse habitats might have great variation in structural complexity due to increased intraspecific trait variation (Coverdale and Davies, 2023). For example, pine forests may be highly vertical structured at different stages of juvenile recruitment, medium-aged adult individuals, and mature trees. This successional or gap dynamic may influence intra-specific structural patterns related to different vertical layers of the same species. Hence, even a species poor forest might show high structural complexity.

Mature, less disturbed habitats may exhibit higher structural complexity due to increased species richness, vegetation layering, and the presence of deadwood from a higher species richness (Casas *et al.,* 2016; Coverdale and Davies, 2023; Perles-Garcia *et al.,* 2021). However, we do note that structural complexity may peak before maturity of a habitat – a mid-successional habitat may be more heterogenous as the dominant species of a mature ecosystem are not yet eliminating space for greater species richness (Qianwen *et al.,* 2022; Sferra *et al.*, 2017). For example, the *Morella-Erica* heath which occurs in disturbed or transitional areas between scrub and laurel forest, can exhibit dense, twisted vegetation indicative of high structural complexity, potentially exceeding that of mature laurel forest (Bermúdez *et al.,* 2007).

4.2 Components of Structural Complexity

Numerous vegetation traits can contribute to habitat structural complexity. Seidel *et al.* (2019a) show that crown traits such as crown size from individual trees have a positive relationship to forest plot stand structural complexity, whilst tree architecture from branching patterns (direction, density, etc.) further result in unique tree morphologies (Seidel *et al.,* 2019b), strongly influencing overall habitat structural complexity (Koller *et al.,* 2025). Community trait 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 are present within our non-forested habitats, albeit at different scales, thus likely contributing similarly to habitat structural complexity in scrubs. With traditional forest inventories typically focusing on tree height and diameter at breast height, Koller et al. (2025) demonstrate the importance of tree branching architecture in habitat structural complexity (specifically contributing towards MeanFRAC), which suggests that these attributes be even more considerable in scrub habitats where vertical stratification is less pronounced.

Our results of the PCA indicate that structural features contribute differently to habitat complexity across habitats. For taller habitat stands, such as in the forests, the vertical stratification, or ENL, is a more defining feature. De Conto *et al.* (2024) demonstrated a positive relationship between forest structural complexity (derived from GEDI waveforms) and canopy height, dependent on location and forest type, whilst noting that leaf area and canopy cover or density may be influential in other systems. Consistent with this, our PCA showed that in scrub habitats, structural indicators such as mean distance from the stand and MeanFRAC were more influential, suggesting that complexity in these habitats is shaped by other features.

For example, in the cardonal coastal scrub, this community is more speciose, with a variety of species morphology (the cactus-like *Euphorbia canariensis*, versus the umbrella shaped *E. lamarckii, Plocama pendula* has hanging branches, whilst the presence of climbers such as *Periploca* exist), thus increasing structural complexity. However, the community has a lower species density, which would conversely limit the horizontal packing and consequently habitat structural complexity.

The tabaibal coastal scrub is dominated by *Euphorbia balsamifera*; a species that grows in a hemispherical shape and displays a high branching density from the ground to the top of the shrub's canopy. In one plot, a single scan yielded an extreme SSCI value of 44.02, What can initially be viewed as an extreme outlier, may likely indicate dense branching architecture and high canopy cover (Figure 6). This supports our PCA finding of a negative relationship between mean distance from the stand (a possible proxy for canopy cover or density) and SSCI. 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 sparse canopies of the southern coastal and summit scrubs, further supporting the contribution of vegetation cover and density to structural complexity.

Figure 6. Branching architecture of *Euphorbia balsamifera* (left) and resulting terrestrial laser scan preview (right) of the associated plot.

4.3 Future Considerations and Management Applications

We did not consider other structural complexity indices (Batchelor *et al.,* 2022; Reich *et al.,* 2021; Seidel, 2018), as the SSCI is advantageous for rapid capture of single scans in field and the simple algorithm processing; ideal for island- based monitoring by stakeholders. We argue that the definition of structural complexity should not differ across ecosystems. Thus, the SSCI captures components of structural complexity (as we measured it) comparable across habitats. We note that the structural attributes chosen to define a structural complexity index will yield different values (Reich *et al.,* 2022) and future research could compare alternative metrics. The choice of index should be determined by its purpose; in our case, enabling simple, repeatable monitoring of structural complexity over time and across habitats.

With these considerations in mind, we propose future research directions to try disentangling the direct and indirect drivers of habitat structural complexity. Ehbrecht et al. (2021) highlight the abiotic drivers of structural complexity in defining habitat floral composition and biomass distribution. We extend this by incorporating across and within habitat variation, adding complexity through intraspecific trait variation (Figure 7). We could predict that higher intraspecific trait variation (arising from varying growth rates, stem characteristics, branching structure, or leaf production and characteristics, for example) would lead to greater within habitat variation. Additionally, variation in structural components differ by habitat type; habitats with little height differentiation between species may show higher structural complexity with increased divergence of horizontal structural components.

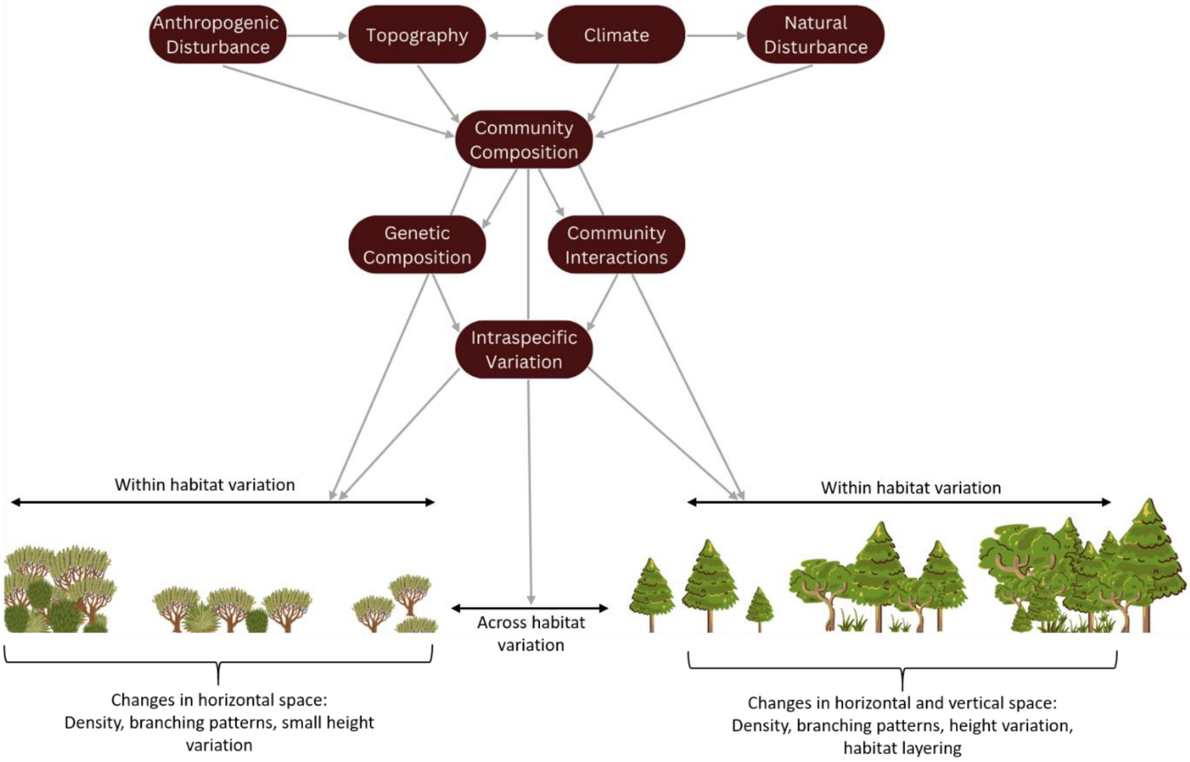

Figure 7. Cascading effects of abiotic and biotic drivers of structural complexity leading to across and within habitat variation in structural complexity. Figure adapted from Ehbrecht *et al.,* 2021.

Structural complexity must also be considered beyond woody species; vertical and horizontal components of structure exist in grasslands, but their fine-scale spatial organisation proves difficult to measure. How these proportionally constitute the habitat structural complexity warrants further investigation. This requires sampling across environmental and disturbance gradients, accounting for trait variation of individuals within and between species (Westerband *et al.*, 2021).

With the TLS pertinent for use in forestry management and planning applications (Perles-Garcia *et al.,* 2021; Saarinen *et al.,* 2021; Zemp *et al.,* 2019), we argue that this can be initiated across habitats. TLS is valuable for resource quantification, understanding biodiversity patterns, and making conservation decisions based on the quantified habitat structural complexity of an area (Caviedes and Ibarra, 2017). With repeat scanning of habitats, change can be indicated, highlighting issues with management practices or disturbance, for example (Penman *et al.,* 2023). The TLS can subsequently track improvements in structural complexity as a result from restoration efforts or changes in management. With broader applicability of the TLS for quantifying structural complexity that we demonstrate here, common workflows can be developed for stakeholder uptake that can be directed to ecologists, habitat managers, and conservation planners. By expanding our understanding of habitat structural complexity across habitats in our study, management practices can ensure the retention of vital structural components.

We encourage the use of the TLS for long-term monitoring of structural complexity changes across habitats, with the endeavour to provide new monitoring protocols that can be instigated more globally. This is fundamental in underrepresented locations that are witnessing unprecedented change. Consequently, we can deliver conservation and management efforts that maintain the unique biodiversity found on oceanic islands.

Declarations

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Author Contributions

Conceptualisation: SS, DCZ, RO, JMF-P, LdN, NG-R, HK. Data collection: SS, FRA, RO, NSC, CZ, NGR, JMF-P. Writing: SS. Expert Input: RO, JMF-P, LdN, ME. Revising: DCZ, JMF-P, RO, LdN, ME, NG-R, FRA, NSC, HK.

Competing Interests

The authors declare no competing interests.

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Supplementary Materials

Supplementary Note 1.

Preliminary tests were performed to investigate the adaptation of the SSCI index for non-forested habitats, explore the applicability of utilising the UCI instead of the SSCI in our shrub habitats, and to try address errors encountered in post-processing of the data.

Expanding the Point Cloud Distribution: Algorithm Adaptation of Structural Complexity

We conducted preliminary adjustments of the SSCI and UCI to see if the indices would require changes that were more applicable to the construction of structural complexity within the shrub habitats. Initial exploration of the TLS images demonstrated that a large portion of the coastal scrub images are “empty” – as in they do not contain vegetation information. It was questioned whether this space may influence the results of the SSCI of habitats with low-lying vegetation. To see if the more information on structural complexity could be captured within the scrub habitats which have lower lying vegetation, the algorithm for the SSCI and UCI was adapted to remove this empty space. The SSCI is calculated from point clouds above the scanner height (1.3 m above the ground), whilst the UCI is calculated from points within 0.8 to 1.8 m from the scanner height. Both were adapted to take points from the ground (-1.3 m), and to the top of the scrub canopies for the UCI (15 m).

T Tests were used to test if adjusting the algorithm of SSCI and UCI computation significantly affected the value of these indices within the scrub habitats. This was primarily used to explore the influence of empty space in the scans of the scrub habitats on the indices. Assumptions were tested and met.

By altering the algorithm for computing the SSCI and UCI, this resulted in 12 of the summit scrub, 21 of the tabaibal coastal scrub, and 14 of the cardonal coastal scrub scans unable to process. A T Test showed that the differences in original SSCI and UCI and the adapted SSCI and UCI values were non-significant (t = 0.10939, df = 45.401, p-value = 0.9134, and t = -0.79488, df = 29.591, p-value = 0.433 respectively) with changes to the algorithm. These adjustments did not improve the computation of structural complexity or ultimately make more sense for these habitats and, as such, the original algorithm was determined suitable for all habitat types we surveyed

SSCI versus UCI for Scrub Habitats

The UCI was, on average, the highest, within the tabaibal coastal scrub habitat, with a mean UCI of 4.20. On average, the lowest UCI values were found in the pine forest with a mean

UCI of 2.05. Within habitat variation in SSCI and UCI was largest in the tabaibal coastal scrub with a mean plot SSCI standard deviation of 4.67 and UCI standard deviation of 5.58. Whilst the smallest within habitat variation in SSCI and UCI was found in the pine forest, resulting in a mean plot SSCI standard deviation of 0.59 and UCI standard deviation of 0.91 (Figure S1).

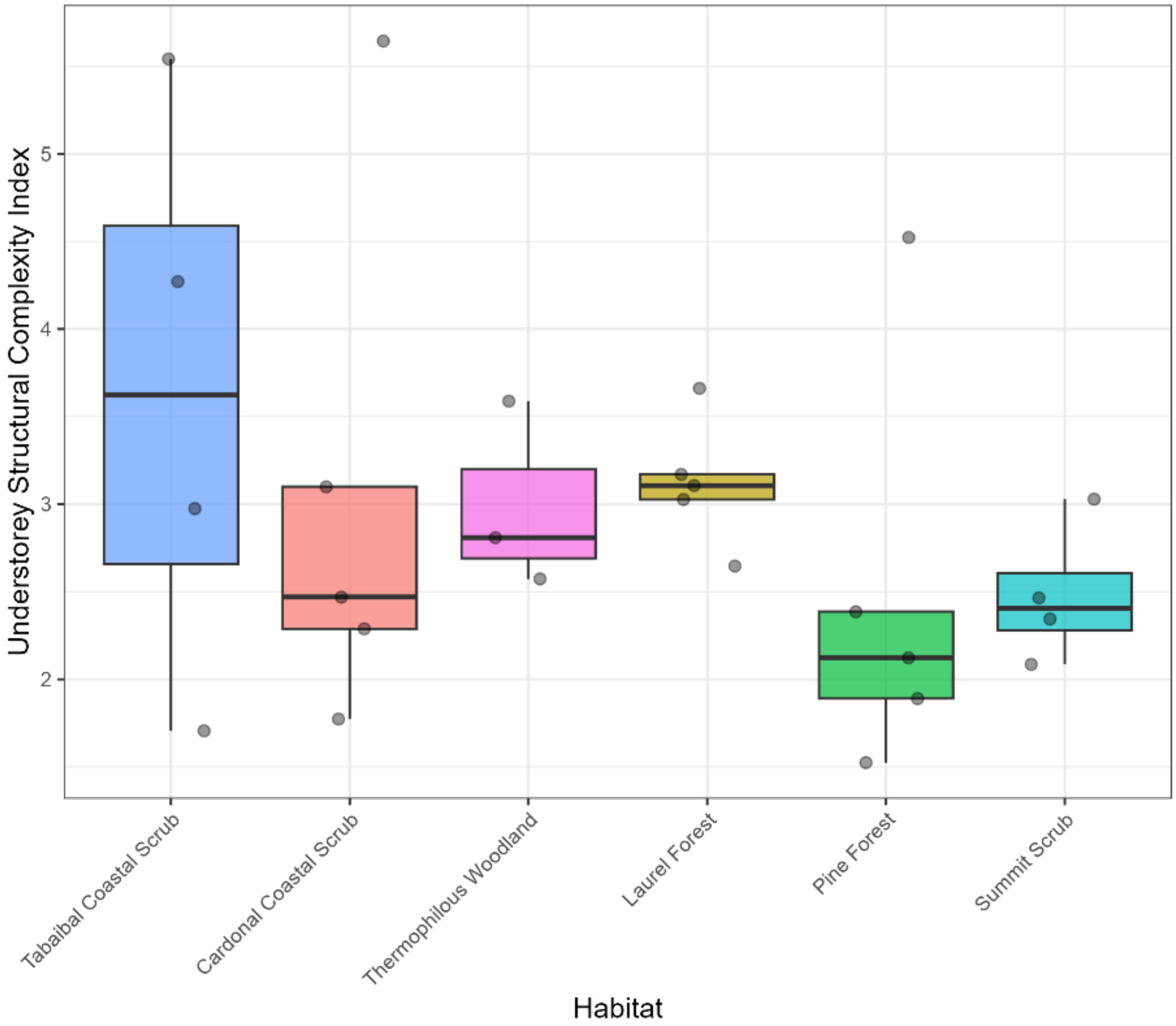

Figure S1. Distribution of plot mean understorey structural complexity values by habitat type across Tenerife.

We considered the use of the UCI solely for the shrub habitats for the measurement of structural complexity. We thought the UCI may contain further structural information that may be more relevant for low lying vegetation, as this is calculated for vegetation between 0.8 – 1.8 m from the scanner height. Due to the height constraints, we hypothesised that the UCI would miss structural information outside of this range. We adjusted the UCI to include all points across the scrub stands as a substitute for the SSCI. For the shrub habitats, we wanted to investigate whether the stand was largely made up from vegetation within the defined understorey height or distributed wider across the entire stand (as defined by the SSCI). We compared the SSCI and UCI values for each scan of the three scrub habitats (summit, tabaibal coastal, and cardonal coastal). Assumptions of normality could not be met, so for each habitat, a paired Wilcoxon test was used.

The mean SSCI value for the cardonal coastal scrub was 3.02 versus 3.06 for the UCI. There was no significant difference found between the means of the index values ($p = 0.098$). For the summit scrub, the mean SSCI value was 2.65 versus a mean UCI value of 3.28. The mean values between the SSCI and UCI were not significantly different for the summit scrub ($p = 0.083$). The mean SSCI value in the tabaibal coastal scrub was 5.06, whilst the mean UCI value was 4.20. We did not conduct the paired Wilcoxon test, because only six of the scans had both SSCI and UCI values.

The UCI itself is not directly comparable to the SSCI, which uses MeanFRAC compared to a single fractal dimension index value needed for the UCI, only considers points within 15 m horizontally from the scanner, and does not consider the ENL of the habitat for index computation (Willim *et al.,* 2019). In the end we determined, based on our definition of structural complexity, the ENL (vertical space occupation) must be included in all stands structural complexity calculations regardless of habitat type. When considering our definition of structural complexity which is consistent across habitats, it is still important to incorporate the vertical stratification of the habitat. Without this scaling, the structural complexity values in shorter vegetation stands may be inflated, as the UCI only considers the horizontal complexity. The extreme values of structural complexity that we found in shorter habitat stands such as the tabaibal coastal scrub demonstrate the structural complexity that these habitats can reach because of their horizontal structural components. Even with the reducing effect on structural complexity resulting from minimal vertical structure in the scrub habitats, we can see the extent that horizontal structure can bring to the overall habitat structural complexity

Computation of Structural Complexity

For SSCI computation 14 scans were unable to be processed, of which 1 was from the thermophilous woodland, 10 were from the tabaibal coastal scrub, and 2 were from the cardonal scrub habitat. More issues were associated with the computation of the UCI where 15 scans did not process: 1 within the summit scrub and 14 within the tabaibal coastal scrub. For scans where the canopy height was calculated at 1 m, the SSCI did not correctly calculate where the ENL derived also gave a value of 1. The extent of the vertical distribution of the vegetation (beyond canopy height), therefore, may limit the use of the SSCI within habitats with very small vegetation heights. Other instances of SSCI computational failure resulted from negative MeanFRAC values calculated. These occurred mostly in the coastal scrubs, and once in the thermophilous woodland. A negative MeanFRAC can result when thresholds in the size of the polygon areas or lengths that are constructed from the point cloud are not met. This could occur even from only one negative fractal value in one of the 1280 cross-sections, suggesting there is less occupied space in one horizontal direction. This may be more likely to occur within sparsely vegetated habitats, but we argue that where any vegetation occurs, the structural complexity can still be captured.

Protocols for calculating structural complexity exist, and, for the SSCI here, are centred around forest habitats. Perhaps this exact protocol cannot be applied to lower lying vegetation. We considered the possibility to adjust the height of the TLS to be lower, ideally below the canopy for all habitats. However, for some of the scrub habitat plots, this was still not possible for a large portion of the plots, as the tripod was still too high off the ground at the lowest setting. Potentially, a habitat specific set up would need to be developed where the TLS can be placed as low to the ground as possible. This was not possible within the scope of our study but necessitates further research.

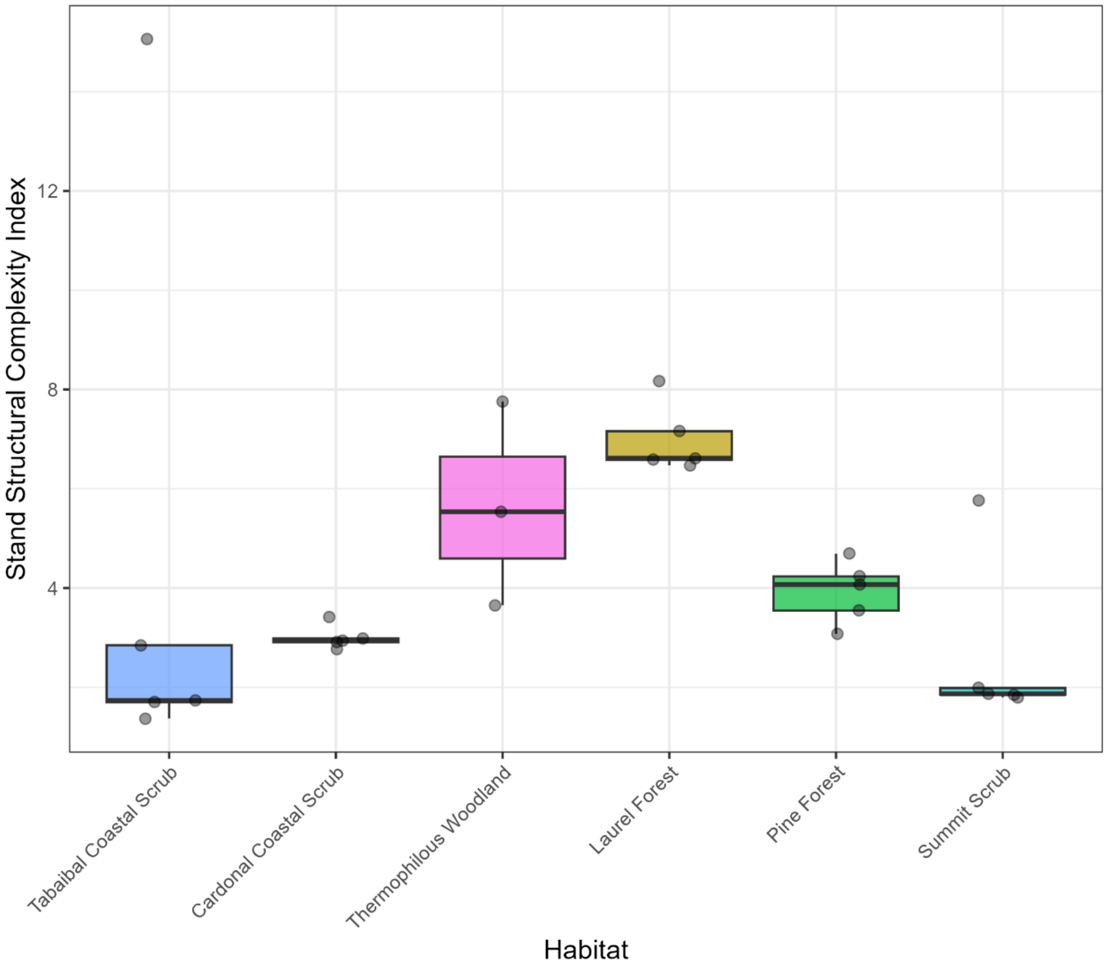

Figure S2. Distribution of mean plot stand structural complexity by habitat type across Tenerife.

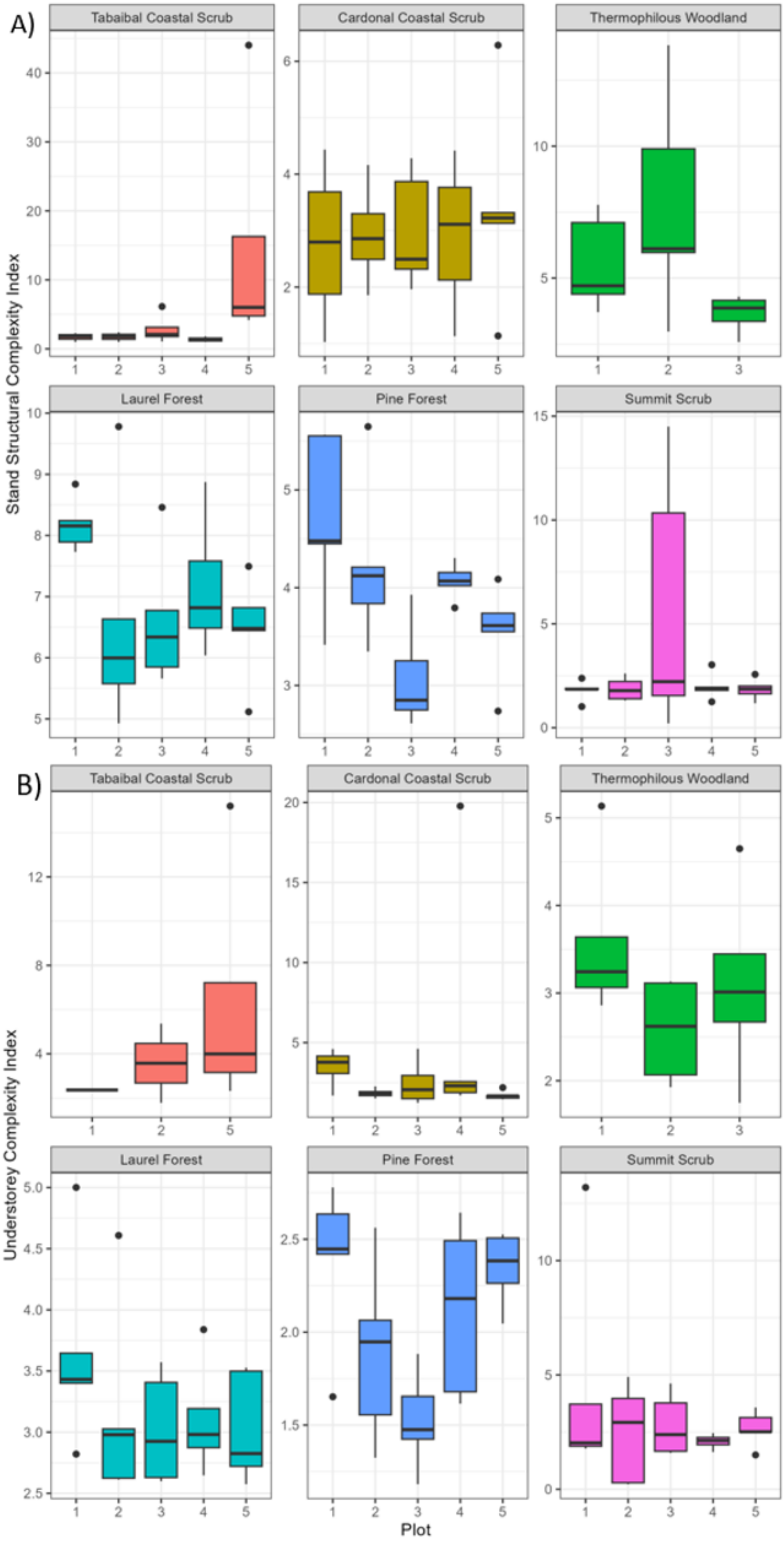

Figure S3. Within plot variation of A) stand structural and B) understorey structural complexity across habitats in Tenerife. NB: Y axes are not scaled to clearly depict within habitat variation.

Supplementary Note 2

Drivers of Structural Complexity

We conducted further analysis using the robust linear mixed effects model and saw that the relationship between annual precipitation and UCI across habitats was not significant (t = -0.507, p = 0.612). This led us to theorise that precipitation is ultimately influencing vertical structural components to a greater extent than horizontal structural components. We, therefore, tested the relationship between annual precipitation and average plot ENL. Although we found evidence of a positive relationship (Figure S4) between annual precipitation and mean plot ENL (t = 1.923) this was non-significant (p = 0.055). We found a non-significant relationship between annual precipitation and mean plot MeanFRAC (t = 1.525, p = 0.127)

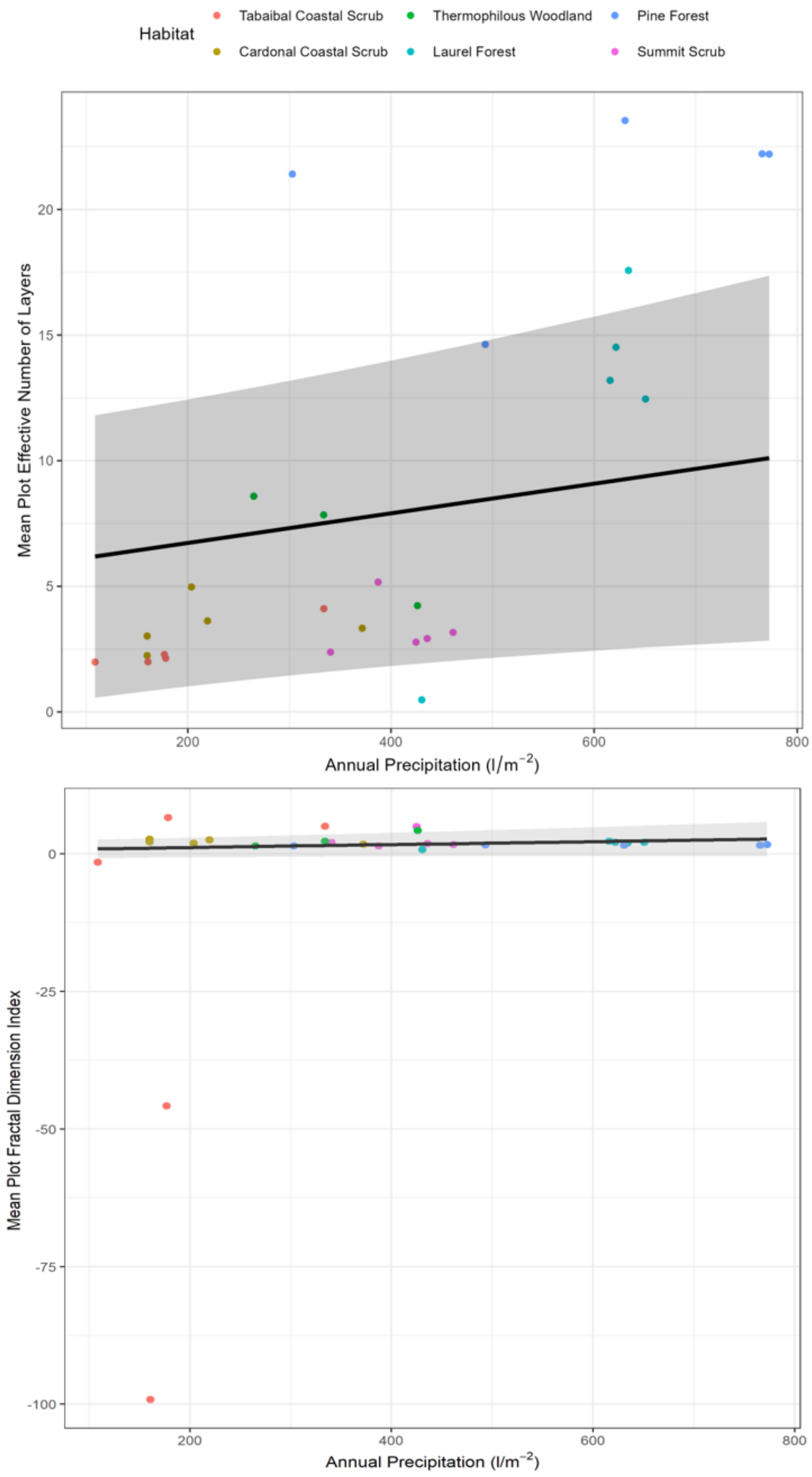

Figure S4. Relationship between annual precipitation and mean plot (top) effective number of layers and (bottom) mean fractal dimension index, across habitats in Tenerife. The black lines show the fixed-effect prediction of precipitation, with the 95% confidence interval (shaded areas). Each point represents a sampled site, coloured by habitat.