Peer-reviewed version available at *Remote Sens.* **2020**, *12*, 1407; doi:10.3390/rs12091407

Article

Compatibility of Aerial and Terrestrial LiDAR for Quantifying Forest Structural Diversity

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Abstract: Structural diversity is a key feature of forest ecosystems that influences ecosystem functions from local to macroscales. The ability to measure structural diversity in forests with varying ecological composition and management history can improve the understanding of linkages between forest structure and ecosystem functioning. Terrestrial LiDAR has often been used to provide a detailed characterization of structural diversity at local scales, but it is largely unknown whether these same structural features are detectable using aerial LiDAR data that are available across larger spatial scales. We used univariate and multivariate analyses to quantify cross-compatibility of structural diversity metrics from terrestrial versus aerial LiDAR in seven National Ecological Observatory Network sites across the eastern USA. We found strong univariate agreement between terrestrial and aerial LiDAR metrics of canopy height, openness, internal heterogeneity, and leaf area, but found marginal agreement between metrics that describe heterogeneity of the outer most layer of the canopy. Terrestrial and aerial LiDAR both demonstrated the ability to distinguish forest sites from structural diversity metrics in multivariate space, but terrestrial LiDAR was able to resolve finer-scale detail within sites. Our findings indicate that aerial LiDAR can be of use in quantifying broad-scale variation in structural diversity across macroscales.

Keywords: ALS; forest ecology; forest structure; NEON; macrosystems biology; TLS

1. Introduction

Forest structural diversity is the physical arrangement and variability of the living and non-living biotic elements within canopies, that support many essential ecosystem functions [1]. As a critical driver of forest function, estimates of structural diversity are a useful proxy for predicting forest ecosystem functions. For example, structural diversity can be used to predict light interception [2], microclimate [3], hydrology [4], and resilience to disturbance [5]. Forest structural diversity arises from the complex interactions of a range of abiotic and biotic factors that influence the growth and the quantity of vegetation [6–8]. A wide variety of structural diversity metrics can be estimated using methods that range from traditional forest inventory approaches (e.g. basal area [9]) to next-generation remote sensing techniques (e.g. canopy traits or multivariate structural types [7]). The complex and dynamic nature of forest structure has proven challenging to measure accurately across scales and forest types [10,11], but such measurements could substantially improve predictions of forest ecosystem functions [12].

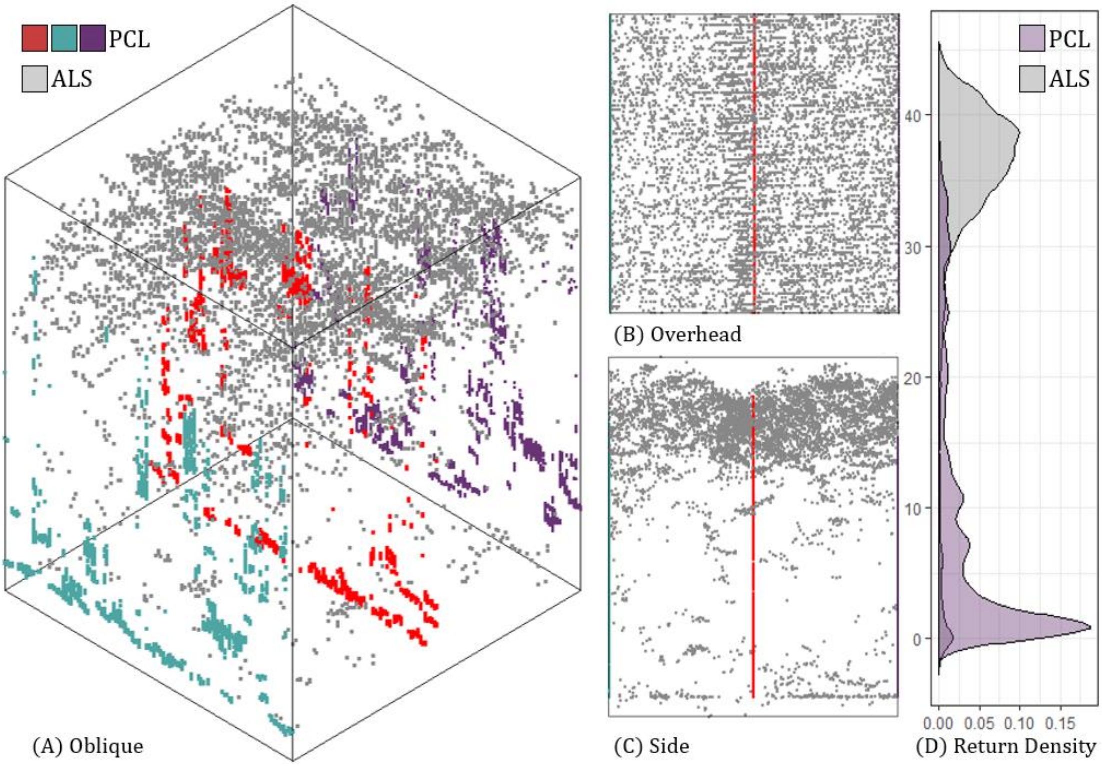

Fig. 1. Comparison of ALS and TLS point clouds for the NEON Great Smoky Mountains plot GRSM_053 (40 x 40 m) from oblique (A), overhead (B), and side angles (C). Vertical profiles of return heights from raw LiDAR returns (D) demonstrate the occlusion experienced by both LiDAR methods as a result of their respective view angles (return density refers to the proportion of total points or relative densities of returns from each platform).

LiDAR remote sensing may be particularly useful in quantifying structural diversity by providing detailed three-dimensional location and attribute data on features such as stems, canopy elements (leaves and branches), and deadwood, but each LiDAR platform has trade-offs in resolution [13]. LiDAR is a useful tool for the multi-dimensional characterization of forest structure that has versatile terrestrial and aerial deployment platforms spanning a multiple of spatial extents and resolutions [14–18]. Terrestrial laser scanners (TLS) and aerial laser scanners (ALS) have both been shown to be effective at quantifying components of forest structural diversity [14–20], however, each LiDAR platform has trade-offs for data resolution and spatial coverage. TLS and ALS scan the forest from opposite angles and occlusion by the canopy constrains the capacity of each to obtain data from portions of the canopy distal to the instrument [21] (Fig. 1). TLS measures the forest from within, providing high resolution data on complex, fine-scale internal features of canopy structural diversity [22]. However, TLS data are less reliable for the upper canopy due to occlusion by intervening foliage [23]. Conversely, ALS measures the forest from above, providing the highest level of detail on the outer canopy surface with declining capacity to resolve canopy features with increasing canopy depth [23].

It is unknown if it is possible to obtain similar estimates of structural diversity with high density TLS data and low density ALS data across ecologically heterogeneous macroscales. TLS and

ALS may not be able to resolve the same aspects of structural diversity well due to their opposing viewing angles. Previous studies within a single site or forest type dominated by one tree species demonstrated that TLS and ALS estimates of forest structural diversity were correlated [23–26]. However, forests vary in structure and species composition substantially from local to regional scales [27]. The ability to scale high resolution TLS metrics of structural diversity with spatially extensive ALS data would help improve the understanding of links between structural diversity and ecosystem function across scales. It is therefore necessary to compare their ability to estimate forest structural diversity across different forest types within ecologically heterogeneous macroscales.

We compared the characterization of structural diversity using TLS and ALS across seven forested sites in the eastern USA from the National Ecological Observatory Network (NEON) (Table 1). We focused on the types of structural diversity metrics (i.e. canopy structural traits) that can be measured by LiDAR methods. First, we examined the univariate correlations of computationally comparable ALS and TLS structural diversity metrics. Second, we tested for intercorrelations between ALS and TLS suites of structural diversity metrics. Third, we compared the multivariate suites of ALS and TLS structural diversity metrics to compare their relative abilities to categorize plots from different forest types. Our study results have implications for providing a reliable remote sensing toolkit for linking structural diversity and ecosystem functions in forest macrosystems.

Table 1. Seven forested NEON sites measured for TLS and ALS across the eastern USA.

Site (ID)	Ecoclimatic domain	Dominant forest type	N_{Plots}
Harvard Forest (HARV)	Northeast	Mixed temperate	19
Smithsonian Conservation Biology Institute (SCBI)	Mid-Atlantic	Mixed temperate	6
Smithsonian Environmental Research Center (SERC)	Mid-Atlantic	Temperate deciduous	13
Ordway-Swisher Biological Station (OSBS)	Southeast	Pine Savannah	20
University of Notre Dame Environmental Research Center East (UNDE)	Great Lakes	Mixed temperate	8
Great Smoky Mountain National Park (GRSM)	Appalachians & Cumberland Plateau	Temperate rainforest	10
Talladega National Forest (TALL)	Ozarks Complex	Pine savannah	12

2. Materials and Methods

2.1 LiDAR Data Collection and structural diversity metrics

To evaluate the potential for combining TLS and ALS structural diversity metrics into a more comprehensive assessment of forest structural diversity at large spatial scales, we analyzed data

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acquired using both platforms within 40 m x 40 m distributed sampling plots (n=88) at seven NEON sites in the eastern USA (Table 1). These sites are located in 6 ecoclimatic domains that span a wide gradient of structural diversity and forest community composition. Structural diversity metrics derived from both ALS and TLS are grouped into four different categories that all describe traits of the canopy [10]. These categories include: (1) *canopy height*, (2) *canopy cover and openness*, and (3) *canopy heterogeneity* (internal and external; [1]), and (4) *vegetation area*.

Table 2. Categories of forest structural diversity and metrics from TLS and ALS platforms. Details on the derivation and R functions used to calculate structural metrics can be found in Atkins et al. [10] for TLS and Table S2 for ALS. The abbreviations of metric names are listed in parentheses.

Category		ALS metric	TLS metric
Height		Mean canopy height (H), Mean outer canopy height (MOCH), Maximum canopy height (Hmax)	Mean leaf height (Mean H), Mean outer canopy height (MOCH), Maximum canopy height (Max.can.ht), Mean of squared leaf height model (Mode.2), Mode.el (Model.el), Mean height of maximum VAI (Max.el), Root mean square height (meanHRMS), Mean height variability (meanHvar), SD of mean height (Height.2)
Cover and openness		Deep gaps (DG), Deep gap fraction (DGF), Cover fraction (CF), Gap fraction profile (GFP)	Deep gaps (DG), Deep gap fraction (DGF), Sky fraction (SF), Cover fraction (CF)
Heterogeneity	External	Top rugosity (TR), Rumple (Rumple)	Top rugosity (TR), Rumple (Rumple)
	Internal	SD of vertical SD of height (StdStd), Entropy (Entropy), Height SD (HSD: rLiDAR), Height SD (StdH: lidR), Vertical complexity index (VCI)	Canopy rugosity (Rugosity), Mean of vertical SD (MeanStd), SD of vertical SD (StdStd), Effective number of layers (ENL)
Vegetation area		Vegetation area index (VAI)	Mean VAI (Mean.VAI), Mean peak VAI (Mean.peak.VAI)

We characterized canopy structural diversity with 21 metrics (Table 2) from TLS data. TLS data were collected using a portable canopy LiDAR (a type of TLS) (Riegl LD90-3100VHS-FLP; Table S1) from each site in 2016. The system consists of an upward facing 900 nm laser rangefinder mounted on a wearable frame that is moved along a pre-defined transect through the plot. The data collected corresponds to a vertical two-dimensional cross section through the canopy with approximately 500 - 2,000 data points collected per linear meter (Fig. 1). The full description of the design, operation, and validation of the TLS system is found in Parker et al. [22]. For this study, three parallel transects of 40 m each in length were measured per NEON plot (Fig. 1A; see [2] for data collection methods).

This TLS data was then used to characterize canopy structural diversity from a suite of 21 metrics (Table 2) in the *forestr 1.0.1* package [10] in R v.3.5.2 [28], which creates 1 m^2 bins of returns along the 40 m 2D LiDAR point cloud to quantify the 21 structural diversity metrics.

We derived a suite of 15 structural diversity metrics from level-1 discrete return ALS data (Product No. DP1.30003.001) that is collected by the NEON Aerial Observation Platform. This ALS consists of a 1,064 nm whiskbroom scanning laser (Optech ALTM Gemini; Table S1) flown over the study sites at 1,000 m AGL, producing a three-dimensional point cloud with a final point density of 1 - 4 points m^2 (Table S1). Detailed methods on the NEON ALS data collection methods and all data can be found on the NEON Data Portal [29]. ALS data were collected for each site in 2016 (TALL, OSBS, GRSM, HARV, UNDE) or 2017 (SCBI, SERC). Return heights were corrected for topographic variation using A digital terrain model (DTM) was created from the *grid_terrain* function in order to correct return heights for topographic variation in the *lasnormlize* function of the *lidR* package [30]. A 100 m buffer zone was included around each plot center to minimize potential edge effects when correcting for topographic variation. A point cloud encompassing the 1,600 m^2 plot area was then clipped from the buffer point cloud. We used the *lidR* [30] and *rLiDAR* R packages [31] to measure 15 structural diversity metrics (Table 2). The definitions and R functions used to calculate each of the 15 structural diversity metrics are found in Table S2. There were fewer ALS than TLS metrics because the point density of ALS is much lower than TLS. Therefore, low density ALS cannot be used to describe some of the TLS metrics that require fine-scale data on the absence of laser pulses intersecting vegetation in the subcanopy (e.g. the porousness of gaps between vegetative materials such as leaves, [10]). Finally, we compared the data collection methods of ALS and TLS, by measuring the distance at which structural diversity metrics stabilized from slices of varying widths taken from ALS data (see the Supplemental Information Section 1). The analysis supported our approach of averaging multiple 2D canopy slices of TLS data to estimate plot structural diversity, so that we could then compare these values to whole plot ALS metrics of structural diversity.

2.2 Data Analysis

To investigate the univariate strength and direction of correlations between ALS and TLS structural diversity metrics, we calculated a non-parametric Spearman's correlation coefficient (r) between equivalently estimated structural diversity metrics and each pairwise combination of metrics between LiDAR platforms. To facilitate interpretation, we considered an $|r| \geq 0.7$ as a strong correlation, $|r| \geq 0.5$ as a moderate correlation, and a $|r| \leq 0.5$ as a weak correlation.

We performed multivariate analyses to assess differentiation in the clustering of plots from different sites based on all the structural diversity metrics provided by the two LiDAR methods. First, we performed non-metric multidimensional scaling (NMS) ordination on plot-level data sets of the TLS and ALS suites of structural diversity metrics. Ordinations were conducted in PC-ORD v.5.31 [32] with Sorensen's distance measure and the "slow-and-thorough" auto-pilot setting, using 250 runs of real data and 250 Monte Carlo randomizations to assess the robustness of the solution [33]. Ordinations were conducted on matrices with all metrics first relativized to the maximum value that the metric obtained to scale all metrics equivalently. We tested for differences among groupings in each data set (TLS, ALS) in multivariate suites of canopy structural metrics using Multiple Response Permutation Procedure (MRPP) with Sorensen's distance measure in PC-ORD [33]. We performed hierarchical agglomerative clustering on matrices of structural diversity metrics to determine

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clustering of plots into canopy structural types [7]. Clustering was performed with PC-ORD using Ward's Method and Euclidean distance measures [33]. The optimal cluster grouping level was determined by conducting Indicator Species Analysis and deriving mean p-values for indicator values across all metrics for each level of grouping [33]. The grouping level with the lowest mean p-value was selected as the optimal grouping level or cluster for the data. Finally, we compared the classification of plots between the ALS and TLS-derived classifications by creating a confusion matrix with TLS classifications utilized as the "ground-truth" data for assessing the classification produced by the ALS system.

3. Results

3.1 Univariate Comparison of ALS and TLS Metrics

Many metrics from ALS and TLS were correlated (r = 0.44 - 0.92) within and across structural diversity categories (Fig. 2). First, there were significant moderate to strong correlations of r > 0.6 among eight metrics that have equivalent measurements of the same structural aspect of canopies (Table 3). The only exception was in the category of external heterogeneity, where there was a weak significant correlation between ALS and TLS metrics of top rugosity (r = 0.44), but not rumple (r = 0.09) (Table 3, Fig. 2). Second, ALS and TLS metrics within the same category of structural diversity, but not necessarily the equivalent measurement of the same metric, varied in how strongly they were correlated (Fig. 2). Height and vegetation area metrics were both moderately to strongly positively correlated (Fig. 2). Cover and openness metrics were strongly correlated between TLS and ALS (Fig. 2). When comparing ALS and TLS, heterogeneity metrics were much more variable in their correlation strength, which varied from neutral to strongly positively correlated (Fig. 2). Third, there was significant and frequent intercorrelation among metrics of structural diversity from different categories (Fig. 2). Overall, this analysis suggests that ALS-derived metrics of structural diversity can provide statistically similar estimates of structural diversity compared to TLS, though the accuracy of these estimates vary depending on the specific structural metric.

Table 3. Spearman correlations between equivalently estimated structural diversity metrics with TLS and ALS. * indicates that values were significant at $\alpha < 0.05$.

Category	ALS	TLS	r
Height	MOCH	MOCH	0.80*
	H	H	0.72*
	Hmax	Max.can.ht	0.92*
Cover and openness	DGF	DGF	0.66*
	CF	CF	0.74*
External heterogeneity	Rumple	Rumple	0.09
	TR	TR	0.44*
Internal heterogeneity	StdH	MeanStd	0.61*
	StdStd	Rugosity	0.74*
Vegetation area	VAI	VAI	0.87*

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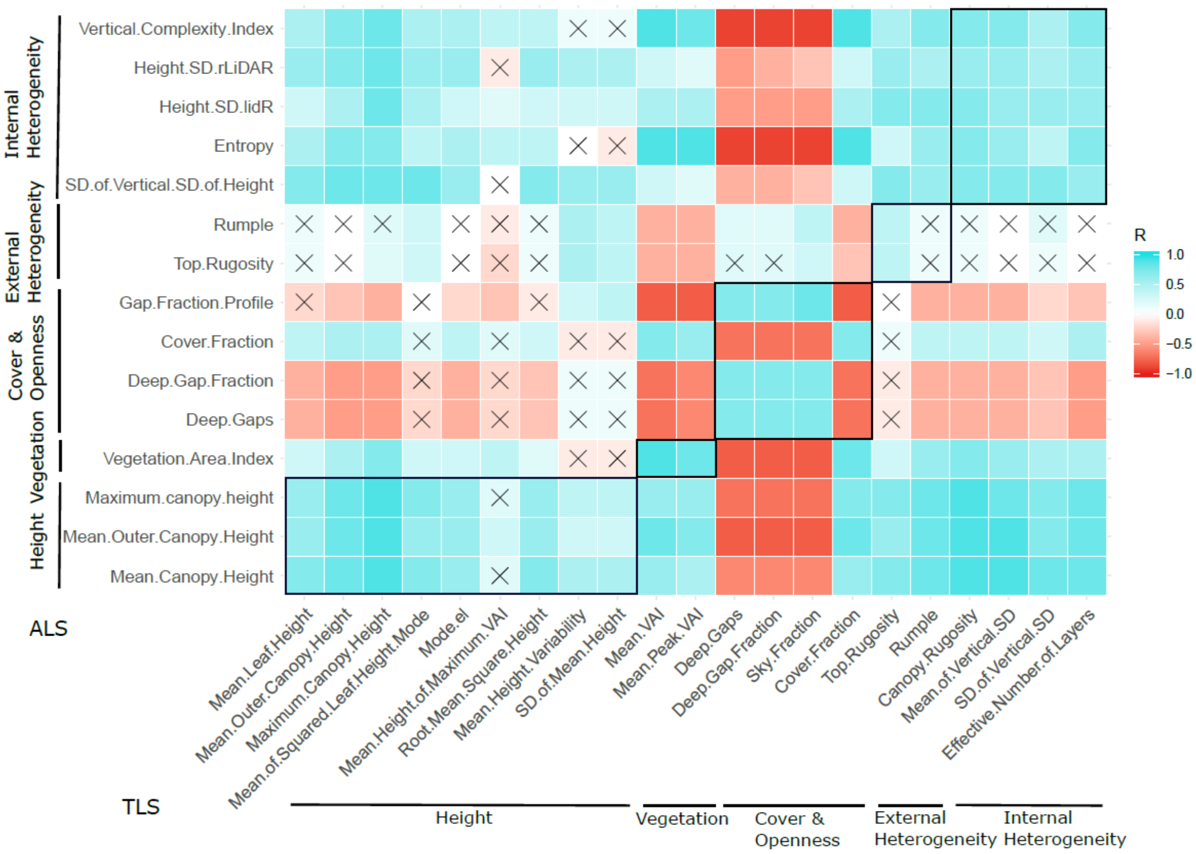

Fig. 2. Pairwise Spearman correlation coefficients between ALS (Y-axis) and TLS LiDAR metrics (X-axis). Colors of the squares indicate the strength of each correlation; an X indicates a relationship was not significant at $\alpha < 0.05$.

3.2 Multivariate Comparison of ALS and TLS Classifications

There was strong agreement in the general multivariate classification of plots from different forest sites by ALS and TLS metrics of structural diversity (Fig. 3), demonstrating the ability of both systems to resolve forest type differences at the macroscale. NMS ordination of structural diversity derived from ALS data had a two-dimensional solution with a mean Stress of 7.811, which was significant relative to randomized data (p = 0.004) and explained a 98.2% of the variation in the original data matrix (Fig. 3A). The first axis explained 73.4% of the variation and was driven most strongly by VAI and maximum canopy height. The second axis explained an additional 24.8% of the variation and was most strongly driven by vertical variation in canopy height. There was relatively strong separation between sites in the ALS-based ordination space (Fig. 3A) and MRPP analysis indicated significant differentiation among sites in structural diversity (A = 0.50, p < 0.001). Classification of the TLS structural diversity metrics was also explained in two dimensions of multivariate structural space (Fig. 3B). The NMS ordination based on TLS structural diversity metrics had a two-dimensional solution that was significant relative to randomized data (p = 0.004; mean Stress = 8.665) and explained a 97.9 % of the variation in the original data matrix. The first axis explained 80.6% of the variation and was driven by vegetation area and openness. The second axis explained an additional 17.4% of the variation and was driven by canopy height and internal heterogeneity. NMS ordination of structural diversity derived from TLS data illustrated differentiation among sites (MRPP analysis A = 0.45, p < 0.001). Both ALS and TLS suites of structural

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diversity metrics provided similar two-dimensional characterization of plots from different sites (c.f. Fig. 3A, 3B), indicating that both LiDAR systems are able to resolve differences in structural diversity of plots from different forest types at a sub-continental scale.

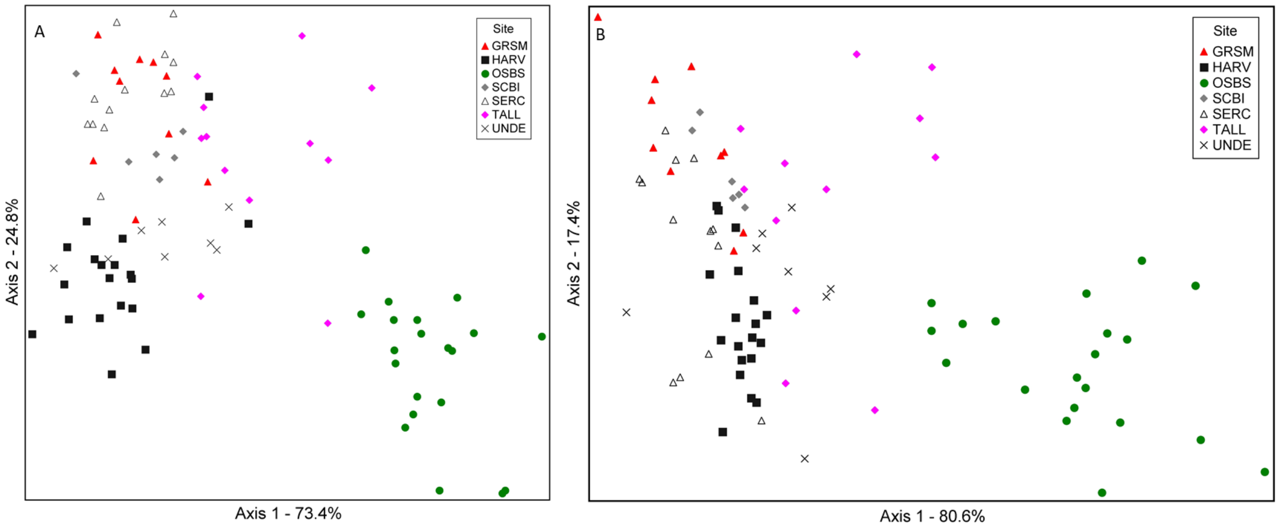

Fig. 3. Non-metric multi-dimensional scaling ordination illustrating variation in multivariate classification of plots across seven NEON forest sites from structural diversity as measured using a) ALS and b) TLS. Site ID abbreviations can be found in Table 1.

While there was broad agreement in the clustering of plots from structurally similar forest sites that vary by height and openness from ALS and TLS metrics of structural diversity, the finer resolution of TLS data provided a greater ability to distinguish plots from within sites that have subtle differences in structural diversity (Fig. 4, Table 4). Hierarchical agglomerative clustering of TLS and ALS structural metrics produced different numbers of clusters in structural diversity space indicating that, as expected, TLS and ALS are sensitive to different canopy structural features. ALS structural diversity metrics were clustered into 3 groups (based on iterative indicator species analysis conducted on grouping levels; minimum average p-value in 3 cluster solution: $p = 0.0002$) (Table 4). These three groups separate plots from sites approximately by geography (latitude) with groups of northern (medium height and high canopy cover), mid-Atlantic/Appalachian (tallest height and high canopy cover), and southern sites (lowest height and open canopy) (Fig. 4A). In contrast, TLS structural diversity metrics grouped canopies into 5 clusters (minimum mean p-value from ISA – $p = 0.001$) (Table 4). These clusters split the plots from the following groups of sites: HARV/SERC, GRSM/SERC, UNDE/SCBI, OSBS, and a subset of TALL (Fig. 4B). The additional groupings distinguished by the TLS data were related to plots with very tall canopy, but low complexity (cluster 5 – TALL site), plots with short canopy, but high VAI (cluster 3 – largely at HARV and UNDE), and plots with extreme vertical complexity (cluster 2 – largely GRSM and SERC). Comparison of the groupings of plots into clusters using the two different data sets illustrated both substantial agreement in some regards and separation in others (Table 4). The two classification systems agreed in placing the OSBS plots into a distinct cluster group, while the other two ALS clusters aggregated plots largely from 2 or 3 of the TLS clusters respectively. The ability of the TLS to split plots from different sites into clusters with plots from other sites illustrates that TLS permits the characterization

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of within-site variability of structural diversity, versus the purely among-site variation that was represented in the ALS ordination and clustering (c.f. Fig. 4A, B).

Table 4. Comparison of plot assignment to groupings derived from hierarchical agglomerative clustering of ALS and TLS illustrating structural diversity variation in multivariate space between LiDAR platforms. Cluster name indicates which plot was assigned to a given TLS or ALS cluster. Numbers indicate the how many plots were assigned to each cluster.

Cluster	TLS1	TLS2	TLS3	TLS4	TLS5	Total
ALS1	12	15	4	0	4	35
ALS2	14	2	16	0	0	32
ALS3	1	0	0	20	0	21
Total	27	17	20	20	4	88

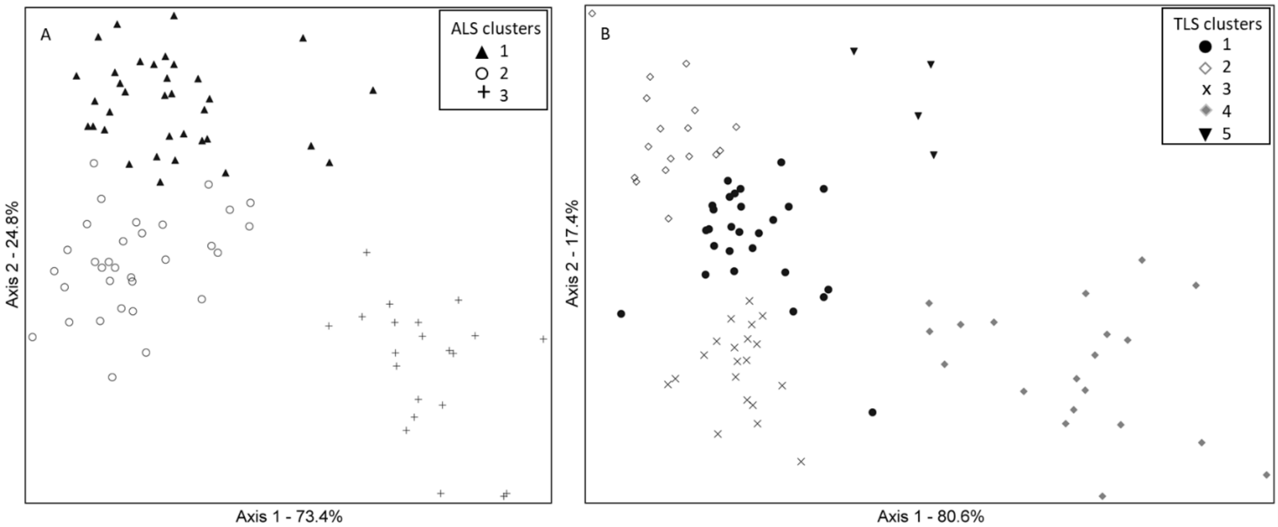

Fig. 4. Illustration of canopy structural type groupings derived from hierarchical agglomerative clustering overlaid on non-metric multi-dimensional scaling ordination of structural diversity across seven NEON sites; A) illustrates cluster groups derived from ALS data and b) cluster groups from TLS data.

4. Discussion

Despite terrestrial and aerial LiDAR systems having trade-offs in their resolution and spatial extent for the characterization of structural diversity, the results of our study show broad agreement between ALS and TLS in the potential to quantify canopy structural diversity across a variety of forest types at a sub-continental scale. We showed robust concurrence among equivalent measures of

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canopy height, cover and openness, vegetation area, and internal heterogeneity. We also show that ALS delineates the multivariate canopy structural types among forest sites at a sub-continental scale. Our results demonstrate that low resolution, large footprint ALS systems may be a useful tool for classifying forests by structural diversity at landscape to sub-continental scales. However, TLS derived metrics may be required to resolve fine-scale structural variation within forest types, such as that related to disturbance history, management, or successional development [24,34]. Previous studies have focused on comparisons of ALS and TLS at a single site or forest type in a localized region, but consistent with our results, these have found that ALS and TLS are comparable in their capacity to delineate features such as canopy height, cover, and vertical stratification [23–26]. TLS systems are a well-established method to provide high resolution, functionally meaningful measurements of structural diversity in forest ecosystems at the stand-scale [2,19,20,22,25,35], but these results demonstrate that ALS could potentially be used to scale the characterization of canopy structural diversity to much broader spatial extents.

The effects of occlusion that plague both bottom-up TLS and top-down ALS methods did not prevent robust agreement for 8 of the 10 equivalent metrics tested here but did result in low agreement for two metrics of external heterogeneity. The top-down view of ALS versus the bottom-up viewing angle of TLS results in a difference of laser beam attenuation that may mean these systems see non-overlapping portions of the canopy volume (Fig. 1). Specifically, ALS typically exhibits decreased capacity to resolve subcanopy vegetation relative to TLS due to increased attenuation. Meanwhile TLS exhibited a decreased ability to clearly characterize upper canopy elements relative to ALS also due increased attenuation [26]. The partial occlusion of the canopy surface in TLS data was apparent in our study, as univariate analyses illustrated only partial agreement among measures of external canopy heterogeneity that estimate structural diversity at the outer canopy surface. A similar issue was observed by Hilker et al. [23], who found that while TLS accurately measured canopy height from the top 10% of points, it underestimated total canopy height by approximately a meter. This suggests a need for caution in relying on the Portable Canopy TLS [22] for measuring outer canopy features (e.g. external heterogeneity), whereas ALS seems better suited for this category of structural diversity metric. Nevertheless, the broad agreement we observed between ALS and TLS methods for quantifying most categories of structural diversity metrics supports the use of ALS to scale up functionally relevant measurements of canopy structure, and further suggests that structural metrics derived from ALS can serve as a reasonable proxy for TLS derived metrics.

The resolution of ALS is sufficient to distinguish between different forest sites based on multivariate structural diversity, but TLS is better suited to resolving within site variation. In our study there was a similar placement of plots from different forest types in multivariate space based on ALS and TLS structural diversity metrics. However, there were both similarities and differences in the hierarchical agglomerative clustering by TLS (5 clusters) and ALS (3 clusters). For example, OSBS, a pine savannah characterized by open canopies and short trees, was always placed in its own cluster by both LiDAR platforms. This illustrates the ability to clearly delineate general structural types among forests for ALS or TLS. Forest sites with denser canopies, dominated by deciduous species (which tend to have broader, rounded crowns), did not cluster similarly and were split among four TLS clusters and two from ALS. This indicates that studies seeking to investigate fine-scale differences in structural diversity within a forest type or single site should rely on TLS to accurately characterize sub-canopy structure. There are ecological and management circumstances for which it is desirable to resolve fine-scale structural variation and its role in forest ecosystem function; for example, to understand differences in local disturbance on the same forest type [24] or to assess the effects of forest management actions [36]. However, previous studies have demonstrated that at larger scales greater variation in structural diversity occurs across forest types and sites rather than within sites [2,18,37]. For example, canopy structural types defined using multi-dimensional metrics of three-dimensional forest structure are useful for predicting forest productivity [7]. We suggest that the derivation of some canopy traits and general canopy structural types across landscapes is feasible with ALS and that ALS could be an appropriate choice for characterizing broad-scale forest variation in forest macrosystem studies (e.g. [38]). We also caution users of ALS to keep the context of structural attributes of forests in mind, because resolving structural diversity in the sub-canopy of open canopies will be easier than dense, closed canopies that pose occlusion issues for low density ALS.

5. Conclusions

The TLS and ALS systems compared here each provide unique benefits for remotely sensing forest structural diversity, and both can be robustly applied across different forest types at a sub-continental scale. The portable canopy LiDAR TLS system we examined is extremely portable and efficient at collecting within-canopy structural diversity data at stand scales—which makes this TLS system useful in small-scale structural diversity analyses where higher point densities are needed. The ALS system has the capacity to measure structural diversity at broader scales, which is advantageous for investigating spatial and temporal dynamics or testing compatibility to model simulations that use spaceborne remote sensing data at larger extents than is feasible to measure with TLS systems. Furthermore, future studies should also compare remotely sensed measures of structural diversity with forest-inventory based-structural diversity metrics (e.g. [9]), because forest managers often make management decisions based on inventory metrics. Advances in the open source coding and the accessibility of ALS, from organizations such as NEON, has a distinct capacity to quantify forest canopy structural diversity at scales that have not been possible until recently. These improvements allow for the incorporation of more comprehensive structural information in ecological models, forest management, and strategic decision making for forest macrosystems. Understanding the limitations and shortcomings of ALS and TLS LiDAR systems, and how we can utilize the complementary strengths of these systems, is a critical step forward for further understanding the complex dynamics that link forest structural diversity with macroscale patterns of ecosystem functioning.

Supplementary Materials: The following are available online, Supplementary methods: 1. Spatial stability of ALS metrics estimated from the TLS 2D canopy slice approach, Figure S1: Breakpoint analysis for VAI, mean outer canopy height, and maximum canopy height, Figure S2: Breakpoint analysis for top rugosity, standard deviation of standard deviation of height, entropy, VCI, standard deviation of height, and rumple, Figure S3: Breakpoint analysis for cover fraction, deep gaps, deep gap fraction, and gap fraction profile, Table S1: LiDAR system specifications, Table S2: Derivation of structural diversity metrics from aerial LiDAR.

Author Contributions: SF and BH conceived the idea. FW and EL wrote the initial draft. EL, FW, JA, BF conducted analyses. All authors contributed to writing and have approved the final version.

Funding: Funding for this work was supported by NSF award #1638702 to S. Fei and B. Hardiman, NSF award #1924942 to S. Fei, B. Hardiman, and E. LaRue, and NSF award # 1926538 to B. Hardiman.

Conflicts of Interest: The authors declare no conflict of interest.

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