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# Spatial Variation in Canopy Structure across Forest Landscapes

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**Abstract:** Forest canopy structure (CS) controls many ecosystem functions and is highly variable across landscapes, but the magnitude and scale of this variation is not well understood. We used a portable canopy lidar system to characterize variation in five categories of CS along $N = 3$ transects (140–800 m long) at each of six forested landscapes within the eastern USA. The cumulative coefficient of variation was calculated for subsegments of each transect to determine the point of stability for individual CS metrics. We then quantified the scale at which CS is autocorrelated using Moran's *I* in an Incremental Autocorrelation analysis. All CS metrics reached stable values within 300 m but varied substantially within and among forested landscapes. A stable point of 300 m for CS metrics corresponds with the spatial extent that many ecosystem functions are measured and modeled. Additionally, CS metrics were spatially autocorrelated at 40 to 88 m, suggesting that patch scale disturbance or environmental factors drive these patterns. Our study shows CS is heterogeneous across temperate forest landscapes at the scale of 10's of meters, requiring a resolution of this size for upscaling CS with remote sensing to large spatial scales.

**Keywords:** forest structure; macrosystems biology; portable canopy LiDAR; rugosity; transect spatial autocorrelation

## 1. Introduction

In forested ecosystems, the density and spatial arrangement of vegetation, or canopy structure (CS), imposes strong controls on many scale-dependent ecosystem functions. CS in the form of leaf area and arrangement exerts a strong influence on forest production, through its effects on light absorption [1] and light-use efficiency [2,3]. CS metrics describing height and heterogeneity affect the turbulent exchange of gases between ecosystems and atmosphere, and regulate canopy net energy balance [4–6]. The spatial scale at which canopy structure exerts functionally meaningful

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effects on ecosystem processes varies depending on forest type and architecture, environmental factors, and the ecosystem functions and the CS element of interest. For example, patterns of light transmittance relate to structure at the scale of individual leaves and small canopy gaps [7], while boundary-layer processes are affected by gap to small landscape-scale canopy structure variation [8]. Inferring and scaling ecosystem functions from remotely sensed measurements of forest structure requires an understanding of how different measures of CS vary spatially across forested landscapes.

CS is an emergent property of multiple underlying ecological factors operating at multiple spatial scales [9–11]. Determinants of CS within landscapes may include at the smallest scales the distribution of individual leaves owing to resource availability and at the landscape scale variation in tree mortality and defoliation (Table 1) [12,13]. Additional within-landscape variation is associated with the combined effects of individual-scale tree crown architecture, neighborhood-scale community taxonomic diversity and competition, and environmental variables that shape biomass production and allocation [14,15]. Variation within and among forest stands in these canopy-shaping forces may determine the spatial scale at which CS stabilizes (i.e., spatial extent within a stand at which heterogeneity in CS stabilizes), and the degree to which scales of stability differ among forested landscapes [12]. Such understanding of the spatial scales and patterns of variation in CS are essential precursors both to understanding the fundamental drivers of this variation as well as to deriving, interpreting, and modeling ecosystem structure and function across forest stands and landscapes.

Recent methodological advances in LiDAR have provided a means to better understand spatial patterns in the variation of forest CS. Terrestrial LiDAR allows for a complete characterization of the arrangement of vegetation throughout the entire canopy volume [16,17] with a level of detail not possible with aerial or satellite forms of LiDAR [18]. Therefore, to advance our understanding of the patterns in variation of forest CS, we choose to use terrestrial lidar to examine and compare variation in landscape-scale CS of mature temperate forests in the northeastern, Great Lakes, and prairie peninsula ecoclimatic domains of the USA (see Thorpe [19] for NEON domains). We used terrestrial lidar to measure CS, which provides high resolution, spatially continuous canopy structure data quantitatively describing vegetation density, arrangement, and heterogeneity [20]. Our primary objective was to identify the magnitude of variation and spatial scale of stability in CS within these forested landscapes. We focused on mature temperate forests to evaluate whether these similarly-aged secondary forests located in the northern continental USA exhibit similar spatial scales of CS stability.

**Table 1.** Examples of drivers and potential sources of spatial variation in canopy structure.

| Driver | Literature source |
|---|---|
| Crown morphology/architecture | [21–25] |
| Disturbance | [26–32] |
| Demographics (community composition, diversity, succession) | [10,28,33–38] |
| Edaphic factors (topography, soil moisture, nutrient status, etc.) | [9,39–43] |

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## 2. Materials and Methods

### 2.1 Portable Canopy LiDAR and Forest Landscapes

We used a portable canopy LiDAR (PCL) system, a type of terrestrial LiDAR to survey CS along a vertical cross section of canopy. The portable canopy LiDAR system contains an upward facing, near-infrared pulsed laser operating at 2000Hz (Riegl LD90 3100 VHS; Riegl USA Inc. Orlando, Florida, USA) that is mounted to a frame worn by a user and operated along a transect at a constant speed. The design and operation of the instrument is outlined in Parker et al. [44]. Laser pulses emitted by the LiDAR unit either reflect off objects in the forest canopy or, when a gap is encountered, are not returned. These reflected and un-reflected pulses are recorded and used to construct a vertical cross-section of forest canopy. These "hit-grid" data (Fig. 1) are then used to calculate metrics of CS [2].

We collected PCL data from six deciduous forested landscapes in Eastern North America (Fig. 2). Five of the six landscapes were characterized by a deciduous, mixed hardwoods species composition, while Harvard Forest (HF) was composed primarily of eastern hemlock (*Tsuga Canadensis*). Within each landscape, we collected PCL data from $N = 3$ transects (140 - 800 m; see Fig. S1 for individual transect lengths). We sampled within contiguous forest landscapes and thus sampling lengths varied among forested landscapes depending on the dimensions and area of each. Sampling after leaf-out occurred during May 2018 in Indiana locations at McCormick Creek (MCK), Lugar Farm (LUG), and Martell Forest (MTL); August 2017 at Harvard Forest (HF); during summer 2016 at the University of Michigan Biological Station, and August 2017 at Hubbard Brook Experimental Forest (HBEF).

### 2.2 Canopy Structural Complexity

We focused our analysis on five metrics of CS broadly demonstrated to be functionally important, particularly with respect to canopy light interception and carbon uptake [1]. These metrics fall within five different CS categories: 1) vegetation height (mean maximum outer canopy height, MOCH); 2) vegetation density, volume, and area (mean vegetation area index, VAI); 3) arrangement and distribution (canopy rugosity, $R_C$); 4) cover and openness (deep gap fraction, GF); and 5) vegetation variability (porosity, PC) [20]. The detailed definitions, derivation, and calculation of each of the 5 metrics are available in Atkins et al. [20]. The raw PCL data were processed using the *forestr* package [20], available in R 3.4.4 (R Core Team, 2018).

### 2.3 Statistical Analyses

Our first analysis identified the sampling distance at which CS metrics stabilized within each sampled forested landscape. Changes with sampling distance in the coefficient of variation (CV) of each CS metric was derived from cumulative 10-m means and variances across each transect (i.e. 0 - 10, 0 – 20, 0 - 30, . . . up to the maximum transect length, varying from 140 - 800 m). The distances at which additional canopy structural information no longer significantly shifts in variance, hereafter termed "stability points", were estimated from Bayesian changepoint analysis using the *bcp* package (Wang et al. 2015) in R 3.4.4 (R Core Team, 2018). The distance at which stability in the CV of CS metrics occurred was recorded using both methods and then averaged for a conservative

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transect level measure of stability distance. We tested for differences in the mean stability point among forested landscapes for each CS metric with one-way ANOVAs. Stability points for $R_C$ did not meet the assumption of normality, therefore we used a Kruskal-Wallis test to assess differences in mean stability points among forested landscapes. If the landscape effect was not significant, we calculated a mean stability point across forested landscape; if the effect was statistically significant, then we conducted post hoc Tukey tests to compare stability points among forested landscapes.

We conducted a second analysis with Incremental Autocorrelation analysis to assess spatial clustering patterns among CS metrics and across forested landscapes. For each forested landscape and CS metric combination we calculated Moran's *I* for all points separated by a given distance as a measure of autocorrelation by distance. We calculated the level of *I* at 10m distance increments for the full range of possible sampling distances, starting at 10m and ending at 150 (LUG, UMBS) or 200m (all other sites). For each distance increment the *z*-score and *p*-value associated with the Moran's *I* test statistic were calculated and then *z*-scores were compared across distances. The distance (or distances) at which the *z*-score peaked was determined from the data and utilized as an indicator of spatial clustering for each metric and site combination. Incremental Autocorrelation analysis was conducted using the Spatial Analyst toolbox in ArcGIS v. 10.3 (ESRI; Redlands, CA, USA).

## 3. Results

### 3.1 *Transect lengths at which CS metrics stabilize*

The stability points for two of the five CS metrics differed significantly among forested landscapes. Significant differences were observed among forested landscapes in the distance at which variation (i.e., as CV) in mean outer canopy height (Fig. 3A) and VAI (Fig. 3E) stabilized. Specifically, the stability point of mean outer canopy height for HF (262 m) was significantly greater than that of MLT (94 m) and MCK (92 m) (Fig. 3A). Additionally, the stability point for VAI at HF (241 m) was greater than that of LUG (87 m) and MCK (101 m). However, there were no significant differences in stability points among forested sites for gap fraction (Fig. 3B), canopy rugosity (Fig. 3C), or porosity (Fig. 3D). Average stability points among forested landscapes for gap fraction, canopy rugosity, and porosity were 115 m, 125 m, and 144 m, respectively. All CS metrics exhibited a tendency to converge toward similar values at sufficiently long transect lengths (~300 m), regardless of site (Fig. S1). At all sites, CS metrics demonstrated sensitivity to putative ecotones or edaphic gradients as illustrated by sudden shifts in the value of their running mean (Fig. S2-5).

### 3.2 *Scales of canopy structure autocorrelation*

Peak spatial autocorrelation along transects varied among CS metrics and forested landscapes. Mean peak spatial autocorrelation distances of the five CS metrics varied substantially among CS metrics, ranging from 40 to 88 m (Table 2). Mean outer canopy height, VAI, and canopy rugosity displayed peak spatial autocorrelation at shorter distances than gap fraction and porosity (Table 2). While among forested landscapes, peak distances of spatial autocorrelation in CS metrics were highly variable, from 20 to 180 m (Table 2). For example, peak spatial autocorrelation of canopy rugosity ranged among landscapes from 20 to 150 m (mean = 53 m; Fig. 4), with MTL significantly peaking at both 30 and 150 m (Fig. 4). Similarly, VAI and porosity of MCK and mean out canopy height of MTL exhibited peak autocorrelation at multiple distances, indicating

correspondence of VAI at multiple spatial scales. Deep gap fraction, which was zero along many 10 m transect subsegments, displayed significant peak autocorrelation distances in only two of six forested landscapes. One forested landscape, UMBS, exhibited a statistically significant peak distance of autocorrelation for porosity and canopy, but not for the other three CS metrics. Overall, peak autocorrelation when it occurred, varied substantially among forested landscapes for different CS metrics.

**Table 2.** Distance or distances (in meters) at which the z-score from Incremental Autocorrelation analysis reached a statistically significant peak for canopy structural complexity metrics across six forested landscapes in eastern USA. "---" indicates no significant peak was found in the data, number in parentheses indicates the distance of the non-significant peak z-score on the curve if there was one.

| Site | MOCH | GF | Rc | Porosity | VAI | Mean |
|---|---|---|---|---|---|---|
| UMBS | --- | --- | 20 | 20 | --- | *20* |
| HEBF | 30 | 50 | 20 | 40 | 150 | *58* |
| HF | 30 | 30 | 50 | 110 | 50 | *54* |
| LUG | 40 | --- | 50 | 20 | --- (70) | *37* |
| MCK | 20 | --- | --- (80) | 30/100 | 30/140 | *64* |
| MTL | 20/120 | --- | 30/150 | 180 | 70 | *95* |
| **Mean** | *43* | *40* | *53* | *71* | *88* | |

MOCH: Mean Outer Canopy Height; GF: Gap Fraction; Rc: Canopy Rugosity; VAI: Vegetation Area Index

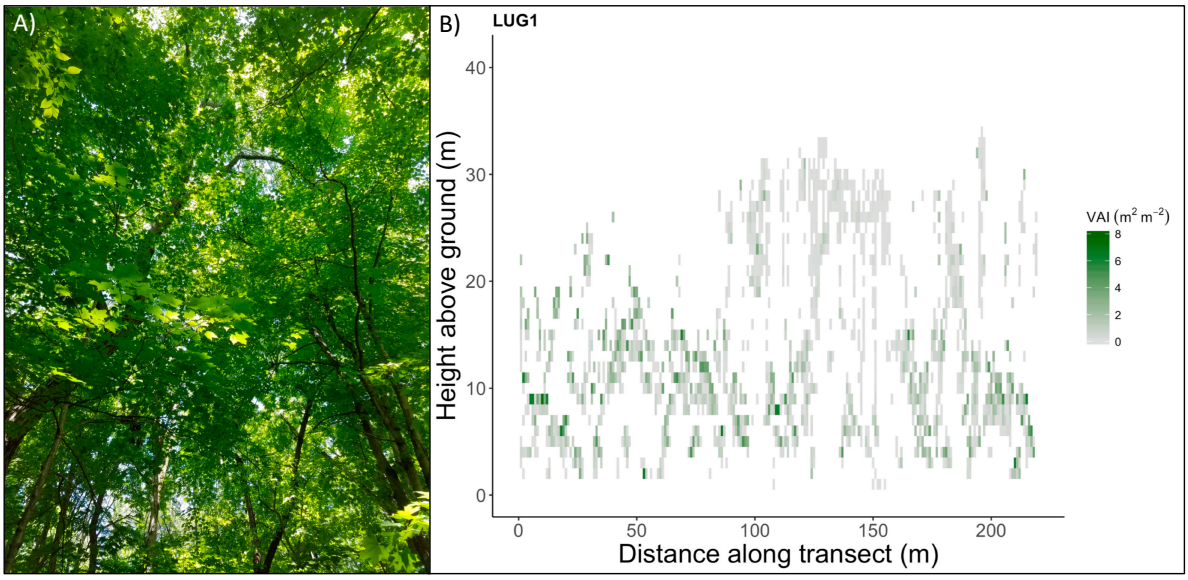
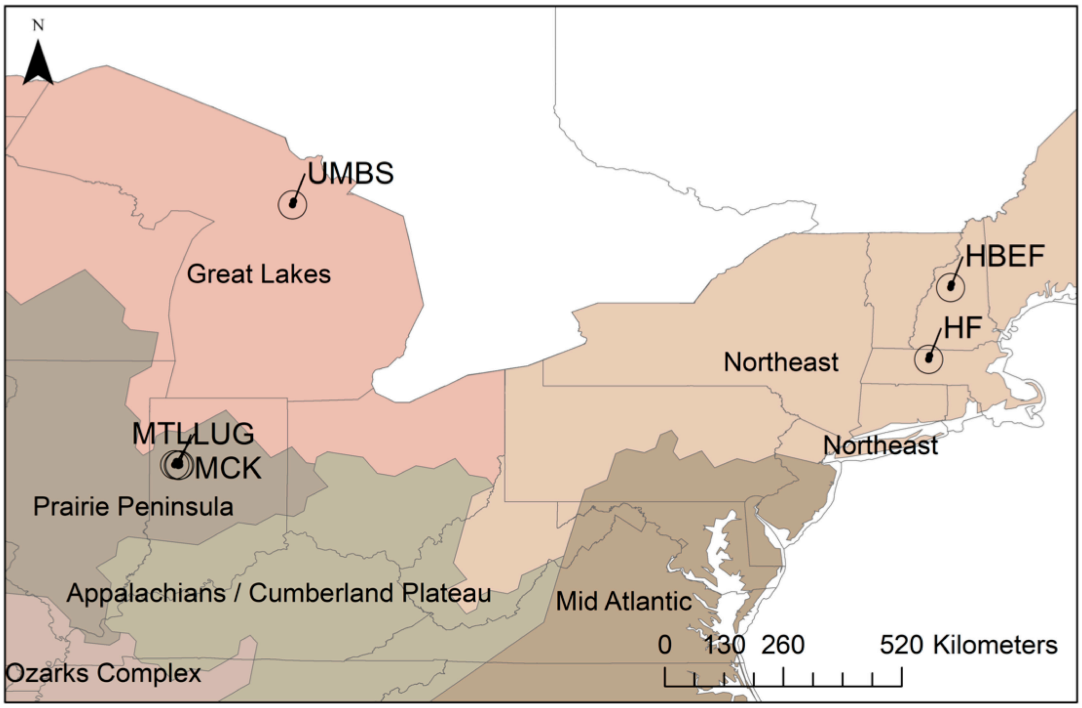



**Figure 1**. An example vertical cross section of a forest canopy collected from the portable canopy LiDAR. The transect was 250 m long and was collected within the Purdue University Lugar Farm Research Area, Indiana, USA. A) An image of the canopy at 0 m on the transect. B) Vegetation area index (VAI) was calculated using data collected along a 250 m transect with the portable canopy LiDAR unit. Each pixel in the cross section corresponds to a 1 $m^2$ bin containing values of VAI. The lighter to darker green shading corresponds to increasing values of VAI.

175




176

177 **Figure 2**. Sampling locations of the six forested landscapes for which portable canopy LiDAR data
178 was collected in eastern USA. Martell Forest (MTL), McCormick Woods (MCK), and Lugar Farm
179 (LUG) are located in the Prairie Peninsula ecoregion, Hubbard Brook (HBEF) and Harvard Forest
180 Hemlock plot (HF) are in the Northeast ecoregion, and (UMBS) is in the Great Lakes forest
181 ecoregion

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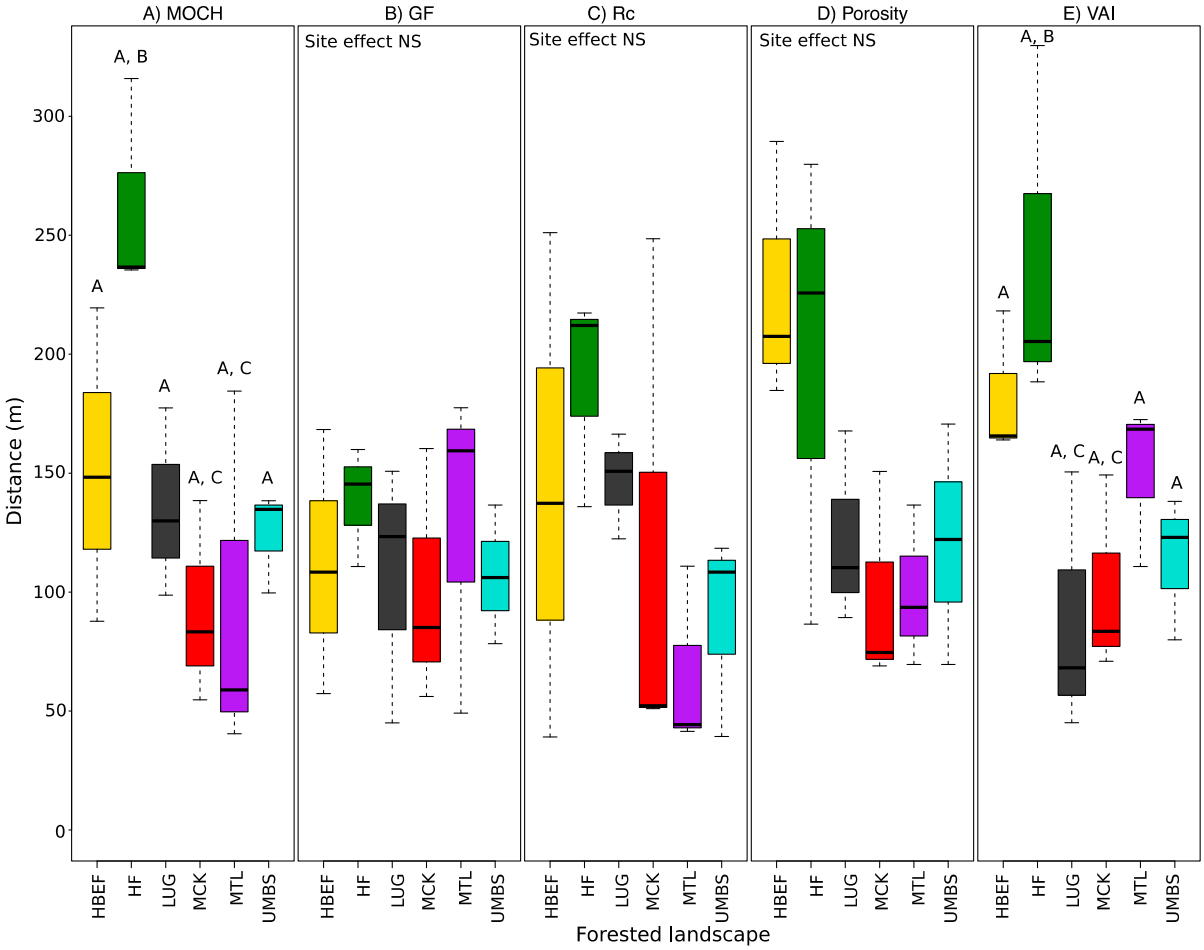
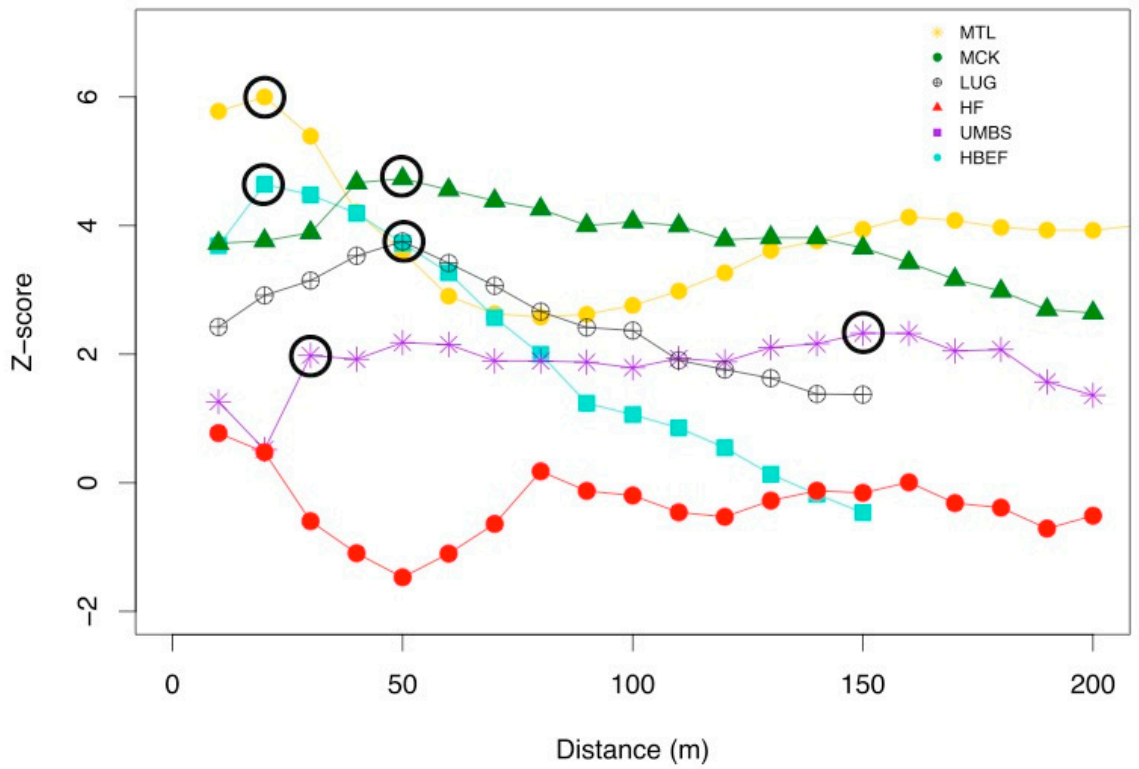



183

184 **Figure 3**. Estimated stability points of canopy structural complexity metrics from Bayesian
185 changepoint analysis along forested transects from six forested landscapes in eastern USA. CS
186 metrics included A) mean outer canopy height (MOCH; $F_{5,12} = 4.31$, $P = 0.01$), B) percentage of deep
187 gap fractions (GF; $F_{5,12} = 0.26$, $P = 0.92$), C) canopy rugosity (Rc; $X^2 = 17$, $P = 0.45$), D) porosity ($F_{5,12} =$
188 2.61, $P = 0.08$), and E) mean vegetation area index (VAI; $F_{5,12} = 4.37$, $P = 0.01$). $N_{Transects} = 3$ per forested
189 landscape. Letters above bars indicate significantly different groups in post hoc Tukey tests if the
190 main effect of forested landscape in the univariate ANOVA or Kruskal-Wallace test was significant.

191




192

193 **Figure 4**. Peak spatial autocorrelation of canopy rugosity along transects from six forested
194 landscapes in eastern USA. The peak z-score from Incremental Autocorrelation analysis indicates
195 the distance at which spatial clustering of canopy rugosity is greatest along a transect. Circled
196 symbols indicate a statistically significant peak z-score for a forested landscape. $N_{Transects}$ = 3 per
197 forested landscape.

198

## 4. Discussion

### 4.1 *Spatial variation and autocorrelation of canopy structure*

CS varied substantially across spatial scales both within and among forest landscapes but, despite this variation, all CS metrics reached stable values within 300m. The distance at which CS stabilized varied substantially among forested landscapes, with midwestern sites generally achieved stability at shorter distances, suggesting greater structural homogeneity, than eastern sites. Among CS metrics, mean outer canopy height and VAI varied significantly among forested landscapes, while gap fraction, canopy rugosity, and porosity did not. Even so, all CS parameters and sites reached stability between 50 to 300 m indicating geographically and biologically distinct forested landscapes, and different measures of CS, reach stability at similar spatial scales of tens to hundreds of meters. This broad convergence of stability within 300 m shows that different structural measures within various landscapes align with many fundamental ecosystem functions that operate, and are measured and modeled at similar spatial scales, including net ecosystem production and evapotranspiration [4,45].

The spatial scale of CS autocorrelation suggests that the drivers creating this structure are likely to be local disturbance patterns or environmental quality. The mean spatial autocorrelation across forested landscapes ranged between 40 - 88 m. This local scale of spatial autocorrelation reveals the potential for landscape patterns of patchiness in CS features to emerge, with differences among landscapes occurring [46]. Such differences among metrics in spatial clustering likely reflect the underlying ecological drivers of each structural measure such as the variety in crown architecture and disturbance history in the specific forests that were sampled. For example, the CS metric with the shortest peak distance was gap fraction, which likely reflects the ubiquitous distribution of small gaps in the mature forest examined [47–49]. Likewise, VAI had the longest distance of peak autocorrelation, likely reflecting spatial differentiation within landscapes as a function of variable soil fertility and management history. For some CS metrics we observed a high degree of consistency across most or all forested landscapes (GF, Porosity, VAI) suggesting a common driver of these metrics, while the other metrics may be driven primarily by forest stand-specific factors such as recent disturbances. Indeed, forests at HF and HBEF have recently experienced well documented disruptions to CS prompted by widespread tree mortality [32,50,51]. Accounting for this spatial autocorrelation in the design of a sampling plan can improve the robustness of studies that rely on the characterization of CS across space [52]. Our study clearly sheds light on the need to understand spatial scales of autocorrelation in CS, because the potential for patchiness in CS within and across landscapes will influence design of robust empirical studies and strategies for modeling forest processes.

While approaches to describing CS have become increasingly sophisticated with aerial LiDAR technologies, improving the understanding of how CS varies across spatial scales within stands, across landscapes, and among forest types may require the coupling of terrestrial and aerial LiDAR [53,54]. Our study shows that the spatial scale of stability in CS may be best characterized by terrestrial LiDAR, and then scaled up to a larger footprint with aerial LiDAR. Terrestrial LiDAR platforms provide an advantage over downward looking aerial LiDAR [18] by providing a characterization of the arrangement of canopy elements throughout the full canopy volume. CS metrics from terrestrial LiDAR have proven to have high value in describing structures that are

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important to ecosystem functioning [1,55]. Similar information could be extracted from aerial LiDAR data, especially from full waveform or Geiger-mode platforms, but the correct scale at which to describe such CS metrics (which has generally been constrained in terrestrial LiDAR studies by sampling schemes) is not well understood. Recent studies have documented the substantial influence of CS, as measured by TLS, on remote sensing observations of forests (e.g., Landsat; [56]), demonstrating potential new methods to derive additional information from existing data streams. However, despite these linkages, the spatial coherence of terrestrial and aerial measures of structure is uncertain due to differences in the scale of measurement. Coupling the two will require understanding of how stable or, conversely, variable CS metrics are within contiguous area of forestland.

### 4.2 *Relevance to canopy structural scaling and modelling efforts*

Our results suggest that surveys of CS are likely to correspond well with functions examined at a 'foot-print' scale. For example, the maximum stability point of 300 m corresponds with the area of measurements of forest carbon exchange by eddy covariance towers [4,45]. Analysis of stability points and autocorrelation scales for CS metrics indicate that CS can be robustly estimated and upscaled within an area of observation typical of that already employed by some forest ecological studies. While all metrics achieved stability within 300 m, some categories of CS metrics do appear inherently more spatially variable regardless of landscape (Fig. 3), suggesting that upscaling some metrics may necessitate coarser resolution of outputs. Given the spatial variation in stability points and auto-correlation across forest landscapes and parameters, scaling and modeling of CS requires a nuanced approach. Our analysis indicates that while CS is stable within landscapes, it tends to shift across landscapes, suggesting that scaling of contiguous landscape units may be important.

Improved characterization of spatial variation of CS has several potential benefits for understanding and modelling scale-dependent forest ecosystem processes. First, ecosystem models greatly simplify complex CS to improve computational tractability [57,58]. While computational tractability is desirable, output from such models often fails to accurately describe forest process and responses to disturbance [59]. More accurate representation of CS could improve model performance by increasing biological realism. Second, many ecosystem models accommodate some degree of vertical variation in vegetation distribution, but most do not explicitly incorporate horizontal heterogeneity in vertical variation, limiting their ability to accurately represent spatially heterogeneous processes such as disturbance events which are known to influence CS and functions such as carbon cycling [26,29]. Third, incorporating CS and the spatial variation thereof in ecosystem models offers opportunities to represent disturbance and successional changes through their effects on CS itself rather than by attempting to capture and represent the mechanism of disturbance itself.

## 5. Conclusions

We conclude that, although CS metrics stabilize within forested landscapes at different spatial scales, all approach stability at distances under 300 m. This is a range that is well aligned with the spatial scale at which many fundamental ecosystem functions are quantified using measurements and models. This finding has important implications for remote sensing, upscaling, and modeling

of CS and functions inferred from structure. New remote sensing platforms, such as terrestrial lidar, are increasingly available and are likely to become a common component of the forest ecology toolkit in the near future. The data generated by these tools will help to answer ecological questions requiring a rigorous understanding of the scales at which CS vary across the landscape. Furthermore, there are likely to be many drivers of landscape variation in canopy structure; future research should investigate the underlying causes of variation in CS across and within spatial scales.

**Supplementary Materials:** The following are available online at www.mdpi.com/xxx/s1, Figure S1: Coefficient of variation of canopy structural complexity metrics from *N*=3 individual transects at each of six forested landscapes in Eastern North America.

## Author Contributions:

Conceptualization, Brady S. Hardiman and Jeff W. Atkins; Data curation, Jeff W. Atkins and Franklin W. Wagner; Formal analysis, Elizabeth A. LaRue, Jeff W. Atkins and Robert T. Fahey; Funding acquisition, Brady S. Hardiman, Robert T. Fahey and Christopher M. Gough; Methodology, Elizabeth A. LaRue, Jeff W. Atkins, Robert T. Fahey and Franklin W. Wagner; Project administration, Brady S. Hardiman, Robert T. Fahey and Christopher M. Gough; Resources, Brady S. Hardiman and Christopher M. Gough; Supervision, Brady S. Hardiman; Visualization, Elizabeth A. LaRue and Jeff W. Atkins; Writing – original draft, Brady S. Hardiman, Elizabeth A. LaRue, Jeff W. Atkins, Robert T. Fahey and Christopher M. Gough; Writing – review & editing, Brady S. Hardiman, Elizabeth A. LaRue, Jeff W. Atkins, Robert T. Fahey and Christopher M. Gough.

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

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