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Community and structural constraints on the complexity of eastern North American forests

Christopher M. Gough[1] | Jeff W. Atkins[1] | Robert T. Fahey[2] | Brady S. Hardiman[3] | Elizabeth A. LaRue[3]

[1]Department of Biology, Virginia Commonwealth University, Richmond, Virginia, USA

[2]Department of Natural Resources and the Environment & Center for Environmental Sciences and Engineering, University of Connecticut, Storrs, Connecticut, USA

[3]Forestry and Natural Resources and Environmental and Ecological Engineering, Purdue University, West Lafayette, Indiana, USA

Correspondence
Christopher M. Gough, Department of Biology, Virginia Commonwealth University, Box 842012, 1000 West Cary St., Richmond, VA 23284, USA.
Email: cmgough@vcu.edu

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Abstract

Aim: Canopy structural complexity, which describes the degree of heterogeneity in vegetation density, is strongly tied to a number of ecosystem functions, but the community and structural characteristics that give rise to variation in complexity at site to subcontinental scales are poorly defined. We investigated how woody plant taxonomic and phylogenetic diversity, maximum canopy height, and leaf area index (LAI) relate to canopy rugosity, a measure of canopy structural complexity that is correlated with primary production, light capture, and resource-use efficiency.

Location: Our analysis used 122 plots distributed across 10 ecologically and climatically variable forests spanning a > 1,500 km latitudinal gradient within the National Ecological Observatory Network (NEON) of the USA.

Time period: 2016–2018.

Taxa studied: Woody plants.

Methods: We used univariate and multivariate modelling to examine relationships between canopy rugosity, and community and structural characteristics hypothesized to drive site and subcontinental variation in complexity.

Results: Spatial variation in canopy rugosity within sites and across the subcontinent was strongly and positively related to maximum canopy height (r^2 = .87 subcontinent-wide), with the addition of species richness in a multivariate model resolving another 2% of the variation across the subcontinent. Individually, woody plant species richness and phylogenetic diversity (r^2 = .17 to .44, respectively) and LAI (r^2 = .16) were weakly to moderately correlated with canopy rugosity at the subcontinental scale, and inconsistently explained spatial variation in canopy rugosity within sites.

Main conclusions: We conclude that maximum canopy height is a substantially stronger predictor of complexity than diversity or LAI within and across forests of eastern North America, suggesting that canopy volume places a primary constraint on the development of structural complexity. Management and land-use practices that encourage and sustain tall temperate forest canopies may support greater complexity and associated increases in ecosystem functioning.

KEYWORDS
canopy height, canopy structural complexity, diversity, leaf area index, LiDAR, National Ecological Observatory Network, NEON, phylogenetic diversity, richness, rugosity

1 | INTRODUCTION

Canopy structural complexity, which describes horizontal and vertical variation in vegetation density, height or distribution, is an emergent ecosystem property that may be viewed as a product of several forest community and structural features (Ali, 2019; Ali et al., 2019; Ehbrecht, Schall, Juchheim, Ammer, & Seidel, 2016; Forrester, 2019; LaRue, Hardiman, Elliott, & Fei, 2019; Seidel, 2018; Wilkes et al., 2016). *Plant taxonomic and phylogenetic diversity* supports complexity by supplying interspecific genetic diversity and the related crown architectural variety required to build complex canopy structures (Figure 1a; Ali et al., 2019; Fotis et al., 2018; Jucker, Bouriaud, & Coomes, 2015; Kunz et al., 2019; Pretzsch et al., 2015; Seidel, Annighofer, et al., 2019). *Leaf mass or area* provides the construction materials with which to manufacture complex canopy structures (Figure 1b; Hardiman, Bohrer, Gough, Vogel, & Curtis, 2011; Pretzsch et al., 2016). Additionally, *canopy height* constrains the physical space or volume in which complex canopy configurations can develop (Figure 1c; Bottalico et al., 2017; Castro-Izaguirre et al., 2016). When compared with plant diversity, leaf area, and canopy height, canopy structural complexity often emerges as a superior predictor of ecosystem functioning, including primary production, nutrient cycling, light capture, and avian habitat quality (Atkins, Fahey, Hardiman, & Gough, 2018; Fahey, Fotis, & Woods, 2015; Gough, Atkins, Fahey, & Hardiman, 2019; Hardiman et al., 2011; LaRue et al., 2019; Liang et al., 2016; Reich, 2012; Zellweger, Braunisch, Baltensweiler, & Bollmann, 2013). The predictive strength of canopy structural complexity may arise from its inherent integration of community and structural characteristics with independent ties to ecosystem functioning (Forrester, 2019).

Despite the recent introduction of several novel canopy structural complexity indexes, the community and structural characteristics that underpin such metrics are not fully resolved, even though this knowledge is fundamental to understanding their ecological significance and utility (Forrester, 2019; Gough et al., 2019). Moreover, unlike regional to global assessments of patterns in plant species diversity (Staudinger et al., 2013) and leaf area index (LAI; Disney et al., 2016), analysis and interpretation of canopy structural complexity have generally been limited to sites or landscapes. Studies conducted at these scales suggest that multiple, rather than individual, community and structural characteristics give rise to structurally complex canopies. For example, species diversity along with the arrangement of stems or LAI may predict variation in complexity within and among sites and landscapes (Ehbrecht, Schall, Ammer, & Seidel, 2017; Fotis et al., 2018; Peck, Zenner, Brang, & Zingg, 2014). Elsewhere, a combination of structural (Bottalico et al., 2017; Seidel, Ehbrecht, Annighofer, & Ammer, 2019) or compositional (Juchheim, Ehbrecht, Schall, Ammer, & Seidel, 2019; Kasel, Bennett, Aponte, Fedrigo, & Nitschke, 2017; Munro, Fischer, Wood, & Lindenmayer, 2009) characteristics explained site to regional spatial variation in canopy structural complexity. Though a lack of consensus among studies may be associated with variable definitions of complexity and structural properties, a question relevant to ecological theory, observation, and application persists: what characteristics underlie

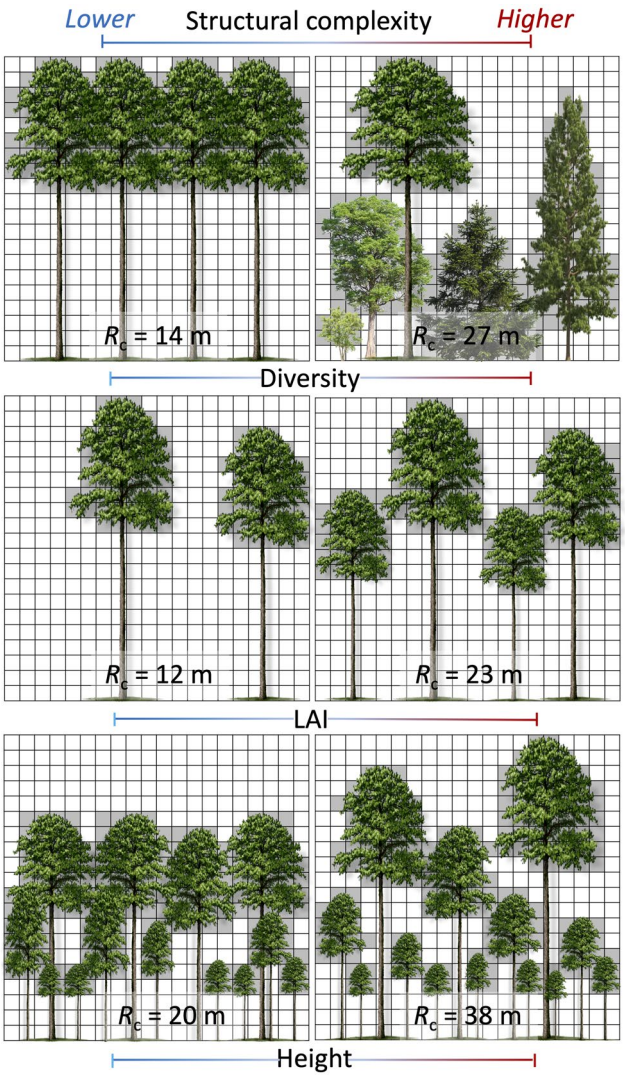

FIGURE 1 Conceptual illustration of the hypothesized relationships between canopy structural complexity – here, expressed as canopy rugosity – and plant diversity, leaf area index (LAI) and canopy height. Filled grey shaded boxes depict 1-m^2 grid-cells from which canopy rugosity is derived using terrestrial portable canopy Light Detection and Ranging, or LiDAR (PCL). Hypothetical canopy rugosity (R_c) values were generated from a random draw of vertical LAI distributions of < 5.5 or < 6.0 for low and high complexity canopies, respectively

differences in canopy structural complexity within sites and across a subcontinental gradient encompassing compositionally and structurally variable forests? While a number of different community and structural characteristics correlate with complexity indexes, plant diversity, canopy height and LAI are among the most strongly implicated as both determinants of complexity (Figure 1) and functioning (Fahey et al., 2019; LaRue et al., 2019).

We build on site to landscape scale studies, asking whether diversity, LAI and height drive variation in canopy structural complexity within and across eastern temperate forests of the United States. Recognizing that the term structural complexity is variously defined (Fahey et al., 2018), we focus our analysis on the measure 'canopy rugosity', which summarizes the degree of spatial heterogeneity in vegetation density and strongly predicts primary production, resource-use efficiency, and light capture at local to subcontinental scales (Atkins, Fahey, et al., 2018; Fahey et al., 2015; 2019; Fotis & Curtis, 2017; Gough et al., 2019; Hardiman, Bohrer, Gough, & Curtis, 2013; Hardiman et al., 2011; Hardiman, Gough, et al., 2013; Scheuermann, Nave, Fahey, Nadelhoffer, & Gough, 2018). In comparison to some metrics of structural complexity, canopy rugosity is multidimensional, high-resolution, and describes variation within the canopy interior. Forests with higher canopy rugosity values are more multi-layered and, as a result, more completely absorb and efficiently use light to drive plant growth (Hardiman et al., 2011; Hardiman, Gough, et al., 2013). In eastern North American temperate forests, the strong relationship between canopy rugosity, and light-use efficiency and light absorption explains its superiority as a subcontinental predictor of net primary production (NPP) over plant species diversity, LAI and other measures of complexity (Gough et al., 2019). Focusing on community and structural characteristics that have been linked individually with structural complexity and ecosystem functions, including NPP, we limited our investigation to plant taxonomic and phylogenetic diversity, LAI, and maximum canopy height (Forrester, 2019). We hypothesized that canopy rugosity would be greatest when diversity, LAI, and canopy height are high, reasoning that these characteristics confer a broader variety of plant architectures (Seidel, Annighofer, et al., 2019), a larger pool of raw materials (Hardiman et al., 2011), and more physical space in which to build complex canopy structures (Bottalico et al., 2017), respectively (Figure 1). Acknowledging a high likelihood of autocorrelation among community and structural characteristics, we examined the influence of each on canopy rugosity separately via univariate models and together using multivariate model selection.

2 | METHODS

2.1 | Study sites

We characterized the canopy rugosity, woody plant and phylogenetic diversity, LAI, and maximum canopy height of 122 forest plots at 10 climatically and ecologically variable National Ecological Observatory Network (NEON) sites distributed across > 1,500 km (Supporting Information Figure S1.1). Our study sites, surveyed during full canopy leaf-out in 2016, were: Bartlett Experimental Forest (BART); Great Smoky Mountains National Park (GRSM); Harvard Forest (HARV); Mountain Lake Biological Station (MLBS); Ordway-Swisher Biological Station (OSBS); Smithsonian Conservation Biology Institute (SCBI); Smithsonian Environmental Research Center (SERC); Talladega National Forest (TALL); Treehaven (TREE); and University of Notre Dame Environmental Research Center (UNDE). These sites encompass deciduous broadleaf forest and evergreen needleleaf forest plant functional types and span mean annual air temperature and precipitation gradients of 4.5 to 20 °C and 800 to 1,450 mm, respectively (Supporting Information Table S1.1). The same cluster of NEON sites was used to examine how subcontinent-wide NPP, light absorption and light-efficiency relate to several community and structural characteristics, demonstrating that canopy rugosity was most strongly correlated with ecosystem functioning at the macroscale (Atkins, Fahey, et al., 2018; Gough et al., 2019). Descriptions of each site along with dates of data collection are detailed in Supporting Information Table S1.1 and provided by Gough et al. (2019). The general NEON sampling design is described by Thorpe et al. (2016) and illustrated in Supporting Information Figure S1.2.

Because our study sites are members of a coordinated network, data collection and analysis followed standardized published protocols implemented by NEON or, in the case of terrestrial Light Detection and Ranging (LiDAR), methods published by the authors (Atkins, Bohrer, et al., 2018). All data were collected from NEON's 40 m × 40 m 'tower base' plots nested within the footprint of a nearby meteorological tower. The number of tower base plots sampled ranged between 6 to 20 at each site depending on the area and dimensions of the associated meteorological tower footprint.

2.2 | Canopy structural complexity and height

We used a terrestrial portable canopy LiDAR (PCL; Parker, Harding, & Berger, 2004) to characterize canopy rugosity and maximum canopy height. An in-depth description of the design, operation, and use of the PCL at our NEON study sites along with the mathematical derivation of canopy structural measures from terrestrial LiDAR is presented in a series of publications (Atkins, Bohrer, et al., 2018; Atkins, Fahey, et al., 2018; Gough et al., 2019). Briefly, PCL is a rangefinder operating at a maximum pulse frequency of 2,000 Hz (Riegl LD90 3100 VHS; Riegl USA, Inc., Orlando, FL). Laser pulse point returns are binned to create a 2-dimensional metre-squared grid of vegetation density arrayed in vertical columns and horizontal rows depicting a cross-sectional 'slice' of the canopy. For our study, LiDAR sampling within each plot was conducted along three parallel 40-m-long transects spaced 20 m apart, for a total of 120 vertical columns with vegetation densities resolved to a 1-m^2 gridded resolution. Canopy rugosity and maximum canopy height were then computed from vegetation grids using *forestr* in the R programming language (https://CRAN.R-project.org/package=forestr, R Core Team, 2018)

(Atkins, Bohrer, et al., 2018). Maximum canopy height (m) was the vertical distance of the tallest vegetated 1-m-wide column within a plot. The multi-step derivation of canopy rugosity (R_c, m) used here is detailed in Appendix S1 of Atkins, Bohrer, et al. (2018) and and was applied to several prior studies of R_c and ecosystem functioning, disturbance, or above/belowground structure–R_c relationships (Atkins, Fahey, et al., 2018; Fahey et al., 2019; Gough et al., 2019; Hardiman, Bohrer, et al., 2013; Hardiman, Gough, et al., 2013; Hardiman et al., 2017; 2018; Hickey et al., 2019; Scheuermann et al., 2018); for continuity and consistency, we retain in Equation 1 the nomenclature and abbreviations used in these studies. We note that our mathematical definition of R_c differs from its conceptual formula described by Hardiman et al. (2011), and Atkins, Bohrer, et al. (2018) should be consulted for the full mathematical derivation and ecological principles underlying Equation 1. Briefly, R_c of each plot was calculated from the transect-long (L_t) standard deviation (σ) in column vegetation area index (VAI)-weighted mean heights ($\overline{H}$):

$$R_c = \left(\frac{\overline{\sigma_H^2}}{L_t} - \left[\frac{\overline{\sigma_H}}{L_t} \right]^2 \right)^{0.5} \quad (1)$$

VAI within each 1-m^2 grid is estimated from LiDAR return densities (Hardiman, Bohrer, et al., 2013). R_c is derived by first calculating vertical column H from 1-m^2 gridded values and then computing the σ of all column H values along a horizontal transect. R_c, therefore, summarizes the heterogeneity of VAI density and distribution along horizontal and vertical axes of the canopy interior, with higher values indicating a more variable distribution and density of vegetation. Importantly, while VAI density and heights are required for the calculation of R_c, canopy rugosity does not scale geometrically with these vegetation properties. Because R_c is a function of the *variability* rather than magnitude of VAI density or height, short and tall canopies with similarly uniform vegetation arrangements can achieve the same hypothetical canopy rugosities. Our calculation of *canopy* rugosity, derived from multiple dimensions of the canopy interior, differs from related measures of structural complexity such as *top* rugosity and rumple, which focus on the variation in or surface area of the outer canopy (e.g. Kane et al., 2010). We centre our analysis on canopy rugosity because prior investigation of the 10 NEON sites examined in this study revealed that canopy rugosity was superior to top rugosity and rumple as a predictor of ecosystem functioning, including forest net primary production, light-use efficiency and canopy light interception (Atkins, Fahey, et al., 2018; Gough et al., 2019).

2.3 | Leaf area index

We obtained PCL-independent estimates of plot LAI from NEON's Airborne Observation Platform (AOP) *LAI-spectrometer-mosaic* data product (NEON.DOM.SITE.DP3.30012.001). LAI is calculated from the soil adjusted vegetation index using an airborne imaging spectrometer, a push broom visible-to-shortwave infrared sensor that measures surface reflectance with 424 discrete band passes at 5-nm bandwidth (from 382 to 2,512 nm) at 1-m resolution (Krause, Kuester, Johnson, McCorkel, & Kampe, 2011). Plot LAI was calculated as mean LAI within a 20-m radius of each plot centre.

2.4 | Diversity and phylogenetic indexes

We used NEON *Woody plant vegetation structure* data (NEON.DOM.SITE.DP1.10098.001) to estimate plot-level woody plant richness and Shannon's index of diversity along with phylogenetic species diversity. Inclusive of all plots in our analysis, 27,938 individual vines, shrubs and trees > 130 cm tall were identified to the species level in 2017 following the standardized NEON sampling protocol detailed by Thorpe et al. (2016). Hypothesizing that plant architectural redundancy at the species level would obscure richness- and Shannon's-complexity relationships, we additionally evaluated richness at the genus and family taxonomic ranks. For richness, we summed the number of unique vine, shrub and tree species, genera or families found in each plot. To account for abundance and evenness of species, genera and families, we derived separate Shannon's index of diversity estimates from stem count data binned by taxonomic level. We also examined three measures of phylogenetic species diversity – phylogenetic species clustering (PSC), phylogenetic species richness (PSR) and phylogenetic species variability (PSV) – to account for potential trait redundancy not explicitly represented in taxonomic diversity measures (Helmus, Bland, Williams, & Ives, 2007). To characterize phylogenetic species diversity measures, we created a phylogeny of species in each plot using the V.PhyloMaker R package (Qian et al., 2019; Qian & Jin, 2016). We then used the picante R package (Kembel et al., 2010) to calculate phylogenetic species diversity measures from each plot-level phylogeny. PSV, which measures the variability (divergence) among species across the phylogeny, is an index ranging from 0 (low variability) to 1 (high variability). PSC quantifies the degree to which phylogenetic branch tips are divergent or clustered relative to one another, ranging from 0 (low divergence) to 1 (high divergence). PSR measures the phylogenetic richness of the plant community from the distance of phylogenetic branches among species and the number of overall different species, which as a metric of richness has positive values without an upper limit. For concision, we use the term 'diversity' to encompass richness, Shannon's index and phylogenetic species diversity measures.

2.5 | Statistical analysis

Our statistical analysis focused on comparing univariate and multivariate relationships of woody plant richness, Shannon's index and phylogenetic diversity, LAI, and maximum canopy height with cross- and within-site variation in canopy rugosity. For cross-site univariate analysis, we fit linear and nonlinear relationships between candidate explanatory variables and canopy rugosity, retaining the function with the highest adjusted r^2 (to account for the trade-off between

model complexity and goodness-of-fit). Within sites, we applied only linear models to avoid overfitting our limited sample size (≤ 20 per site). To determine which combination of community and structural characteristics predicts canopy rugosity, we applied Akaike information criterion (AIC) and Bayesian information criterion (BIC) separately to our stepwise model selection, retaining and reporting models with the lowest scores. These stepwise model selection procedures account for autocorrelation among community and structural characteristics, eliminating computationally redundant model parameters. All regression models were examined for approximate normal distribution of residuals and constant variance of errors via a diagnostic panel generated using PROC REG in SAS 9.4 (SAS Institute Inc., Cary, NC) that included normal probability and residual distribution plots. Cook's distance (*d*) was calculated to assess the leverage or influence of individual data points on model parameters. Fewer than 0.4% of data points had $d > 2$ and all observed values were within the range of prior published data; thus, no data points were deemed outliers or ecologically spurious and, accordingly, all were included in our analysis. Data analysis was conducted using PROC REG and PROC STEPWISE in SAS 9.4.

3 | RESULTS

3.1 | Diversity and complexity

Richness and Shannon's indexes at all taxonomic levels were positively correlated with canopy rugosity at the subcontinental (i.e. cross-site) but not site scale. Across all sites, plot woody plant species richness varied from 2 to 28, declining to a maximum of 18 at the family level. The strength of the linear relationship between richness and canopy rugosity increased with taxonomic level, with the goodness-of-fit (r^2) for species (.17) < genus (.23) < family (.28) richness (Figure 2). Though richness was generally a poor predictor within sites, canopy rugosity within SCBI was negatively correlated with richness at all taxonomic levels; one other site, MLBS, exhibited a weakly negative canopy rugosity–species richness relationship (Table 1). Relationships between Shannon's index of family, genus and species diversity were similarly positive but weaker than those of richness, explaining 12 to 17% of the variance in subcontinental canopy rugosity (Supporting Information Figure S1.3).

Phylogenetic species diversity measures varied substantially in relation to canopy rugosity. Phylogenetic species variability was a stronger predictor of canopy rugosity than richness, explaining 44% of the variability in subcontinental scale complexity when fitted with an exponential decay function (Figure 2). Across all plots, those containing higher woody plant PSV, and, therefore, supporting species with more distant phylogenetic relatedness, had lower canopy rugosity values. Similarly, three sites displayed significant negative relationships between canopy rugosity and PSV. PSC was negatively and PSR positively but weakly correlated with canopy rugosity across the subcontinent (Supporting Information Figure S1.4), individually resolving 7 and 3% of the subcontinental variation in complexity, respectively.

Because Shannon's index and PSC and PSR were much weaker predictors of canopy rugosity than richness and PSV, respectively, we focus hereafter on the stronger correlates of complexity, while presenting subcontinental relationships with Shannon's index, PSC and PSR in Supporting Information Figures S1.3 and S1.4.

3.2 | Leaf area and complexity

Among the hypothesized predictors of canopy structural complexity, LAI was the most weakly correlated with canopy rugosity (Figure 3). LAI across all plots ranged from < 1 to 10 and was positively but weakly correlated with canopy rugosity, explaining 16% of the subcontinental variation in structural complexity. Within sites, LAI only exhibited a significant positive relationship with canopy rugosity at the TALL and OSBS sites.

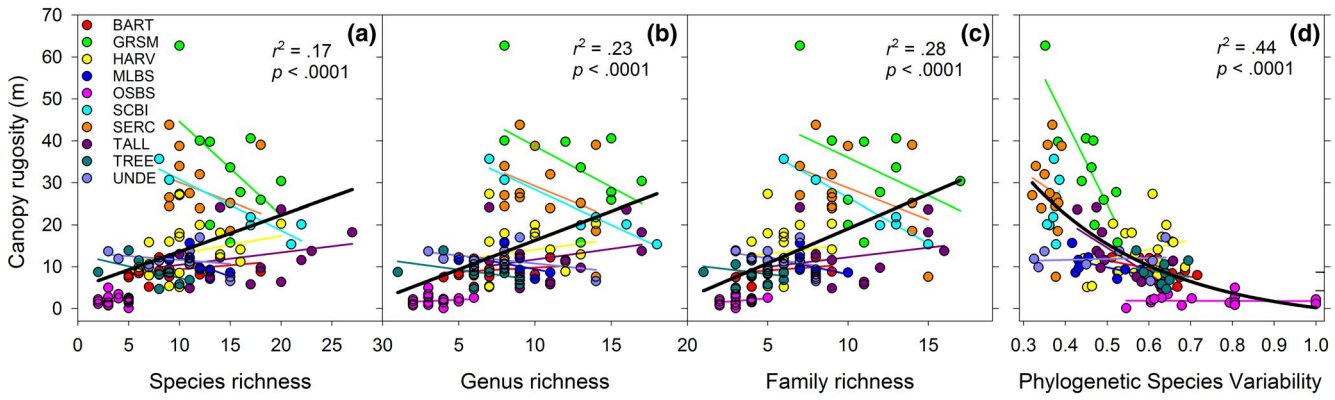

FIGURE 2 Canopy rugosity (R_c) at the site (coloured lines) and subcontinental (black lines) scales in relation to richness at multiple taxonomic levels and to phylogenetic species variability. Site abbreviations are defined in the Methods. All site and subcontinental models (a–c) are linear and the subcontinental model presented in (d) is a 3-parameter exponential decay model, where $R_c = y0 + a^*\exp(-b^*x)$. r^2 is the goodness-of-fit for subcontinental models, presented with corresponding *p*-values

TABLE 1 Site-level slopes (illustrated in Figures 2 to 4) for linear relationships between canopy rugosity and diversity indexes, leaf area index and maximum canopy height

Site	*n*	Species richness	Genus richness	Family richness	Phylogenetic species variability	Leaf area index (LAI)	Maximum canopy height (m)
BART	15	–	–	–	−19.5**	–	0.93***
GRSM	10	–	–	–	−200.6***	–	2.93***
HARV	19	–	–	–	–	–	1.87***
MLBS	9	−0.91*	–	–	–	–	–
OSBS	20	–	–	–	–	0.88*	0.31***
SCBI	6	−1.22***	−1.68***	−2.20***	–	–	2.75***
SERC	13	–	–	–	–	–	1.87***
TALL	12	–	–	–	−63.1***	1.55*	1.08***
TREE	10	–	–	–	–	n.d.	0.50**
UNDE	8	–	–	–	–	–	1.04*

BART = Bartlett Experimental Forest; GRSM = Great Smoky Mountains National Park; HARV = Harvard Forest; MLBS = Mountain Lake Biological Station; OSBS = Ordway-Swisher Biological Station; SCBI = Smithsonian Conservation Biology Institute; SERC = Smithsonian Environmental Research Center; TALL = Talladega National Forest; TREE = Treehaven; UNDE = University of Notre Dame Environmental Research Center. n.d. - no data

*$p < .1$; **$p < .05$; ***$p < .01$.

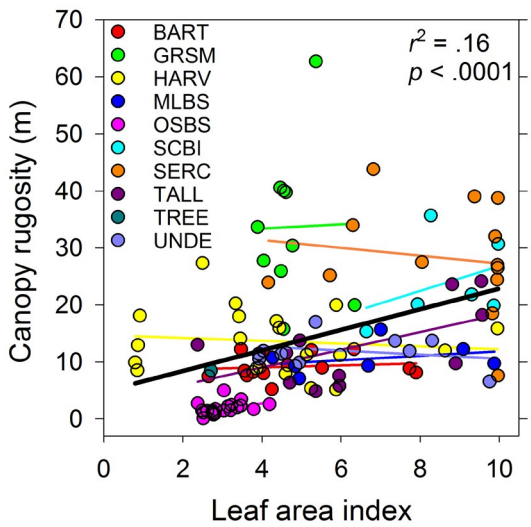

FIGURE 3 Canopy rugosity at the site (coloured lines) and subcontinental (black line) scales in relation to leaf area index. Site abbreviations are defined in the Methods. Site and subcontinental models are linear. r^2 is the goodness-of-fit for the subcontinental model, presented with its corresponding *p*-value

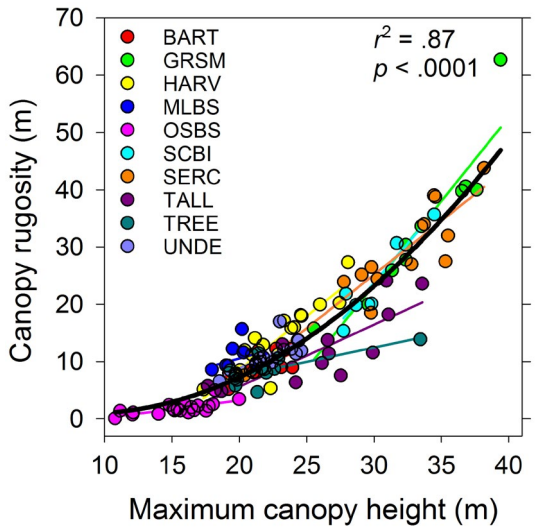

FIGURE 4 Canopy rugosity at the site (coloured lines) and subcontinental (black line) scales in relation to maximum canopy height. Site abbreviations are defined in the Methods. All site models are linear and the subcontinental model is a quadratic polynomial model. r^2 is the goodness-of-fit for the subcontinental model, presented with its corresponding *p*-value

3.3 | Canopy height and complexity

Relative to other hypothesized drivers of structural complexity, maximum canopy height was the strongest individual correlate of canopy rugosity across and within sites (Figure 4). Across all plots, maximum canopy height varied from *c*. 10 to 40 m and, when fitted with an exponential model, explained 87% of the variation in canopy rugosity. Similarly, plot-scale canopy rugosity within nine of ten sites was positively correlated with maximum canopy height, highlighting the consistent strength of maximum canopy height as a predictor of complexity at site and subcontinental scales (Table 1). Maximum canopy height explained > 75% of the within-site variation in canopy rugosity at four sites (GRSM, HARV, SCBI, SERC) and a low of 48% at UNDE .

3.4 | Synthesis: Multivariate predictors of canopy rugosity

Acknowledging autocorrelation among community and structural characteristics (Figure 5), we conducted multivariate model selection to determine which parameter combination most strongly predicts canopy rugosity at the subcontinental scale. When the hypothesized characteristics of canopy structural complexity (including all taxonomic and phylogenetic diversity indexes) were considered simultaneously through AIC and BIC stepwise model selection, maximum canopy height was retained as the strongest positive predictor with species richness a weakly negative predictor of canopy rugosity (Table 2, Figure 6). Together, maximum canopy height and species richness accounted for 89% of the variation in canopy rugosity across the subcontinent, only 2% more than that explained by maximum canopy height alone. When maximum height was omitted to test whether diversity and LAI are comparable joint predictors of canopy rugosity, phylogenetic species variability and family richness were retained, together explaining half of the variation (44%) accounted for by models containing maximum canopy height. LAI was not retained as a predictor of canopy rugosity in either multivariate model selection, reinforcing results from univariate

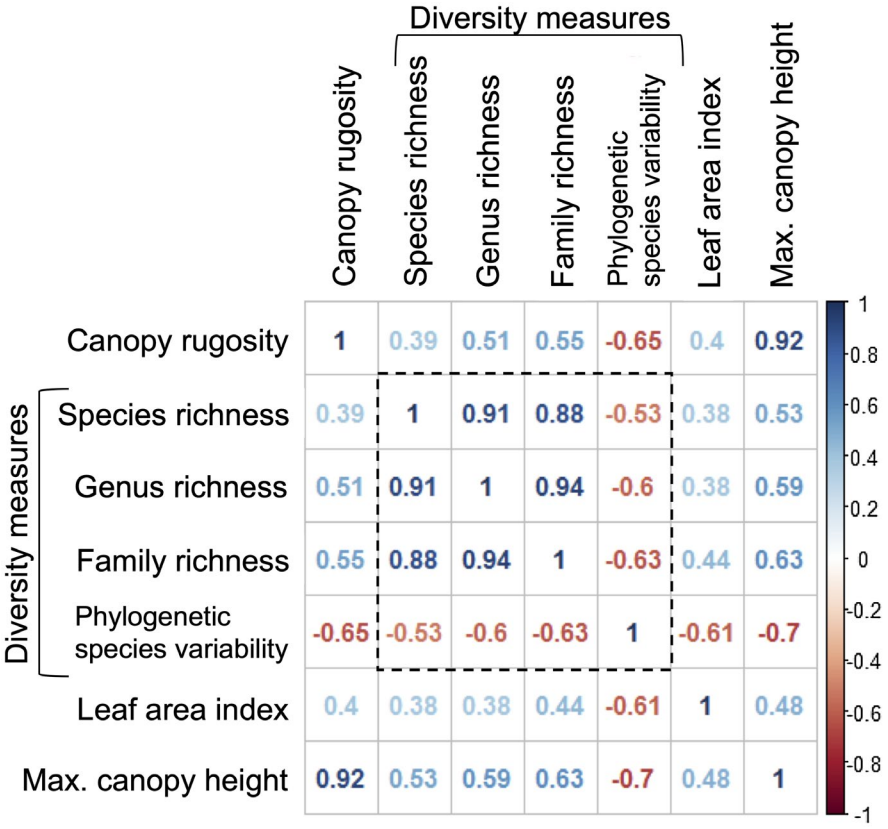

FIGURE 5 Correlation coefficient matrix for the linear relationships between canopy rugosity, richness and phylogenetic species variability measures, leaf area index, and maximum canopy height. The dashed-line box highlights diversity measures

TABLE 2 Multivariate linear models of canopy rugosity (R_c) retained by stepwise selection using Akaike information criterion (AIC) and Bayesian information criterion (BIC)

		Parameter		Model ranking statistics		
Parameter		Estimate	Partial r^2 (x100)	Total r^2(x100)	AIC	BIC
With max. height	*Intercept*	*−5.00*	–	*88.8*	*416.0*	*308.4*
	Species richness	*−0.073*	*16.8*			
	Maximum height^2	*0.033*	*70.0*			
Without max. height	Intercept	31.3	–	43.6	597.0	492.1
	Phylogenetic species variability	−38.9	40.9			
	Family richness	0.652	2.7			

Note.: Italicized values present statistics for a full model selection containing all possible variables, while plain text model selection omitted the highly influential parameter maximum height of the canopy. Maximum height was squared (^{2}) to represent its nonlinear relationship with R_c.r^2, the goodness-of-fit, was multiplied by 100 to express the percent variation in R_c explained by model parameters.

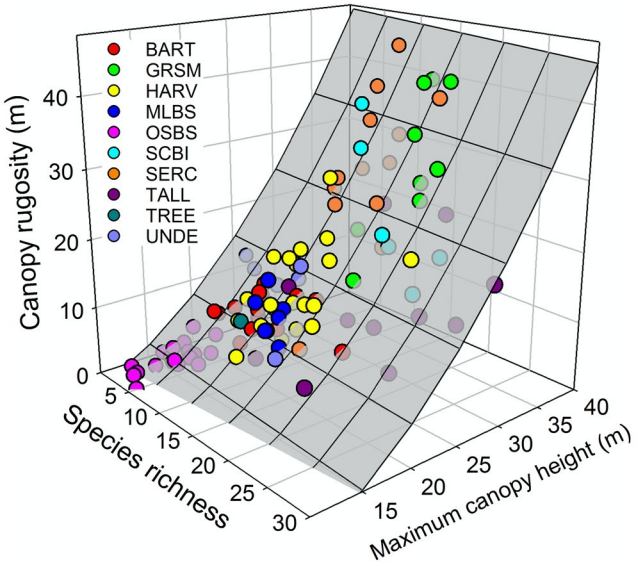

FIGURE 6 Three-dimensional relationships between modelled (surface) and observed (filled circles) canopy rugosity, species richness, and maximum canopy height at the subcontinental scale. The response surface was produced using model parameters provided in Table 2. $r^2_{adj} = .89$, $p < .0001$. Site abbreviations are defined in the Methods

regression analysis that show LAI is a weak indicator of subcontinent-wide canopy structural complexity.

4 | DISCUSSION

Our investigation in eastern North American forests of the community compositional and structural characteristics hypothesized to constrain canopy structural complexity yielded three principal findings. First, we found that the influence of forest community and structural characteristics on spatial variation in canopy rugosity was stronger at the subcontinental than site scale. Second, at subcontinental scales when multiple characteristics were simultaneously considered, maximum canopy height was substantially stronger than species diversity or LAI as a predictor of canopy complexity. Lastly, in the forests that we examined, autocorrelation among the hypothesized constraints on canopy rugosity limits full statistical disentanglement of the unique contributions of canopy height, species diversity, and LAI. Although community compositional and structural characteristics are ecologically interconnected (Forrester, 2019), and, therefore, correlated, a better understanding of how individual characteristics shape canopy complexity could prove valuable to the prediction and management of forest functions coupled with complexity.

The scale dependency of correlations between canopy rugosity and community compositional and structural characteristics indicates caution is warranted when assessing and interpreting complexity at fine spatial scales. Our plot perimeter of 40 m is less than the 300-m transect length at which canopy structural complexity stabilizes in eastern North American forests (Hardiman et al., 2018). Consequently, at the site level, small-scale heterogeneity resulting from individual tree mortality, for example, and limited spatial coherence of compositional and structural characteristics may have obscured relationships between canopy rugosity and, in particular, plant diversity and LAI (Hardiman et al., 2018). Moreover, in patchy, non-homogenous landscapes, the spatial scale at which variation in canopy rugosity and LAI stabilizes may differ, resulting in scale dependencies in correlation strength between structural characteristics. Similar to other studies of complexity, as the numeric breadth of canopy rugosity and vegetation characteristics increased with inclusion of sites across eastern North America, stronger patterns emerged that may have been masked by limited site-level sample sizes and ranges (Kukunda et al., 2019). The scale dependency of community compositional and structural characteristics is particularly acute for indexes and measures relying on count data, such as taxonomic richness, for which the probability of encountering a unique taxon increases with sampling area (Rahbek, 2005). For these reasons, we refrain from overinterpreting the contrary trends between woody plant taxonomic richness and canopy rugosity within- and across-site relationships. Though taxonomic richness and canopy rugosity were uniformly positive across the subcontinent, we observed negative within-site relationships in two of ten sites. Together, our results suggest that the relationships of canopy structural complexity with community compositional and structural characteristics are more robust across broader spatial scales encompassing an array of stand characteristics, particularly in the case of diversity and LAI.

Our finding that maximum canopy height was a consistently positive predictor of canopy rugosity across scales demonstrates that taller forest canopies support more complex vegetation arrangements. Across the subcontinent, we found maximum canopy height explained 87% of the variation in plot canopy rugosity and was a significant, positive predictor of canopy rugosity within nine of ten sites. The addition of species richness resolved a small amount (2%) of remaining variance in canopy rugosity across all sites. A similarly positive relationship between canopy structural complexity and canopy height was observed in a Mediterranean forest (Bottalico et al., 2017). We included canopy height in our analysis because taller and more voluminous canopies may provide the physical space needed to build complex structural arrangements along with the breadth of microhabitat required to support a variety of plant growth forms (Seidel, Ehbrecht, et al., 2019). Given the mathematical definition of canopy rugosity, structural complexity does not automatically scale with canopy height, but rather increases with the addition of heterogeneously arranged vegetation to interstitial canopy space. For example, a two-layered canopy in which vegetation density (as VAI) is held constant in rows of the lowest and highest strata will yield the same canopy rugosity whether contained within a short or tall canopy. Therefore, our findings imply a broad and conserved ecological relationship between canopy height and complexity. As canopy height increases, niche differentiation among and plasticity within species likely augment heterogeneity in leaf and branch morphology

and density, leading to an increase in canopy structural complexity (Ishii, Azuma, & Nabeshima, 2013; Welden, Hewett, Hubbell, & Foster, 1991).

A strongly conserved cross-scale relationship between maximum canopy height and structural complexity suggests forest canopies of a given height converge on a common vegetation arrangement regardless of composition, possibly to optimize the acquisition and efficient use of growth limiting resources (Anten, 2016; Ishii & Asano, 2010; Ishii, Tanabe, & Hiura, 2004; Niinemets, 2012). In our analysis, ecologically and climatically distinct ecosystems fell along a common positive canopy height–structural complexity continuum. Across the same group of sites, increasing canopy rugosity and height were correlated with greater light absorption and light-use efficiency (Gough et al., 2019). Taller, deeper and more heterogeneously arranged canopies absorb more light and use light more efficiently to power production, even when plant diversity is low, such as in giant sequoia (*Sequoia sempervirens*) forests (Van Pelt, Sillett, Kruse, Freund, & Kramer, 2016). Similarly, the canopy structural complexity of a planted, monospecific forest increased with canopy height in the absence of taxonomic or phylogenetic diversity (Hickey et al., 2019), consistent with our observation that forest canopies of a given height converge on a common canopy rugosity irrespective of composition. Together, these findings suggest that taller forest canopies are inherently more complex and, consequently, through improved resource acquisition and efficiency, are likely to be more productive. Moreover, our finding of a strong canopy rugosity–height relationship along with prior observations linking canopy rugosity directly to resource-use (e.g. Hardiman, Gough, et al., 2013) suggest structural complexity, rather than canopy height, is more directly coupled to the mechanisms limiting forest production.

In contrast to canopy height, diversity (including richness, Shannon's and phylogenetic indexes) and LAI were weakly to moderately correlated with canopy rugosity. As hypothesized, we found that between sites canopy rugosity was greatest where taxonomic, particularly family, richness was high. Crown morphological divergence in more diverse forests (Benavides, Scherer-Lorenzen, & Valladares, 2019; Kunz et al., 2019) may enhance complexity by supplying a variety of architectures, heights and forms. In our study, crown morphological redundancy may explain why family – rather than species or genus – richness was more highly correlated with canopy rugosity. Overlapping evolutionary histories may give rise to convergent crown architectures and consequently morphological redundancy may have been reduced when richness was expressed at progressively higher taxonomic levels. Somewhat counterintuitively, phylogenetic species variation was negatively related to canopy rugosity, indicating that complexity was greatest when species within a plot were phylogenetically similar. Though this result may appear to be at odds with uniformly positive richness–complexity relationships, species-rich plots contained a larger assemblage of more phylogenetically similar species, which may lead to an inverse relationship between richness and phylogenetic diversity indexes (Helmus et al., 2007). Overall, the low to moderate correlation strength between canopy rugosity and diversity may be caused, in part, by a lack of consideration for intraspecific phenotypic plasticity in these indexes, which may contribute substantial variation in crown architecture (Aiba & Nakashizuka, 2009; Sapijanskas, Paquette, Potvin, Kunert, & Loreau, 2014). Finally, given prior within-site observations from an eastern North American temperate forest (Hardiman et al., 2011), we anticipated but failed to observe strong relationships between LAI and canopy rugosity. A weak correlation with LAI could be associated with the limited accuracy of remotely sensed LAI, which may saturate and underestimate leaf area in dense canopies, or an indication that complexity, as in tropical forests (Castro-Izaguirre et al., 2016), is only marginally tied to the quantity of leaves with which to construct complex structures. Though further investigation is required, the latter suggests that complex canopy structures – along with associated enhancements in ecosystem functioning – are plausible in low-LAI forests.

Though we observed a statistically strong canopy rugosity–height relationship, a lack of ecological independence among canopy height, diversity, and LAI prohibits the full disentanglement of these community compositional and structural characteristics. For example, across the subcontinent, we found that plot maximum canopy height was positively correlated with plant family richness ($r = .63$) and LAI ($r = .48$). Prior observational studies report autocorrelation among community compositional and structural characteristics, including canopy height and diversity (Castro-Izaguirre et al., 2016; Kasel et al., 2017; Mao et al., 2018), canopy height and LAI (Atkins, Fahey, et al., 2018; Ma, Song, Wang, Xiao, & Fu, 2014), and diversity and LAI (Forrester et al., 2019; Pretzsch, 2005), though the interdependence of these relationships is not universal (Kohler & Huth, 2010). Manipulative experiments in which one community compositional or structural characteristic varies while others remain constant may aid in identifying the specific contribution of each feature to canopy structural complexity (Williams, Paquette, Cavender-Bares, Messier, & Reich, 2017). However, our widespread observations of eastern North American forests along with ecological theory (Van Pelt et al., 2016) indicate that diversity, height and LAI are inherently intertwined, suggesting that experiments varying single characteristics may not mimic the reality of nature.

Our findings have implications for the modelling and management of canopy structural complexity. First, our analysis shows that maximum canopy height, a property that is readily measured with high certainty using inexpensive field-based equipment and, increasingly in temperate forests, openly available airborne and spaceborne remote sensing approaches (Kampe, Johnson, Kuester, & Keller, 2010; Lim, Treitz, Wulder, St-Onge, & Flood, 2003), may be used as a proxy for more onerous estimations of canopy rugosity. Whether the strength of height as a predictor of canopy rugosity extends beyond the minimally disturbed, middle to late successional forests that we examined, however, requires additional investigation. Canopy structural complexity is shaped by factors not considered in our study, including the stage of ecological succession (Scheuermann et al., 2018), disturbance history (Meigs & Keeton, 2018), and management (Fahey et al., 2018), each of which could modify height–complexity relationships. Second, and related, for the purpose of forest

management, field recorded tree height may be useful for estimating and forecasting changes in stand complexity over time and in response to silvicultural treatments. More specifically, our findings imply that the silvicultural cultivation of tall canopies may enhance complexity, which, in turn, could augment ecosystem functioning (LaRue et al., 2019). Management for various forms of increased canopy structural complexity is associated with an increase in ecosystem goods and services, including wood production and wildlife habitat quality (Fahey et al., 2018; Keeton, 2006; LaRue et al., 2019).

5 | CONCLUSIONS

From our results we conclude that, among diversity, height and LAI, maximum canopy height is the primary constraint on canopy rugosity in forests of eastern North America, with taller canopies supporting greater complexity at site and subcontinental scales. We found minimal support for our hypothesis that taxonomic and phylogenetic diversity, LAI, and canopy height exert unique influences over canopy structural complexity. Rather, our findings reinforce observations that these compositional and structural characteristics covary in forest ecosystems across the subcontinent. Finally, we conclude that canopy height, a routinely obtained structural characteristic, could serve as a proxy for structural complexity in the context of forest complexity management and modelling, thereby aiding in forecasts of ecosystem functioning.

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DATA AVAILABILITY STATEMENT

Data and associated code are available via: doi.org/10.5281/zenodo.3755983 and github.com/atkinsjeff/LaserQuest/releases/tag/0.1.1

ORCID

Christopher M. Gough https://orcid.org/0000-0002-1227-7731
Jeff W. Atkins https://orcid.org/0000-0002-2295-3131
Robert T. Fahey https://orcid.org/0000-0001-7246-8292
Brady S. Hardiman https://orcid.org/0000-0001-6833-9404
Elizabeth A. LaRue https://orcid.org/0000-0002-9535-0630

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BIOSKETCH

'Laserquest' investigators use remote sensing to advance understanding of structure–function relationships across spatial scales, from the eco- to macrosystem. The extended research team includes physiological, community, ecosystem ecologists, carbon cycling scientists, applied forest ecologists, remote sensing scientists, and ecosystem and earth system modellers. Through partnerships with observing networks such as NEON and Ameriflux, and using novel ecological observations obtained with the aid of new technologies, Laserquest researchers seek to improve model representation of ecosystem structure. All Laserquest data – including those from this study – are open via: github.com/atkinsjeff/NEON_csc_npp.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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