


LETTER

Defining a spectrum of integrative trait-based vegetation canopy structural types

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Abstract

Vegetation canopy structure is a fundamental characteristic of terrestrial ecosystems that defines vegetation types and drives ecosystem functioning. We use the multivariate structural trait composition of vegetation canopies to classify ecosystems within a global canopy structure spectrum. Across the temperate forest sub-set of this spectrum, we assess gradients in canopy structural traits, characterise canopy structural types (CST) and evaluate drivers and functional consequences of canopy structural variation. We derive CSTs from multivariate canopy structure data, illustrating variation along three primary structural axes and resolution into six largely distinct and functionally relevant CSTs. Our results illustrate that within-ecosystem successional processes and disturbance legacies can produce variation in canopy structure similar to that associated with sub-continental variation in forest types and eco-climatic zones. The potential to classify ecosystems into CSTs based on suites of structural traits represents an important advance in understanding and modelling structure–function relationships in vegetated ecosystems.

Keywords

Canopy, complexity, lidar, structure, traits.

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INTRODUCTION

The structural characteristics of vegetation canopies are a defining feature of terrestrial ecosystems and a fundamental driver of ecosystem functioning (Ishii et al. 2004). Canopy structure is an emergent property of the organisation of vegetation elements, at leaf to crown scales, by plant individuals and communities with variable crown architecture and shade tolerance (Parker et al. 1989; Hardiman et al. 2013a; Fotis et al. 2018). The development of these emergent canopy structures is driven by optimisation of leaf to canopy resource use efficiency and by competition among individuals, within the biotic and abiotic constraints determined by the broader context in which the ecosystem is situated (Niinemets 2007; Ishii & Asano 2010). As an emergent property of vegetated ecosystems, canopy structure integrates ecologically important characteristics of individuals, species, communities, ecosystems and biophysical regions (e.g. Aber et al. 1982; Ellsworth & Reich 1993; Ishii et al. 2004). For this reason, characterisation of broad, readily categorisable vegetation structural types has been a focus of the foundational work of biogeography, ecology and remote sensing (Whittaker 1970; Running et al. 1995; Box 1996).

Quantification of canopy structure is highly important in studying terrestrial ecosystems both because of its role as an integrator of ecological factors and as a basis for studying fundamental structure–function relationships. Canopy

structure is most commonly quantified using the density metric ‘leaf area index’ (LAI), which has become ubiquitous because of its combination of relative simplicity (in quantification and application) and potential for predicting ecosystem functioning (e.g. Reich 2012). However, vegetation canopies are inherently three-dimensional (3D) and the integrated vertical and horizontal arrangement of canopy elements provides additional predictive capacity on ecosystem processes and functions such as light harvesting and light use efficiency (LUE; Ellsworth & Reich 1993; Ishii & Asano 2010; Fotis & Curtis 2017; Atkins et al. 2018b), air movement (Reich et al. 1990; Parker et al. 2004b; Maurer et al. 2015), vertical temperature and humidity gradients (Niinemets 2007), productivity (Hardiman et al. 2011; Cushman & Kellner 2019; Gough et al. 2019), and disturbance resilience (Gough et al. 2013; Hardiman et al. 2013b; Fahey et al. 2016). There is no widely accepted framework or set of metrics to characterise the 3D structure of vegetation canopies (Nadkarni et al. 2008). This fact is not surprising given that a broad definition of canopy structure incorporates several disparate concepts describing the spatial positioning of canopy elements or open space, and also because there has been limited work pairing functional data with integrative measures as a way of testing their functional significance (Atkins et al., 2018c).

The wide variety of canopy structure metrics that have been described (including LAI) can be viewed as structural ‘traits’ of vegetation canopies (Reich 2012). However, recognising

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that individual aspects of canopy structure (e.g. height, LAI) do not fully describe functionally relevant variation in structure among canopies, we propose a multivariate, trait-based approach to the study of variation in canopy structure among vegetated ecosystems. The multivariate structural trait composition of a canopy can be used to place vegetated ecosystems within a hypothesised global canopy structure spectrum (Fig. 1). Characterisation of terrestrial vegetation types has long been strongly focused on vegetation structure (alongside aspects of phenology and general physiognomy; Bailey 2009), and the general canopy structural types (CSTs) that make up this spectrum are the basis for global to regional-scale vegetation classifications (e.g. grasslands vs. savannas vs. tropical forests; Fig. 1a; Whittaker 1970). These vegetation structural types can be viewed as an agglomeration of canopy traits describing the arrangement of vegetation elements in canopy space and generally relate to three primary components of variation: canopy height, vertical layering and horizontal openness/patchiness (Aber et al. 1982; Brokaw & Lent 1999; Ehbrecht et al. 2016; Paynter et al. 2018; Cushman & Kellner 2019), as well as higher-order metrics that combine or describe variation in these traits to characterise the arrangement of canopy elements in two-dimensional (2D) or 3D space (Hardiman et al. 2011; Chen et al. 2012; Seidel et al. 2016).

The structure of vegetation canopies has an inherent spatial dimension constrained by several biotic factors (e.g. crown

form, plant height and leaf angles; Horn 1971; Givnish 1982; Anten 2004; Verbeeck et al., 2019), but is perhaps most fundamentally defined by the scale of individual leaves, which are ultimately the unit of allocation for organisms exploring canopy space and optimising light capture and resource use (Hikosaka & Anten 2012; Niinemets 2012). Leaf size is relatively consistent across plants that vary in overall size by several orders of magnitude, and so is the amount of space that can be filled or explored by those leaves (Fotis & Curtis 2017). Variation among ecosystems in total height, vertical layering and horizontal openness, therefore, affects the potential for complex arrangement of leaf area in space and differentiation in canopy structural characteristics (Ishii et al. 2004; Fotis et al. 2018). Less complex (i.e. shorter, more horizontally and vertically uniform) canopies inherently have less canopy space that can be explored to promote optimal light harvesting and drive differential interception of diffuse radiation (Montgomery & Chazdon 2001; Fotis & Curtis 2017). Therefore, a framework separating ecosystems based on total canopy height and vertical layering has grounding in allocation and optimisation theories (Anten 2004; Hikosaka & Anten 2012; Niinemets 2012), as well as copious evidence to support functional importance (e.g. Ishii & Asano 2010; Hardiman et al. 2011).

A canopy structural trait-based classification system can be viewed as analogous to other trait-focused frameworks for

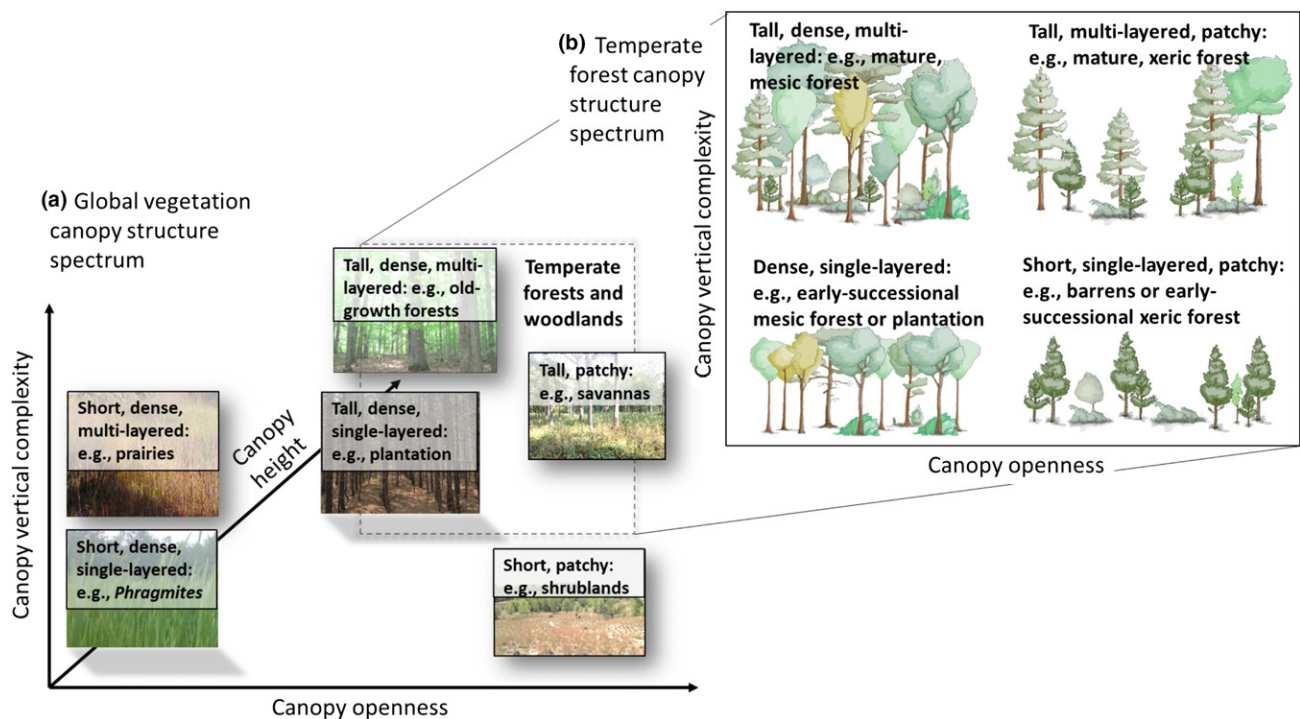


Figure 1 Illustration of the proposed (a) global canopy structure spectrum and (b) the sub-set of temperate forest canopy structure that was evaluated in the present study with hypothesised canopy structural types represented by forest illustrations. The conceptual model presented here separates ecosystems based on canopy height and horizontal and vertical complexity because these factors are most commonly used to delineate vegetation types and have been previously related to ecosystem functioning. The characterisation of canopies as more or less complex focuses on the interspersed open space within the canopy volume that allows transmission/movement of energy or material and also provides potentially explorable space for placement of new leaf area. The temperate forest sub-set is depicted without canopy height as an axis to reflect the expected lower importance of this variable as a delineating factor among temperate tree-dominated ecosystems, which all have relatively similar total canopy height (vs. a prairie-forest comparison).

classifying vegetated ecosystems, such as plant functional types (PFT; Box 1996; Bugmann 1996) or the global leaf economics, wood economics and leaf size spectrums (Westoby & Wright 2003; Wright et al. 2004; Chave et al. 2009; Wright et al. 2017). Canopy structural traits and types likely embody functional information not currently represented by conventional forest types (which are often qualitatively assigned), PFTs based on growth forms/leaf habits or non-integrative leaf and plant traits. A quantitative framework for characterising canopy structure could aid in isolating the role that physical structure plays in mediating ecosystem functional responses and thus has direct implications not only for vegetation and ecosystem modelling (Hurt et al. 2010) but also for testing underlying basic ecological assumptions of structure–function relationships (Ishii et al. 2004).

Differentiation of broad vegetation structural types is driven by biophysical and environmental factors such as seasonality and temperature gradients (Fig. 1a) and characteristics of the regional-scale biota (e.g. gamma diversity; Prentice et al. 1992; Box 1996). However, the arrangement of ecosystems among and within these broad categories of CSTs is also likely to be related to fine-scale environmental variation (e.g. soil water holding capacity, topography; Aber et al. 1982; Jucker et al. 2018), species, crown type, PFT, and trait composition of the local community (Ishii & Asano 2010; Verbeeck et al., 2019), stand to landscape-level community characteristics (e.g. alpha and beta diversity; Dial et al. 2004; Jucker et al. 2015) and historical factors such as successional processes and disturbance legacies (Scheuermann et al. 2018). Understanding how CSTs develop and how they vary within and among vegetation types and eco-climatic domains is essential to assessing structure–function relationships broadly and modelling the distribution of these relationships across landscapes.

Here, we explore the foundational ecological topic of conceptualising and characterising vegetation canopy structure, using novel analytic methods and an extensive, sub-continental-scale data set that combines detailed canopy structure data with information on environmental gradients, community composition, and ecosystem processes and functions. Our overall research goal was to quantify a spectrum of potential CST that characterise hypothesised variation among temperate forest ecosystems as a sub-set of a global canopy structure spectrum (Fig. 1b). Our specific research objectives were to (1) describe variation among a broad suite of canopy structural traits across large, heterogeneous data sets, (2) implement and test a novel method and framework for deriving synthetic canopy structure gradients and CSTs and (3) assess potential drivers and importance of variation in canopy structure by relating CSTs to environmental gradients, community composition and ecosystem functioning. To address this goal, we developed and tested multivariate analytical frameworks for deriving synthetic canopy structural complexity gradients and generalised CSTs, based on approaches adopted from analysis of ecological communities. We utilised data sets representing a range of spatial scales (sub-continental, landscape and stand) and different dominant gradients driving variation in vegetation characteristics (eco-climatic domains, landscape ecosystems, successional stages and disturbance severity).

MATERIALS AND METHODS

Study systems and sampling methods

To analyse patterns of variation in canopy structure, we utilised four data sets spanning different dominant gradients (environmental, successional, and disturbance) and a range of spatial scales (stand to sub-continental). Three data sets were focused on the University of Michigan Biological Station (UMBS) in northern lower Michigan, USA. The UMBS area has a mean annual temperature of 5.5 °C and a mean annual precipitation of 817 mm. Forests in the area are primarily *c.* 100 years old, but old forest (200+ years) remnants are also present (Gough et al. 2007). The first UMBS data set ('UMBS-LE') was a landscape-scale (*c.* 4000 ha) plot network originally utilised to characterise landscape ecosystem types (Pearsall 1995). The second UMBS data set ('UMBS-Chrono') included three experimental chronosequences consisting of 15 forest stands varying from 17 to 180 years of age and differing in type and severity of establishing disturbance (clear-cut vs. clear-cut and burned) and forest type (deciduous broadleaf dominated vs. evergreen needle-leaf dominated; Scheuermann et al. 2018). The third UMBS data set ('UMBS-FASET') was a 39 ha experimental disturbance, where 39% of pre-treatment basal area (range of 9–69% at the plot level) was removed through stem-girdling of early-successional species (Gough et al. 2013).

The final data set was a sub-continental-scale network of study areas primarily focused on National Ecological Observatory Network (NEON) sites but also including a mixture of Long Term Ecological Research (LTER) sites, AmeriFlux sites and university field stations (hereafter referred to as 'LQ-NEON') (Atkins et al. 2018b). For this data set, 13 sites were sampled across the eastern US (Table 1) spanning broad gradients in latitude (29.7–46.3 °N), climate (mean annual temperature: 4.5–20.0 °C, mean annual precipitation: 800–1475 mm year⁻¹), forest type (USDA Forest Service Types: oak-pine, oak-hickory, maple-beech-birch, aspen-birch, longleaf-slash pine, loblolly shortleaf pine; Ruffenacht et al. 2008) and six NEON eco-climatic domains: Northeast, Great Lakes, Mid-Atlantic, Appalachians and Cumberland Plateau, Ozarks Complex, and Southeast (Kao et al. 2012).

The number and characteristics of previously established sample plots varied among data sets (Table 1), but canopy structure sampling was conducted with a consistent methodology. Canopy structure was analysed using below-canopy lidar scan data collected using the portable canopy lidar system (PCL; Parker et al. 2004a). PCL transects of 30–50 m in length were located in each plot; total transect length and number of transects were specific to plot type (Table S1), but were sufficient to characterise canopy structural variability based on prior work (Hardiman et al. 2018). We utilised the *forestr* package (Atkins et al. 2018a) in *R* (v. 3.5.0) to process raw PCL scan data into 1 × 1 m grids of vegetation area index (VAI) from which we derived canopy structure metrics. In prior work, we developed a suite of 23 structural metrics (Table S2) that span a gradient of dimensionality and encompass the range of canopy structural descriptions found in the literature, describing functionally meaningful aspects of canopy density, cover, arrangement, height and variability

Table 1 Characteristics of individual data sets, including component study sites within sub-continental data set (LQ-NEON data set) collected at National Ecological Observatory Network (NEON) and other university (UNIV) or USDA Forest Service (USFS) sites, and three plot networks at the University of Michigan Biological Station (UMBS)

Data set/site	Domain	No. Plots	Type	Citation
LQ-NEON		156		Atkins et al. (2018b)
Arnot forest	Northeast	10	UNIV	
Bartlett EF	Northeast	15	NEON*,†	
Fernow EF	Appalachian	13	USFS	
Great smoky Mtns.	Appalachian	10	NEON*,†	
Harvard forest	Northeast	19	NEON*,†	
Mountain Lake BS	Appalachian	10	NEON	
Ordway Swisher BS	Southeast	24	NEON*,†	
Smithsonian CBI	Mid-Atlantic	6	NEON*,†	
Smithsonian ERC	Mid-Atlantic	13	NEON*,†	
Talladega NF	Ozarks	12	NEON*,†	
Treehaven	Great Lakes	10	NEON*,†	
Univ. Notre Dame ERC	Great Lakes	8	NEON*,†	
UVA Obs. Hill	Mid-Atlantic	6	UNIV	
UMBS LE	Great Lakes	91		Pearsall (1995)
UMBS FASET	Great Lakes	19		Gough et al. (2013)
UMBS Chrono	Great Lakes	41		Scheuermann et al. (2018)

*NPPw data available.

†fPAR and LUE data available.

(Ehbrecht et al. 2017; Atkins et al. 2018b). These canopy structural traits are relatable to the canopy structure spectrum proposed in Fig. 1, with six traits describing vertical complexity (e.g. effective number of layers, rugosity), 10 conveying canopy density or openness (e.g. VAI, gap fraction) and 8 describing measures of canopy height (maximum canopy height, mean vegetation height; Table S2). We used the multivariate composition of these canopy structural traits for each plot to describe canopy characteristics and derive CSTs as described below. Additional data on environmental factors, community characteristics and stand structure were used as predictors in analysing drivers of canopy structure and assessing relationships with ecosystem functioning (Table S3).

Data analysis

Our analysis utilised techniques often applied to understanding ecological communities, recognising that analysis of multi-factor canopy structure data, canopy traits and derivation of CSTs has much in common with analysis of species traits and delineation of vegetation communities – namely high dimensionality and strong intercorrelations. To better understand the primary gradients in canopy structure within and across data sets, we performed ordination analysis on matrices of all 24 canopy structure metrics. Ordination was conducted using non-metric multidimensional scaling (NMS) in PC-ORD v.5.31 (McCune & Mefford 2006) with Sorensen's distance measure and the 'slow-and-thorough' auto-pilot setting, using 250 runs of real data and 250 Monte Carlo randomisations to

assess the robustness of the solution (McCune & Grace 2002). Ordination was conducted on a matrix with all canopy structure metrics first relativised to the maximum value that the metric obtained to scale all metrics equivalently. We also included a second matrix of environmental and site information to enable creation of bi-plot and categorical overlays. We tested for differences among groupings in each data set (landscape ecosystem types, eco-climatic domains, stand ages and disturbance severity groups; Table S3) in multivariate suites of canopy structure metrics using multiple response permutation procedure (MRPP) with Sorensen's distance measure in PC-ORD (McCune & Grace 2002).

To produce data-driven CSTs, we performed hierarchical agglomerative clustering on matrices of canopy structure metrics. Clustering was performed with PC-ORD using Ward's Method and Euclidean distance measures (McCune & Grace 2002). 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 (McCune & Grace 2002). The grouping level with the lowest mean p value was selected as the optimal grouping level for the data set and clusters identified at this grouping level were utilised as the CSTs. We then evaluated which metrics were most strongly associated with each CST based on the results of the indicator species analysis for the final grouping level. Plant functional type classifications were produced for the LQ-NEON plots using an equivalent methodology and based on published species PFT classifications (Bugmann 1996; see Supporting Information 1)

To evaluate how CSTs were related to the primary gradients (community, environmental, successional and disturbance) represented in each data set, we conducted a classification tree analysis. We evaluated which predictors (Table S3) were most influential on the separation of plots into distinct CSTs for each data set using the Random Forest algorithm (Breiman 2001), which produces a series of iterative decision trees using binary, recursive partitioning based on predictor values and known classes (Cutler et al. 2007). We evaluated the classification accuracy of the models based on the out of bag error calculation (OOB) and evaluated the relative strength of individual predictors based on the mean decrease in accuracy associated with trees from which each predictor was removed. The predictors with greatest influence on accuracy across all trees were considered the most influential factors in driving CST differentiation. All analyses were conducted using the *randomForest* package (Liaw & Wiener 2018) in R (v. 3.5.0).

To explore relationships of CSTs with ecosystem processes and functioning, we utilised plot-level light interception (fraction of photosynthetically active radiation absorbed by the canopy; fPAR), wood net primary productivity (NPPw) and LUE (as NPPw/fPAR; Hardiman et al. 2013b) data that were available for a sub-set of the NEON plots (Supporting Information 2; also Atkins et al. 2018b). We utilised generalised linear models to evaluate variation in these factors across CSTs and to assess the effect that adding CSTs and PFTs to a model including only eco-climatic domain had on model performance. All analysis was conducted using PROC GLM in SAS v. 9.4 (SAS-Institute (2013)).

RESULTS

Multivariate analysis of canopy structure metrics

Concurrent ordination of all four data sets illustrated strong gradients in canopy structure that aligned primarily along two axes associated with canopy density/openness (VAI and gap fraction) and vertical heterogeneity (Fig. 2). The NMS ordination had a 3D solution that was highly significant relative to randomised data ($P = 0.004$, mean stress = 6.56) and explained a large majority of the variance in the original data matrix (98.1%; mostly on axes 1 and 2—54.1% and 28.6%, respectively). Axis 1 was strongly related to metrics associated with canopy area/density (e.g. mean VAI: $r = -0.85$; full list of correlations in Table S5) and canopy cover/openness (e.g. sky fraction: $r = 0.90$). Axis 2 was strongly related to metrics relating canopy vertical heterogeneity (e.g. SD of vertical return height: $r = -0.86$) and canopy height distribution (e.g. height of maximum return density: $r = -0.77$). Axis 3 explained a minor component of the variation in the original data matrix (15.4%) and was most strongly related to maximum canopy height ($r = -0.93$).

Patterns within the individual data sets illustrated distinct variation across analysis scales and in relation to environmental, disturbance and successional gradients (Fig. 3). Although there was some evidence of separation among eco-climatic domains in multivariate structure space (MRPP: $A = 0.33$, $P < 0.001$), there was also significant overlap of domains within the ordination (Fig. 3a). For the landscape-scale UMBS-LE data set, there was significant but weak ($A = 0.13$, $P < 0.001$) evidence of separation among the primary geomorphic landforms (Fig. 3b) and stronger separation among the more specific landscape ecosystem types (MRPP: $A = 0.26$, $P < 0.001$). Within the UMBS-Chrono data set, there was very strong evidence for differentiation among age classes (MRPP: $A = 0.64$, $P < 0.001$), but the chronosequence types

(disturbance type, forest type) were not as strongly separated (MRPP: $A = 0.28$, $P < 0.001$; Fig. 3c). For the experimental FASET disturbance, there was little evidence of separation among disturbance severity groups in the ordination space (Fig. 3d; MRPP: $A = 0.11$, $P = 0.02$).

Derivation of CSTs

Cluster analysis for the combined data sets indicated six relatively distinct CSTs, each represented across multiple data sets, and which generally aligned with the hypothesised canopy structure spectrum presented in Fig. 1. Incremental indicator analysis on the agglomerative clustering results suggested pruning the dendrogram at six clusters based on the minimum mean P value in the set (across cluster levels 2–7; mean $P = 0.0002$; Table S4). Clusters generally aligned with those predicted in Fig. 1, with the exception being that no forests were found to have very high openness/low density and high vertical heterogeneity. Three of the CSTs (clusters 1, 78 and 166) had strong indicator traits in the indicator analysis (standard deviation >1.0 ; Table S6).

Relationships between CST and environmental and community characteristics

The strongest environmental and community predictors of CSTs differed among the data sets and largely matched the gradients represented by the data sets. For the LQ-NEON data set, the estimated error rate for classification (OOB error rate) was 52.2%, indicating limited potential to predict CSTs at the sub-continental scale. The most important predictors of CSTs in the NEON data were species composition and annual growing degree day accumulation, reflecting macro-scale differentiation in forest type and eco-climatic domains (Fig. 4a). For the UMBS-LE data, the error rate was estimated at

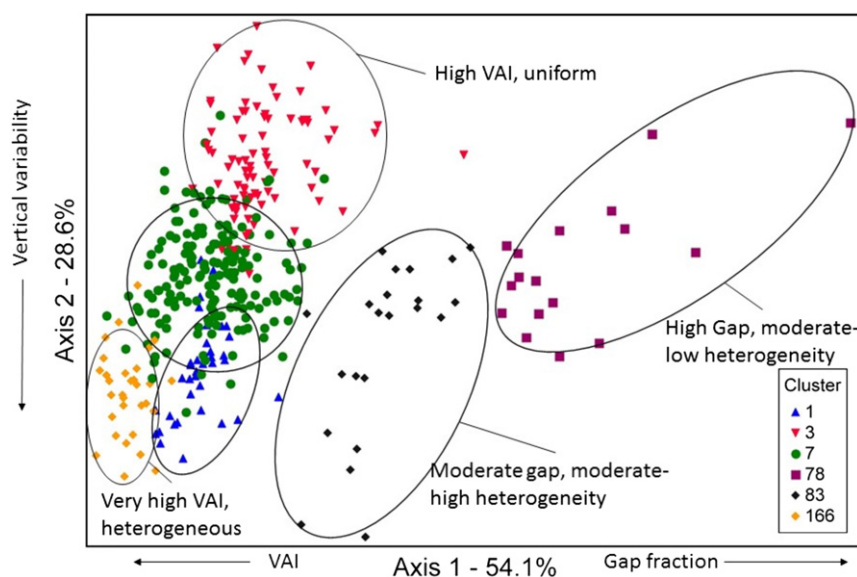


Figure 2 Graphic illustrating position of all study plots in multidimensional canopy structure space based on non-metric multidimensional scaling ordination with overlay of canopy structural types resulting from hierarchical agglomerative clustering. Dominant traits driving separation among plots are indicated for each axis (full list of correlations between traits and axes included in Table S5).

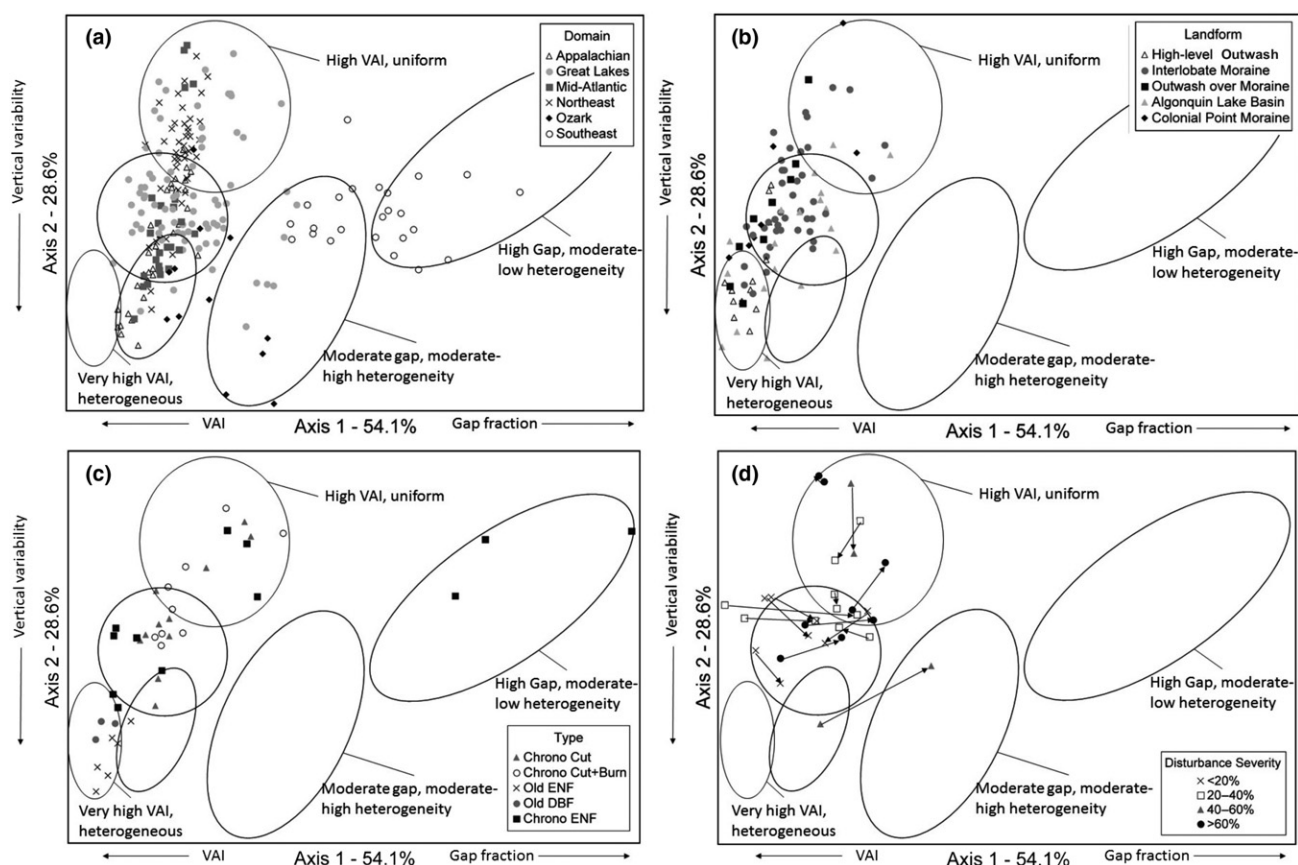


Figure 3 Illustration of plots for each individual data set indicating position of plots in multidimensional canopy structure space. Each panel indicates the same non-metric multidimensional scaling ordination result, but with only the plots for specific data sets illustrated: (a) sub-continental LQ-NEON data set with plot symbols coded by NEON eco-climatic domain, (b) landscape-scale UMBS-LE data set with plot symbols coded by geomorphic landform, (c) successional chronosequences in the UMBS-Chrono data set with plot symbols coded by chronosequence type, and (d) experimental disturbance of the UMBS-FASET data set with symbols coded by disturbance severity and pre- and post-disturbance plots locations connected by vectors. Details of individual data sets and groupings included in the text.

26.7%, with landscape ecosystem type, elevation and soil drainage as the most important predictors, reflecting variation in physiographic factors across a landscape with limited differentiation in composition and diversity among stands (Fig. 4b; Pear-sall 1995). For the UMBS-Chrono data, the error rate was estimated at 6.9% and CSTs were most strongly predicted by stand age, which reflects the strong impact of successional development on stand structure (Fig. 4c). Finally, for UMBS-FASET, the classification error rate was estimated as 31.6% and the most important predictor was species composition, and to a lesser extent disturbance severity, reflecting the limited impact of the moderate severity disturbance on overall canopy structure (Fig. 4d). In the NEON data set, CSTs were significantly associated with PFTs based on contingency table analysis ($X^2_{d.f.=16} = 99.8$, $P < 0.001$). However, there was representation of multiple CSTs across all but one of the PFTs, and all but one of the CSTs likewise included multiple PFTs (Table S8).

Forest productivity in relation to CSTs, PFTs and eco-climatic domains

Plot-level wood NPP ($F_{4,92} = 7.39$, $P < 0.001$), light interception (fPAR; $F_{4,56} = 21.76$, $P < 0.001$) and LUE ($F_{4,56} = 2.93$,

$P = 0.029$) all differed significantly across CSTs (Table 2). For NPPw, the model that included only domain explained 49% of the variation in plot-level NPPw, and the addition of CSTs increased the explanatory power to 59%. A domain-only model explained 79% of the variance in fPAR and the addition of CSTs improved the model slightly ($R^2 = 0.82$). For LUE, a domain-only model explained 49% of the variance and the addition of CSTs to the model increased the explanatory power substantially ($R^2 = 0.66$). In each case, the addition of CSTs added equivalent or greater explanatory power relative to the addition of PFTs (Table 2). Also, for each factor models that included interactions of PFTs and CSTs alongside domains had the greatest explanatory power (Table 2).

DISCUSSION

Our findings demonstrate the potential for deriving functionally relevant CSTs and gradients from multivariate canopy structural data, using temperate mixed coniferous-deciduous forests as a model system. The broad range of forests represented by our sub-continental data set represent a sub-set of a global spectrum of vegetation structural types (Fig. 1) and

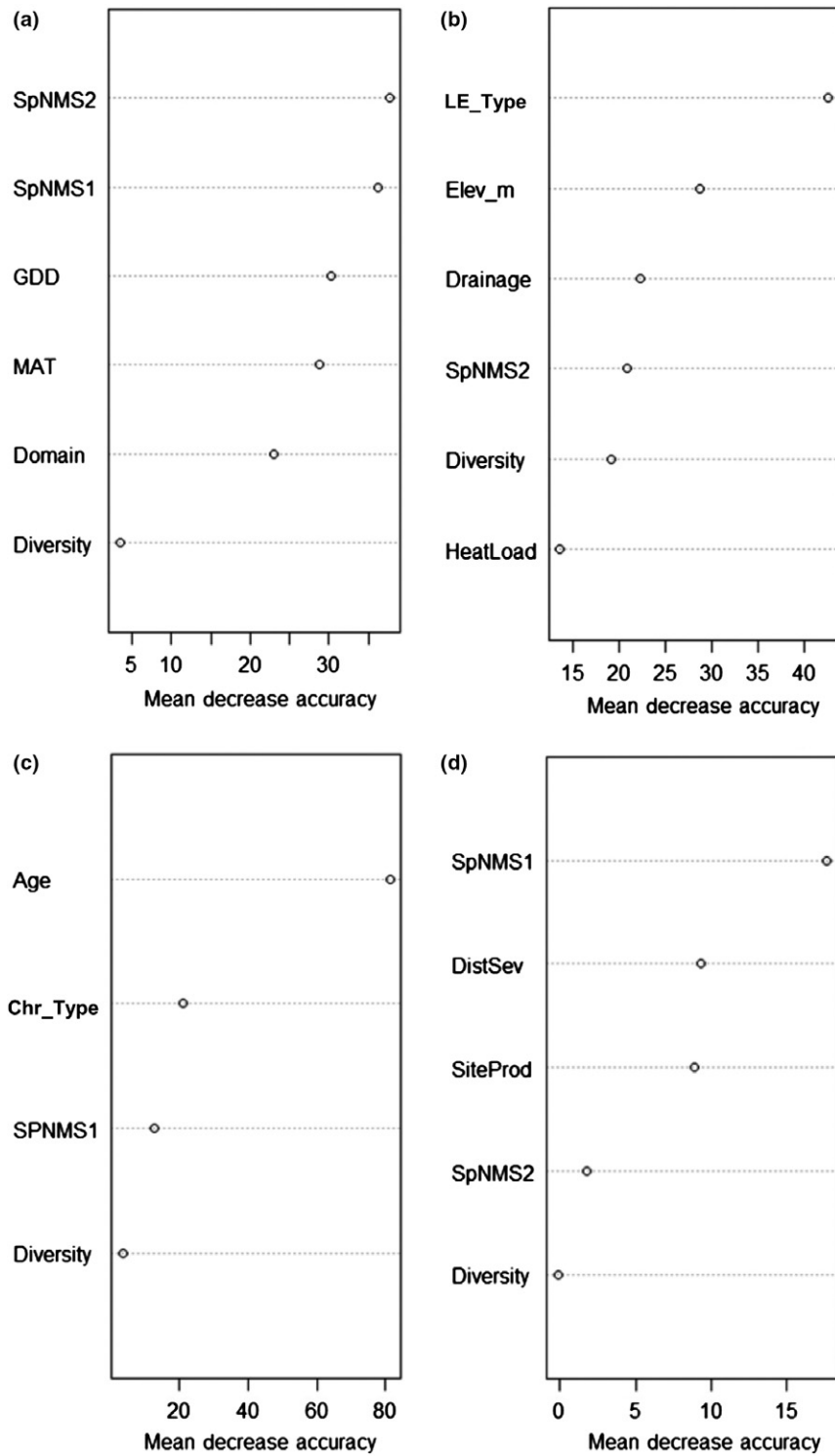


Figure 4 Ranking of predictors in random forest classification tree models for classifying individual plots from four primary data sets (panels a–d same as Fig. 3) into canopy structural types based on mean decrease in accuracy associated with trees from which each predictor was removed. ‘SPNMS’ refers to axes from ordinations of plots by species composition, ‘GDD’ – annual growing degree day accumulation, ‘MAT’ – mean annual temperature, ‘Diversity’ – Simpson’s Index of species diversity, ‘Domain’ – NEON eco-climatic domain, ‘LE_Type’ – landscape ecosystem type for plots from Pearsall (1995), ‘Drainage’ – NRCS soil drainage class, ‘Heatload’ – heat load index calculated using slope and aspect based on methods of McCune and Keon (2002), ‘Chr_Type’ – refers to chronosequence type as described in text, ‘DistSev’ – disturbance severity based on proportion of basal area removed, ‘SiteProd’ – pre-disturbance net primary productivity.

Table 2 Results of generalised linear modelling analysis on relationships of wood net primary productivity (NPPw), light interception (fraction of photosynthetically active radiation absorbed; fPAR) and light use efficiency (LUE as NPPw/fPAR) with eco-climatic domains, plant functional types (PFT) and canopy structural types for a sub-set of the National Ecological Observatory Network sites included in the overall analysis. All analysis was conducted using PROC GLM in SAS v9.4

Model – NPP	R^2	RMSE	F	d.f.	P
Domain	0.49	4.13	7.39	5,91	< 0.001
CST	0.24	3.26	7.20	4,92	< 0.001
CST (Domain)	0.59	3.41	17.52	16,80	< 0.001
PFT	0.44	3.56	17.88	4,92	< 0.001
PFT (Domain)	0.59	3.20	9.19	13,83	< 0.001
CST*PFT (Domain)	0.68	3.11	5.40	27,69	< 0.001
Model – fPAR	R^2	RMSE	F	d.f.	P
Domain	0.79	0.13	40.75	5,55	< 0.001
CST	0.61	0.17	21.76	4,56	< 0.001
CST (Domain)	0.82	0.12	14.97	12,48	< 0.001
PFT	0.67	0.16	28.44	4,56	< 0.001
PFT (Domain)	0.83	0.12	19.44	12,48	< 0.001
CST*PFT (Domain)	0.85	0.13	10.09	22,38	< 0.001
Model – LUE	R^2	RMSE	F	d.f.	P
Domain	0.49	3.24	10.77	5,55	< 0.001
CST	0.17	4.11	2.93	4,56	0.029
CST (Domain)	0.66	2.89	6.44	12,48	< 0.001
PFT	0.39	3.51	9.17	4,56	< 0.001
PFT (Domain)	0.60	3.07	6.06	12,48	< 0.001
CST*PFT (Domain)	0.75	2.73	5.25	22,38	< 0.001

were characterised by two to three primary gradients in canopy structure variability. These gradients were driven by variation not only in canopy density (i.e. LAI) but also vertical canopy layering, horizontal heterogeneity in canopy density and the integrative 3D arrangement of canopy elements in vertical and horizontal space (Fig. 2). The multivariate CSTs derived here delineate forests based on integration of these characteristics and capture variation in canopy structure not characterised by conventional categories of structure based on PFTs, canopy density or vertical layering.

The most important canopy structure gradient driving separation among forests was associated with vegetation density and horizontal heterogeneity in canopy openness (Fig. 2). This finding illustrates that, although canopy density is an important factor separating CSTs, additional variation associated with horizontal heterogeneity in the placement of leaf area is necessary to describe even the first axis of variation in canopy structure. This pattern aligned with our hypothesised canopy structure spectrum (Fig. 1) and is indicative of fundamental differences in vegetation density and gap fraction among forest types ranging from dense, closed-canopy forests to open savannas/barrens. Our results also illustrate strong separation related to vertical variability in canopy density and layering (Fig. 2) but also demonstrate that these integrative traits are not redundant with canopy height (Parker & Brown 2000; Ehbrecht et al. 2016). The importance of the vertical dimension generally matched our expectation, but separation of this variation into two somewhat orthogonal axes (*c.* 70%

orthogonal) did not entirely match the hypothesised framework for temperate forests (Fig. 1b).

Data-driven classification of canopy structure produced six relatively distinct CSTs, which were largely consistent with expectations (Fig. 1), demonstrating expected separation of open-canopied forests from dense, closed-canopy forests and tall, many-layered forests from those with shorter, single-layered canopies (Leiterer et al. 2015; Moran et al. 2018). However, the actual CSTs suggested by the data were somewhat more nuanced than the broad characterisation represented in Fig. 1. For example, the separation of tall forests into top-heavy, two-layered canopies and similarly tall, broadly vertically stratified forests was not represented in Fig. 1, but is a tenet of forest stand dynamics and silviculture (Franklin & Van Pelt 2004). There were also some ‘missing’ CSTs, most notably the lack of differentiation of open-canopied forests based on vertical variability (i.e. along Axis 2 or 3), which could be related to the absence of very tall or very short open-canopied forests (represented in the upper and lower left quadrants of Fig. 1b) in our data set (e.g. no scrub barrens).

Our findings highlight the variable role of factors such as climatic gradients, disturbance history and community assembly in driving the development of canopy structure across scales and ecosystems (Ishii & Asano 2010; Jucker et al. 2015; Scheuermann et al. 2018). At the sub-continental scale, there was significant multivariate separation among eco-climatic zones and forest types in canopy structure, likely reflecting a combination of regional environmental variation and species pools (Prentice et al. 1992), and supporting the basis for hierarchical ecosystem classifications defined according to these factors (e.g. Bailey 2004). A large body of prior work has recognised linkages between species composition and diversity and canopy structure (e.g. Dial et al. 2004; Vojtech et al. 2008; Fahey et al. 2015; Jucker et al. 2015; Fotis et al. 2018), but the distinct role of community assembly of species and related functional traits in driving multidimensional canopy structural variability is largely unresolved (Ishii et al. 2004; Hikosaka & Anten 2012; Jucker et al. 2015).

However, although CSTs varied across eco-climatic domains, our results also illustrated substantial variation in canopy structure within domains and PFTs (Fig. 3a; Table S8). Such variation is not currently represented in broad scale PFT-based frameworks for classifying vegetation structure or models that rely on these frameworks (Hurt et al. 2010). Landscape-scale variation in canopy structure was of relatively similar magnitude to that observed at the sub-continental scale (Fig. 3). For example, plots in the landscape-scale UMBS-LE data set showed separation into four different CSTs (Fig 3b), reflecting the strong influence that fine-grain variation in physiographic factors can have on canopy structural development and that CSTs are integrators of these environmental factors (Aber et al. 1982; Dial et al. 2004; Kane et al. 2010; Nave et al. 2017; Jucker et al. 2018). In addition, the successional chronosequences at UMBS spanned five CSTs and included variation, largely driven by stand age, equivalent to that present in the entire sub-continental LQ-NEON data set. There was a consistent successional trajectory in canopy structure (and sequence of CSTs) across forest types and severities of initiating disturbance

(Fig. 3c), and our findings support several prior studies that have illustrated disturbance legacies on stand to landscape-level canopy structure (Kane et al. 2010; Hardiman et al. 2013a; Scheuermann et al. 2018). However, the effects of the moderate FASET disturbance on forest canopy structure were highly variable (Fig. 3d) and did not generally override pre-disturbance variation in canopy structure (Gough et al. 2013; Stuart-Haëntjens et al. 2015).

Our results indicate that CSTs can provide additional explanatory power beyond that of broad eco-climatic domains and forest functional types in predicting ecosystem processes and functions. The importance of CSTs was especially apparent when assessed within domains, suggesting that variation in canopy physical structure could be an particularly important predictor of functioning at the landscape scale within regions (Cushman & Kellner 2019). Although individual canopy traits have previously been shown to be highly influential on ecosystem functions (Reich 2012; Atkins et al. 2018b; Jucker et al. 2018), a focus on multivariate suites of canopy traits could help further elucidate fundamental ecological mechanisms underpinning ecosystem structure–function relationships and isolate the distinct role of physical structure (e.g. relative to species and functional diversity and environmental gradients) in driving ecosystem functioning. However, further research is needed to fully characterise the potential relevance of CSTs across multiple vegetation types and ecosystem functions.

The characterisation of CSTs and their role in fundamental structure–function relationships provides a basis for studying the mechanistic underpinnings of these relationships (Gough et al. 2016; Fotis & Curtis 2017; Atkins et al. 2018b) and could, thus, be highly useful to terrestrial ecosystem modelling (Hurtt et al. 2010; Shugart et al. 2010). Canopy structural traits or types could be incorporated alongside (or in place of) conventional measures of structure such as LAI, leaf traits and PFTs in ecosystem models or integrated with these factors (e.g. vertical heterogeneity in SLA or leaf N; Niinemets 2007). The inclusion of derived CSTs in ecosystem models could also improve mechanistic fidelity without requiring ingestion of computationally intractable spatially explicit canopy structural data. In addition, understanding and characterisation of the effects of disturbances that do not significantly alter total leaf area or species and trait composition could be greatly improved by analysing shifts in canopy structural traits or CSTs (Seidl et al. 2014; Gough et al. 2016; Scheuermann et al. 2018).

Derivation of canopy structural traits and CSTs is also an important step in fully utilising data being provided by emerging and rapidly expanding technologies such as terrestrial laser scanning and aerial and satellite waveform lidar (Ilankoon et al. 2018; Paynter et al. 2018). In the near term, lidar-based canopy structural data will have increasing geographical coverage and availability from a variety of sources including the NASA Global Ecosystem Dynamics Investigation satellite, NEON Aerial Observation Platform and UAV platforms. Widespread adoption of technologies and analysis techniques focused on quantifying and classifying canopy structure across vegetated ecosystems could represent a paradigm shift in terrestrial ecosystem ecology (Danson et al.

2018), and implementation of canopy trait-based framework for describing canopy structural variation is an important step in that direction.

CONCLUSIONS

Implementation of a multivariate, quantitative structural trait-based framework to describe canopy structure variation across vegetated ecosystems represents an important advance in understanding the functional role of canopy structure, evaluating factors that drive emergence of canopy structures and forest functional types, and meaningfully representing canopy structure in models. Augmenting traditional descriptors of vegetation structure and composition with an integrative canopy trait framework that describes functionally relevant characteristics of the canopy provides a foundation for testing the functional significance of canopy structure via empirical and modelling approaches (Hurtt et al. 2010). Use of CSTs as a basis for future work could substantially improve our ability to elucidate basic structure–function relationships in terrestrial ecosystems (Atkins et al. 2018b), predict ecosystem functions such as wildlife habitat (e.g. Barnes et al. 2016) and carbon sequestration (Gough et al. 2016), and design and implement management practices focused on promoting ecosystem complexity and resilience (Fahey et al. 2018).

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AUTHORSHIP

RTF, JWA, CMG and BSH led the development of the conceptual framework and carried out data analysis. LEN, JMT, KJN, CV, CMS, ESH, LTH, ATF, RR and PSC provided data and conducted initial analyses to support inclusion of data in the analysis framework. RTF wrote the initial

manuscript draft and all authors contributed substantially to final revisions.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.ns674vd>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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