Regional-scale application of lidar: Variation in forest canopy structure across the southeastern US

Andrew J. Hansen [a], Linda B. Phillips [a,*], Ralph Dubayah [b], Scott Goetz [c], Michelle Hofton [b]

[a] Montana State University, Department of Ecology, Bozeman, MT 59717, USA
[b] University of Maryland, Department of Geographical Sciences, College Park, MD 20742, USA
[c] Woods Hole Research Center, Falmouth, MA 02540, USA

ABSTRACT

Canopy structure is a fundamental property of forest ecosystems that influences microclimate, runoff, decomposition, nutrient cycling, forest disturbance, carbon storage, and biodiversity. Unlike ecosystem properties such as vegetation production, canopy structure mapping is limited by measurement constraints and is primarily measured for small areas. Consequently, few large scale studies of carbon budgets, nutrient cycling, and biodiversity use quantitative data on canopy structure. Progress in broad scale mapping of canopy structure has recently been made by merging field, airborne lidar, and satellite data. As a step towards regional mapping of canopy structure with lidar and satellite data, we examine patterns of lidar-derived canopy structure across five ecoregions from Maryland to Mississippi and evaluate relationships with climate, topography, and soils. We used NASA's Laser Vegetation Imaging Sensor (LVIS) to quantify canopy height, canopy cover, diversity of cover, and upper and lower canopy ratio metric along a 4000-km transect. Controlling for stand age, we found that canopy structure varied among undisturbed, closed-canopy stands across the study area. Compared with the Southeast Plains Ecoregion, the Blue Ridge and Central Appalachians ecoregions were greater in canopy height (25%), canopy cover (18%), and cover in the upper third of the canopy (212%). Values in the Piedmont were similar to those in the Southeast Plains. Locations highest in canopy structure were intermediate in temperature, growing season precipitation, topographic complexity and were located on sandy soils. The strength of biophysical models differed among ecoregions, explaining 13% of the variation in canopy height in the Southeastern Plain to 60% in the Ridge and Valley Ecoregion. Canopy structure also differed among disturbance classes. Undisturbed forests were 30% higher in canopy height, 15% higher in canopy cover, and 18% higher in cover of the upper third of the canopy than disturbed forests. Managed pine plantations were intermediate in canopy structure between disturbed and undisturbed forests. This study demonstrates that airborne lidar data can be used to distinguish differences in canopy structure among undisturbed forests in varying biophysical settings and between undisturbed and disturbed forests across sub-continental transects. The results suggest that airborne lidar data in conjunction with data on biophysical gradients can be used as a basis for extrapolating canopy structure at fine spatial scales across regional extents. This would allow for fine-scale characterization of forest structure continuously across large regions. Such methods should allow breakthroughs in the use of canopy structure in ecosystem management and global change studies.

1. Introduction

Canopy structure is a fundamental property of forest ecosystems that strongly influences their characteristics. Canopy structure is typically defined in terms of canopy height, total canopy cover, the distribution of canopy cover among forest height strata, and horizontal variation among these factors (Franklin and Van Pelt, 2004). These elements of canopy structure can influence microclimate (Didham and Lawton, 1999; Parker, 1995), runoff (Brodersen et al., 2000), decomposition and nutrient cycling (Hobbie, 1992), forest disturbance (Frolking et al., 2009), carbon storage (Asner et al., 2010), and biodiversity (MacArthur and MacArthur, 1961; Goetz et al., 2010; Whitehurst et al., 2013).

Because of the importance of canopy structure to ecosystem properties, foresters and ecologists have long invested in methods

of measuring forest structure. Until recently, these methods were laborious field measurements that were restricted to relatively small plots (<0.10 ha) (Whitehurst et al., 2013). The use of aerial and satellite based remote sensing in the past decade has dramatically improved our ability to quantify forest structure (Hyde et al., 2006; Bergen et al., 2009; Lefsky et al., 2005). For example, the light detecting and ranging sensor (lidar) uses return rates of laser pulses to quantify the 3-D structure of forest canopies including canopy height, biomass, canopy cover, and canopy layering in vertical height classes (Dubayah and Drake, 2000; Lefsky et al., 2002; Vierling et al., 2008; Goetz et al., 2007; Swatantran et al., 2012; Whitehurst et al., 2013). Due to the cost of acquiring airborne lidar data, most studies to date have been done within relatively small areas such as specific forest stands or small watersheds (e.g., Hofton et al., 2002; Goetz et al., 2007; Dubayah et al., 2010; Goetz et al., 2010; Swatantran et al., 2012; Whitehurst et al., 2013). Satellite based methods have been used to quantify forest height globally (Lefsky, 2010; Simard et al., 2011), but low accuracies and wide spacing of samples limit the use of these data at regional scales.

In contrast to canopy structure, other ecosystem properties such as climate, vegetation production, and land cover are mapped continentally to globally at annual or finer intervals (Running et al., 2004) and are widely used in studies of carbon budgets, nutrient cycling, ecosystem productivity, and biodiversity. Such studies would benefit from consideration of canopy structure if data were available at appropriate spatial scales. Progress in mapping canopy structure at regional scales has recently been made (Asner et al., 2010, 2011). Data from field sampling, stratified lidar sampling, and Landsat-based mapping of land cover were used to estimate carbon stocks over a 4.3 million ha area in the Amazon and the one-million hectare Island of Hawaii. In these applications, the authors found that canopy structure varied with geologic substrate, landform, vegetation type, land cover and disturbance type.

Knowledge of biophysical and land use effects on canopy structure is critical to designing lidar and field data collection so as to sample the major sources of variation in canopy structure. As a step towards regional mapping of canopy structure with lidar and satellite data in the southeastern US, we examine patterns of lidar-derived canopy structure across five ecoregions stretching from Maryland to Mississippi and evaluate relationships with climate, topography, and soils, biophysical factors that influence forest growth and the development of canopy structure. In his classic monograph on vegetation of the Great Smoky Mountains, Whittaker (1956) examined the influence of environmental gradients on vegetation structure and composition. He concluded that forest stature, growth rates, and species composition varied across the environmental gradients of these mountains, reaching peak levels in particular "favorable" biophysical settings. Forests in the favorable lower elevation cove forests were as much as 50% taller than forests on ridge tops at higher elevations.

Some 50 years after this publication, Whittaker's gradient approach to vegetation distribution is considered foundational to ecology (Begon et al., 2006). Canopy structure is thought to be a product of primary productivity as governed by limiting biophysical factors and disturbance (Spies and Turner, 1999) (Fig. 1). Biophysical factors such as climate, topography, and soils influence resources and conditions within a forest through the mediating effects of canopy structure. These resources and conditions influence plant population growth rates and the capacity of the ecosystem to support species richness (S_K) (Brown et al., 2001). Actual species richness is a product of the size of the regional species pool and how those resources and conditions are allocated among species. Population growth rates and species richness influence primary productivity (Tilman, 2000) and the rate of development of canopy structure (Larson et al., 2008). While primary productivity builds canopy structure, disturbance can destroy plant tissue, kill plants, and thus reduce canopy structure (Pickett and White, 1985). Thus, canopy height and structural complexity are functions of time since disturbance and rates of primary productivity as governed by biophysical conditions.

This model of canopy structure is the basis of the concept of site index in forestry. Site index is used as a measure of site productivity and is defined by maximum tree height at a given time since disturbance (typically 50 years) (Skovsgaard and Vanclay, 2008). Trees are expected to be taller at a given age in sites with favorable climate, soils, and other limiting factors. Consistent with this assumption, Weiskittel et al. (2011) found that site index in western US forests was strongly related to climate and to gross primary productivity. In addition to tree height, the basis of site index, Larson et al. (2008) found that the complex structures of old growth forests developed more quickly in locations of high site index (see also Boucher et al., 2006). Additional evidence that canopy structure varies with biophysical factors comes from Homeier et al. (2010) who found that tree height and basal area were inversely related to elevation across a 700-m elevational gradient in the Ecuadorian Montane Rain Forest and that basal area was correlated with soil nutrients. Moreover, across a subcontinental transect from the maritime climate and favorable soils of the western Oregon and Washington to the continental climate of the Northern Rocky Mountains, a measure of forest structural complexity decreased by about half (Verschuyl et al., 2008).

Despite Whittaker's pioneering work nearly half a century ago, patterns of canopy structure across the forests of the southeastern US and controlling biophysical factors remain poorly known. Consequently, we sampled with an airborne lidar instrument a 4000-km transect from Washington DC to Jackson, MS (Fig. 2). The data were used to quantify canopy height, canopy cover, and canopy layering across five ecoregions. These data offer a unique opportunity to improve understanding of variation in 3-d canopy structure across the biophysical gradients of the SE US. Lidar transects were recently flown over the boreal forest of Canada (Bolton et al., 2013), a region of much harsher climate and lower primary productivity than the southeastern US. We compare our results with those of that study and discuss how the effects of biophysical factors on canopy structure may vary across continental gradients.

The objectives of this study were as follows.

(1) Quantify variation in forest canopy structure within and among ecoregions for forest stands showing no sign of recent disturbance.
(2) Determine the biophysical factors (climate, topography, soils, forest productivity) that best account for this variation.
(3) Evaluate differences in canopy structure among undisturbed, disturbed, and plantation forests.

2. Materials and methods

2.1. Overview

Objectives 1 and 2 focused on local and regional variation of canopy structure of forests across the southeastern US and the influence of biophysical factors on this variation in canopy structure. Data on canopy structure were collected using an airborne lidar system. From among the samples collected along the route, a subset was selected for this analysis that met the criteria of closed-canopy forest with no visual evidence of recent disturbance. Canopy structure of these samples was quantified as the number of canopy height classes represented and the proportional abundance of canopy cover within these height classes. Predictor data were obtained pertaining to climate, soils, topography, and forest productivity. Means and variation in canopy structure of stands of
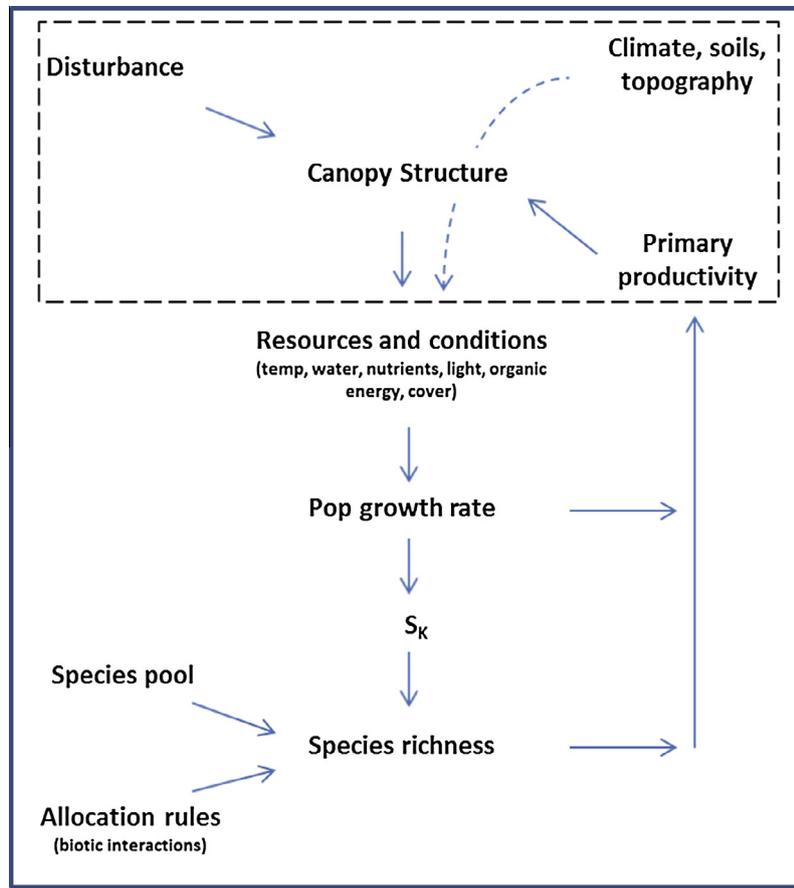
Fig. 1. Conceptual model of the determinants of canopy structure in forest ecosystems. This paper focuses on the portion of the model in the dashed box.
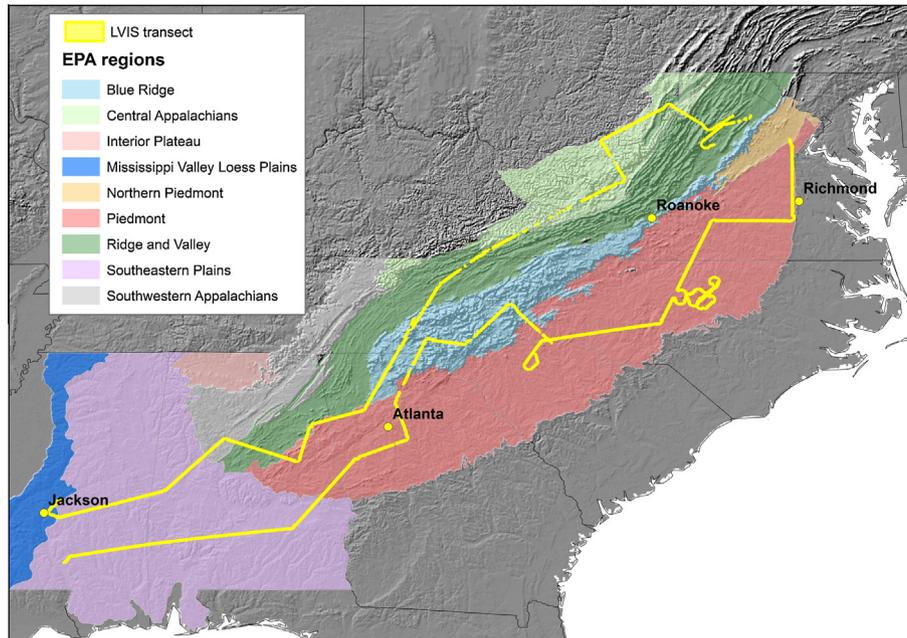
Fig. 2. Map of the study area showing the LVIS transect and ecoregions.

similar age were compared among ecoregions with ANOVA techniques and regression-based model selection techniques were used to quantify the amount of variation in canopy structure accounted for by the biophysical predictors. To gauge how canopy structure of the undisturbed forest differs from those subject to timber harvest, residential development, and other disturbances (Objective 3), we

compared samples of undisturbed forest to samples showing evidence of disturbance and to conifer plantations.

2.2. Study area

Much of the southeastern US is cloaked in forest. With nearly continuous coverage from the Mississippi Delta to Pennsylvania, this area is a portion of the vast Temperate Deciduous Forest of the eastern United States (Olson, 2001). These forests are highly productive (Phillips et al., 2010) and represent an important component of the North American carbon sink (Pan et al., 2011a). They also support high levels of plant and animal biodiversity (Currie, 1991) and contain globally important conservation lands such as Great Smoky Mountain National Park.

While the vast southeastern forest looks relatively homogeneous from an airplane window, the underlying soils, climate, and topography are varied. The area includes the Southeastern Plains, Piedmont, Central Appalachian, Ridge and Valley, and Blue Ridge ecoregions (USEPA, 1999) (Fig. 2 and Appendix A).

The Southeastern Plains are irregular plains with sandy soils. The Piedmont is transitional from the coastal plains to the Appalachian Mountains and his moderately dissected plains and hills. Soils are relatively clayey and infertile. The Blue Ridge includes the Appalachian Mountains with elevations up to 2000 m. Soils vary with slope position and can be deep and loamy in valley bottoms. The Ridge and Valley includes valleys separated by ridges with sandstone caps. Soils are variable from sandy to loamy. The Central Appalachians are a dissected plateau with a mix of soils derived from sandstone, shale and conglomerate parent materials. Climate across the region is relatively hot, humid, with moderate rainfall distributed evenly across the year due to the strong influence of weather systems moving north from the Gulf of Mexico. While the Southeastern Plains and Piedmont are strongly maritime, climate has increasing continental influences to the north and west, thus summer temperatures are somewhat cooler and winters more pronounced. The higher elevations of the Blue Ridge are substantially colder and have prolonged winter conditions. Oak/hickory, maple/beech/birch, and oak pine are the dominant forest types across the Central Appalachians, Ridge and Valley, and Blue Ridge ecoregions (Ruefenacht et al., 2008). These types are also found in the Piedmont and Southeast Plains Ecoregions, but loblolly/shortleaf pine and longleaf/slashpine types are the dominant types.

These ecoregions have all been highly influenced by land use (Goward et al., 2008; Drummond and Loveland, 2010; Goetz et al., 2012). Agriculture and urbanization both led to forest clearing, particularly on the coastal plains and piedmont. Timber harvest is frequent, converting mature forest to earlier seral stages. Fast forest growth rates result in afforestation of abandoned farmlands and rapid forest recovery following disturbance. For example, Li et al., 2011a,b found that 60% of the forests of Mississippi were less than 30 years old due to frequent disturbance and that these disturbed forests reached 80% of maximum height within 30 years following disturbance.

2.3. Transect

NASA's Land, Vegetation, and Ice Sensor (LVIS) (Blair et al., 1999) was flown over a 4000 km loop between Washington D.C. and Jackson MS in July 2009 (Fig. 2). The route was selected to sample vegetation structure across gradients in biophysical factors over the major US EPA Level III ecoregions of the southeastern US, within the land allocation and land use types typical of the region. This route was the longest flight line to date of the LVIS instrument and this study is the first attempt to use this instrument to study regional gradients in canopy structure.

2.4. LVIS data

LVIS is a scanning waveform lidar instrument that is flown, by aircraft, over target areas to collect data on surface topography and vegetation coverage. The instrument is a medium-footprint, full-waveform lidar developed at NASA's Goddard Space Flight Center (Blair et al., 1999). LVIS records the entire outgoing and return signal to provide waveforms that can be used to map sub-canopy topography, canopy height and vertical foliage profiles. The amplitude of the geolocated waveform at a given height is proportional to the amount of canopy material at that height making it suitable for canopy stratification studies (Hyde et al., 2005). LVIS was flown at an altitude that achieved a nominal 20-m diameter footprint on the ground. The footprints overlap slightly in the across- and along-track flight direction to achieve approximately contiguous coverage over the entire imaging swath (about 2 km wide for these flights). A detailed description of LVIS waveform processing is available in Hofton et al. (2002) and Dubayah et al. (2010). Total canopy cover was calculated from the normalized cumulative laser energy (Ni-Meister et al., 2001) and canopy cover at 5 m height intervals was calculated from the cumulative energy return between ground and 60 m, resulting in 10 metrics that approximated the foliage profile following the methods of Swatantran et al. (2012) and Whitehurst et al. (2013). Any height class that had a value of <0.01% cover was converted to 0 so as not to be included in the metric of canopy layer richness (see below) where measurement error may account for canopy cover being represented as present.

The accuracy of LIDAR data has been analyzed in many forest types and has been found to be very high. In wet tropical rainforests, Hofton et al., 2002 found subcanopy topography accuracies to be higher than that of the best digital elevation models. In conifer stands in Western Oregon forest mean stand height had very high accuracy (r^2 = 0.95) (Means et al., 1999), and in wet tropical rainforests plot-level biomass was modeled at r^2 = 0.93 (Drake et al., 2002).

2.5. Estimating canopy cover metrics

The canopy structure metrics included canopy height, canopy cover, and vertical distribution of canopy cover (Fig. 3 and Appendix B). Canopy height (canheight) was defined by the height above the ground where 100% of the return wave form energy was achieved (RH100 in Hofton et al., 2002). Canopy cover (cancover) was the summed cover across 5-m height classes. Shannon Diversity Index (shannon) was calculated as $-\sum (p_i [\ln(p_i)])$, where p_i = proportion of canopy cover in height class i. We also estimated the relative distribution of canopy cover in the lower, middle, and upper third of the canopy in a way that was not influenced by canopy height. Canopy cover was found for 1-m segments from the ground to the top of the canopy. Canopy height was multiplied by 0.33 and 0.66 to find heights representing the lower and middle third of the canopy. Total canopy cover in the, lower, middle and upper third of the canopy was then calculated by summing the canopy cover in the corresponding portion of each waveform. Most of the variation among samples among the canopy thirds was between low and high. Thus, we report the ratio of cover in the upper to lower third of the canopy in the analyses (highlow).

Canopy structure varies with grain size of analysis. We represented canopy structure as mean of the 20 m LVIS samples within 100-m plots. We selected this grain size because it allowed representation of horizontal variation in canopy structure by canopy gaps and because it is within the grain sizes of the biophysical predictor data (30 m to 1 km) (see below). Thus conceptually, a 100-m grid was overlain on the LVIS samples, and means of canopy metrics were estimated within each 100-m plot similar to Dubayah
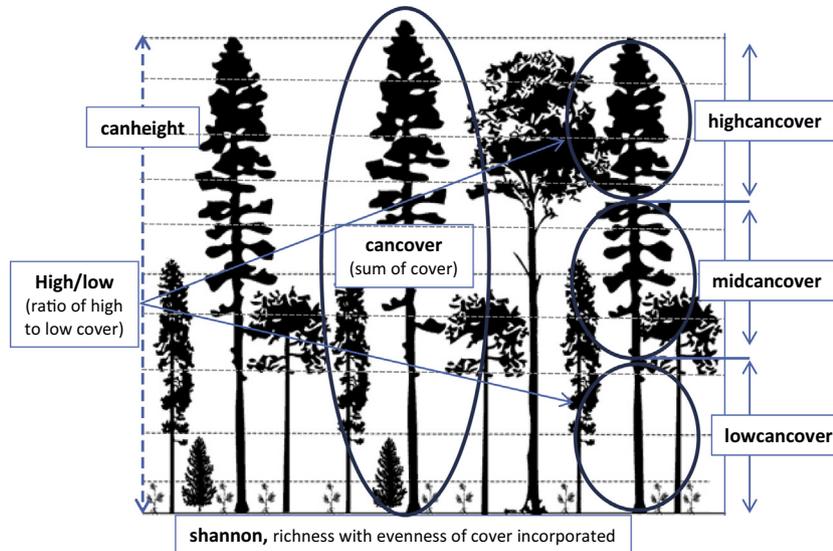
Fig. 3. An illustration of the canopy structure metrics quantified in this study.

et al. (2010). Plots with less than 15 LVIS samples were excluded to ensure adequate sampling of each plot. The resulting data set contained 325, 978, 100-m plots.

2.6. Selection of 100-m sample plots

Computation time for estimating these metrics for the full 100-m data set was prohibitive. Thus we subsampled the data set with a stratified random design to obtain 35,000 samples that were well distributed among the biophysical, forest cover, disturbance classes, land-use classes of interest. The intent of Objectives 1 and 2 were to examine canopy structure for closed canopy forest stands that showed no evidence of disturbance. Thus, we selected for potential sample plots those that met the following criteria:

- Percent of plot in forest = 100% (based on NLCD% forest, Homer et al., 2004; Fry et al., 2011).
- Canopy density >75% (based on NLCD canopy density).
- Home density < exurban levels (based on Theobald, 2005).
- No visual evidence of canopy disturbance on ESRI basemap images.

We reduced this data set still further in order to have similar sample sizes among ecoregions, land allocation types and landforms. Ecoregions were US EPA Units (USEPA, 1999). Land allocation types were private unprotected, public and private protected (from Conservation Biology Institute, 2006). With regards to landform, we distinguished valley bottom from slopes and ridges in the two mountainous ecoregions (Blue Ridge and Ridge and Valley). Landform was relatively homogeneous in the other ecoregions. The resulting data set included 2694 100-m samples.

We evaluated our visual classification of stands with no canopy disturbance against independent data from the North American Forest Dynamics Project (http://daac.ornl.gov/NACP/guides/NAFD_Disturbance_guide.html) (Goward et al., 2008). NAFD used the Vegetation Change Tracker (VCT), an automated forest change analysis algorithm, on temporally dense (annual or biennial) Landsat Time Series Stack (LTSS) of images and produces forest disturbance data products (Huang et al., 2010). They defined "persistent forest" as forest stands that did not show evidence of disturbance during the 1984–2009 analysis period. We compared 100-m plots that we tallied as "undisturbed" to the NAFD persistent forest class in the two ecoregions where their samples overlapped our 100-m

plots (Appendix C). This analysis revealed that plots that we classified as showing no evidence of disturbance were classified as persistent forest by NAFD with accuracies of 90–100% in the Blue Ridge, Ridge and Valley, and Cumberland Plateau ecoregions and 43–59% in the Southeast Plains and Piedmont ecoregions.

For Objective 3, we identified two types of disturbed forest among the 35,000 100-m samples. Stands that had more open canopies, roads, or exposed soil were classified as 'disturbed'. Those dominated by coniferous trees, oriented in rows, typically in rectangular stands, with road access were classified as conifer plantations. These two types were only adequately represented in the Piedmont and Southeast Plains Ecoregions and the analyses were restricted to these ecoregions. Sample sizes were 192 disturbed stands and 841 for conifer plantations.

2.7. Predictor data

The biophysical gradients that have been found to influence canopy structure in undisturbed forests in other studies relate to climate, topography, and soils (Weiskittel et al., 2011; Larson et al., 2008; Homeier et al., 2010). The sources of data used to represent the biophysical predictors (Appendix D) were selected to be the best available with regard to availability across the study area, grain of 1 km or less, representative of the date of lidar sampling (2009), and had published methods and availability of accuracy assessments (see Appendix D for data details). Climate data were obtained from PRISM (Daly et al., 2008) for the time period 2005–2009. Climate metrics were calculated for two time periods: annually and growing season; and are distinguished with a suffix 'an' and 'gs', respectively. Climate metrics are mean temperature (TEMP), mean precipitation (PPT), mean actual evapotranspiration (ET), mean potential evapotranspiration (PET), and an aridity index (PET/PPT). PET and ET were calculated using basic water balance equations (Dingman, 2001). Growing degree day (GDD) was calculated for months with average temperature >5 °C (Sork et al., 2010). Soils data were selected from multiple sources to best represent soil texture, soil nutrient status, and water holding capacity. Soil texture and waterholding capacity largely came from Miller and White (1998) who developed raster data from STATSGO data (Soil Survey Staff, 2012). The finer-scale SSURGO soils data are available in raster form from the NRCS Gridded SSURGO data set. We selected from this data set soil organic carbon (SOC0150), available water stores (AWS015), rooting zone depth (ROOTZONE),

and root zone available water storage (ROOTZONEWS). The CONUS dataset also provided soil metrics of Soil silt fraction (SILT), soil clay fraction (CLAY), soil sand fraction (SAND), depth to bedrock (BED), annual waterholding capacity (AWC2), and soil bulk density (BULK). Data for gross forest productivity (GPP) came from MODIS which uses simulation modeling of biophysical processes using input data from meteorological stations, satellite spectral data and land-cover information. Data representing topography included Aspect (Geesch et al., 2002), Topographic position index (TPI) (Jenness, 2006), mean annual solar radiation (RAD), and a measure of hillslope position (HILLSLOPE).

Time since disturbance or forest age is known to influence canopy structure (see Introduction). We obtained estimates of forest age for our samples from Pan et al. (2011b). They mapped stand age for the year 2000 at a 250 m grain size across the forested portion of the US based on tree ages from Forest Inventory and Analysis Data and NASA Landsat Ecosystem Disturbance Adaptive Procession System. Stated accuracies were generally ±10 years in our study area. We basically controlled for stand age in the analyses.

2.8. Analyses

Differences in mean values of canopy structure among ecoregions types were analyzed with ANOVA. The distributions of stand age differed among ecoregions with older stands being present in the three mountainous ecoregions. To control for stand age, we restricted the comparison of canopy structure among ecoregions to stands 30–70 years of age, which were well represented in all the ecoregions. We chose this age range because forests in the SE US were found to reach 80% of maximum height by 30 years of age (Li et al., 2011a,b). We confirmed the small influence stand age on tree height in this age range with regression analyses (see Table 1). ANOVA was also used to evaluate differences in canopy structure among disturbance types. Regression-based model selection techniques (Burnham and Anderson, 1998) were used to identify best biophysical models predicting canopy structure. Both ANOVA and Regression techniques assume that residuals (error terms) are independent, normally distributed and with constant variance. We first evaluated if univariate models between the response variable and each predictor variable were linear or best fit with a second-degree polynomial. We then examined X–Y plots for outlier observation and histograms for skew in the predictor data. Where the predictor data included outliers or were skewed in distribution, we transformed the predictor (log 10), regressed the response variables on the predictor data and inspected diagnostic plots (R v.3.0.0) for homogeneity of variance and normality of the residuals, and leverage of individual observations.

Stand age was included in candidate models to determine its relationship with canopy structure and to evaluate if stand age was included in best models of canopy structure. This variable explained $\leqslant 8\%$ of the variation in metrics of canopy structure

and was included in the best model only for canheight at the study-area wide level. It was not included in best models for cancover or highlow at the study-area wide level nor for canheight within any of the ecoregions. Thus, within the 30–70 year old forests analyzed, stand age had little effect on canopy structure.

Linear and quadratic forms were evaluated for each predictor and the form resulting in the best model was used in subsequent analyses. For the assessment of the best overall models, all predictors were considered except those found to be highly correlated ($r > 0.75$). All analyses were performed in R (v.3.0.0). The models were analyzed using ordinary least squares regression techniques. The Akaike information criterion (AIC) was the primary criterion for determining best models (Burnham and Anderson, 1998). The AIC provides an estimate of the distance between the specified model and some full truth or reality. We used the difference in AIC values (DAIC) and Akaike weights of evidence (AIC weights) to assess relative model strength (Burnham and Anderson, 2002). We interpreted the cumulative Akaike weights as relative probabilities of importance. However, AIC only provides a measure of model strength relative to other models being examined; it does not inform on the overall model goodness of fit. Hence, we used the coefficient of determination (R^2) as a measure of how much variation in the response variables was explained by the best model.

To determine if spatial autocorrelation was problematic in our data, we examined Moran's I correlograms of the model residuals, since spatial autocorrelation violates the assumption of independent residual values in regression analyses. Moran's I is an index of global autocorrelation ranging between −1 (negative correlation) and 1 (positive correlation). Moran's I was calculated and standardized with the Z value. When spatial autocorrelation was present (Moran-Index $p \leqslant 0.001$), semivariograms were used to determine the spatial relationship and generalized least squares multiple regression models were used to incorporate the spatial structure determined by the semivariogram. The GLS models included the spatial structure in the model, thus controlling for the influence of spatial autocorrelation on sample size. Software used for these analysis was Spatial Analysis for Macroecology (SAM) (v.2.0) (Rangel et al., 2006). We report adjusted R^2 values for the predictor values and for the predictors plus the spatial term.

Some level of collinearity is expected among biophysical variables and this can inflate the variance of coefficient estimates in the model. We reduced correlation between predictors and their squared forms (used to represent nonlinear relationships) by centering the values on their means before squaring them. Additionally we assessed the Variance Inflation Factors (VIF) of terms in the best models and report them. A VIF of 1 means that there is no correlation among a predictor and the remaining predictor variables, and hence the variance of coefficient is not inflated. The general rule of thumb is that VIFs exceeding 4 warrant further investigation, while VIFs exceeding 10 are signs of serious multicollinearity requiring correction.

Table 1
Models relating biophysical predictors to each canopy metric across the study area. DF: 10 and 2705. VIF is variable inflation factor and is reported for the highest value among predictors in the model.

Dependent variable	Best model	Adj R^2 of predictors	Adj R^2 of predictors + space	F-statistic	P-value <	VIF	Variation explained by forest age (adj R^2)
Canheight	Space FORAGE – TEMPAN – TEMPAN^2 PPTGS – PPTGS^2 – TPI – TPI^2 – RAD SAND – BULK	0.27	0.38	100	2.2e−16	2.98	0.06
Cancover	FORAGE – TEMPAN – TEMPAN^2 PPTGS – PPTGS^2 – TPI – TPI^2 – RAD SAND	0.30	Space not significant	126	2.2e−16	2.74	0.08 But not sig in final model
Highlow	–TEMPAN – TEMPAN^2 PPTGS – PPTGS^2 – TPI–TPI^2 – RAD PH SAND	0.30	Space not significant	130	2.2e−16	2.33	0.08 But is not in the best model

3. Results

3.1. Correlation among canopy metrics

The canopy structure metrics were moderately correlated indicating that they carried overlapping information. Correlation coefficients for canheight, cancover, and highlow were between 0.34 and 0.64 (Appendix E). Tall forests were generally higher in canopy cover and had a higher ratio of cover in the upper third of the canopy relative to the lower third. Shannon was highly correlated with canopy height (0.93), indicating that the forest samples differed more in number of 5-m height classes represented in the canopy rather than the proportional abundance of cover among height classes, thus it was dropped.

3.2. Mean and variation canopy structure across ecoregions

Canopy structure for stands of similar age differed substantially among the ecoregions in the study area. The Blue Ridge and Central Appalachians ecoregion had the highest levels of canheight, cancover, and highlow (Fig. 4 and Appendix F). The Ridge and Valley ecoregion had slightly lower values, but the differences were generally not significant. The Piedmont and Southeast Plains Ecoregions were typically significantly lower in these metrics than the other ecoregions. Differences between the highest and lowest values were substantial: canheight (25%), cancover (18%), and highlow (212%).

The tallest forests were disproportionately located within the Blue Ridge, Ridge and Valley and Central Appalachians Ecoregions and on public lands (Fig. 5). Forests 40–50 m in height were largely located in Great Smokey National Park and the surrounding national forests. National forests in the Central Applications Ecoregion also support these tall forests. The Southeast Plains and Piedmont ecoregions had relatively few samples with tall forests and those samples were primarily on public lands.

3.3. Biophysical predictors of canopy structure

Climate predictor variables that were highly correlated (>0.75) were TEMPAN, TEMPGS, PETAN, PETGS, ETAN, ETGS, and GDD. Among these, we chose to use TEMPAN in the analyses. Topographic predictors were not highly correlated. Among soil predictors, ROOTZONE, ROOTZONEWS, and AWS0150 were highly correlated and ROOTZONEWS and AWS0150 were excluded from the analyses.

Stand age (FORAGE) was included as a candidate variable in the models to control for its effects on canopy structure. The canopy structure metrics were positively correlated with stand age, but the relationship was weak, explaining 6–8% of the variation in the canopy structure metrics in the study area wide analyses (Table 1, Appendix G)). Moreover, FORAGE was not included as a predictor in the best models for cancover and highlow. Spatial autocorrelation was present and controlled for in the canheight model but was not significant in the cancover and highlow models.

Across the study area, the canopy structure metrics were most consistently correlated with a subset of biophysical predictors. These included TEMPAN, PPTGS, TPI, RAD, and SAND (Table 1, Appendix H). The relationship between canheight and TEMPAN, for example, was unimodal, increasing to about 12 °C then decreasing and flattening at about 19 °C (Fig. 6a). There was considerable scatter in canopy height across the range of temperatures (R^2 = .16). Samples within ecoregions were relatively nonoverlapping across the regional temperature gradient, with coolest to warmest being: Central Appalachians, Ridge and Valley, Blue Ridge, Piedmont, Southeast Plains. Thus, TEMPAN decreased to the north
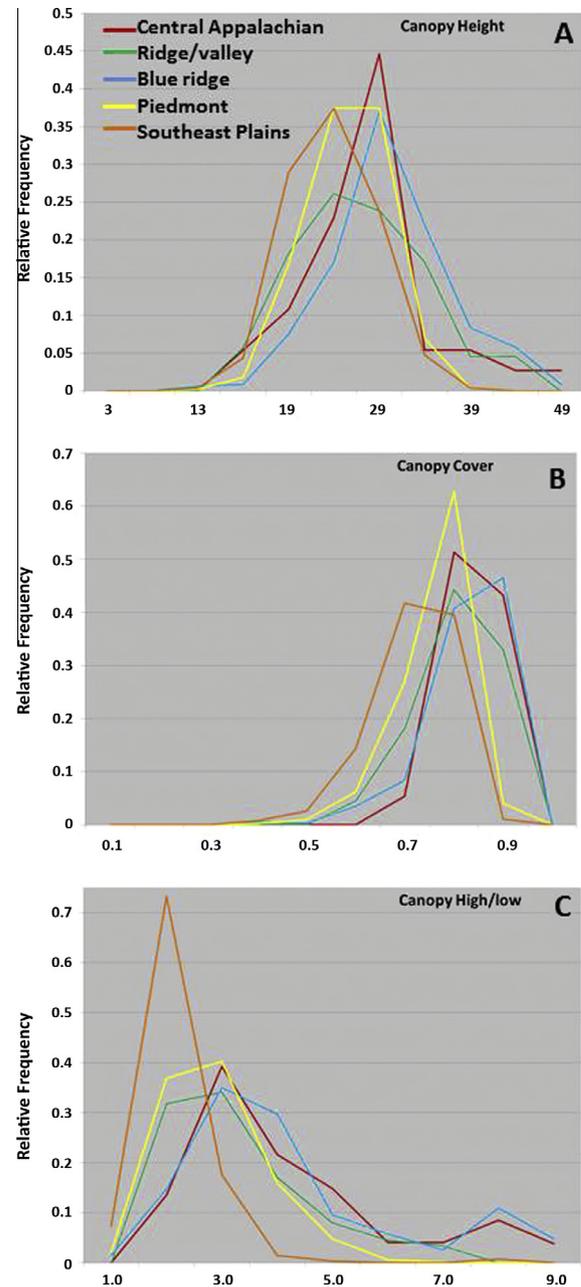
Fig. 4. Comparison of frequency distributions of canopy structure metrics among ecoregions for (A) canopy height, (B) canopy cover, and (C) ratio of cover in the upper third of the canopy to the lower third. Units are (A) meters, (B) percent cover, and (C) dimensionless ratio.

and with elevation (Fig. 7). The best biophysical predictor model for canheight included TEMPAN, PPTGS, TPI, RAD, SAND, and BULK and explained 27% of the variation (Table 1). Locations highest in canheight were intermediate in temperature, growing season precipitation, topographic complexity; were on sandy soils; and were lower in radiation and bulk density of soil. The results for cancover and highlow were similar to those for canheight in terms of best biophysical models (Table 1). Cancover decreased more steeply with TEMPAN (R^2 = .24) (Fig. 6b) as did highlow (R^2 = .24).

The strength of the best biophysical models differed substantially among ecoregions. For example, models for canheight for the Ridge and Valley and the Central Appalachians explained 60% and 45% of the variation (Table 2). Only 13% of the variation in canheight was explained for the Southeast Plain ecoregion. Variation
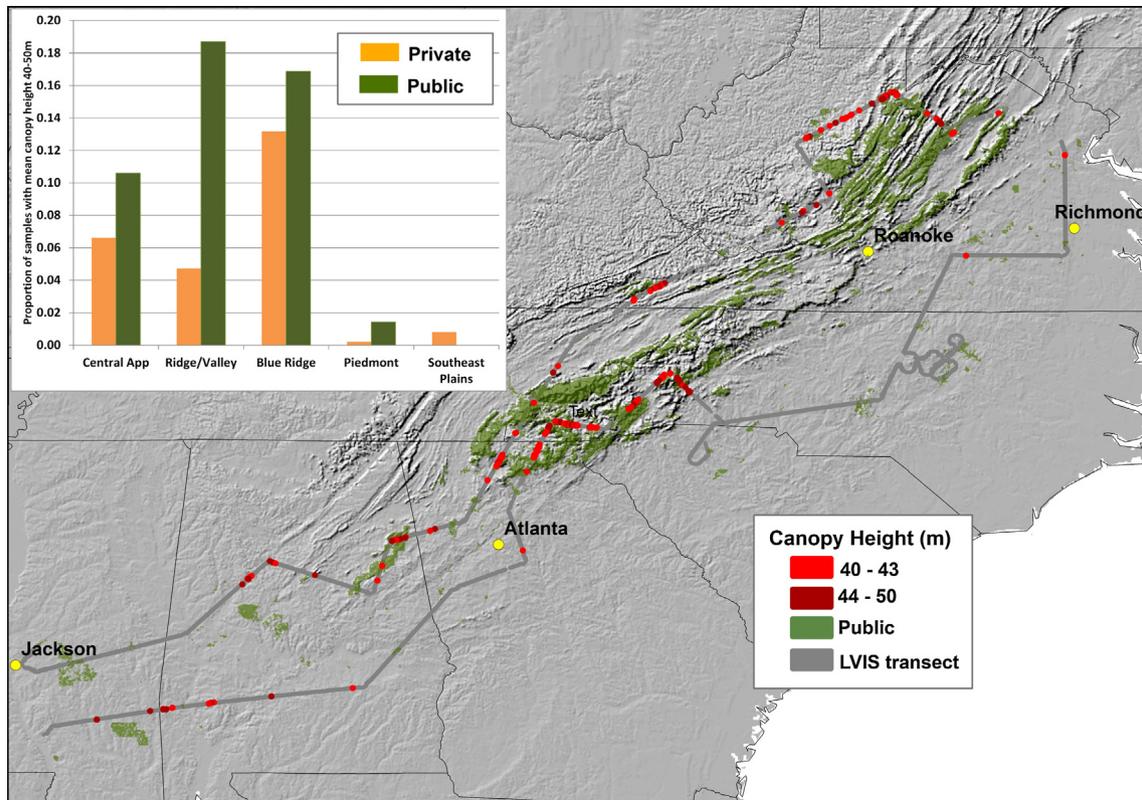
Fig. 5. The location of the tallest forests along the transect and the representation of tall forests among public and private lands and ecoregions.

explained was intermediate for the Blue Ridge (29%) and Piedmont (29%). This difference in strength of best biophysical models was also true for cancover, and highlow (results not shown). Strength of models among ecoregions varied with the range of the biophysical predictors represented within the ecoregions. The Central Appalachians, Ridge and Valley, and Blue Ridge generally spanned greater ranges of temperature, precipitation, aridity index, elevation, and slope than did the Piedmont and Southeast Plains Ecoregions. Spatial autocorrelation was not present in any of the ecoregion biophysical models. The VIF levels were well within acceptable limits for all of these analyses (Tables 1 and 2).

3.4. Canopy structure among disturbance types

Disturbed and plantation disturbance types were poorly represented in the Central Appalachian, Ridge and Valley, and Blue Ridge ecoregions. Thus, only samples from the Piedmont and Southeast Plains Ecoregions were analyzed. Undisturbed samples were higher than plantation and disturbed samples in canheight, cancover, and highcancover (Fig. 8 and Appendix I). Plantation was generally intermediate between the undisturbed and disturbed classes in these canopy metrics. Compared with disturbed samples, undisturbed samples were 30% higher in canheight, 15% higher in canopy cover, and 18% higher in cover of the upper third of the canopy.

4. Discussion

Asner et al. (2010, 2011); Bolton et al. (2013), and this study represent the first applications of airborne lidar to regional gradients in canopy structure and potential underlying biophysical controlling factors. This technology allows quantification of canopy structure attributes that are difficult to obtain in the field and that

are likely to be important determinants of ecosystem function and biodiversity. We represented 3-dimensional canopy structure in terms of the height of the canopy, total canopy cover, the vertical distribution of canopy cover. Vertical distribution was represented as the number of 5-m height classes above the forest floor with canopy presence (richness) and a diversity index that integrates number of canopy height classes represented and the proportional abundance of cover among the height classes. We also developed new metrics to account for the proportion of total cover present in the lower third, middle third, and upper third of the canopy, controlling for canopy height. Recent studies have documented the value of vertical distribution of vegetation for biodiversity in forests relatively equal in canopy height (Swatantran et al., 2012; Whitehurst et al., 2013). Our samples varied substantially in canopy height, thus we defined the three vertical height classes (low, mid, high) within a sample relative to the total height of the forest in that sample. Most of the difference in samples was between the low and high canopy classes, thus we expressed this difference as the ratio of high to low canopy cover.

We found that, controlling for stand age, canopy structure varied substantially across the study area. Among ecoregions, the Blue Ridge ecoregion, which includes the Smoky Mountains studied by Whittaker (1956), and the Central Applications Ecoregion had the fullest development of canopy structure. Samples in these ecoregions were characterized by tall forests with high total cover and proportionally more of the canopy cover in the upper strata. Forests in the Central Appalachian and Ridge and Valley ecoregions were similar in structure to the Blue Ridge. Forests in the Piedmont and Southeast Plains Ecoregions were shorter in height, more open in canopy cover, and had proportionally more cover in the lower canopy strata. Canopy metrics in the mountain ecoregions were 9–25% higher than in the Southeast Plain Ecoregion: in the case of the ratio of high to low canopy cover, the difference was 212%.
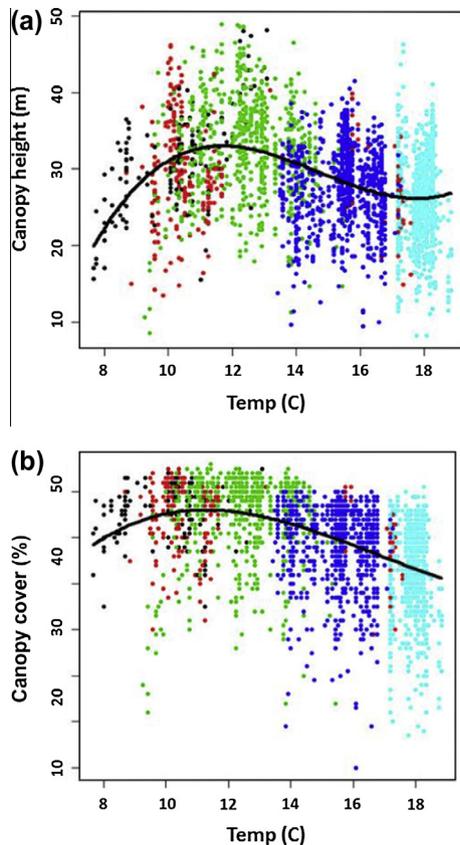
Fig. 6. Relationships between TEMP and canheight (a) and canopy cover (b) across ecoregions. black – Central Appalachians, red – Ridge and Valley, green – Blue Ridge, purple – Piedmont, light blue – Southeast Plains.

Consistent with our conceptual model on the drivers of canopy structure, biophysical factors explained significant variation in canopy metrics. Across the study area, canopy height, canopy cover, and the ratio of high to low canopy cover were greatest in samples with: intermediate levels of temperature, precipitation, and topographic position; higher levels of sand/silt content in soil; and lower levels of solar radiation, PH, and soil bulk density. The samples with more fully developed canopy structure were located in the more northerly and mountainous portions of the study area (e.g., the Central Appalachian, Ridge and Valley, and Blue Ridge ecoregions). Locations with intermediate elevations (ca 1100 m), in the low mountains of the Central Appalachians and Ridge and Valley and the valley bottoms and lower slopes of the Blue Ridge, had the intermediate levels of temperature, precipitation, steeper slopes, and lower levels of radiation where canopy structure was most developed. The Piedmont and especially the Southeast Plains had higher temperatures, higher solar radiation, higher aridity index, lower precipitation and higher sand content in soil associated with shorter forests with lower canopy cover and relatively more of the cover in the lower third of the canopy.

The hypothesis that canopy structure varies with environmental favorableness is the basis for the widely used method in forestry of quantifying the productivity of a site based on the height of trees on the site at a given age (e.g., site index) (Skovsgaard and Vanclay, 2008). Weiskittel et al. (2011) confirmed this relationship finding that 78% of the variation in site index across western North America was explained by climate and 70% by gross primary productivity. Additional evidence on the influence of biophysical factors on canopy structure comes from Fang et al. (2012) who found that tree diameter, tree height, and total basal area all

increased significantly with summer temperatures in temperate forests in northeast China. Substrate geology or age predicted carbon stocks in forests in the Amazon and in Hawaii (Asner et al., 2010, 2011). Additionally, Larson et al. (2008) found that an index of old-growth forest structural complexity was positively related to site productivity in coniferous forests in Western Washington. Similarly, Boucher et al. (2006) concluded that in productive sites in boreal forests of Quebec, Canada, forest stands become uneven-sized earlier than unproductive stands and also maintain greater diameter diversity. Finally, Moles et al., 2009 found that precipitation in the wettest month was the best biophysical predictor of plant height globally, explained 26% of the variation.

The effects of biophysical factors on canopy development likely vary with the level of the limiting biophysical factor relative to the tolerances of forest vegetation. For example, site index has been found to asymptote for given tree species, presumably because factors other than site quality set limits on maximum tree height in the most favorable sites (Skovsgaard and Vanclay, 2008, Fig. 1). Evidence for a positive flattening relationship between site index and gross primary productivity comes from Weiskittel et al., 2011 who found that tree height increased steeply between 3 and 15 Mg C/ha/year but showed no relationship with GPP at levels of GPP > 15 Mg C/ha/year. Similarly, canopy cover is known to asymptote in increasingly favorable sites because light extinction sets upper limits on the benefits for photosynthesis of increased leaf area (Chapin et al., 2011). Further evidence comes from comparing the results of Bolton et al. (2013) with our results. In the Canadian Boreal Forest where gross primary productivity (GPP) is relatively low (about 2–12 Mg C/ha/year), Bolton et al. (2013) found that canopy cover was significantly positively related to GPP in six of the ecoregions and correlation coefficients were relatively high (0.27–0.74). In our southeastern US study area where GPP is among the highest in North America (10–19 Mg C/ha/year) we found no relationship between canopy structure and GPP.

In addition to being high in GPP, we found that levels of temperature and precipitation were likely at threshold levels in the study area. Canopy structure had a unimodal relationship with mean annual temperature and with precipitation, suggesting that our study area may be at the asymptote in the continental gradient of between canopy structure and the interaction of temperature and precipitation. If so, studies in colder or drier environments would be expected to find stronger relationships, as did Bolton et al. (2013) with regards to temperature.

Another obvious factor influencing the strength of models of biophysical factors and canopy structure is the range of biophysical conditions in the samples. Both our study and Bolton et al., 2013 had the strongest models in ecoregions with the widest span in biophysical predictors. In our case, biophysical factors explained only 13% of the variation in canopy structure in the relatively homogenous Southeastern Plains Ecoregion, but 60% of the variation in the mountainous and heterogeneous Blue Ridge ecoregion.

More studies are needed to delineate the strength and shapes of the relationships between canopy structure and biophysical predictors across subcontinental to continental areas. The evidence presented above suggests that these relationships can be nonlinear with flattening or slightly unimodal functions.

4.1. Considerations

Canopy structure is known to vary with stand age (time since the last stand-initiating disturbance). We drew on a published data set (Pan et al., 2011a,b) to derive estimates of stand age for our samples and then controlled for stand age in the analyses. Our samples were 100-m cells, however, and unknown level of error in stand age for our samples due this difference in spatial resolution. Pan et al. (2011a,b, pg. 719) report that most of the standard

deviations in stand age in eastern forests were around 10 years, which we consider reasonably good for this application. Accurate age data collected within our samples, however, would have allowed for more rigorous control of stand age effects on our analyses.

A second consideration is that we draw inference about biophysical correlates with canopy structure only for those biophysical settings that are currently forested. Land use may have preferentially converted the most productive biophysical settings to agriculture, pasture, or other non-forest cover types, as was found by Asner et al. (2010) in Amazonia. If so, such biophysical settings would not have been included in our samples and the possible positive effect of such settings on canopy structure would not have been detected.

4.2. Implications

The major conclusions of this study are:

- Canopy structure of 'undisturbed' forests varies substantially across the southeastern US, with average canopy height, for example, being 25% greater in the Blue Ridge ecoregion than then Southeastern Plains Ecoregion.
- Gradients in climate, topography and soil factors likely contributed to these differences in canopy structure across the region. Canopy height, for example, was greatest in locations that were intermediate in temperature, growing season precipitation, and topographic complexity; were on sandy soils, and were lower in radiation, PH, and bulk density of soil.
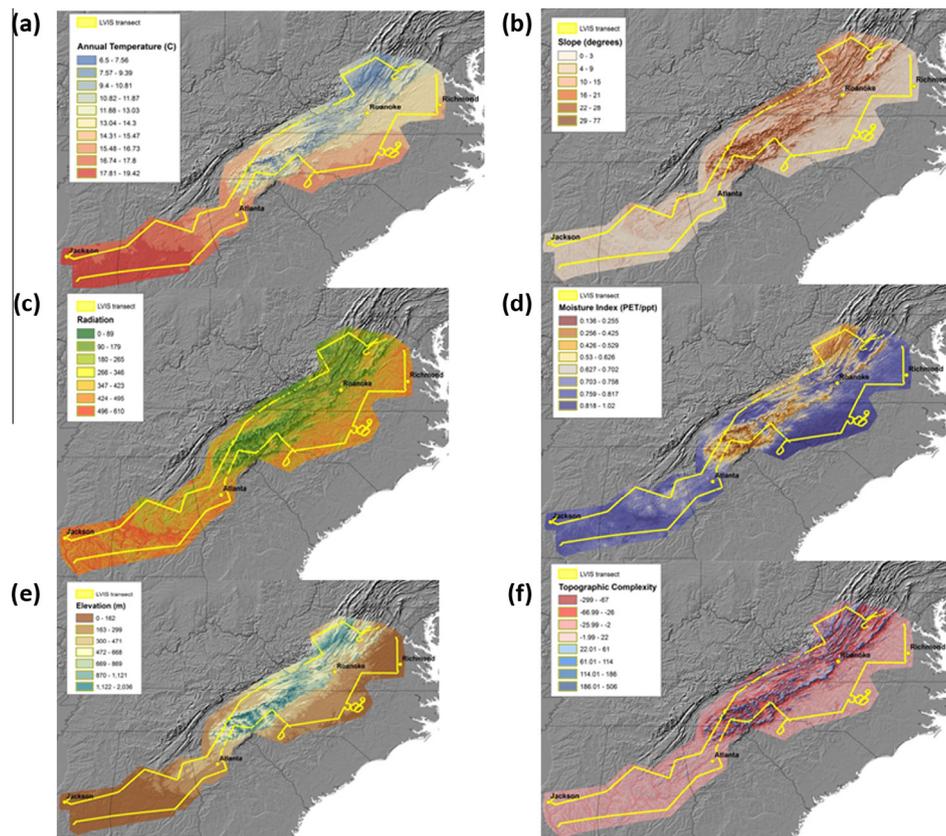
Fig. 7. Maps of predictor variables, (a) annual temperature (b) slope (c) solar radiation (d) aridity (e) elevation (f) topographic complexity.

Table 2
Models relating biophysical predictors to canheight within ecoregions.

Ecoregion	N	Best Model	Adj R^2 of predictors	Adj R^2 of predictors + space	F-statistic	P-value <	VIF	Variation explained by forest age (adj R^2)
Central Appalachians	133	TEMPAN PPTGS – TPI – ASPECT SAND	0.45	Space not significant	23.4	2.2e−16	4.3	0
Ridge and Valley	255	TEMPAN PPTGS PPTGS^2 – RAD – ASPECT – ROOTZONE PH SILT–	0.60	Space not significant	47.6	2.2e−16	2.25	0.02
Blue Ridge	638	–TEMPAN – TEMPAN^2 – PPTAN – PPTAN^2 – TPI –TPI^2 RAD – ASPECT SAND –PH – HILLSLOPE	0.29	Space not significant	17.1	2.2e−16	2.32	0
Piedmont	857	FORAGE TEMPAN – TEMPAN^2 – PPTGS PPTAN^2 – TPI – RAD SAND – PH – SILT	0.29	Space not significant	34.3	2.2e−16	2.7	0.03
Southeast Plains	872	TEMPAN – TEMPAN^2 PPTGS – TPI TPI^2 ASPECT – RAD	0.13	Space not significant	17.6	2.2e-16	1.5	0
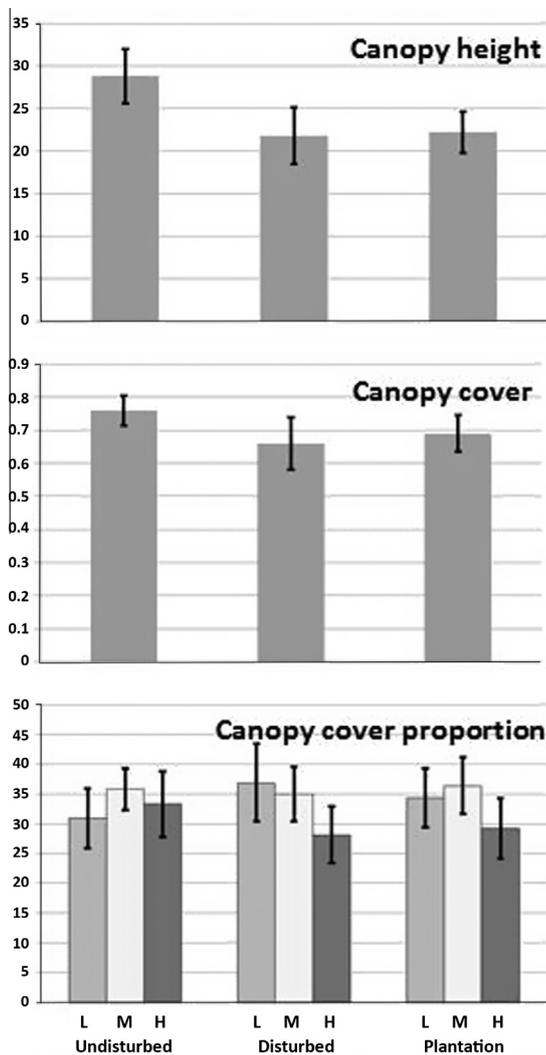
Fig. 8. Differences in canopy metrics among undisturbed, disturbed and plantation forests. Error bars denote on standard deviation. "L" is lower third of canopy, "M" is middle third of canopy, and "U" is upper third of canopy.

- Disturbance strongly influenced canopy structure in the study area. Conifer plantations, for example, were 30% lower in canopy height than 'undisturbed' forests.

One implication of these results is that current estimates of ecological properties related to canopy structure can be improved through consideration of biophysical gradients on canopy development. Forests in the southeast US play a particularly important role in the US Carbon cycle. Owing to favorable temperature and moisture conditions, the Southeast US has some of the fastest-growing forests in North America (Goetz et al., 2012). The region has been, and continues to be, subject to intensive human management and land-use change, both cropland establishment and cultivation and cropland abandonment and subsequent forest regrowth (Chen et al., 2006). This frequent disturbance and rapid regrowth has led to the southeast US having with the greatest increase in net primary productivity in the 1980s and 1990s among regions in North America (Hicke et al., 2002). Consequently, this part of the US is thought to be the largest carbon sink across the conterminous US (Pacala et al., 2001, Chen et al., 2006). Thus, accurate carbon accounting in this regional is vital to national estimates.

Carbon accounting in this region needs to take into account fast overall growth rate, spatial variation in forest structure and growth rates due to biophysical gradients, and disturbance history. Current

field-based methods estimate tree stocking densities from Forest Inventory and Analysis field plots and convert these data to estimates of biomass and carbon using allometric equations (Birdsey et al., 2000). These methods are not designed to take into account biophysical gradients between plots and estimates are considered accurate only at the spatial scales of counties or above.

Estimates of carbon storage could be improved by integrating Landsat, lidar, and field sampling methods largely along the framework of Asner et al. (2010, 2011). As summarized by Goetz et al. (2012), high frequency analyses of Landsat imagery has been used to reconstruct forest disturbance history with unprecedented temporal detail (Huang et al., 2009, 2010; Kennedy et al., 2010; Powell et al., 2014). These methods allow wall-to-wall mapping of forest disturbances at sub-hectare spatial resolution (Li et al., 2009a, 2009b). As demonstrated in this paper, airborne lidar remote sensing allows assessment of structure at fine spatial resolution along transects that bisect gradients in biophysical factors and land use. Stratified random sampling of forest structure with lidar across biophysical and land use gradients can be used to derive carbon estimates for the fine-scale land cover type and seral stage classes derived from high-frequency Landsat analysis leading to much more accurate mapping of carbon stocks than is currently available for the southeast region. Application of such methods in Hawaii found that total aboveground carbon was 56% lower than estimates that ignored gradients in soils, climate, and disturbance. Moreover, knowledge of local variation in forest growth and stature would allow carbon management strategies to be tailored to these gradients.

The southeast US is also of high interest for biodiversity and conservation. Tree and amphibian diversity are the highest in North America (Currie, 1991). Many of the rare or sensitive species here are associated with forests of complex canopy structure, including the guild of forest interior neotropical migrant birds that have been the subject of long-term conservation efforts (Robbins, 1980, Sauer et al., 2011). The vertical layering of forest canopies is an element of niche partitioning for some species of plants and animals and influences species abundances and community diversity (MacArthur and MacArthur, 1961; Carey, 1998; Hunter, 1999; Bell et al., 1991). Knowledge of variation in the capacity of forests to support complex structure would improve conservation and management efforts aimed at protecting such species. The locations of the especially tall forests identified in our results may be particularly important to target for conservation measures.

A third implication of this study relates to evaluation of lidar airborne and satellite campaigns. The need for remotely sensed lidar data over regional to global areas has been widely recognized (Lefsky et al., 2002). Various current studies (including this one) are aiming to assess the types and quality of information about ecological response variables that can be derived from different lidar instruments, platforms, and spatial scales (Vierling et al., 2008; Goetz and Dubayah, 2011). Such knowledge would provide guidance to remote sensing agencies as to design criteria for future lidar-based campaigns. One implication of our results along with those of Asner et al. (2010, 2011), and Bolton et al. (2013) is that such tests should be done with reference to continental gradients in canopy structure and biophysical gradients. Given the nonlinear relationships described above, the strength of relationships between canopy structure and biophysical predictors within an ecoregion will likely vary with mean and range of biophysical predictors within that ecoregion relative to broader scale gradients. Hence, conclusions about the information derived from a particular lidar system may be erroneous if only locations with weaker expected relationships are sampled. This situation is not unique for lidar. Modis GPP, for example is known to be less accurate in wet tropical forests where plant growth is less constrained by biophysical factors than other biome types (Running et al., 2004).

Careful design of sampling strategies integrating field, lidar, and satellite data have considerable promise for mapping forest structure continuously at fine grain across regional extents and greatly improving current understanding of carbon budgets, biodiversity, fuel loading and other ecological response variables.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2014.06.009.

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