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High rates of primary production in structurally complex forests

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Abstract. Structure–function relationships are central to many ecological paradigms. Chief among these is the linkage of net primary production (NPP) with species diversity and canopy structure. Using the National Ecological Observatory Network (NEON) as a subcontinental-scale research platform, we examined how temperate-forest NPP relates to several measures of site-level canopy structure and tree species diversity. Novel multidimensional canopy traits describing structural complexity, most notably canopy rugosity, were more strongly related to site NPP than were species diversity measures and other commonly characterized canopy structural features. The amount of variation in site-level NPP explained by canopy rugosity alone was 83%, which was substantially greater than that explained individually by vegetation area index (31%) or Shannon's index of species diversity (30%). Forests that were more structurally complex, had higher vegetation-area indices, or were more diverse absorbed more light and used light more efficiently to power biomass production, but these relationships were most strongly tied to structural complexity. Implications for ecosystem modeling and management are wide ranging, suggesting structural complexity traits are broad, mechanistically robust indicators of NPP that, in application, could improve the prediction and management of temperate forest carbon sequestration.

Key words: carbon cycling; complexity; forests; fPAR; leaf area index; light; National Ecological Observatory Network; net primary production; species diversity; structure–function.

Introduction

Positive effects of plant species diversity and leaf area on net primary production (NPP) are nearly universal (Hooper et al. 2005, Reich 2012). Ecosystems with diverse plant assemblages often have higher NPP because functional complementarity optimizes whole-ecosystem light acquisition and light-use efficiency (Williams et al. 2017). Canopy traits (sensu Reich 2012), including vegetation or leaf area index, describe the physical structure of vegetation within an ecosystem and most often relate to NPP through their effects on canopy light absorption (Atkins et al. 2018*b*). Novel, complexity-focused canopy traits summarizing multidimensional variation in vegetation distribution and density (Fig. 1) may be even more strongly tied to NPP through their positive effects on both light acquisition and light-use efficiency (Hardiman et al. 2013, Atkins et al. 2018*b*). Structurally variable, multilayered canopies absorb more light and, because their leaves occupy a range of light environments and span a physiological spectrum, they may use light more efficiently to drive NPP (Niinemets 2012).

The derivation of next-generation canopy structural measures is being advanced by terrestrial light detection and ranging, or lidar, technology. Terrestrial scanning lidar, which uses high-frequency laser pulses to map vegetation density and arrangement within the canopy interior, provides an unprecedented information-rich perspective from which to describe novel canopy features. By integrating structural information across multiple dimensions, canopy structural complexity may be a potent indicator of numerous ecosystem functions such as NPP, equal in significance to other widely measured and managed canopy structural features and community characteristics such as species diversity (Pedro et al. 2017). However, unlike relationships of production with species

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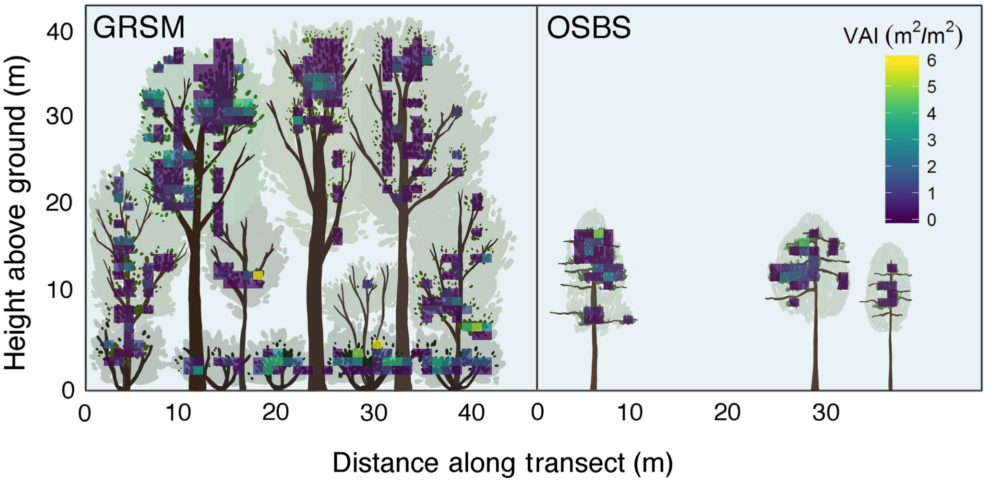

FIG. 1. Terrestrial lidar-generated vegetation area index (VAI) grids overlaying illustrated vegetation for Great Smoky Mountains National Park (GRSM) and Ordway-Swisher Biological Station (OSBS) temperate forest sites. The ground-based portable canopy lidar (PCL) system uses high-frequency laser pulses to map a two-dimensional (horizontal and vertical) “slice” of gridded VAI from within the canopy interior, providing a spatially rich lens through which to characterize canopy traits. Vegetation area, height, arrangement, and cover traits are derived from VAI distribution and/or density along a single vertical or horizontal axis. Canopy structural complexity traits describe the degree of variability in VAI distribution and/or density along both horizontal and vertical axes (Appendix S1: Table S2, Video S1). GRSM, a productive mixed deciduous forest, has a structurally complex canopy with high tree species diversity and VAI. Conversely, OSBS, a sparsely vegetated low-productivity pine savannah, is low in canopy structural complexity, species diversity, and VAI. Illustration: Catherine McGuigan.

diversity and conventional structural features, biome-wide canopy structural complexity–NPP relationships and their mechanistic underpinnings have not been investigated (Hardiman et al. 2011, 2013, Fahey et al. 2015).

Here, we ask whether the strong positive linkage of forest NPP with novel traits describing canopy structural complexity, previously observed in site-level studies, spans North America’s temperate forest biome. We then compare how NPP relates to canopy structural complexity, species diversity, and conventional measures of canopy leaf area, height, arrangement, and cover. Finally, we assess whether light acquisition and light-use efficiency mediate broad spatial scale linkages between canopy properties, including canopy structural complexity, and NPP. To address these questions, we evaluated relationships of aboveground wood NPP, hereafter NPP for brevity, with a suite of canopy traits (derived from terrestrial lidar) and tree species diversity indices for 10 National Ecological Observatory Network (NEON) sites spanning a >1,500-km latitudinal gradient in eastern North America (Appendix S1: Fig. S1, Table S1).

METHODS

Study sites

Our analysis paired site-level estimates of canopy structural traits, tree species diversity, canopy light absorption, and NPP from 10 climatically and ecologically variable temperate forests in the NEON (Appendix S1: Fig. S1, Table S1). Study sites included Bartlett Experimental Forest (BART), Great Smoky Mountains National Park (GRSM), Harvard Forest (HARV), Mountain Lake Biological Station (MLBS), Ordway-Swisher Biological Station (OSBS), Smithsonian Conservation Biology Institute (SCBI), Smithsonian Environmental Research Center (SERC), Talladega National Forest (TALL), Treehaven (TREE), and University of Notre Dame Environmental Research Center (UNDE). Lidar sampling of canopy structural traits, ceptometer measurements for calculating the fraction of photosynthetically active radiation (fPAR) absorbed by the canopy, and vegetation analysis for the derivation of species diversity and NPP co-occurred within NEON’s 40 × 40 m “tower base” plots (Appendix S1: Fig. S2). The total number of tower base plots sampled across all sites was 106, and ranged between 6 and 20 at each site depending on the site-specific footprint of an associated meteorological tower. For our analysis, we generated site-level means for all factors based on averages across sampled tower base plots. Our sampling density, distribution, and measurement co-location (e.g., of NPP and canopy structure) are modeled after prior studies investigating these relationships in temperate forests (Hardiman et al. 2011, Fahey et al. 2015, Atkins et al. 2018*b*).

Canopy traits and species diversity

We focused on lidar-derived canopy traits that correlate with temperate forest canopy light absorption (i.e., fPAR; Atkins et al. 2018*b*) and thereby may be mechanistically tied to broad-scale variation in NPP. In 2016, a portable canopy lidar (PCL) system with a maximum pulse frequency of 2,000 Hz (Riegl LD90 3100

VHS; Riegl USA, Inc., Orlando, Florida) was used to map the two-dimensional (i.e., horizontal and vertical) vegetation arrangement and density of fully leafed-out canopies at each site (Fig. 1). Specific details on the design, operation, and validation of the PCL system are outlined in Hardiman et al. (2011). In each tower base plot, lidar data were collected along three parallel 40-m transects, which resulted in a total of 720–2,400 m sampled per site, depending on the number of tower base plots. The cumulative distances sampled at each site exceed the ~300-m minimum length for estimating canopy structural traits from terrestrial lidar in spatially heterogeneous temperate forests (Hardiman et al. 2018). Canopy traits were computed from vertical and horizontal vegetation hit-grids using *forestr* in the R programming language (R Development Core Team, 2018; Atkins et al. 2018*a*). Canopy traits fall within five broad categories describing vegetation density/area, height, arrangement, cover, or canopy structural complexity. The nine specific canopy traits used in our analysis are defined in Appendix S1: Table S2 and full mathematical derivations are supplied by Atkins et al. (2018*a*). A conceptual visualization of the canopy traits derived from terrestrial lidar is presented in Video S1. Tree species diversity indices, including richness and Shannon’s, and Simpson’s indices, were calculated using the basal-area weighted values of tree species, supplied by NEON, via *Vegan* in the R programming language.

Net primary production

Wood NPP was calculated for each site from the 2015 or 2016–2017 diameter-at-breast-height (DBH) increment of live stems, which totaled 11,686 across sites. The NEON “woody plant vegetation structure” sampling protocol subdivides each 40 × 40-m tower base plot into four, 20 × 20-m quadrats, two of which are randomly selected for repeated DBH measurements of live stems >5 cm (Thorpe et al. 2016). The total area sampled per site was 4,800–16,000 m^2 depending on the number of tower base plots. Wood mass was inferred from DBH using generalized allometries (Jenkins et al. 2003), with tower base plot NPP calculated from the total wood mass difference between sampling years. We estimated NPP uncertainty as the quadrature sum of error originating from natural variation (i.e., variation among plots), DBH measurement error (assuming $\pm$ 0.05 cm), and allometric equation uncertainty (Yanai et al. 2010, Appendix S1: Table S3). The latter two errors were estimated using Monto Carlo simulations drawing from a normal distribution of variance over 1,000 iterations.

Canopy light absorption and light-use efficiency

Canopy light absorption was assessed for 7 (GRSM, HARV, OSBS, SCBI, TALL TREE, UNDE) of 10 sites as fPAR (Atkins et al. 2018*b*); sampling conditions were not favorable during the time of measurement for the remaining three sites. Briefly, under- and over-canopy photosynthetically active radiation (PAR) were measured under clear-sky conditions within 2 h of solar noon along the same transects as the portable canopy lidar using a Meter Environment ACCUPAR LP-80 ceptometer. fPAR is the ratio of light (i.e., PAR) absorbed by the canopy to total incoming light above the canopy. Light-use efficiency was calculated as NPP/fPAR (Hardiman et al. 2013).

Data analysis

We used regression analysis and model selection to examine how NPP relates to nine different canopy traits and three species diversity measures: six conventional indices of vegetation area, height, arrangement, and cover; three canopy structural complexity indices that summarize the variability of leaf distribution in horizontal and vertical directions; and tree species diversity expressed as richness, Simpson’s and Shannon’s indices ($P \leq 0.1$; Appendix S1: Table S3). The regression analysis compared the goodness-of-fit (r^2), Akaike information criterion (AIC), and mean-squared-error (MSE) values of separate linear models regressing NPP against canopy trait or species diversity measures. Though such associations may be nonlinear, without exception three-parameter exponential and curvilinear models failed to achieve significance and, accordingly, we limited our analysis to more parsimonious linear models. AIC and stepwise selection procedures were used to rank simple and multivariate models, with the latter using the Schwarz Bayesian criterion (SBC) to account for our limited site sample size.

An additional analysis used structural equation modeling (SEM) to examine whether canopy structural complexity, canopy rugosity in our example, vegetation area index (VAI), and species diversity were mechanistically coupled to NPP through the mediating effects of canopy light absorption, as fPAR, and light-use efficiency (Hardiman et al. 2011). We used *lavaan* in the R programming language to produce AIC_c scores, stipulating a confirmatory factor analysis (CFI) value $\geq$0.90. Though our sample size for the SEM was limited to seven sites (because three sites lacked fPAR data) and its broader inference should be interpreted with caution, the forests in the model span the full continuum of NPP, canopy traits, and tree species diversity, and include the most (GRSM) and least (OSBS) productive and structurally complex sites. With the exception of NPP (which considered multiple sources of error), site-level estimates are accompanied by standard errors calculated from the site-specific variance among plots and tower base plot number (Appendix S1: Table S4). Statistical analyses were performed in SAS 94 or R 3.1.0.

RESULTS

Three findings point to a strongly positive, mechanistically grounded, biome-wide relationship between NPP and canopy structural complexity, with complexity-focused canopy traits more strongly linked to production than conventional canopy structural or species diversity measures. First, among the 12 canopy traits and diversity indices examined, canopy structural complexity measures were the most strongly correlated with site NPP, individually explaining a majority of the variation in production among temperate forests (Fig. 2; Appendix S1: Table S5). A comparison of simple linear models by AIC scores, MSE, and goodness-of-fit ($P \leq 0.1$, r^2 presented parenthetically) yielded the following ranking: canopy rugosity (0.83) > rumple (0.77) > top rugosity (0.58) > mean outer canopy height (0.40) > VAI (0.31). Among diversity indices, only Shannon's index was significantly ($P = 0.1$) correlated with site NPP ($r^2 = 0.30$; Fig. 2j–l). Secondly, a stepwise model selection considering linear combinations of canopy traits and species diversity indices retained only canopy rugosity and, unlike other canopy trait categories and diversity indices, AIC-ranked models varying in parameter number all contained at least one structural complexity trait (Appendix S1: Table S6). Lastly, our SEM comparison indicated that canopy light absorption (i.e., fPAR) and light-use efficiency—processes positively tied to site NPP—were more strongly predicted by canopy rugosity ($\mathrm{AIC_c} = 34.0$) than by vegetation area index ($\mathrm{AIC_c} = 40.7$) or Shannon's index ($\mathrm{AIC_c} = 41.5$; Appendix S1: Table S7).

Though structural complexity measures were the strongest predictors of site-level NPP, a high degree of autocorrelation among canopy structural features and species diversity indices highlights the interrelatedness of canopy traits and species diversity (Appendix S1: Fig. S3) Canopy structural complexity was greatest in temperate forests with high levels of vegetation area and tree species diversity, with VAI and Shannon's index of species diversity positively correlated with canopy rugosity, the most robust structural complexity predictor of NPP. For example, canopy rugosity was relatively high in montane GRSM and MLBS mixed temperate forests, which also exhibited high species diversity and VAI values. Conversely, OSBS, a pine savannah with very low species diversity and VAI values, had the lowest canopy rugosity value among temperate forests surveyed (Appendix S1: Table S7).

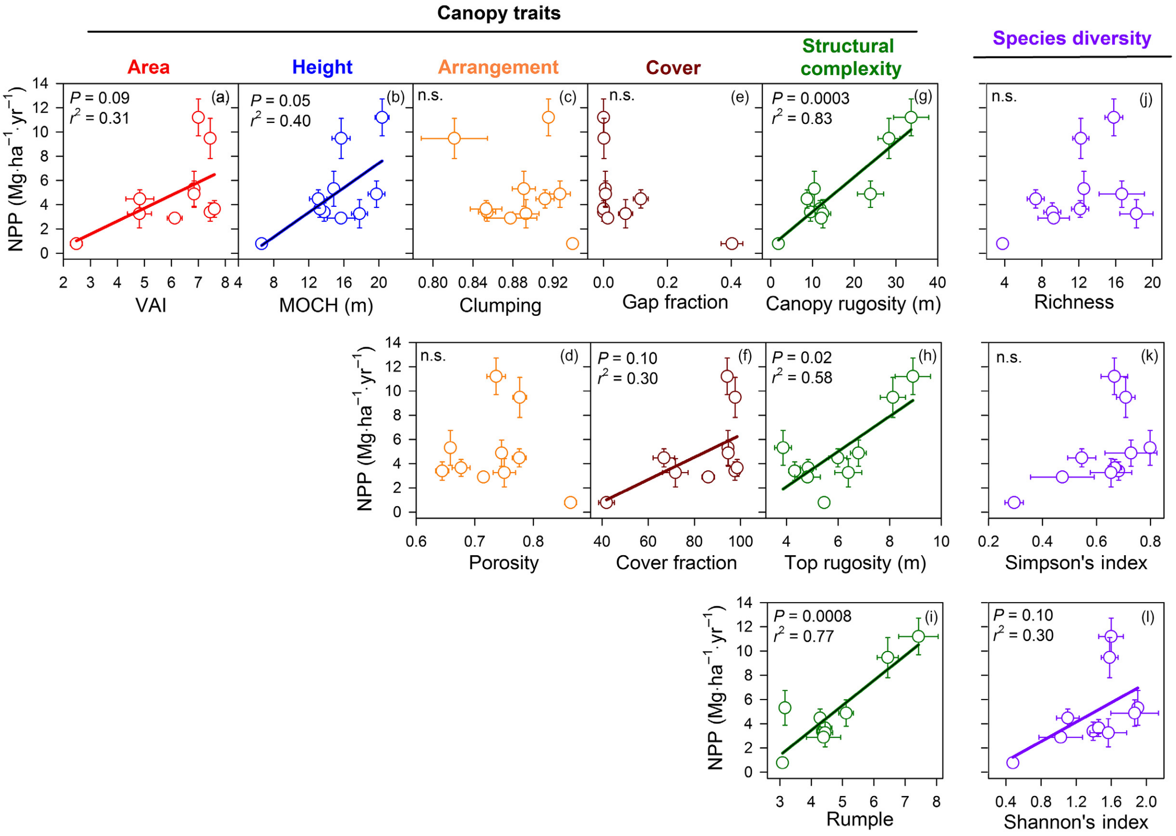

FIG. 2. Site-level wood net primary production (NPP) in relation to the canopy traits and tree species diversity of 10 National Ecological Observatory Network (NEON) temperate forest sites. Canopy traits are presented categorically following the taxonomy of Atkins et al. (2018*a*). Dimensionless or unidimensional canopy traits are (a) vegetation area index (VAI), an area measure; (b) mean outer canopy height (MOCH), a height measure; (c) clumping and (d) porosity, indices of leaf arrangement; and (e) gap fraction and (f) cover fraction, describing canopy cover. Multidimensional canopy traits describing structural complexity are (g) canopy rugosity, summarizing variability in the vertical and horizontal distribution and density of vegetation; (h) top rugosity, describing variability in maximum canopy height; and (i) rumple, the ratio of the canopy top outer surface area to the ground surface area. Tree species diversity indices are (j) richness, (k) Simpsons's index, and (l) Shannon's index. Site level means ± 1 SE.

Discussion

Our results point to a widespread positive relationship between canopy structural complexity and production in temperate forests. We found that multidimensional canopy characteristics summarizing heterogeneity in vegetation distribution are mechanistically grounded indicators of NPP. Moreover, our results suggest that structural complexity traits could serve as broad-scale predictors of forest production, rivaling or exceeding in utility the conventional canopy traits and species diversity measures commonly used in the scaling and modeling of regional to global NPP. The strong biome-wide associations we observed between canopy structural complexity and NPP, along with the underlying mechanisms of improved canopy light absorption and light-use efficiency, are consistent with site-level analyses, indicating that these relationships traverse spatial scales (Hardiman et al. 2011, 2013).

Canopy structural complexity may be a strong, biome-wide indicator of NPP because it is inherently an emergent ecosystem property, arising from and integrating functional information embedded in species diversity and conventional canopy traits. Positive correlations among site-level structural complexity traits, vegetation area index, and species diversity indices support the hypothesis (Gough et al. 2016) that canopies require the crown architectural variety supplied by a diverse plant community and, additionally, a critical mass of vegetation with which to build complex structure. Though species diversity and VAI were positively related to canopy structural complexity (i.e., canopy rugosity) and, through this dependency, may convey redundant functional information, we found that canopy rugosity was most strongly related to canopy light acquisition and light-use efficiency. This finding is congruent with theory and modeling asserting that structurally complex forests composed of species and individuals possessing a diversity of leaf physiological traits are more optimally organized to acquire and use light to assimilate carbon (Anten 2016). Multilayered, heterogeneously arranged canopies absorb more light (Ligot et al. 2016) and they contain a complement of sun and shade leaves functioning optimally under a range of light conditions. The consequence is improved overall leaf-level physiological functioning, whole-canopy light-use efficiency, and NPP (Niinemets 2012).

Our findings have implications for the derivation, modeling, and management of ecosystem structure–production interactions. A quarter century of theory and observation linking species diversity and canopy traits to production has substantially advanced the mechanistic understanding of these relationships, while exposing the limitations of conventional species diversity and canopy structural features as indicators of ecosystem functioning (Loreau et al. 2001, Hooper et al. 2005). The strong mechanistic underpinnings and predictive capacity of structural complexity traits suggest that augmenting the long-standing canon of conventional traits, particularly those focused on vegetation quantity or area, could improve fundamental understanding of structure–function relationships while supporting advances in forest ecosystem modeling and management. In particular, remote sensing tools such as lidar and hyperspectral imaging offer novel ways to characterize canopy structure, and their broad adoption by ecologists is key to the development and scrutiny of functionally focused canopy traits (Asner et al. 2015). Our observation that structural complexity measures outperform conventional canopy traits as predictors of NPP suggests that ecosystem models, which characterize structure in vastly different ways (Fisher et al. 2018), may enhance their mechanistic rigor by representing vegetation in multiple spatial dimensions. In application, forest management and land-use policies that promote or preserve temperate forest canopy structural complexity may aid in sustaining the biome's carbon sink.

Advancing knowledge surrounding relationships of ecosystem structure with production and, more broadly, function, will require the deliberate integration of ecological disciplines with remote sensing science and earth system modeling. Our findings, which derive from a limited number and variety of light-limited temperate forests, may not be directly transferable to biomes where other resources are more growth limiting. In addition, our results only begin to disentangle the mechanistic contributions of highly autocorrelated canopy structural and species diversity traits (Fig. 3; Appendix S1: Fig. S3). Testing

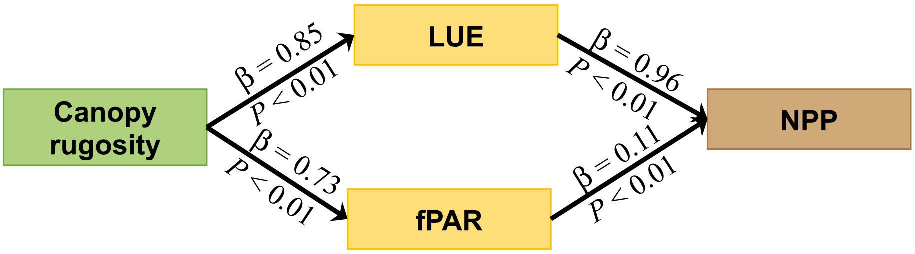

Fig. 3. Structural equation modeling provides support for the hypothesis that canopy rugosity, a structural complexity trait strongly correlated with production (Fig. 2), exerts a positive influence over both canopy light-use efficiency (LUE) and light absorption (as fPAR, the fraction of photosynthetically active radiation absorbed by a canopy), and consequently wood net primary production (NPP). The comparative fit index (CFI = 1.00) and second-order Akaike information criterion ($AIC_c = 33.98$) indicate canopy rugosity is more closely coupled to NPP through fPAR and LUE than either vegetation area index (CFI = 0.99; $AIC_c = 40.74$) or diversity (CFI = 0.99; $AIC_c = 41.54$; Appendix S1: Table S7). β is the standardized regression coefficient.

whether our findings apply to nontemperate forest ecosystems and determining which canopy structural traits and tree diversity indices produce complementary rather than redundant information also necessitates enhanced interdisciplinarity within the field of ecology. Significant advances are likely when physiological, community, and ecosystem ecologists—often pursuing questions of ecosystem structure and function separately—work together toward more integrative theoretical development, experimentation, and application. The exploration of new, scalable canopy traits is already underway, facilitated by a proliferation of ecosystem and Earth observatory networks providing openly available lidar and spectral data from the ground, air, and space and an array of accompanying functional data (Schimel and Keller 2015). The outcome of this joint effort will offer a unified foundation upon which theorists, modelers, and empiricists alike characterize, simulate, and interpret next-generation ecosystem structure–function interactions.

Acknowledgments

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2864/suppinfo

Data Availability

Data in Figs. 2 and 3 are available on Figshare: https://doi.org/10.6084/m9.figshare.7322042.v1. Raw lidar, DBH, and inventory data along with R code are available on Zenodo: https://doi.org/10.5281/zenodo.3359986.