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PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

Effects of canopy structure and species diversity on primary production in upper Great Lakes forests

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Abstract

Canopy structure and tree species diversity, shaped by succession, disturbance, and community composition, are linked to numerous ecosystem functions, including net primary production (NPP). Understanding of how ecosystem structural metrics are interrelated and mechanistically link to NPP, however, is incomplete. We characterized leaf area index (LAI), Simpson's index of Diversity (D', a measure of species diversity), and canopy rugosity (R_c, a measure of canopy physical complexity) in 11 forest stands comprising two chronosequences varying in establishing disturbance, and in three late successional communities. We related LAI, D', and R_c to wood NPP (NPPw), and examined whether absorption of photosynthetically active radiation and light use-efficiency (LUE) link NPPw with ecosystem structure. We found that recovery of LAI and D' was delayed following more severe establishing disturbances, but that the development of R_c was strikingly conserved regardless of disturbance, converging on a common mean value in late-successional stands irrespective of differences in leaf area index and species diversity. LAI was significantly correlated with NPPw in each stage of ecosystem development, but NPPw was only correlated with R_c in early successional stages and with D' in late successional stages. Across all stands, NPPw was coupled with LAI and R_c, (but not D') through positive relationships with light absorption and LUE. We conclude by advocating for better integration of ecological disciplines investigating structure–function interactions, suggesting that improved understanding of such relationships will require ecologists to traverse disciplinary boundaries.

Keywords Chronosequence · Canopy structure · Net primary production · Canopy rugosity · LiDAR · Leaf area index · Ecosystem structure · Disturbance · Succession · Diversity · Eastern temperate forest · Light use efficiency

Introduction

Canopy structure, species diversity, and other ecosystem structural features are strongly related to ecosystem functions, including primary production, and these relationships

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are shaped by successional development and disturbance history, edaphic factors, and plant community composition (Pedro et al. 2015). Linkages between canopy structure and species diversity, and net primary production (NPP)—the rate of C accrual in plant biomass—feature prominently in ecological theory and texts (Chapin et al. 2002; Niinemets and Anten 2009) and empirical studies (Cardinale et al. 2011; Hardiman et al. 2011), and are the foundation upon which many ecosystem models simulate carbon cycling processes (Medvigy et al. 2009). Numerous studies have related ecosystem structural features with forest growth, but mechanistic understanding of how features such as canopy structure and species diversity drive primary production is limited (Cardinale et al. 2011; Danescu et al. 2016; Pedro et al. 2015). Moreover, prior studies generally examined how either plant community composition and species diversity (Castro-Izaguirre et al. 2016; Musavi et al. 2016; Stoy et al. 2008; Vanderwel et al. 2016) or canopy structure (Fahey et al. 2015, 2016; Hardiman et al. 2011; Reich 2012) relates to NPP, with few concurrently investigating canopy structure and species diversity, or their mechanistic linkages with primary production (Danescu et al. 2016; Pedro et al. 2017). The consequence of focusing separately on either canopy structure or species diversity is limited understanding of whether different structural features, individually shown to correlate with NPP, embody unique or redundant information relevant to primary production (Pedro et al. 2017).

The degree to which canopy structure, species diversity, and primary production change synchronously or independently during stand development has been theorized (Pedro et al. 2017), but minimally evaluated empirically (Danescu et al. 2016). Functionally important ecosystem structural features that change through succession and have been linked with primary production include: leaf area index (LAI, Dronova et al. 2011; Kashian et al. 2005; Reich 2012); canopy structural complexity (as the heterogeneity of vegetation arrangement; Hardiman et al. 2011; Pretzsch et al. 2015); and plant species diversity and community composition (Danescu et al. 2016; Liang et al. 2016; Niinemets et al. 2015; Pedro et al. 2015). Separate observational and theoretical studies suggest similar trajectories of development and overlapping mechanistic roles among some canopy structural and species diversity measures, making the unique functional roles of each particularly challenging to disentangle (Pedro et al. 2017). LAI rapidly increases in young forests prior to crown closure, and is related to primary production through its positive effect on canopy light interception (Myneni and Williams 1994). Plant species diversity, which often peaks during the middle stages of ecosystem development, is linked with improved light-use efficiency and light capture (Danescu et al. 2016; Forrester and Albrecht 2014; Stoy et al. 2008). Canopy complexity measures describing the heterogeneity of vegetation arrangement are positively correlated with primary production via changes in light-use efficiency, increasing into late stages of ecosystem succession and declining or increasing following disturbance (Hardiman et al. 2011; Stark et al. 2012; Williams et al. 2017). Though untested empirically, model simulations suggest the principal ecosystem structural predictor of primary production may change from one successional stage to the next, with plant community composition and then canopy complexity driving NPP during early and late stages of succession, respectively (Hardiman et al. 2013b; Pedro et al. 2017). While these prior studies offer important clues about ecosystem structure–primary production relationships, distinguishing the effects of multiple structural features on primary production requires concurrent observations of leaf area index, canopy complexity, and species diversity (Pedro et al. 2017).

Here, we used an empirical approach to evaluate how canopy structure and species diversity measures relate to one another, to wood NPP, and to putative mechanisms linking these features to wood NPP. Our first objective (Obj. 1) was to characterize successional trajectories of canopy structure and tree species diversity following two different establishing disturbances. We hypothesized that LAI, canopy complexity (as canopy rugosity, R_c), and tree species diversity (as Simpson's index, D') would all initially increase with forest age (Pedro et al. 2017), but that the recovery of these ecosystem structural measures would be delayed in more severely disturbed stands (Gough et al. 2007). Our second objective (Obj. 2) included two related parts centered on relationships between wood NPP and ecosystem structural features. Obj. 2a examined whether LAI, R_c, and D' correlate with wood NPP across stands spanning all successional stages and initiating disturbances. Obj. 2b evaluated relationships of LAI, R_c, and D' with wood NPP across stands within early, middle, and late successional stages. For Obj. 2a, prior results from our site led us to predict LAI, R_c, and D' would be positively correlated with wood NPP across stands spanning successional stages and initiating disturbances, with stronger relationships within a plant functional type (Gough et al. 2010; Hardiman et al. 2011). For Obj. 2b, we hypothesized that wood NPP would be most strongly correlated with LAI during early succession (Gough et al. 2007; Law et al. 2003), R_c in middle succession (Hardiman et al. 2013b), and D' in compositionally distinct late successional stands (Fahey et al. 2015). Our third objective (Obj. 3) was to determine whether canopy light absorption and light use-efficiency (LUE) mechanistically link these canopy structural and species diversity measures with wood NPP. We hypothesized that canopy light absorption would be most closely coupled with LAI (Myneni et al. 1997; Turner et al. 2003), and LUE more strongly correlated with D' and R_c (Niinemets 2016; Retkute et al. 2015).

Materials and methods

Study site description

Our study location was the University of Michigan Biological Station (UMBS) in Northern Lower Michigan, USA (45.6°N, −84.7°W), a forest landscape with physiography, soils, disturbance history, and forest composition that represent the range of variation across the upper Great Lakes region (Frelich 1995; Nave et al. 2017). Study sites included stands forming two well-characterized forest chronosequences differing in severity of establishing disturbance, and three associated late successional forest communities (Gough et al. 2007). Our 11 total forest stands spanned ~200 years of ecological succession and were within 14 km of one another. The upper Great Lakes region, including stands in both chronosequences, experienced widespread clear-cut and fire disturbance during the late nineteenth and early twentieth centuries (Gough et al. 2007). Following this region-wide disturbance, stands in a systematically clear-cut forest chronosequence were harvested but not burned afterward (hereafter “Cut Only”) in 1911, 1952, 1972, and 1987. A more intensively disturbed chronosequence includes four stands experimentally clear-cut harvested and burned (hereafter “Cut and Burn”) in 1936, 1954, 1980, and 1998 (Gough et al. 2007). Bigtooth aspen (*Populus grandidentata*) emerged as the dominant tree species following Cut Only and Cut and Burn disturbances, consistent with regional patterns of disturbance-related aspen dominance a century ago. Three regionally representative late successional forest stands, the eldest initiated before 1850, escaped the widespread deforestation occurring a century ago. A mostly coniferous evergreen site (hereafter “ENF” for evergreen needleleaf) had an upper canopy dominated by red pine (*Pinus resinosa*) and a white pine (*Pinus strobus*) understory. A mixed coniferous–deciduous site (hereafter “MIX” for mixed) included red pine and white pine canopy dominants with the additional presence of deciduous bigtooth aspen and subcanopy Northern red oak (*Quercus rubra)* and red maple (*Acer rubrum*). A primarily deciduous site (hereafter “DBF” for deciduous broadleaf) had a canopy of American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and Northern red oak, with lesser representation from Eastern hemlock (*Tsuga canadensis*). The site had an average annual air temperature of 5.5 °C and precipitation of 817 mm (Hardiman et al. 2013a, b). Additional stand characteristics are detailed in Supplementary Table 1.

Because our study includes experimental chronosequences initiated decades ago and late successional remnant forests, stand area shapes and sizes are not uniform. Each stand contained two or three 0.1 ha plots, with one exception noted below, for a total of 29 sampling plots, and plots were treated as replicates for calculating stand means and error. Plots were circular with the exception of the Cut and Burn stand initiated in 1998, which, due to size constraints of the treatment area, consisted of two rectangular plots of 0.14 and 0.06 ha. Soils and climate are relatively uniform among chronosequence stands and our chronosequences were systematically clear-cut harvested and burned using the same experimental protocol (Gough et al. 2007); however, limitations with space-for-time substitutions, including differences among stands in atmospheric and climate conditions, necessitate caution when interpreting results (Walker et al. 2010). Even so, our approach follows that of several prior influential studies employing chronosequences to examine long-term C cycling processes (Bond-Lamberty et al. 2004; Law et al. 2003).

Measures of ecosystem structure

We derived three measures of canopy structure and species diversity previously shown to correlate with primary production at our site and elsewhere: leaf area index (Dronova et al. 2011; Reich 2012), canopy rugosity (Hardiman et al. 2011, 2013b), and tree species diversity as Simpson’s index (Drake et al. 2011; Pretzsch et al. 2015).

Leaf area index

We used hemispherical imaging to estimate stand leaf area index (LAI), a canopy structural measure describing leaf surface area. Three images were taken at 1.5 m height in each plot: one in plot center and two additional randomly assigned locations. A north-facing, leveled Nikon D3200 outfitted with a 5.8-mm 180° circular fisheye lens was used under uniform diffuse sky conditions. Images were analyzed with Gap Light Analyzer (Hardy et al. 2004) for effective LAI between zenith angles 0°–60° to minimize error from nearby canopies outside plots. Automatic threshold levels for each image were determined using ImageJ (Chopping 2011). Prior analysis at our site established strong correspondence ($r^2 = 0.87$) between independently derived hemispherical and litter-trap-based LAI (Stuart-Haentjens et al. 2015).

Canopy rugosity

We characterized canopy structural complexity as canopy rugosity (R_c) using below-canopy LiDAR (Hardiman et al. 2013a; Parker and Russ 2004; Stark et al. 2012). A Portable Canopy LiDAR (PCL) system (Parker et al. 2001) generated canopy two-dimensional hit-maps along two 40-m transects within each stand, one running from north to south and another east to west through stand center. A modified

PCL sampling protocol was followed for the irregularly shaped 1998 origin Cut and Burn plots with shortened parallel transects (10 and 20 m) running north to south. PCL returns were pooled in 1-m^2 bins vertically (with height) and horizontally (along the transect), and canopy rugosity and maximum canopy height were calculated using MATLAB code (Hardiman et al. 2013a). Canopy rugosity expresses structural complexity as the variance in the horizontal and vertical distribution of vegetation:

$$R_c = \sigma\left(\sigma[\mathrm{VAI}]_Z\right)_X, \tag{1}$$

where R_c is the product of standard deviations (σ) in horizontal (x) and vertical (z) vegetation area indexes (VAI) for each 1-m^2 bin. Maximum canopy height is the highest recorded value along the vertical axis in each transect. VAI is similar to LAI, but includes all vegetative tissues.

Tree species diversity

To assess tree species diversity, we calculated Simpson's index of diversity *(D′)* from tree stem count data (DBH > 8 cm) collected in 2014. This metric was shown to correlate with NPP (wood only and total) in nearby study sites (Gough et al. 2010) and other forest ecosystems (Danescu et al. 2016), and incorporates both species richness and evenness where values closer to 1 indicate highest diversity.

Wood net primary production

To examine relationships among canopy structure, species diversity, and primary production, we derived plot annual wood NPP from repeated measurements of stem diameter. In 2014, tree dendrometer bands were fitted within each plot to 10–20% of trees with diameter at breast height (DBH) > 8 cm, including all dominant canopy species. DBH was recorded in 2014 and 2015 for each tree with a dendrometer band, and site-specific allometric equations and wood C density data used to derive wood C mass from DBH. Stand wood NPP was calculated as the plot average kg wood C mass increment from 2014 to 2015 scaled to a hectare (Gough et al. 2010).

fPAR and light-use efficiency

We quantified canopy light capture and light-use efficiency for each plot, and examined whether these processes mechanistically link canopy structure and species diversity with wood NPP. Instantaneous photosynthetically active radiation (PAR) was recorded in seven locations within each plot at 0 and 1 m heights, using an AccuPAR LP-80 Ceptometer (Decagon Devices Inc., Pullman, Washington, USA). Coincident above-canopy PAR was interpolated from nearby open-field measurements taken within 30 min of below-canopy PAR measurements, adjusted for solar angle and atmospheric conditions using the APOGEE Clear Sky Calculator parameterized with air temperature and relative humidity values measured by a nearby (within 10 km) meteorological tower. All measurements were taken between 10:30 and 14:30 on clear days during late July to early August 2015. The mean fraction of PAR (fPAR) intercepted by a canopy was calculated from concurrent below- and above-canopy PAR measurements. Canopy (excluding ground vegetation) LUE was calculated for each stand as mean wood NPP divided by mean absorbed light as fPAR recorded at 1 m above the forest floor (Hardiman et al. 2013b; Stuart-Haentjens et al. 2015).

Statistical analysis

Our statistical approach was linked with our objectives, investigating whether: establishing disturbance affects the recovery patterns of canopy structure and species diversity, and wood NPP (Obj. 1); wood NPP correlates with canopy structure and species diversity across all stands or stands within a single plant functional type (Obj. 2a) and across stands within each successional stage (Obj. 2b); and fPAR and LUE mechanistically couple ecosystem structural measures to wood NPP (Obj. 3). With a priori empirical and modeling evidence for non-linear changes in canopy structure over time (Hardiman et al. 2013b; Pedro et al. 2017), we tested linear and curvilinear model fits; however, our model fitting procedure showed that a three-parameter curvilinear model fitted to our small sample size ($n = 4$ stands/chronosequence) amounted to overfitting in all but one case, with adjusted r^2 values of the curvilinear model generally lower than those of linear models. Therefore, in most instances we present more parsimonious simple linear models.

To address Obj. 1, we compared the rates of change in LAI, R_c, and D', and primary production separately for Cut and Burn and Cut Only chronosequences. When slope estimates had non-overlapping 95% confidence intervals, we present separate regression lines for each chronosequence; otherwise, a single regression line combining data from both chronosequences is plotted. We used ANOVA followed by post hoc Least Significant Difference (LSD) analysis to compare the means of late successional plant functional types (ENF, MIX, DBF). To investigate Obj. 2a, we conducted regression analyses with all 11 stands to evaluate whether variation in wood NPP, irrespective of stand age, disturbance history, and community composition, was explained by ecosystem structural metrics, and an additional within functional-type analysis including only the nine deciduous broadleaf forest stands (i.e., Cut and Burn, Cut Only, and DBF). For Obj. 2b, we compared the correlation coefficients

(r) of wood NPP and LAI, R_c, and D' within each of three stages of ecosystem succession. We assessed correlations for Cut and Burn and Cut Only chronosequences separately, grouping plots into the following development stages: early succession, pre-crown closure; middle succession, post-crown closure and pre-senescence of pioneer tree species (aspen and birch); and late succession, post-crown closure and post-senescence of pioneer tree species. Obj. 3 used the same regression approach as Obj. 2a to examine whether structural features correlated with wood NPP also were correlated with fPAR and LUE. Models, correlation coefficients, and mean differences were considered significant when $P < 0.1$. Analysis was conducted in SPSS 12.5 or R 3.1.0 statistical software.

Results

Trajectories of structural characteristics through stand development

We found the more severe Cut and Burn establishing disturbance stunted the successional recovery of tree species diversity and leaf area index but not canopy structural complexity (Obj. 1). LAI in Cut and Burn stands increased ($P = 0.02$, $r^2 = 0.93$; Fig. 1b) and approached the higher and more stable values observed in the less intensively disturbed Cut Only stands several decades following stand initiation. Similarly, Simpson's index was relatively low following higher severity establishing disturbance, with Cut and Burn ($P = 0.06$, $r^2 = 0.82$; Fig. 1c) tree species diversity recovering during middle succession to levels observed in the Cut Only stands ($P = 0.003$, $r^2 = 0.90$; Fig. 1c). In contrast, canopy rugosity increased similarly with stand age regardless of disturbance intensity ($P = 0.0001$, $r^2 = 0.95$; Fig. 1a).

Though late successional communities had significantly different LAIs and Simpson's index values, the three stands converged on a common mean canopy rugosity of 26 m (Fig. 1a). Tree species diversity expressed as Simpson's index was significantly lower ($P < 0.1$) in ENF relative to both MIX and DBF, and LAI was much higher in DBF (LAI = 3.15) than in ENF (LAI = 1.58) and MIX (LAI = 1.77) forests ($P < 0.1$; Fig. 1b, c).

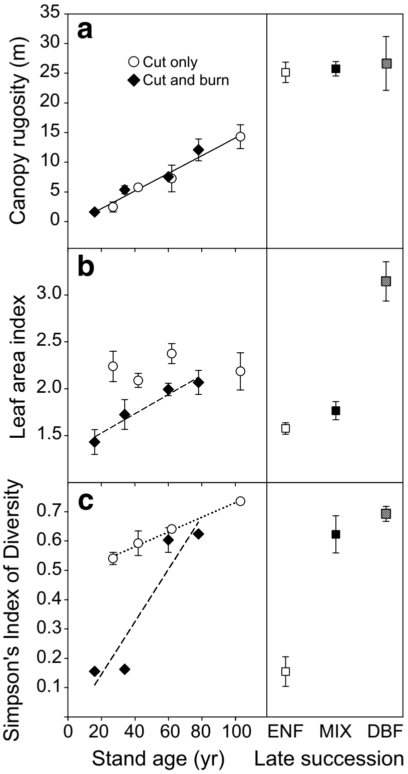

Fig. 1 Canopy rugosity (**a**), leaf area index (**b**), and Simpson's index of (canopy tree) Diversity (**c**) (mean ± 95% CI) in "Cut Only" and "Cut and Burn" chronosequence stands, and in late successional forest stands. Dotted and dashed lines denote significant ($P < 0.1$) chronosequence-specific changes with age in "Cut Only" and "Cut and Burn" stands, respectively, while a single solid line indicates a significant ($P < 0.1$) common trend. Non-overlapping 95% confidence intervals between late successional communities illustrate significant differences between means. **a** Combined $r^2 = 0.95$; **b** "Cut and Burn" $r^2 = 0.93$; **c** "Cut Only" $r^2 = 0.99$ and "Cut and Burn" $r^2 = 0.82$

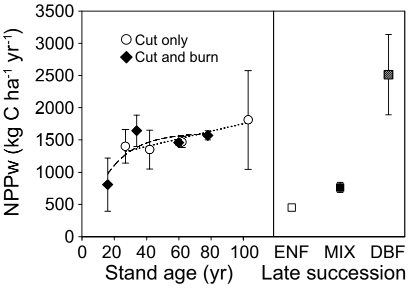

Fig. 2 Annual wood net primary production (NPPw; mean ± 95% CI) in relation to stand age in "Cut Only" and "Cut and Burn" stands, and in late successional communities. Dotted and dashed lines denote significant ($P < 0.1$) chronosequence-specific changes with age in "Cut Only" ($r^2 = 0.82$) and "Cut and Burn" ($r^2 = 0.64$) stands, respectively

Relationship of production with ecosystem structure through stand development

The successional trajectories of wood NPP were similar for the two chronosequences, but values varied among late successional stands. Wood NPP increased with stand age in both chronosequences (Fig. 2). Cut Only wood NPP increased linearly ($P = 0.06$, $r^2 = 0.82$), reaching a maximum of 1810 kg C ha^{-1} year^{-1} in the century-old stand. Cut and Burn chronosequence stands, which started at an earlier age than Cut Only, followed a curvilinear increase ($P = 0.1$, $r^2 = 0.64$) to a maximum approaching 1570 kg C ha^{-1} year^{-1} in the

68-year-old stand. Among late successional forest communities, wood NPP of DBF (2510 kg C ha^{-1} $year^{-1}$) was significantly higher than that of MIX (760 kg C ha^{-1} $year^{-1}$) and ENF (450 kg C ha^{-1} $year^{-1}$) ($P < 0.1$).

Across all stands and stands within the deciduous broadleaf forest plant functional type, relationships varied between wood NPP, and LAI, canopy rugosity, and species diversity (Obj. 2a; Fig. 3). Canopy rugosity was not strongly correlated with wood NPP when all 11 stands were analyzed, but this canopy structural complexity measure was positively related to wood NPP when only deciduous forests were included in a model ($P = 0.0006$, $r^2 = 0.81$; Fig. 3a). In contrast, wood NPP and LAI were positively correlated across all stands ($P = 0.001$, $r^2 = 0.72$; Fig. 3b). Simpson's index of Diversity was not significantly correlated with wood NPP when all stands or only deciduous forest stands were analyzed (Fig. 3c).

Similarly, across stands within successional stages, relationships between wood NPP and different metrics of ecosystem structure varied in strength (Obj. 2b). The results from correlation analyses (Table 1) suggest strong positive ($P < 0.1$) coupling of wood NPP with canopy rugosity ($r = 0.93$) and LAI ($r = 0.95$) during early succession in Cut and Burn, but not in Cut Only plots. Leaf area index emerged as a significant negative correlate ($P = 0.011$, $r = -0.96$) in Cut Only middle successional stands. Among late successional communities, which unlike early and middle successional stands span three different plant functional types, LAI ($P < 0.001$, $r = 0.99$) and Simpson's index of diversity ($P = 0.058$, $r = 0.65$) were highly correlated with wood NPP.

Canopy light absorption and use-efficiency

Canopy light interception varied with establishing disturbance and among late successional stands. Although ground-level measurements of canopy light absorption, expressed as fPAR, did not differ significantly among stands (Fig. 4a), at 1 m height (i.e., above the ground-layer vegetation) successional trajectories of fPAR diverged in the two chronosequences. fPAR at 1 m height in Cut Only stands followed a positive trend with age ($P = 0.068$, $r^2 = 0.80$; Fig. 4b), while the more severely disturbed Cut and Burn stands exhibited no significant trend. Canopy light interception at 1 m was significantly higher in DBF than in either MIX or ENF ($P > 0.1$), with fPAR above 1 m approaching 97% in the late successional deciduous forest (Fig. 4a, b).

Light-use efficiencies (LUE, wood NPP/fPAR at 1 m) were similar among stands in the two chronosequences,

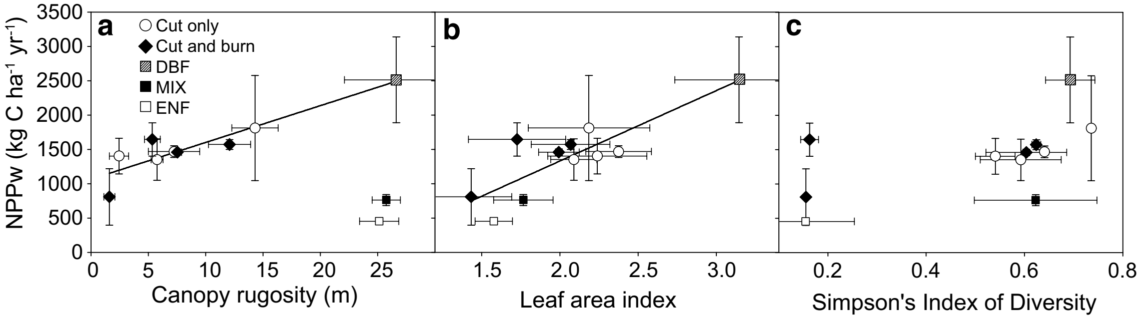

Fig. 3 Wood net primary production (NPPw) in relation to canopy rugosity (**a**; $r^2 = 0.81$, $P < 0.1$), leaf area index (LAI, **b**; $r^2 = 0.72$, $P < 0.1$), and Simpson's index of (canopy tree) Diversity (**c**; not significant). Modeling of NPPw–canopy rugosity excluded pine-dominated ENF and MIX late successional stands, and NPPw–LAI included all stands. Means ± 95% CI

Table 1 Correlation coefficients (r) and P-values summarizing wood net primary production's relationship with ecosystem structural (Canopy rugosity and leaf area index) and compositional (Simpson's index of diversity) parameters at different stages of ecological succession in the Cut Only and Cut and Burn chronosequences, and late successional stands

Successional stage (plot sample size)	Canopy rugosity		Leaf area index		Simpson's index	
	R	*P*	*R*	*P*	*R*	*P*
Early/cut only (6)	−0.01	0.982	−0.28	0.588	−0.22	0.677
Early/cut and burn (5)	**0.93**	**0.023**	**0.95**	**0.012**	0.43	0.470
Mid/cut only (5)	0.26	0.675	**−0.96**	**0.011**	0.28	0.652
Mid/cut and burn (4)	0.85	0.151	0.10	0.896	0.46	0.540
Late (9)	0.45	0.224	**0.99**	**< 0.001**	**0.65**	**0.058**

Significant ($P < 0.1$) relationships within a successional stage are highlighted in bold text

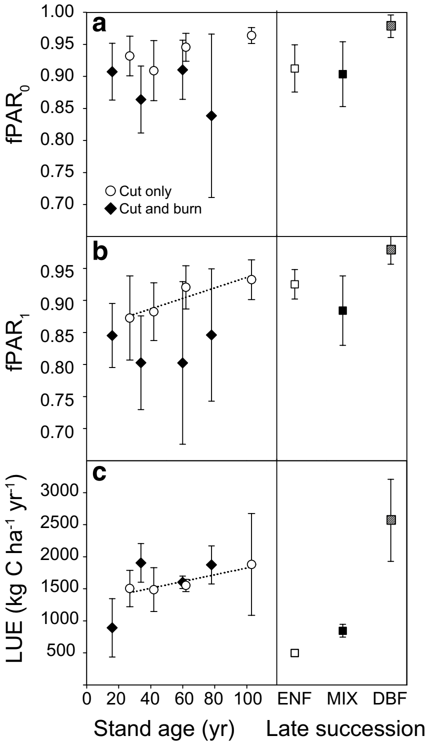

Fig. 4 Canopy light absorption and use-efficiency (mean ± 95% CI) in "Cut Only" and "Cut and Burn" chronosequence stands, and in late successional forest communities. Canopy light absorption is expressed as the fraction of above-canopy photosynthetic active radiation at 0 m ($fPAR_0$, **a**) and 1 m ($fPAR_1$, **b**) above the forest floor, and light use efficiency (LUE, **c**) is the quotient of NPPw and $fPAR_1$. The dotted line denotes a significant ($P < 0.1$) chronosequence-specific change in $fPAR_1$ with age in the "Cut Only" ($r^2 = 0.80$) stands

but significantly different among late successional stands (Fig. 4c). Chronosequence stand LUE varied from ~ 1530 to 2050 kg C ha^{-1} $year^{-1}$, with the exception of lower LUE in the youngest, 16-year-old Cut and Burn stand (960 kg C ha^{-1} $year^{-1}$, Fig. 4c). LUE was markedly different across all three late successional plant functional types, with DBF (2570 kg C ha^{-1} $year^{-1}$) ≫ MIX (860 kg C ha^{-1} $year^{-1}$) > ENF (490 kg C ha^{-1} $year^{-1}$) stands ($P < 0.1$; Fig. 4c).

Canopy rugosity and LAI, which were significantly correlated with wood NPP (Fig. 3), were also correlated with fPAR and light-use efficiency. fPAR at 1 m increased significantly with canopy rugosity ($P = 0.039$, $r^2 = 0.32$ l; Fig. 5a) and LAI ($P = 0.1$, $r^2 = 0.29$; Fig. 5b). As with wood NPP, light-use efficiency increased with canopy rugosity across deciduous forest stands (i.e., when late successional MIX and ENF stands were excluded; $P = 0.002$, $r^2 = 0.74$; Fig. 5c), and with LAI when all stands were analyzed ($P = 0.004$, $r^2 = 0.59$; Fig. 5d). We excluded analysis of Simpson's index because this measure of species diversity was not significantly correlated with wood NPP (Fig. 3c).

Discussion

Our investigation of stands varying in successional stage and establishing disturbance showed that canopy structure and species diversity were dynamic, did not parallel one another, and were variable in their relationship with wood NPP. Canopy structural complexity (i.e., canopy rugosity) exhibited a strikingly similar pattern over successional development regardless of the severity of establishing disturbance,

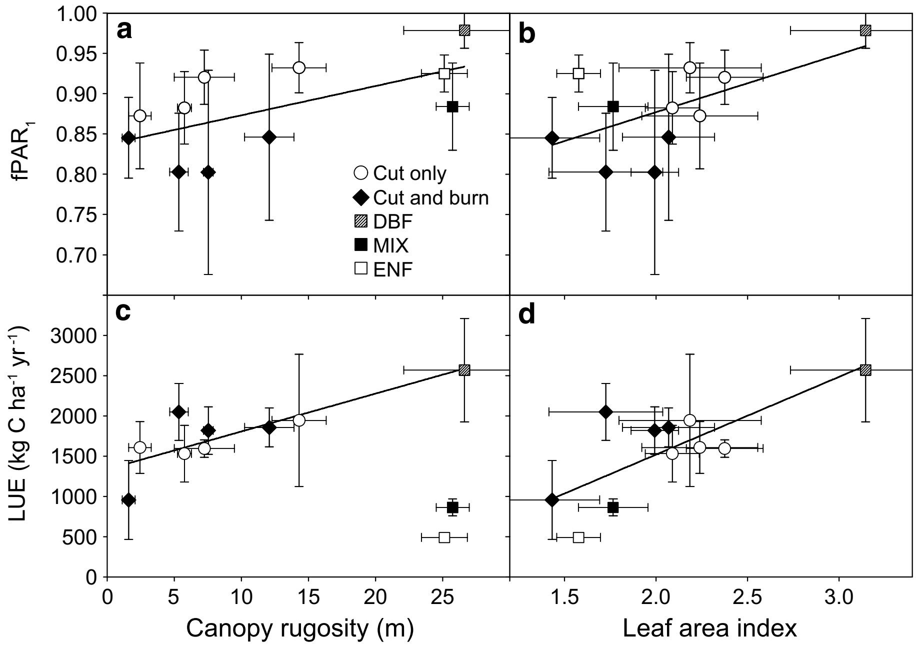

Fig. 5 Canopy light absorption, as the fraction of photosynthetic active radiation at and 1 m ($fPAR_1$; **a**, **b**), and light-use efficiency (LUE; **c**, **d**) in relation to canopy rugosity area index (LAI) in "Cut Only" and "Cut and Burn" chronosequence stands, and in late successional forest communities. Regression models include all stands, with the exception of LUE–canopy rugosity, which excluded pine-dominated MIX and ENF stands. **a** $r^2 = 0.32$; **b** $r^2 = 0.29$; **c** $r^2 = 0.74$ DBF only, ns. when MIX, ENF included; **d** $r^2 = 0.59$

increasing linearly in young stands and then plateauing to a common mean value in late successional stands. This fixed pattern of development in canopy structural complexity was in stark contrast to that of LAI, and tree species diversity (i.e., Simpson's index of diversity) both of which exhibited delayed recovery following more severe establishing disturbance. Differences among stands in wood NPP were mediated, in part, by light acquisition and use-efficiency, which were correlated with canopy rugosity and LAI. However, pine-dominated late-successional communities did not fall along the same canopy rugosity–wood NPP continuum as deciduous broadleaf forest stands, indicating this measure of canopy structural complexity did not capture processes underlying wood NPP variation across plant functional types.

Each canopy structure and species diversity measure that we examined—LAI, canopy rugosity, and Simpson's index of diversity—exhibited a distinct increasing trend through successional development. However, these ecosystem structural features displayed varying sensitivity to establishing disturbance, as more severe disturbance delayed the recovery of LAI and Simpson's index, but not canopy rugosity. An exception to this trend was LAI in the less severely disturbed Cut Only chronosequence, which did not change with stand age, possibly because recovery had already occurred in the youngest 27-year-old stand. Delayed recovery of LAI and tree species diversity following high-intensity disturbance is consistent with numerous studies (Nakashizuka 2001; Zhang et al. 2009), and may be caused by a loss in nitrogen capital (Fahey et al. 1998; Gough et al. 2007) along with a reduction in advance seedling regeneration and the seed bank (Mou et al. 1993). Conversely, a material legacy of established subcanopy plants and greater nitrogen availability in the less intensely disturbed Cut Only chronosequence may have accelerated the recovery of LAI and species diversity (Johnstone et al. 2016).

More surprising was the strikingly conserved development of canopy rugosity, which increased linearly through a century of ecosystem succession and converged on a common mean value in late successional stands varying in LAI or tree species diversity. Counter to our observations, theory posits that canopy structure and species diversity measures are intrinsically linked because the breadth of phenotypic structure, including that which arises from interspecific variation in crown morphology, shapes and constrains canopy structural complexity measures (Danescu et al. 2016; Gough et al. 2016; Ishii et al. 2004; Niinemets 2016; Pedro et al. 2017). However, our observations indicate that canopy structure and species diversity follow distinct successional trajectories, and demonstrate that canopies with different leaf quantities and tree architectures may converge on a similar vegetation arrangement. The successional development of canopy rugosity at our site reflects in part the fundamental role of canopy height in constraining physical structural complexity (Supplementary Fig. 1; Hardiman et al. 2013a), with progressive increases in canopy height providing the additional physical space necessary to accommodate more complex vegetation arrangements (Parker et al. 2001). Given the autocorrelation of many canopy structural features (Hardiman et al. 2013a), future work is needed to disentangle their functional roles.

The positive relationships we observed linking wood NPP with LAI and canopy rugosity, the latter evaluated within deciduous broadleaf forest stands only, coincided with increases in fPAR and light-use efficiency, suggesting complementary and interrelated mechanisms could couple these structural features with primary production. The mechanistic relationship between primary production and LAI is well understood (*cf*. Reich 2012), with greater leaf surface area increasing the quantity of light absorbed by canopies and, consequently, boosting whole-canopy carbon assimilation. The mechanisms underlying positive relationships of canopy rugosity with fPAR and light-use efficiency are less understood, but may be explained by corresponding increases in subcanopy vegetation light interception and photosynthetic rates, which together elevate whole-canopy carbon fixation (Hardiman et al. 2011; Williams et al. 2017). Specifically, more vertically and horizontally heterogeneous vegetation arrangements allow for deeper light penetration into the canopy and, when paired with higher LAI, lead to greater light interception by the subcanopy and thus the canopy as a whole (Forrester 2014; Rohrig et al. 1999). This supplement of light to the subcanopy may lead to proportionally greater additive effects on carbon assimilation because, unlike light-saturated leaves of the upper canopy, photosynthesis rates of subcanopy leaves are generally light limited and sensitive to small increases in light availability (Niinemets 2007; Niinemets and Anten 2009). However, the deviation of pine-dominated stands from the canopy rugosity–light-use efficiency continuum observed in deciduous broadleaf forests suggests that variation in light-use efficiency among plant functional types may be driven by biological features not represented by canopy structure alone. While the mechanisms underpinning these observed differences require further investigation, the remarkably fixed successional trajectory of canopy rugosity and its coupling to fPAR and light-use efficiency in deciduous broadleaf forest stands suggests that leaf arrangement within a plant functional type may develop to maximize light capture and use-efficiency, paralleling mechanisms thought to underlie plant community assembly rules (Anten 2016; Li and Waller 2016; Zhang et al. 2009).

We found that the correlation of wood NPP with LAI, canopy rugosity, and tree species diversity varied within each stage of ecological succession. These results are consistent with ecological theory and observations showing the ecosystem structural features that drive primary production vary as succession progresses (Pedro et al. 2017) and, in the case of late-successional stands, across plant functional types (Spies 1998). For example, our findings are congruent with studies reporting strong relationships between NPP and LAI during multiple successional stages (Kashian et al. 2005; Zha et al. 2009), and with those showing plant species diversity is an important correlate of primary production across compositionally variable forest stands (Liang et al. 2016). Our observation that canopy rugosity was correlated strongly with wood NPP in early and, more marginally, in middle successional stands is aligned with results from a nearby study site (Hardiman et al. 2011). Canopy rugosity, which varied little across compositionally different late successional stands, failed to explain variation in wood NPP among older forests. However, unlike early and middle successional stages, these oldest stands represented three different plant functional types and we cannot discard the possibility that canopy rugosity–wood NPP relationships are significant during late succession within plant functional types. Elucidating why the coupling of primary production with different ecosystem structural features varies over time and in space remains a fundamental knowledge gap, and is important to improving models that simulate ecosystem processes using structural information (Antonarakis et al. 2011; Fischer et al. 2016).

Taken together, our results offer novel insights into ecosystem structure–primary production interactions while raising many new questions. Of primary significance was the observation that canopy rugosity developed along a predictable successional trajectory, suggesting that canopies may physically develop to maximize resource acquisition and use-efficiency during stand development, regardless of the quantity of structural materials (i.e., leaves) and species-driven variability in crown architecture (i.e., reflected in tree species diversity). Additional findings meriting investigation include observations that the strength of correlation of canopy structure and tree species diversity with primary production may fluctuate among periods of stand development, and that leaf area index, and tree species diversity, and canopy rugosity exhibit different successional trajectories. The latter is significant because it demonstrates that complex canopy structures can develop without reliance on the architectural variety afforded by species diversity. Last, our results have implications for ecologically focused forest management and ecosystem restoration, indicating that the canopy structure and tree species diversity features prioritized through manipulations may affect the breadth and degree to which ecosystem services are provided. Additional research is necessary to understand whether the cultivation of different ecosystem structural features promotes the rise of co-occurring ecosystem functions including carbon storage, timber production, ecosystem resilience and stability, and animal biodiversity (Thompson et al. 2011). These findings, and the outstanding questions that remain, argue for more deliberate and integrative collaborative investigations across ecological disciplines engaged in advancing understanding of ecosystem structure–function relationships, including physiological, community, and ecosystem ecology.

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Author contribution statement CMS, LEN, KJN, and CMG conceived and designed the experiments. CMS, LEN, and CMG performed the experiments. CMS, RTF, and CMG analyzed the data. All authors wrote the manuscript and provided editorial advice.

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