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Stand age, disturbance history and the temporal stability of forest production

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ABSTRACT

Sustaining the terrestrial carbon (C) sink requires knowledge of the forest properties supporting stable production under increasingly variable climate conditions. We examined how stand disturbance history and age, structural complexity and species diversity, and leaf properties relate to the 10-yr stability of above-ground wood net primary production (NPPw) in northern temperate forests of Michigan, USA. Our investigation centered on separate deciduous, evergreen, and mixed late successional stands initiated over a century ago and free of recent disturbance, a “Cut Only” chronosequence established following clearcut harvesting, and a “Cut and Burn” chronosequence that regenerated following experimental clearcut harvesting and fire. The temporal stability of stand production was calculated from the 10-yr coefficient of variation (CV) of annual NPPw estimated from tree cores; canopy rugosity, a measure of structural complexity, was estimated using terrestrial LiDAR; and > 1500 subcanopy leaves were sampled for leaf mass area and chlorophyll fluorescence intensity. The temporal stability of stands differed by > 2-fold, from 5% to 11% CV of NPPw. Counter to expectations, we found that NPPw stability was greatest in the more severely disturbed Cut and Burn stands and lowest in late successional stands. Despite similar successional patterns of species diversity and structural complexity, NPPw stability increased in Cut Only stands and declined in Cut and Burn stands as age, diversity and canopy rugosity increased. The NPPw of more diverse, late successional deciduous forests was more temporally stable than that of evergreen forests. We conclude that management for maximal rates of production may not confer temporal stability, indicating future studies are needed to elucidate the stand and canopy properties that support both high production rates and stability.

1. Introduction

Maintaining and managing for a sustainable future forest carbon (C) sink requires knowledge of what structural and functional properties confer temporal stability on production under an increasingly variable climate. A quarter century of investigation in grasslands suggests species diversity promotes functional stability, including net primary production (NPP, Tilman and Downing, 1994; Hooper et al., 2005; De Boeck et al., 2018). A less conclusive body of forest-focused literature, however, indicates both positive (Stoy et al., 2008; Jucker et al., 2014; Dragoun et al., 2015; del Rio et al., 2017; Musavi et al., 2017) and negative (DeClerck et al., 2006; Tamrakar et al., 2018) effects of species diversity and stand structural complexity on production temporal stability. For example, a global analysis of forests established that species richness is a weakly positive predictor of gross primary production temporal stability across sites (Musavi et al., 2017). Conversely, within a montane landscape, lower diversity forest stands containing a prevalence of drought tolerant species exhibited greater NPP temporal stability than more diverse stands (DeClerck et al., 2006), suggesting the mechanisms stabilizing forest production may vary depending on the ecosystem and scale (i.e., across vs. within landscapes) of observation. Structural complexity – defined here as the degree of variation in vegetation distribution and quantity – has been shown to be superior to species diversity as a predictor of NPP *magnitude* in some

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forests, but its effect on temporal *stability* is not known (Scheuermann et al., 2018).

Although both species diversity and structural complexity are likely to have some impact on temporal stability of productivity, the relative impact of these stand characteristics on stability and the specific mechanisms underlying, in particular, structural complexity-C cycling stability interactions are not fully understood (Pretzsch et al., 2015; Forrester et al., 2018; Zeller and Pretzsch, 2019). Canopy structural complexity and species diversity are both expected to affect NPP and stability in NPP by increasing resource use efficiency and complementarity (Liang et al., 2016; Forrester, 2019). However, the effect of these stand-level characteristics on temporal stability is also likely to be strongly mediated by their effects on fine scale variation in leaf traits and resource environments. The canopies of species diverse and structurally complex forests are micro-climatically variable and contain a broader complement of leaf morphological and physiological traits (Fotis et al., 2018). Canopy heterogeneity in expressed leaf traits is a function of inter-specific trait variability and the intra-specific trait plasticity of individuals in response to their local resource availability. A canopy containing functionally diverse leaves may stabilize whole-stand NPP by acquiring limiting resources more thoroughly and evenly via complementarity, resulting in collectively steady rates of plant growth over a range of environmental conditions (Garcia-Palacios et al., 2018; Mudrak et al., 2019).

Within patchy forested landscapes, an array of stand disturbance and developmental histories may lead to variation in species diversity and structural complexity which, along with associated leaf functional attributes, could drive the temporal stability of production. Disturbance history and stage of stand development following disturbance affect not only tree species diversity but also structural complexity features such as canopy rugosity, a measure of the vertical and horizontal variation in leaf area distribution that is broadly linked to forest NPP across scales (Gough et al., 2019; Hardiman et al., 2011; Hardiman et al., 2013a; Hardiman et al., 2013b; Fahey et al., 2015; Scheuermann et al., 2018). Moreover, stand disturbance history and age are primary determinants of leaf functional properties, including photosynthetic capacity and morphology, thought to underlie stand-scale production stability (Loreau and de Mazancourt, 2013). The effect that different stand and leaf functional characteristics have on the stability of production across gradients in disturbance history and stand development, though not known, is relevant to improved fundamental understanding and management for production stability in forested landscapes.

We examined how the temporal stability of annual aboveground wood NPP (hereafter NPPw) relates to stand disturbance history and age, species diversity and structural complexity, and subcanopy leaf morphology and physiology, with the principal goal of elucidating the factors that confer greater forest production stability. We chose to emphasize the structural complexity measure "canopy rugosity" because of its strength as a predictor of mean NPP (Gough et al., 2019). Though there are several components of ecosystem "stability" (Hillebrand et al., 2018), we focus on temporal stability expressed as interannual variation in NPPw (Musavi et al., 2017). Our analysis complements prior studies, including work in the same study system that coupled stand structural and leaf properties to the magnitude, but not stability, of NPP and C storage (Gough et al., 2007; Stuart-Haentjens et al., 2015; Scheuermann et al., 2018), as well as global-scale analysis that examined drivers of production temporal stability (Musavi et al., 2017). Our objectives were to evaluate relationships of NPPw temporal stability, as the coefficient of interannual variation (CV) in NPPw, with: stand disturbance history and age (Obj. 1); species diversity and structural complexity (Obj. 2); and the degree of variation in subcanopy leaf morphology and physiology (Obj. 3). We hypothesized that less severely and less recently disturbed stands would exhibit greater NPPw stability, with greater species diversity, structural complexity, and more heterogeneous subcanopy leaf traits in these stands conferring greater temporal stability in NPPw.

2. Methods

2.1. Study site

Our study site (45°35′N 84°43′W) was the University of Michigan Biological Station (UMBS), located in northern Michigan, USA. Region-wide clear-cut harvesting and subsequent fires in the late 1800s and early 1900s decimated most primary forest in the area and promoted the establishment of early successional bigtooth aspen (*Populus grandidentata*) and paper birch (*Betula papyrifera*) (Frelich and Reich, 1995). As these secondary forests advance in age, red oak (*Quercus rubra*) and red maple (*Acer rubrum*) increased in the abundance, with lesser representation from sugar maple (*Acer saccharum*), eastern white pine (*Pinus strobus*), red pine (*Pinus resinosa*) and American beech (*Fagus grandifolia*) (Gough et al., 2010). The landscape, though dominated by century-old secondary forests, is a mosaic of forest stands varying in age and disturbance history (Nave et al., 2017). Late-successional stands occupy a small proportion of the region's forested area (Frelich, 1995; Hanberry and He, 2015) and provide an important measure of ecosystem functioning in the absence of recent stand-replacing disturbance.

Our study encompasses this local to regional variability in stand development and disturbance history, centering on two chronosequences with different establishing disturbances and three late successional legacy forests that survived deforestation a century ago

Table 1
Characteristics of 11, 1-ha forest stands comprising two experimental chronosequences and three late successional stands.

Name	Disturbance History	Year Established	Plot Number	Stems ha^{-1}	Mean DBH	Landform	Soils	Dominant taxa (> 8 cm DBH)
Cut and Burn	Twice cut, twice burned	1936	2	1335	17.1	high-level plain	sandy Haplorthod	POGR, PIST, ACRU
		1954	2	1355	14.1			POGR, QURU, PIST
		1980	3	1597	11.4			POGR, QURU, ACRU
		1998	2	725	9.2			POGR, QURU
Cut Only	Twice cut, once burned	1911	3	793	21	high-level plain	sandy Haplorthod	POGR, QURU, PIST
		1952	2	1090	16.6			QURU, PIST, POGR
		1972	3	1960	12.5			POGR, QURU, ACRU
		1987	2	1523	10.6			POGR, QURU, ACRU
DBF	Late Succession	1850	3	433	34	gently sloping moraine	sandy over loamy Haplorthod	FAGR, TSCA, QURU, ACRU
ENF	Late Succession	1885	3	753	28.8	low-level plain	sandy over gravelly Haplorthod	PIRE, POGR, BEPA
MIX	Late Succession	1885	3	657	26.8	high-level plain	sandy Haplorthod	PIRE, POGR, PIST

Dominant taxa collectively comprise a majority of canopy cover (Scheuermann et al. 2018). POGR = *Populus grandidentata*, QURU = *Quercus rubra*, ACRU = *Acer rubrum*, PIST = *Pinus strobus*, PIRE = *Pinus resinosa*, BEPA = *Betula papyrifera*, FAGR = *Fagus grandifolia*, TSCA = *Tsuga canadensis. i.*

(Table 1). Each of the chronosequences included four stands located on a common soil series and landform that were experimentally clear-cut harvested ("Cut Only") or clear-cut harvested and burned ("Cut and Burn") over a period of nearly a century. We also examined three > 130-yr-old late successional forest communities categorized as deciduous broadleaf forest (DBF), evergreen needleleaf forest (ENF), or mixed deciduous-conifer forest (MIX). Chronosequence stands were positioned on an outwash plain of moderate site productivity and late successional stands, located on more productive outwash plains or moraine landforms (Nave et al., 2019), were remnant stands that escaped the region-wide deforestation occurring a century ago (Nave et al., 2017). All stands were within 14 km of one another. For categorical analysis of disturbance history, we delineated the following groups: late successional (i.e., disturbed over a century ago), Cut Only (i.e., disturbed by harvesting only in last century), and Cut and Burn (i.e., disturbed by harvesting and fire in last century). Each approximately 1-ha stand contained two or three circular, 0.1 ha plots (n = 29), with the exception of the 1998 stand, which, because of its irregular dimensions, included two rectangular 0.14 and 0.06 ha plots (Table 1).

Though our chronosequences were comprised of unreplicated stand ages, our study design and analysis employed space-for-time substitution best practices broadly used in ecological investigations when long-term time-series observations are not practical (Walker et al., 2010; Blois et al., 2013; Davies and Gray, 2015). Foremost, the soils, climate, and landform were uniform among our multi-decadal chronosequence stands (Table), which were systematically clearcut harvested and burned using identical experimental protocol (Gough et al. 2007). Limitations with space-for-time substitutions, including differences among stands in atmospheric conditions during growth, necessitate caution when interpreting results (Walker et al. 2010). Even so, our approach was modeled after several prior influential studies employing unreplicated chronosequences to examine long-term C cycling processes (Law et al., 2003; Bond-Lamberty et al., 2004; Irvine et al., 2004; Kashian et al., 2013).

2.2. Air temperature and light

To evaluate whether year-to-year climate variability was large enough to drive interannual variability in wood NPP, we examined time-series of mean annual air temperature and photosynthetically active radiation (PAR), the principal environmental drivers of year-to-year variation in C fluxes at our site (Gough et al., 2008). For long-term context, we present mean annual temperatures from 1897 to 2016 for Emmet County, MI (NOAA, National Centers for Environmental Information). We also calculated from this time-series the 10-yr coefficients of variation (CV) in air temperature, with the most recent CV coincident with the period (2006–2016) of NPPw measurement. Century-long records of PAR were not available; instead, we present above-canopy PAR during the period of wood NPP observation, collected by the nearby US-UMB AmeriFlux meteorological tower (Gough et al., 2013).

2.3. Net primary production of aboveground wood

We estimated the 10-yr annual aboveground wood net primary production (NPPw) of each plot using a dendrochronological approach in which stand-scale NPPw was inferred from annual growth rings. Our derivation of temporal stability using 10 years of NPPw data exceeds the minimum of 4 years applied to the global analysis of Musavi et al. (2017). In 2017, all stems > 8 cm diameter at breast height (DBH) within a plot were censused for DBH and species. In an effort to representatively sample all primary contributors to production, an increment borer was used to core a minimum of two randomly selected stems from each species that constituted > 5% total basal area within a plot, resulting in a total of nine to 14 stems sampled per plot and 318 total trees cored across all 29 plots (~20% of the total population).

We used WinDENDRO (Regent Instruments, Québec, Canada) software paired with an EPSON Expression 12000XL (Regent Instruments LA2400) scanner to image cores and estimate their yearly growth increment (YGI, i.e., annual ring width) from 2006 through 2016. YGIs were subtracted from the 2017 reference DBH to calculate the annual DBH of each associated tree. From reconstructed DBH values, wood biomass was calculated using species and site- or region-specific wood biomass allometries (Gough et al., 2007). The 10-yr annual wood production of each tree was calculated as the wood biomass difference between years. Subsequently, an annual relative growth rate (RGR) time-series was generated by dividing the annual wood production of an individual tree by its coincident wood biomass. Total stand-scale NPPw was estimated by multiplying year-, species- and plot-specific RGR values by the allometry-derived wood biomass values of non-cored individuals, and summing the wood production values for each individual tree within a plot. Our approach does not account for tree ingrowth and mortality during the 10-yr sampling period, but we generally find good long-term agreement between independent inventory and flux tower based estimates of production at our site (Gough et al., 2008). Dry weight NPPw was converted to C using a site-specific C density of 0.48 (Gough et al., 2008). Lastly, we used the approach of Musavi et al. (2017) to express the stability of NPPw as the coefficient of variation (CV) in 10-yr NPPw (2006–2016), where a lower number indicates greater temporal stability (or less variability) in NPPw. While NPPw from repeated DBH measurements was reported by Scheuermann et al. (2018), we supply independently derived dendrochronological NPPw to provide context for our core CV of NPPw results.

2.4. Structural complexity and species diversity

We evaluated relationships between NPPw temporal stability and both structural complexity and species diversity, features previously linked with the magnitude (but not stability) of NPPw at our site (Scheuermann et al., 2018). We used terrestrial LiDAR to derive a structural complexity measure termed "canopy rugosity", which is a spatially integrated measure of the vertical and horizontal variation in leaf density and arrangement (Hardiman et al., 2011). Canopy rugosity was estimated using the *forestr* (Atkins et al., 2018) package in R 3.5 (R Core Team, 2019) from 2-dimensional vegetation hit-grids constructed via upward-facing portable canopy LiDAR (PCL) sampling during 2017 along a 40-m transect passing through the center of each plot (n = 28, with one plot not sampled). We expressed stand-scale species diversity as the Shannon-Wiener (hereafter, "Shannon" for brevity) Index, which accounts for species' abundance and evenness. We estimated the Shannon Index of each plot (n = 29) from stem count and species data collected during the 2017 census (Scheuermann et al., 2018).

2.5. Leaf physiological and morphological traits

Hypothesizing a positive linkage between NPPw temporal stability and leaf trait variation, we characterized variation in subcanopy leaf morphology and physiology, similar to the approach of Garcia-Palacios et al. (2018) in which sampling distribution and intensity are intended to capture the variability within a plot. Without access to upper canopy leaves, we limited our sampling to 3 m above the forest floor, reasoning that the degree of subcanopy morphological and physiological variation – which was our interest – mirrors that of the upper canopy. Though the physiological competency and morphological features of canopy and subcanopy leaves are different, the subcanopy can be viewed as a "negative imprint" of the upper canopy, containing a mix of sun and shade-acclimated leaves formed in response to upper canopy vegetation cover and the resulting light environment (Stuart-Haentjens et al., 2015). Balancing our goal of quantifying subcanopy variation with sampling effort, we focused leaf mass area (LMA, n = 1542 total) sampling on three broadleaf (red maple, red oak, and beech) species and, because sampling is rapid, fluorescence intensity (Fs, n = 2541 total) measurements on the same broadleaf species plus two needleleaf (red and white pine) species. In each plot, three leaves were sampled from up to eight randomly selected individuals within each species. Fs, which serves as a high throughput surrogate of leaf photosynthetic rate under ambient conditions, was measured *in situ* on clear, windless days using an Opti-Sciences Y(II) Meter (Opti-Sciences Inc. Hudson, NH, USA). Broadleaves were harvested, scanned for area using a LI-3100C Area Meter (LI-COR Inc. Lincoln, NE, USA), weighed following drying at 55 °C, and LMA calculated as the quotient of leaf mass and area.

2.6. Statistical analysis

Our statistical analysis mapped onto our objectives, examining: (Obj. 1) how disturbance history and stand age relate to wood NPP temporal stability; (Obj. 2) whether more structurally complex and more diverse stands exhibit greater wood NPP temporal stability; and (Obj. 3) the degree to which subcanopy leaf trait variability relates to NPPw temporal stability. We used ANCOVA to evaluate how mean NPPw and the CV of NPPw relate to stand age, disturbance history, and the interaction between the two. We treated stand age as continuous and disturbance history as categorical variables, respectively, in the ANCOVA, with Cut Only (N = 4), Cut and Burn (N = 4) and late successional (N = 3) stands, respectively, considered true replicates because they shared a common disturbance history. We tested for pairwise differences among disturbance histories in the CV of NPP using Fisher's LSD (Obj. 1). The results of the ANCOVA additionally informed whether the Cut Only and Cut and Burn chronosequences warranted separate or common regression models. Based on *a priori* evidence of non-linear changes in NPPw with age (Hardiman et al., 2013b; Scheuermann et al., 2018), we fit and ranked linear and two- and three-parameter rise to maximum and exponential decay regression models, applying separate regressions to each chronosequence when the ANCOVA disturbance history × stand age interaction was significant ($P < 0.05$, Obj. 1). We used the same regression modeling approach to investigate how CV of NPPw relates to canopy rugosity and Shannon Index of Diversity (Obj. 2), and trait variability (Obj. 3). We omitted the analysis of age effects in late successional stands since they do not form a developmental continuum. We also evaluated whether a common (multivariate) model containing canopy rugosity, Shannon Index, and/or trait variability parameters predicts CV of NPPw regardless of stand disturbance history and age, using the Akaike Information Criterion (AIC) to rank and select significant model parameters. In figures, we present stand means with standard errors displaying spatial (i.e., plot-to-plot) variation within stands. Analysis was conducted in SAS 94 and SigmaPlot 14.0, reporting $P < 0.1$.

3. Results

3.1. Climate trends and mean wood NPP

Local air temperatures increased in the last century, with inter-annual variability in air temperature and photosynthetically active radiation (PAR) during the period of NPPw observation large enough to drive historical year-to-year variation in forest production at our site (Gough et al. 2008). A significant rise from 1897 to 2016 in mean annual air temperature, of 1.7 °C, was recorded for Emmet County, MI (Fig. 1A; $P < 0.0001$, $R^2 = 0.25$). Interannual variability in air temperature, expressed as the 10-year coefficient of variation (CV), reached a maximum of > 25% in the 1920′s and exceeded 15% in the most recent decade (Fig. 1B). From 2006 through 2016, our period of NPPw observation, we found that mean annual air temperature and mean photosynthetically active radiation (PAR) varied from year to year by as much as 4 °C (Fig. 1C) and > 100 μmol m^{-2} s^{-1} (Fig. 1D).

Our dendrochronological estimates of mean (10-yr) NPPw were similar in magnitude and trajectory to those derived by Scheuermann et al. (2018) through repeated DBH measurements. We observed an initial increase with stand age in Cut and Burn NPPw, which approached that of the already asymptotic Cut Only NPPw at ~40 years (Fig. 2). Chronosequence stand NPPw averaged from 500 to 900 kg C ha^{-1} yr^{-1}, with the youngest Cut and Burn stand exhibiting the lowest production. Consistent with Scheuermann et al. (2018), we found that NPPw was greatest in late successional DBF (> 1200 kg C ha^{-1} yr^{-1}) and lower by half or more in ENF and MIX stands.

3.2. Wood NPP stability and disturbance history

Counter to our hypothesis, we observed high NPPw temporal stability (i.e., lower CV of NPPw) in the most severely disturbed Cut and Burn stands. The mean CV of NPPw was lowest for stands in the Cut and Burn chronosequence and greatest in late successional stands ($P < 0.05$, Fig. 3), with clearcut harvested and burned stands exhibiting 25% greater temporal stability in NPPw than late successional stands.

3.3. NPPw stability, canopy rugosity, and species diversity in relation to stand age

We observed contrasting patterns of NPPw temporal stability with increasing age in the Cut Only and Cut and Burn chronosequences. Over seven decades of stand development, the CV of NPPw in Cut Only stands declined by nearly half, though this trend was largely driven by high variation of 11% in the youngest stand (Fig. 4A: p = < 0.0441, Adj R^2 = 0.31). In Cut and Burn stands, the pattern of wood NPP stability and age was the opposite, with CV of NPP_w increasing slightly from 5% to 8% over a ~60-yr period (Fig. 4A: p = 0.0619, Adj R^2 = 0.31). The CVs of NPPw in the > 130-yr-old late successional stands were 7% to 10%, falling within the range of values for the younger chronosequence stands. In late successional stands, mean CV of NPPw was ENF > MIX > DBF ($P < 0.05$), indicating that older stands with a larger evergreen component displayed less stable NPPw over time.

Unlike NPP_w temporal stability, we found age-species diversity and -canopy rugosity patterns were the same regardless of disturbance history. In both chronosequences, the Shannon Index of species diversity increased rapidly with age in the younger stands (< 50 yrs) and increased more gradually in middle successional stands (Fig. 4B: p = 0.0002, Adj R^2 = 0.53). The Cut and Burn and Cut Only stands exhibited a common significant, linear increase in canopy rugosity (Fig. 4C, p = < 0.0001, Adj R^2 = 0.77). Late successional canopies were 1.5–2 × more rugose than the oldest chronosequence stand. Our independent estimates of species diversity and canopy rugosity are similar to those derived two years earlier by Scheuermann et al. (2018).

3.4. Wood NPP stability as a function of diversity and canopy rugosity

Species diversity and canopy rugosity exerted variable effects on the temporal stability of NPPw. Shannon Index of species diversity was negatively correlated with the CV of NPPw in Cut Only (Fig. 5A, p = 0.0588, Adj R^2 = 0.27) and late successional stands (Fig. 5A, p = 0.0016, Adj R^2 = 0.75). Conversely, we observed a moderate increase in the CV of NPPw with rising Shannon Index in the Cut and Burn stands (Fig. 5A, p = 0.0066, Adj R^2 = 0.63). With canopy rugosity-age trajectories tightly conserved, we found that relationships between NPPw temporal stability and canopy rugosity in the Cut Only and Cut and Burn chronosequences mirrored those of NPPw temporal stability and stand age (Fig. 5B). The CV of NPPw of stands in the Cut Only chronosequence declined nonlinearly as canopy rugosity increased, falling from 11 to 7% (Fig. 5B, p = 0.0345, Adj R^2 = 0.34). Conversely, The CV of NPPw for Cut and Burn stands increased significantly with rising rugosity, signaling diminishing temporal stability of NPPw in more complex stands (Fig. 5B, p = 0.0487, Adj R^2 = 0.37). Canopy

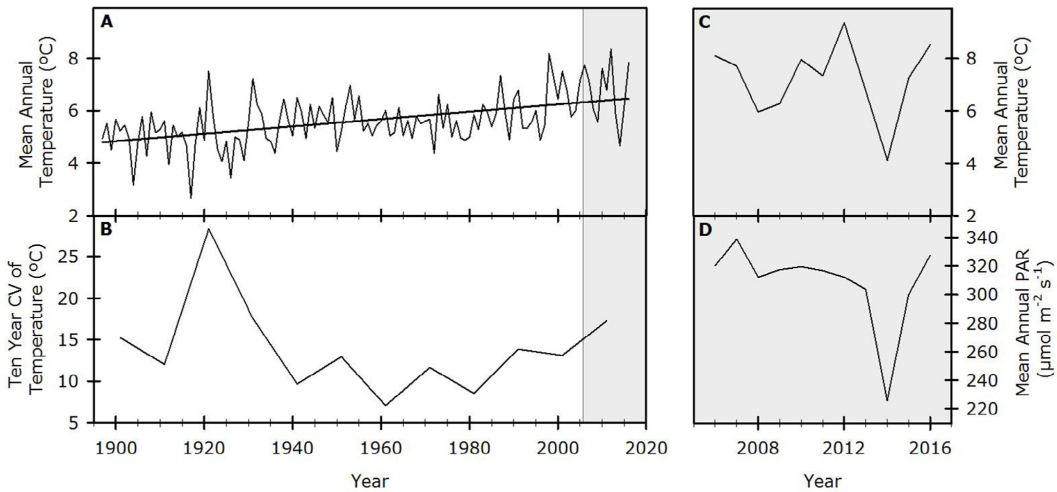

Fig. 1. Emmet County, MI annual mean (A: $P < 0.0001$, $R^2 = 0.25$) and coefficients of variation (CV) in temperature (B, 10-year increments) from 1897 to 2016. Inset C and D highlight mean annual air temperature and photosynthetically active radiation (PAR) at our site from 2006 to 2016 (gray shading), the period during which we examined net primary production stability. Long-term (A, B) data obtained from NOAA (National Centers for Environmental Information) and short-term, 10-year (C, D) data obtained from the UMB AmeriFlux tower. Mean annual air temperature and PAR were previously shown to be the primary environmental drivers of interannual variation in production at our site (Gough et al., 2008).

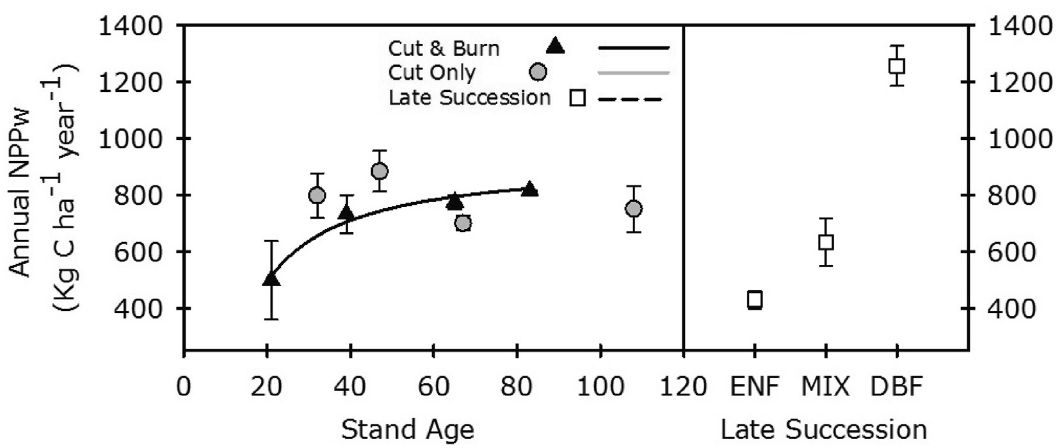

Fig. 2. Relationships between mean (10-yr) annual NPPw and Cut & Burn and Cut Only stands, and mean annual NPPw for late successional communities. Annual NPP_w for the "Cut & Burn" chronosequence is significantly related to stand age ($p = 0.011$, Adj $R^2 = 0.57$). Means ± 1 S.E.

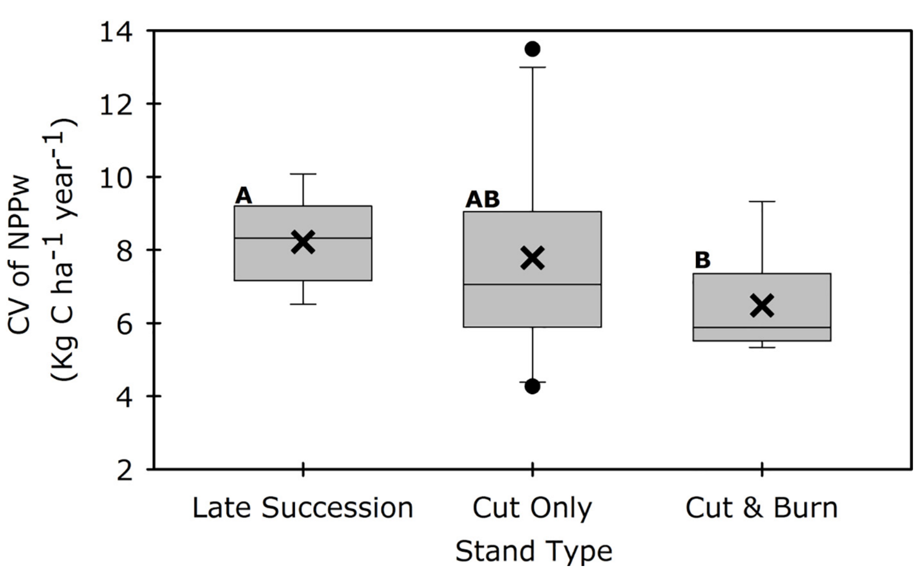

Fig. 3. Differences in the coefficient of variation (CV) in wood net primary production (NPP_w) for stand types differing in disturbance history. Unique letters indicate significant mean differences ($\alpha = 0.05$). X – mean; upper and lower whiskers – maximum and minimum values, respectively; upper and lower edges of box – interquartile range; line inside box – median; dots – outliers. N = 3 stands for late succession and N = 4 stands for Cut Only and Cut & Burn stand types.

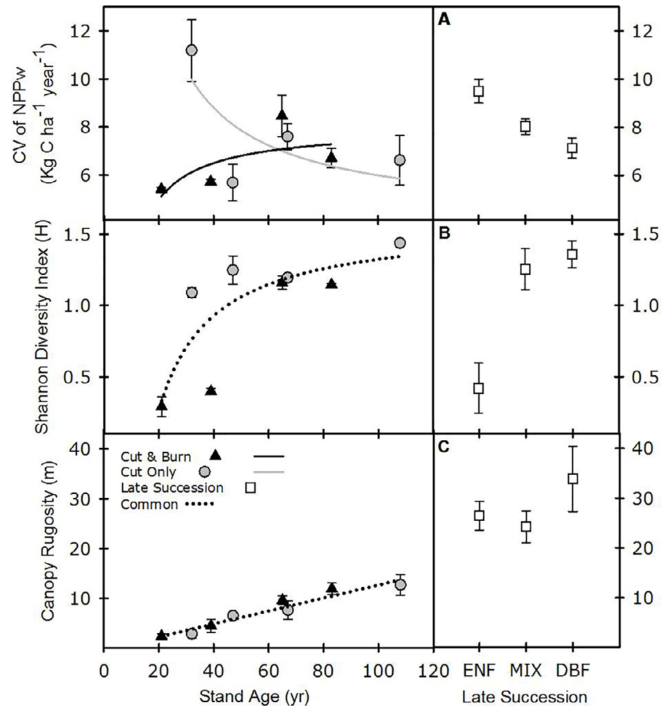

Fig. 4. Forest stand age and late succession functional type in relation to stand coefficient of variation (CV) in annual wood net primary production (NPP_w, A), Shannon Diversity Index (H, B) and canopy rugosity (C). CV of NPPw is negatively related to age in the "Cut Only" (A: p = < 0.0441, Adj R^2 = 0.31) chronosequence and positively related to age in the "Cut and Burn" (A: p = 0.0619, Adj R^2 = 0.31) chronosequence. "Cut Only" and "Cut and Burn" stands exhibited common relationships between stand age and both Shannon Diversity Index and canopy rugosity (B: p = 0.0002, Adj R^2 = 0.53; C: p < 0.0001, Adj R^2 = 0.77). Means ± 1 S.E.

rugosity did not explain variation in the temporal stability of NPPw among late successional stands.

3.5. Sub-canopy leaf morphological and physiological traits

With one exception, subcanopy leaf morphological and physiological variation poorly predicted NPPw temporal stability (Fig. 6). The CVs of LMA and Fs varied nearly 2-fold among stands, indicating substantial differences in the range of leaf traits present in subcanopies. However, these differences generally did not correspond with significant changes in the CV of NPPw when individual or combined models were fitted to chronosequence and late successional stands. The exception was a weakly significant positive relationship between CV of Fs and CV of NPPw in late successional stands (Fig. 6B, p = 0.0966, Adj R2 = 0.07), in which the DBF stand exhibited high NPPw temporal stability and low subcanopy leaf physiological variation.

3.6. Multivariate model selection for a common model

Inconsistent univariate relationships between the CV of NPPw and candidate explanatory variables limited the development of a common multivariate model predicting temporal stability of NPPw regardless of disturbance history and age. In our AIC model selection, none of the four candidate explanatory variables were retained as significant parameters explaining variation among all 11 stands in the CV of NPPw. Specifically, P-values were: 0.5204 for canopy rugosity; 0.5282 for Shannon Index; 0.9628 for CV of LMA; and 0.8371 for CV of Fs.

4. Discussion

We found that the temporal stability of production in the temperate forests surveyed was high relative to forests globally. Most studies examining the temporal stability of primary production center on grasslands, which display relatively high CV of NPP values of up to 60% (Cadotte et al., 2012; Polley et al., 2013; Zelikova et al., 2014). Comparatively, the CV of gross primary production was 2–38% for forests globally (Musavi et al., 2017), with most sites falling below 20%. Similarly, a survey of European forests reported CV of aboveground NPP values of 12.5 to 25% (Jucker et al., 2014). Our CV of NPPw values of 5–11% indicate that the forests we sampled exhibit high temporal stability, even across a broad range of stand structural complexity, diversity, and prior disturbance. Though much more limited in breadth relative to global values, the > 2-fold difference among stands in temporal stability highlights the importance of local – in addition to large spatial scale ecoclimatic – factors in determining the degree of interannual variation in production.

In contrast to our hypothesis, more recently and severely disturbed Cut and Burn stands displayed greater NPPw temporal stability than late successional stands established over a century ago. Our finding is at odds with theoretical and empirical studies reporting greater *structural* temporal stability in less disturbed ecosystems (Gunderson, 2000; Loreau and de Mazancourt, 2013). However, the effect of disturbance history on the temporal stability of ecosystem *functions*, such as NPP, remains unclear because of a paucity of studies on the topic (Anderegg et al., 2016; Hillebrand et al., 2018). Though examples from forest

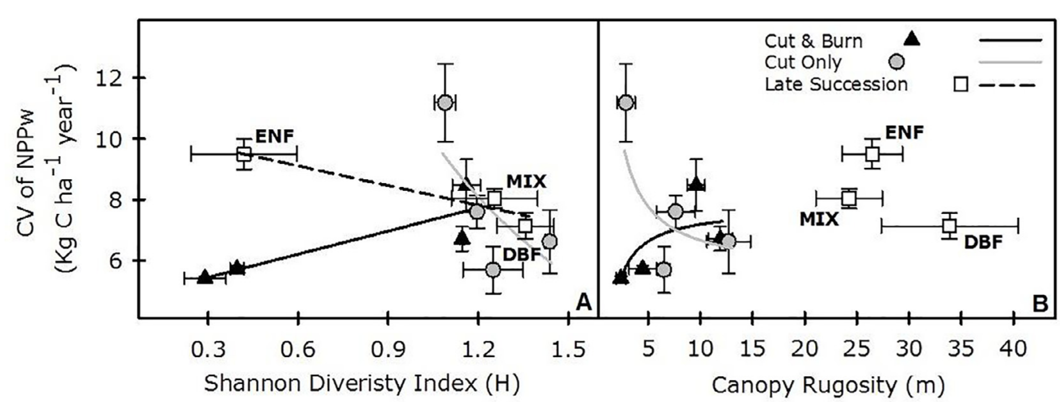

Fig. 5. Stand coefficient of variation (CV) of annual wood net primary production (NPPw) in relation to canopy rugosity and Shannon Diversity Index for "Cut and Burn" and "Cut Only" chronosequences, and three late successional stands. As Shannon diversity index increased, the CV of NPPw declined in the Cut Only chronosequence (A: p = 0.0588, Adj R^2 = 0.27) and late successional stands (A: p = 0.0016, Adj R^2 = 0.75) and increased in the Cut and Burn chronosequence (A: p = 0.0066, Adj R^2 = 0.63). CV of NPPw increased significantly with canopy rugosity in the "Cut and Burn" (B: P = 0.0487, Adj R^2 = 0.37) chronosequence and declined in the "Cut Only" (B: p = 0.0345, Adj R^2 = 0.34) stands. Means ± 1 S.E.

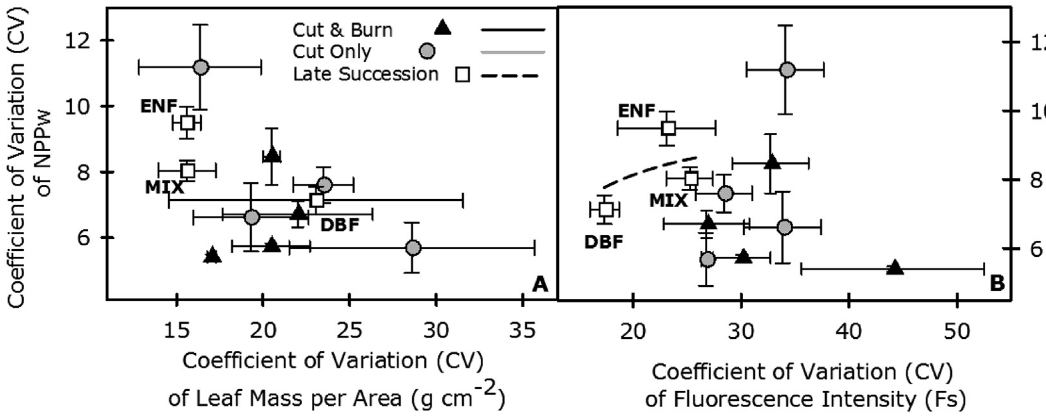

Fig. 6. Stand coefficient of variation (CV) of annual wood net primary production (NPPw) in relation to stand subcanopy leaf trait variability. Subcanopy leaf traits include leaf mass per area (LMA; A, not significant) and chlorophyll fluorescence intensity (Fs, B: $p = 0.0966$, Adj $R^2 = 0.07$). Means ± 1 S.E.

ecosystems are lacking, a grassland study found the stability of different ecosystem functions varied in response to a common disturbance, suggesting some functions may be more sensitive than others to disturbance (Saruul et al., 2019). Direct effects of disturbance history aside, more severely disturbed Cut and Burn stands may display greater temporal stability because the expressed range of NPPw is narrower than that of more productive older stands (Scheuermann et al., 2018). Temporal stability may be relatively low in highly productive stands with a broader and more dynamic range of functioning; conversely, when production is low, the range of variability and potential for the ecosystem to respond to changing conditions may be more limited (Stone et al., 1996). Prior investigation in our study system demonstrated that the more severe Cut and Burn disturbance diminished long-term nitrogen availability (Nave et al., 2019), a factor known to affect the degree of variation in year-to-year production (De Boeck et al., 2018).

Also departing from expectations, we observed opposite trends in the relationship between CV of NPPw and age in the two chronosequences, suggesting that the temporal stability of production does not automatically increase as forests age. At the biome-scale, Musavi et al. (2017) reported strong positive effects of age on the gross primary production temporal stability (similarly defined as CV over time) for temperate forests, speculating that a progressive improvement with age in the complementary use of growth-limiting resources stabilizes production. Counter to the analysis of Musavi et al. (2017) that encompassed a range of forest types varying in age, we found that within the same forest type the more severely disturbed Cut and Burn chronosequence exhibited a slight decrease in NPPw temporal stability with stand age. In these stands, severe fire disturbance imposed long-term nutrient limitations (White et al., 2004; Nave et al., 2019) that stunted structural and functional redevelopment (Scheuermann et al., 2018) and prompted a long-term trajectory of low production – and thus less production variability – in young stands (Gough et al., 2007). The discrepancies between our results and those of Musavi et al. (2017) reinforce calls for studies that broadly address the mechanisms supporting functional stability at multiple spatial scales (Pretzsch et al., 2015; Forrester et al., 2018; Hillebrand et al., 2018).

Our findings indicate variable effects of species diversity, structural complexity, and subcanopy leaf properties on temporal stability of production. This somewhat contrasts with our expectation that older, more structurally complex, species diverse, and multi-layered forest canopies would contain a broader complement of (or display greater variance in) subcanopy leaf physiological and morphological traits and that this would enhance NPPw temporal stability. We and others have observed positive effects of species diversity and structural complexity on the magnitude of NPP (Hardiman et al., 2011; Fahey et al., 2015; Danescu et al., 2016; Liang et al., 2016; Juchheim et al., 2017; Pedro et al., 2017), with leaf trait complementarity (Zhang et al., 2012) potentially conferring greater whole-ecosystem resource-use efficiency (Zhang et al., 2012; Forrester, 2019). The mixed relationships observed here between variability in NPP and both canopy complexity (rugosity) and species diversity (Shannon Index) suggest the lack of a uniform effect of ecosystem and community structure on the temporal stability of production, at least within our study system. Similarly, we found that the degree of variation in leaf morphology and physiology was nominally predictive of variation in stand-scale production temporal stability. Our observations do not support forest model simulations predicting leaf functional diversity increases carbon cycling stability following disturbance (Pedro et al., 2015) or the empirical analysis of dry ecosystems establishing a positive relationship between NPP temporal stability and variation in specific leaf area, the reciprocal of leaf mass area (Garcia-Palacios et al., 2018). Though the reliance of ecosystem functioning on leaf morphological and physiological properties is widespread (Wang et al., 2012; Poorter et al., 2016; Fisher et al., 2018), relationships are not universal among ecosystems or consistent across leaf traits (Finegan et al., 2015; Xu et al., 2018). Similarly, whether stand structure exerts a positive or negative influence on NPP temporal stability may be a function of how complexity features are operationally defined, measured, and derived (Forrester, 2019). A lack in uniformity across ecosystems in how and which structural and leaf properties influence ecosystem-scale processes such as primary production exposes the need to better understand the mechanisms that underlie these putative connections (Forrester, 2019; Gustafsson and Norkko, 2019), particularly within the understudied context of ecosystem stability.

With few studies available for direct comparison, particularly in forest ecosystems, our results and conclusions should be qualified and carefully contextualized. First, the use of unreplicated chronosequence studies, though valuable for space-for-time substitutions (Johnson and Miyanishi, 2008; Walker et al., 2010), may introduce uncertainty associated with co-varying factors, other than age, from stand to stand such as soil properties and atmospheric conditions during development. Despite known limitations, our approach, which used experimentally created chronosequences positioned on a common soil series and landform, followed best practices for space-for-time substitution studies (Davies and Gray, 2015). Second, when considering stand structure-production stability interactions, we focused on a subset of diversity and complexity indices correlated with rates of NPP at our site (Hardiman et al., 2011; Hardiman et al., 2013b; Scheuermann et al., 2018); however, our results indicate that stand properties correlated with rates of NPP may not strongly or consistently predict NPP temporal stability, suggesting a mismatch between structural features that regulate production rates and stability. Lastly, our analysis of subcanopy leaf trait variability, though drawing from a relatively large sample size averaging > 140 leaves per stand, did not extend to upper canopy leaves. Subcanopy sampling, though logistically tractable and related to upper canopy environmental and leaf physiological properties, may have undersampled the breadth of functionally relevant variation in leaf traits within the canopy.

5. Conclusion

We conclude that the temporal stability of wood net primary production varies > 2-fold among species and structurally diverse upper Great Lakes forests varying in age and disturbance history, highlighting a large degree of variability among stands in the stability of annual carbon accumulation in wood. The causes for differences among forest stands in the temporal stability of wood primary production are less clear from our results, with structural complexity, species diversity, and subcanopy leaf traits variably tied to stability. While these mixed findings preclude us from making firm management recommendations, our results suggest the following for foresters and land-use specialists focused on the C management of upper Great Lakes forests: 1) a history of severe disturbance may not degrade the temporal stability of production; 2) in late successional forests, more species diverse and structural complex stands, as defined in our analysis, may be associated with greater temporal stability; and 3) structural complexity, while predictive of production rate, is a capricious indicator of temporal stability. We recommend that future work center on understanding why some canopy structural and compositional features confer greater rates of production but not stability, and identify the stand characteristics that can be cultivated through management to balance goals of maximal C sequestration and stability.

Data availability

All data presented in figures 2–6 is provided numerically with metadata via figshare DOI: https://figshare.com/projects/Wales_et_al_2020_-_Forest_Ecology_and_Management/74226.

CRediT authorship contribution statement

Shea B. Wales: Conceptualization, Data curation, Formal analysis, Investigation, Writing - original draft. **Mark R. Kreider:** Data curation, Investigation, Methodology, Writing - original draft. **Jeff Atkins:** Formal analysis, Investigation. **Catherine M. Hulshof:** Data curation, Formal analysis. **Robert T. Fahey:** Data curation, Supervision, Writing - original draft. **Lucas E. Nave:** Data curation, Methodology, Project administration, Writing - original draft. **Knute J. Nadelhoffer:** Data curation, Methodology, Project administration, Writing - original draft. **Christopher M. Gough:** Data curation, Methodology, Project administration, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.117865.

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