

Disturbance has variable effects on the structural complexity of a temperate forest landscape

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ABSTRACT

The temporal dynamics of forest canopy structure are influenced by disturbances that alter vegetation quantity and distribution. While canopy structural indicators such as leaf area index (LAI), canopy cover, and canopy height have been widely studied in the context of disturbance, the post-disturbance temporal dynamics of structural complexity, which summarizes the heterogeneity of vegetation arrangement, are poorly understood. With the goal of advancing conceptual and empirical understanding of the temporal dynamics of structural complexity following disturbance, we synthesized results from three large-scale disturbance manipulation experiments at the University of Michigan Biological Station (UMBS): the 4-year Forest Resilience Threshold Experiment (FoRTE) manipulating levels of disturbance severity; the decade-long Forest Accelerated Succession Experiment (FASET), in which all early successional tree species were stem-girdled within 39 ha in the same landscape; and forest chronosequences established following clear-cut harvesting. We found that the temporal dynamics of canopy structure following disturbance were dependent upon three factors: (1) the source and severity of disturbance; (2) the spatial and temporal scales of analysis; and (3) the measure of structure assessed. Unlike vegetation area index and canopy cover, which initially decreased in response to disturbance, structural complexity measures such as canopy and top rugosity did not consistently respond to moderate levels of disturbance severity. Over multi-decadal timescales, structural complexity increased to a maximum, regardless of whether fire occurred at the time of stand establishment, but intervening low-to-moderate severity disturbance in regrown century-old forests altered trajectories of canopy rugosity. We conclude that structural complexity indicators display a more nuanced temporal and directional response to disturbance than conventional leaf area and cover indexes. Predicting what disturbance conditions modify trajectories of structural complexity remains critical to disturbance characterization and the inference of ecosystem functioning.

1. Introduction

Forest canopy structural features, shaped by succession and disturbance, are potent indicators of ecosystem functioning across spatial and temporal scales. Commonly measured canopy structural indicators such as leaf area index (LAI), canopy cover, and canopy height are related to core ecosystem processes, including primary production, water-use

efficiency, and biogeochemical cycling rates (Asner et al. 2003; Reich 2012). Such indicators can also be used to characterize the spatial extent and severity of disturbance from ground inventories and via airborne and satellite remote sensing (Gough et al. 2022). LAI, canopy cover, and canopy height generally decline immediately following disturbance (Atkins et al. 2020; Parker 2020; Stovall et al. 2019), and then gradually increase to a maximum over successional timescales following a pattern

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that is largely consistent across forest ecosystems (Franklin et al. 2002; Gough et al. 2021b). This knowledge of how disturbance and time interact to affect canopy structure has helped improve ecological modeling (Antonarakis et al. 2011; Bondeau et al. 1999), the interpretation of remote sensing of ecosystem stress, disturbance, and functioning (Lindroth et al. 2008; Townsend et al. 2012), and forest management (Glatthorn et al. 2017). However, such understanding is limited to a few widely measured structural indicators (Ali 2019; Parker 2020).

Less is known about the post-disturbance temporal dynamics of canopy structural complexity, which may be more closely coupled with ecosystem functioning than conventional indicators of structure (Hart and Kleinman 2018; Juchheim et al. 2017; Pedro et al. 2017). The term “structural complexity” encompasses indicators describing the multidimensional heterogeneity of vegetation density and/or distribution in the canopy interior or outer surface (Atkins et al. 2018a; Ehbrecht et al. 2017; Ehbrecht et al. 2016; Franklin et al. 2002; Gough et al. 2020). Contemporary measures of structural complexity may be particularly robust indicators of ecosystem functioning because they are spatially integrative, summarizing 2- to 3-dimensional arrangements of canopy vegetation rather than spatially averaged dimensionless (e.g., LAI) or 1-dimensional (e.g., canopy height) indicators. Greater structural complexity is associated with optimized resource use and more complete resource acquisition (Hardiman et al. 2013b), similar to the mechanisms underlying plant diversity-ecosystem functioning relationships (Williams et al. 2017). Unlike LAI, canopy cover, and height (Hardiman et al. 2013a), but similar to diversity (Thom and Seidl 2016), complexity may decrease (Hardiman et al. 2013a), increase (Fahey et al. 2020; Meigs and Keeton 2018; Reed et al. 2022), or stay the same following disturbance (Fahey et al. 2015). Like more commonly measured structural indicators and diversity, complexity generally increases with forest age, reaching a maximum in late successional forests (Hickey et al. 2019; Scheuermann et al. 2018).

Prior studies, including our own, examining structural complexity's response to disturbance vary in duration of observation, source of disturbance, and forest type, limiting synthetic and theoretical advancement of disturbance-time-complexity interactions (Mathes et al. 2021). To address this limitation, we synthesized three large-scale experiments from the University of Michigan Biological Station (UMBS) to understand how disturbance interacts with succession to shape trajectories of structural features with ties to ecosystem processes. Rather than an exhaustive assessment of canopy structural indicators, we focus on a subset of lidar-derived canopy structural metrics coupled to ecosystem functioning at our site and others: vegetation area index (VAI), cover fraction, mean outer canopy height (MOCH), canopy rugosity, top rugosity, and rumple; the latter three are measures of interior or outer canopy complexity (defined in detail below). Our analysis synthesizes separate large-scale disturbance manipulation experiments varying in timescale of interest, and source and severity of disturbance, specifically asking the following questions (Q): **Q1** How does disturbance severity and the orientation of disturbance within the canopy affect short-term changes in forest structure?; **Q2** How does disturbance that kills early successional tree species affect decadal structural change? **Q3** How do two different stand-replacing disturbances (clear-cut only, clear-cut + fire) affect forest structure over multi-decadal (i.e., successional) time-scales? An overarching synthesis question (**Q4**) tying the three experimental disturbances together is: which canopy structural features respond similarly over time to the disturbances above, and which ones exhibit variable responses? We conclude by proposing a conceptual model of structural complexity's response to disturbance across time-scales and in response to different disturbance sources and severities.

2. Methods

2.1. Sites and experiments

The University of Michigan Biological Station (UMBS) in northern lower Michigan, USA (45.56 N, 84.67 W) hosts three large-scale

disturbance experiments. The landscape encompasses a range of forest ecosystems, disturbance histories, and ages that are representative of the upper Great Lakes region (Nave et al. 2017). With few exceptions, primary forests were clear-cut harvested during the early 20th century and, in most cases, subsequently burned (Frelich 1995). Presently, the UMBS landscape is mostly comprised of regrown 100-yr-old forest once dominated by early successional pioneer bigtooth and trembling aspen (*Populus grandidentata* and *P. tremuloides*, respectively) and paper birch (*Betula papyrifera*) (Gough et al. 2010), and rapidly giving way to later-successional red oak (*Quercus rubra*), eastern white pine (*Pinus strobus*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*). Defoliating and phloem-disrupting disturbances across UMBS that cause patchy, moderate tree mortality are increasing, and include forest tent caterpillar (*Malacosoma disstria*), spongy moth (*Lymantria dispar*), emerald ash borer (*Agrilus planipennis*), and the beech bark disease complex. Mean annual air temperature is 5.5 °C and mean annual precipitation is 817 mm (Gough et al. 2021b).

Our forest disturbance treatments, detailed below, were implemented asynchronously at stand/plot (0.1–1 ha) to landscape (33 ha) scales and simulate both the historical severe, stand-replacing disturbance regimes and the contemporary low-to-moderate severity disturbance regime driven by biotic or age-related senescence (Fig. 1a). All experimental plots and landscapes are within 14 km of one another (Fig. 1b). The duration of observations following experimental disturbance and the timescale of interest varied among experiments from years to centuries. Each of the three disturbance manipulations and their biogeochemical (i.e., carbon, nitrogen, and/or water cycling) and, to a lesser extent (see below), canopy structural effects are detailed in prior, separate publications; disturbance effects on canopy structure have not been synthesized across experiments. We summarize each experiment below and in Table 1, referencing key publications.

2.1.1. The forest Resilience Threshold Experiment (FoRTE, Q1)

The Forest Resilience Threshold Experiment (FoRTE) was established in 2018 to evaluate how disturbance severity and orientation within the canopy affect C cycling processes, and vegetation structure and composition (key references: Atkins et al. 2021; Gough et al. 2021a). The study design consists of four levels of disturbance severity and two disturbance orientations replicated in four different forest ecosystems spanning a range of productivities, compositions, and structures present in the upper Great Lakes region (Lapin and Barnes 1995). Disturbance treatments were implemented via stem girdling, which, like wood boring insects (e.g., emerald ash borer), kills woody plants once carbohydrate reserves are exhausted over a period of two to three years (Dietze et al. 2014; Gough et al. 2013). Following a year (2018) of pre-treatment data collection, >3600 trees with stems >8 cm diameter at breast height (DBH) were selected experiment-wide for girdling in May 2019. Species- and site- or region-specific allometries (Gough et al. 2008) relating DBH to leaf area were used to target gross LAI reductions within each plot of 0% (control), 45%, 65%, or 85%. Gross defoliation levels were assigned at random to four, 0.5 ha circular whole plots, which were split into 0.25 ha halves and randomly designated “top-down” or “bottom-up” disturbance orientations. For the “top-down” treatment, the largest trees were girdled first, irrespective of species, starting with the highest leaf-area individual and sequentially girdling lower leaf-area trees until the assigned plot disturbance severity was reached. For the “bottom-up” treatment, individual trees > 8 cm DBH with the lowest leaf area were stem girdled first, followed by sequentially larger trees up to the targeted disturbance severity. Circular, 0.1 ha sampling subplots were established within each disturbance severity × type treatment in each of the four replicates (n = 32 subplots total) and surrounded by a 5-m wide measurement-free treatment buffer. Canopy structure was characterized in 2018 (before disturbance) and 2021 (three years after disturbance). Detailed methodology and results are found in vignettes contained within the project's open field notebook: <https://fortexperiment.github.io/fortedata/> (Atkins et al. 2021).

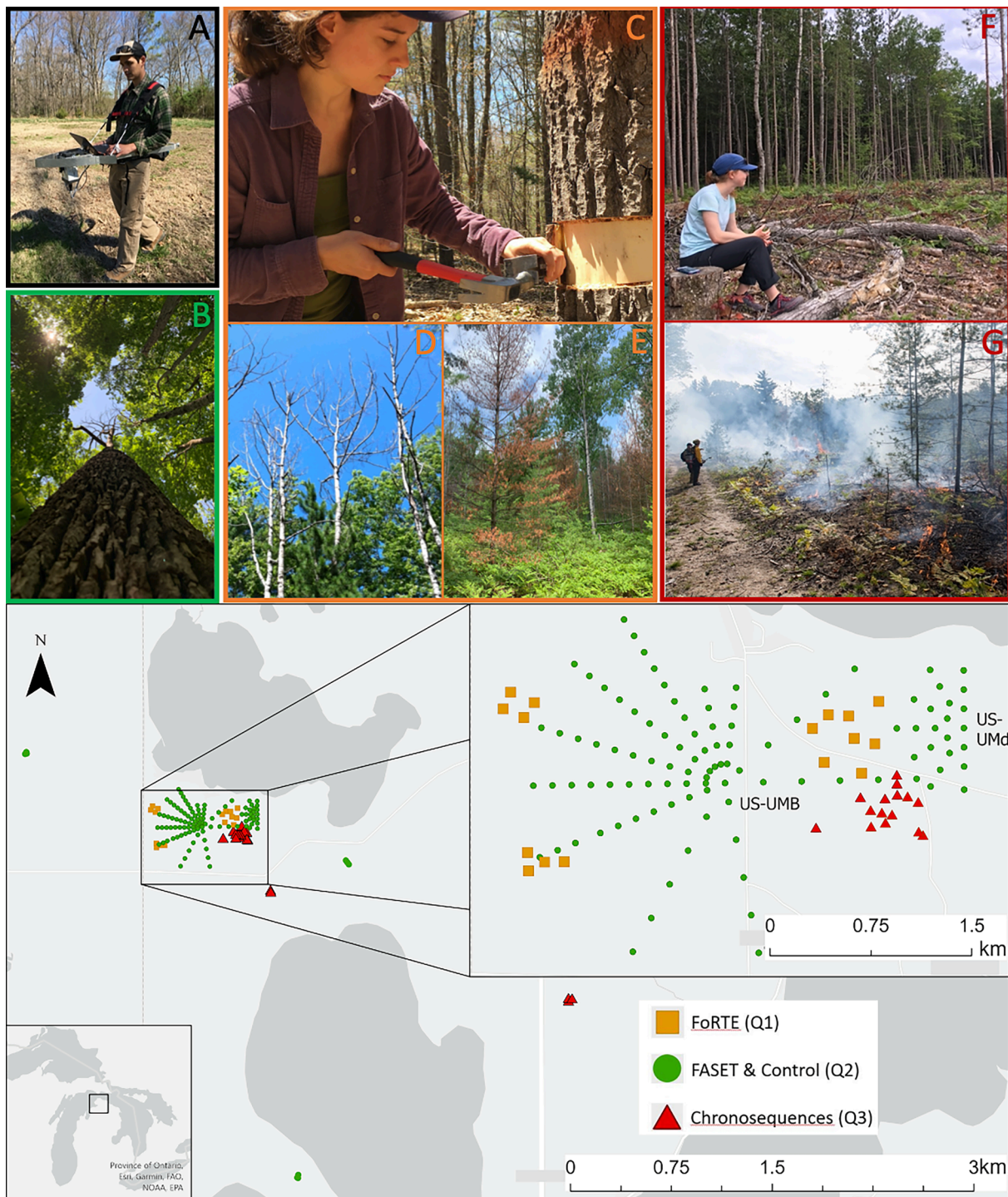


Fig. 1. We used a portable canopy lidar (PCL, A) to derive forest canopy structural metrics summarizing vegetation area, cover, height, and complexity. PCL Sampling occurred in: unmanipulated control/baseline forests (B); forests in which ~ 10,000 trees total were stem-girdled (C) to achieve different levels of tree mortality at landscape (D) and plot (E) scales; and 100-yr forest chronosequences initiated following experimental clear-cut harvesting only (F) and clear-cut harvesting and fire (G). Timescales of interest included years, decades, and centuries, and encompass multiple disturbance sources and severities, and spatial scales. The map illustrates the locations of PCL sampling plots within each experimental manipulation, organized by research question (Q). US-UMB (<https://ameriflux.lbl.gov/sites/siteinfo/US-UMB>) and US-UMd (<https://ameriflux.lbl.gov/sites/siteinfo/US-UMd>) are Ameriflux site identifiers.

Table 1

Site summaries for the Forest Resilience Threshold Experiment (FoRTE), the Forest Accelerated Succession Experiment (FASET), and the Cut and Burn and Cut only forest chronosequences. The year each experimental disturbance treatment was implemented is provided; for late successional references, stand establishment dates are specified. Stem density and diameter at breast height (DBH) are for trees with DBH > 8 cm. The three most dominant woody plant taxa by basal area are provided.

Experiment/ PFT	Description	Established	Plot N	Stems ha ⁻¹	Mean DBH	Dominant taxa	References
FoRTE	Stem girdled to achieve disturbance severities of 0, 45, 65, 85% gross defoliation	2019	32	865	19.5	POGR, ACRU, QURU	Atkins et al. 2021; Gough et al. 2021a
FASET/ Control	Stem girdling all mature POGR, BEPA	2008	21/ 81	750	19.3	POGR, ACRU, QURU	Gough et al. 2021b; Gough et al. 2013; Nave et al. 2011
Cut and burn	Twice cut, twice burned	1936	2	1335	17.1	POGR, PIST, ACRU	Gough et al. 2007; Nave et al. 2017; Nave et al. 2019; Scheuermann et al. 2018; Wales et al. 2020
		1954	2	1355	14.1	POGR, QURU, PIST	
		1980	3	1597	11.4	POGR, QURU, ACRU	
		1998	2	725	9.2	POGR, QURU	
	Twice cut, once burned	1911	3	793	21	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	
Late successional	DBF	1850	3	433	34.0	FAGR, TSQA, QURU	
	ENF	1890	3	753	28.8	PIRE, POGR, BEPA	
	MIX	1890	3	657	26.8	PIRE, POGR, PIST	

PFT = Plant functional type (late successional stands only); DBF = Deciduous Broadleaf Forest, ENF = Evergreen Needleleaf Forest, Mix = Mixed deciduous evergreen forest; POGR = *Populus grandidentata*, QURU = *Quercus rubra*, ACRU = *Acer rubrum*, PIST = *Pinus strobus*, PIRE = *Pinus resinosa*, BEPA = *Betula papyrifera*, FAGR = *Fagus grandifolia*, TSQA = *Tsuga canadensis*.

2.1.2. The forest accelerated succession experiment (FASET, Q2)

The Forest Accelerated Succession Experiment (FASET) was established in 2008 to identify how disturbance from age-related senescence and succession affect C cycling in aging mixed temperate forests (key publications: Gough et al. 2021b; Gough et al. 2013; Nave et al. 2011). In May 2008, >6,700 early successional aspen and birch trees were stem girdled within a 33 ha contiguous landscape, thereby accelerating the transition to a composition and structure that approximates longer-term changes projected for forests regionally. Experimental defoliation from girdling was compounded by patchy forest tent caterpillar (*Malacosoma disstria*) herbivory in 2010 (Gough et al. 2013). An undisturbed forested landscape, ~1 km away, serves as a control. The FASET treatment is contained within the primary C flux footprint of Ameriflux tower US-UMd (Gough et al 2016-) and the control is in the footprint of the US-UMB tower (Gough et al 1999-). Canopy structural observations were conducted at the FASET manipulation in a single 1-ha sampling plot at the base of the tower and three, 0.1 ha plots spaced 100-m apart along each of seven 250- or 300-m-long transects (n = 22 total plots). Observations within the control landscape were conducted in one, 1-ha center plot and 80, 0.1 ha plots separated by 100 m along 500- to 1000-m long transects radiating from the base of the tower (n = 81 total plots). Canopy structural data were collected during peak leaf-out between 2009 and 2018.

2.1.3. Clear-cut harvesting and fire disturbance forest chronosequences (Q3)

Two experimental forest chronosequences were established to investigate decadal-to-century patterns of forest biogeochemical cycling, composition, and structure following stand-replacing disturbances of the early 20th Century (key publications: Gough et al. 2007; Nave et al. 2017; Nave et al. 2019; Scheuermann et al. 2018; Wales et al. 2020). Stands in a clear-cut only forest chronosequence were harvested

in 1911, 1952, 1972, or 1987; a second chronosequence was established following experimental clear-cut harvesting and burning in 1936, 1954, 1980, or 1998. Soils, climate, and landform were uniform among chronosequence stands. In addition, three late successional “legacy” stands were identified that represent forest compositions and structures that would be present in the upper Great Lakes region today in the absence of widespread deforestation a century ago. These > 130-yr-old late successional stands include three plant functional groups: deciduous broadleaf forest (c. 1833), evergreen needleleaf forest (c. 1890), and mixed deciduous-conifer forest (c. 1891). Each approximately 1-ha stand contained two or three circular, 0.1 ha sampling plots (n = 29 total), with the exception of the 1998 stand, which, because of its irregular dimensions, included two rectangular 0.14 and 0.06 ha plots. Canopy structural data were collected during peak leaf-out in 2021.

2.2. Canopy structure

2.2.1. PCL scanning and derivation of canopy structure

We characterized canopy structure in each of the 164 experimental plots or subplots using a terrestrial portable canopy LiDAR (PCL) system (Parker et al. 2004). The system has been used previously at our site to: relate canopy structure to net primary production in the control US-UMB tower footprint (Hardiman et al. 2011; Hardiman et al. 2013b); investigate initial (2008–2011) canopy structural changes following tree mortality in the FASET manipulation (Hardiman et al. 2013a) and elsewhere (Atkins et al. 2020); contrast decade-long patterns of canopy structural-C cycling change in control and FASET landscapes (Gough et al. 2021b); and interpret structure-C cycling interactions at century time-scales (Scheuermann et al. 2018; Wales et al. 2020). Thus, our synthesis integrates for the first time a subset of already-published canopy structural data reported in separate experiment-specific contexts in addition to newly reported observations. The PCL is based on an

upward facing, near-infrared pulsed-laser operating at up to 2000 Hz (model LD90-3100VHS-FLP, Riegl USA, Inc., Orlando, FL, USA). Our system was mounted on a custom-built frame worn by operators while walking along transects that passed through the center of each sub/plot. While sub/plot areas and dimensions varied, PCL transects were standardized to a minimum of 40 m, which is longer than the 30 m minimum length at which structural metrics stabilize within contiguous forest stands at our site (Hardiman et al. 2018). We binned the raw data horizontally and vertically into 1-m² grids for structural analysis, and derived estimates of canopy structure using the *forestr* package (Atkins et al. 2018a) in R 4.1 (R Core Team, 2021).

2.2.2. Description of canopy structural metrics

We focus on ecological indicators of functional significance to temperate forests. Therefore, we limit our reporting to canopy structural measures correlated with forest primary production, light-use and nitrogen-use efficiency, and canopy light absorption at our site and/or the broader eastern deciduous biome (Atkins et al. 2018b; Gough et al. 2019; Hardiman et al. 2013b). These include: mean outer canopy height (MOCH; m); vegetation area index (VAI; dimensionless, includes leaf and woody biomass); canopy rugosity (m; vertical and horizontal vegetation density and distribution variability); top rugosity (m; outer canopy surface vegetation density and distribution variability); rumple (dimensionless; ratio of canopy outer surface area to ground surface area); and canopy cover (%; ratio of bins returning lidar hits to the total bin number). Three of these measures – canopy rugosity, top rugosity, and rumple – summarize stand-scale complexity, describing different but related aspects of canopy physical structural heterogeneity (Gough et al. 2020). In-depth descriptions and mathematical derivations of each structural measure are found in Atkins et al. (Atkins et al., 2018a).

2.3. Analysis

Our statistical analysis examined changes over time in canopy structure in response to each of the three disturbance manipulations, comparing: (Q1) 3-year changes in canopy structure across FoRTE's disturbance severity gradient and with bottom-up/top-down disturbance orientations; (Q2) decadal trends in canopy structure in the FASET and control landscapes; and (Q3) decade-to-century trajectories of canopy structure following clear-cut harvesting or clear-cut harvesting and fire. To address each question, we first used linear regression to determine whether disturbance treatment $\times$ time interactions were significant ($\alpha = 0.1$). If interactions were significant, then disturbance treatments were modeled separately using linear and non-linear regression to account for variation among canopy structural indicators in patterns of change over time (Hardiman et al. 2013a; Hardiman et al. 2013b); if interactions were not significant, a single model was fit to data irrespective of treatment. Linear vs non-linear model selection was determined using AIC scores, though small sample sizes limited the application of non-linear models. For Q1, in addition to regression models evaluating canopy structural relationships with disturbance severity before (2018) and after disturbance (2021), we evaluated the significance of pre- and post-disturbance differences in canopy structure within disturbance severity and bottom-up/top-down treatment categories. We present regression trendlines and associated p-values when $P < 0.1$. All data and SAS (V9.2) and R code associated with our analysis are available via <https://data.ess-dive.lbl.gov/view/ess-dive-c6f3f2c564bcc45-20220413> T200325029 and <https://doi.org/10.5281/zenodo.6452902>.

3. Results

3.1. Q1: Short timescale (0–3 years): Disturbance severity and canopy structure

We tracked canopy structure for 3 years following FoRTE's disturbance severity and orientation manipulations, assessing responses in two ways. For the first, we evaluated canopy structure's relationship with disturbance severity before (in 2018) and 3 years following (in 2021) disturbance, treating gross defoliation as a continuous variable. While canopy structure-disturbance severity relationships were not significant before disturbance, three years after disturbance we observed significant declines in stand VAI and canopy cover, and, conversely, an increase in one of three complexity indicators as disturbance severity increased from 0% to 85% gross defoliation (Fig. 2). VAI and canopy cover declined by $\sim 20\%$ across the disturbance severity gradient, less than the 85% gross defoliation level targeted experimentally via stem girdling. Conversely, top rugosity increased by $\sim 20\%$ across disturbance severities, indicating that an increase in gross defoliation augmented the heterogeneity of outer canopy vegetation density as tree crown height became more variable following patchy mortality. Significant trends across severities did not emerge for MOCH, canopy rugosity, or rumple following disturbance.

A second complementary analysis assessed the significance of changes in canopy structure from pre- (2018) to post- (2021) disturbance categorically by disturbance severity (gross defoliation) and treatment orientation (bottom-up/top-down). Complexity measures generally increased at the highest (65% and 85%) disturbance severities, while displaying no significant temporal change in response to disturbance orientation (Fig. 3). VAI and canopy cover declined from 2018 to 2021 in all disturbance treatments, except the control. Mean outer canopy height exhibited no change over time. However, top rugosity and rumple increased over the 3-year period in 65% and 85% gross defoliation treatments, while canopy rugosity increased only at the 65% level. Treatment orientation (i.e., bottom-up/top-down girdling) did not significantly alter complexity measures. These findings show that declines in VAI and canopy cover were associated with commensurate increases in structural complexity of the outer, and to a lesser extent, interior canopy, as the FoRTE disturbance enhanced the spatial heterogeneity of vegetation density along vertical and horizontal axes.

Combined, these analyses of canopy structure across disturbance severity levels (Fig. 2) and over time (Fig. 3) demonstrate that moderate levels of disturbance can increase stand structural complexity in the short-term, even while reducing the quantity of vegetation with which to build canopy structure. The degradation of tree crowns in this previously closed canopy forest, in particular, appears to have diversified canopy height and, to a lesser extent, generated interior heterogeneity in vegetation distribution.

3.2. Q2: Decadal timescale: Early successional species decline and canopy structure

We observed similar decadal declines in vegetation area, cover, and height in the control landscape and in the disturbed (FASET) landscape, while complexity measures declined or stayed the same after disturbance (Fig. 4). Decadal reductions in VAI and canopy cover approached 1 unit and 10%, respectively, while mean outer canopy height fell by > 1.5 m in both the control and moderately disturbed landscapes. Canopy rugosity declined over the same time period in the disturbed forest

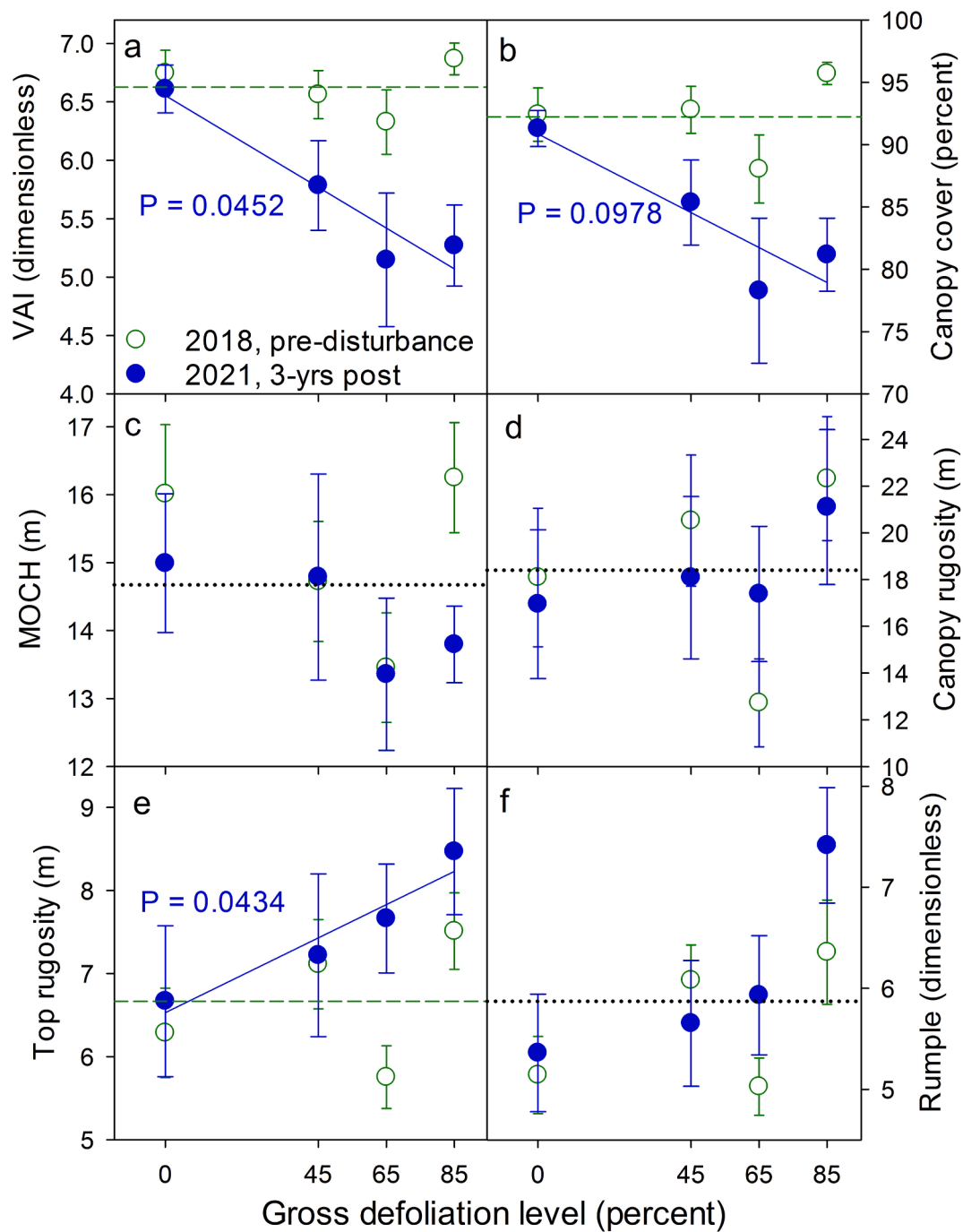


Fig. 2. Vegetation area index (VAI, a), canopy cover (b), mean outer canopy height (c), canopy rugosity (d), top rugosity (e), and rumple (f) across a disturbance severity gradient characterized by the level of gross defoliation, 2018 (pre-disturbance) and 2021 (3 years after disturbance). Dashed and dotted lines illustrate means by year of measurement or for all years when significant trends ($P < 0.1$) were not observed. values Mean ± 1 S.E.

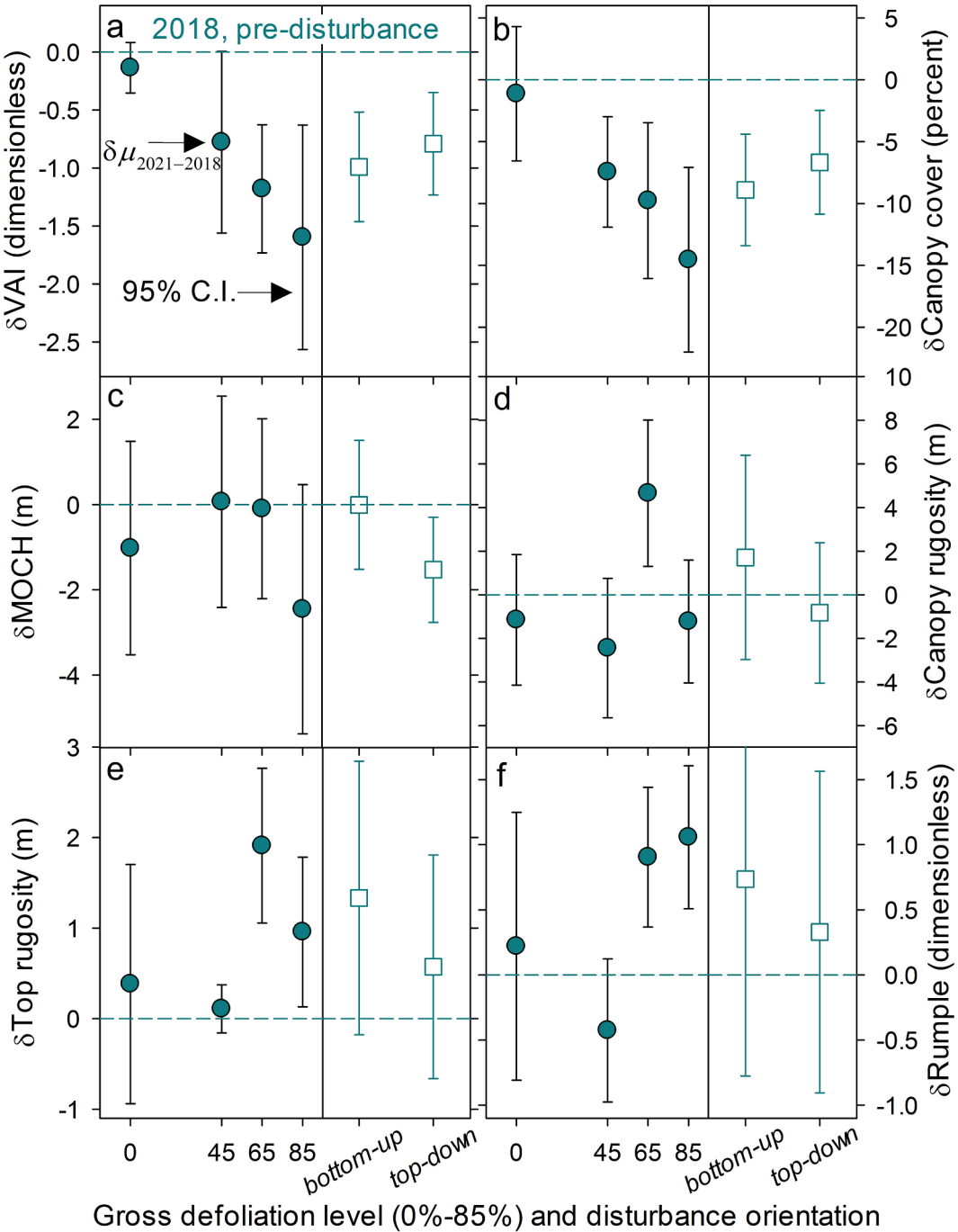


Fig. 3. Mean 3-year differences between pre- (2018) and post- (2021) disturbance vegetation area index (VAI, a), canopy cover (b), mean outer canopy height (c), canopy rugosity (d), top rugosity (e), and rumple (f) within gross defoliation and bottom-up/top-down treatment categories. Mean differences $\pm$ 95% confidence intervals (C.I.), with non-overlapping C.I.s indicating significant changes after disturbance.

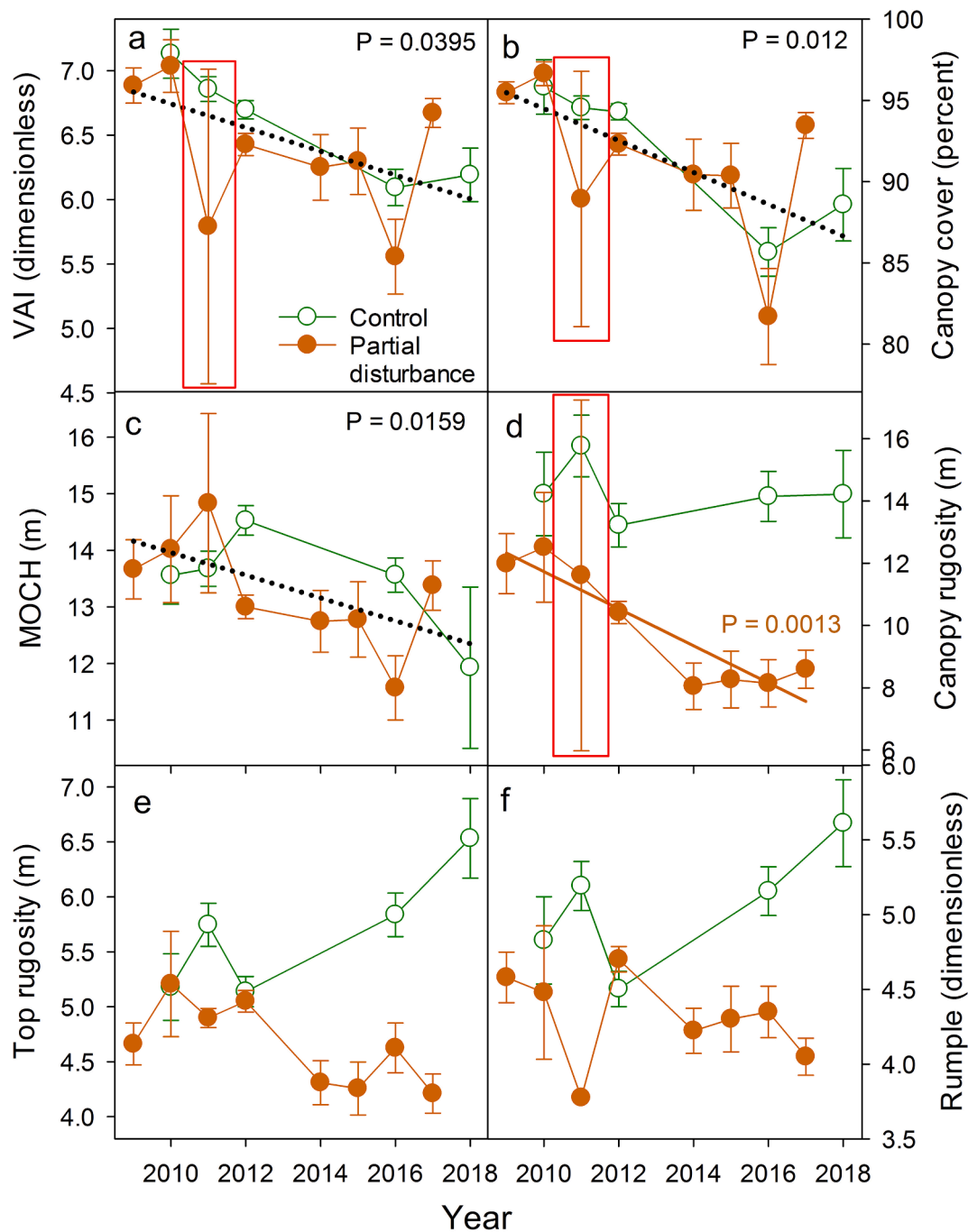


Fig. 4. Vegetation area index (VAI, a), canopy cover (b), mean outer canopy height (c), canopy rugosity (d), top rugosity (e), and rumple (f) in control and moderately disturbed forest landscapes, 2009–2018. Dotted lines illustrate significant common trends over time for both forest landscapes and the solid orange trendline indicates the significant decline in only the moderately disturbed landscape ($P < 0.1$). Red boxes highlight the high within-landscape variability three years after disturbance. values Mean $\pm$ 1 S.E. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

landscape, while remaining stable in the control. In both the control and treatment forests, top rugosity and rumple displayed high interannual variability, exhibiting no decadal pattern. Thus, the decline of early successional species from the tallest dominant canopy position affected interior rather than outer complexity and, unlike FoRTE's species-nonspecific complexity-enriching disturbance, the FASET disturbance eroded complexity. Large mean standard errors three years after disturbance point to a temporary increase in within-landscape (i.e., cross-plot) canopy structural variation, particularly in VAI and canopy rugosity (red boxes, Fig. 4).

3.3. Q3: Century timescale: Canopy structure following clear-cut harvesting and fire

The addition of fire after clear-cut harvesting had mixed effects on the century-long recovery of canopy structural features (Fig. 5). VAI and canopy cover were higher in stands that experienced fire, and these structural measures increased slightly with stand age. Mean outer canopy height, top rugosity, and rumple increased similarly during successional development, regardless of whether fired followed clear-cut harvesting. Stands that were clear-cut and burned exhibited a significantly higher rate of development (i.e., greater slope) in canopy rugosity

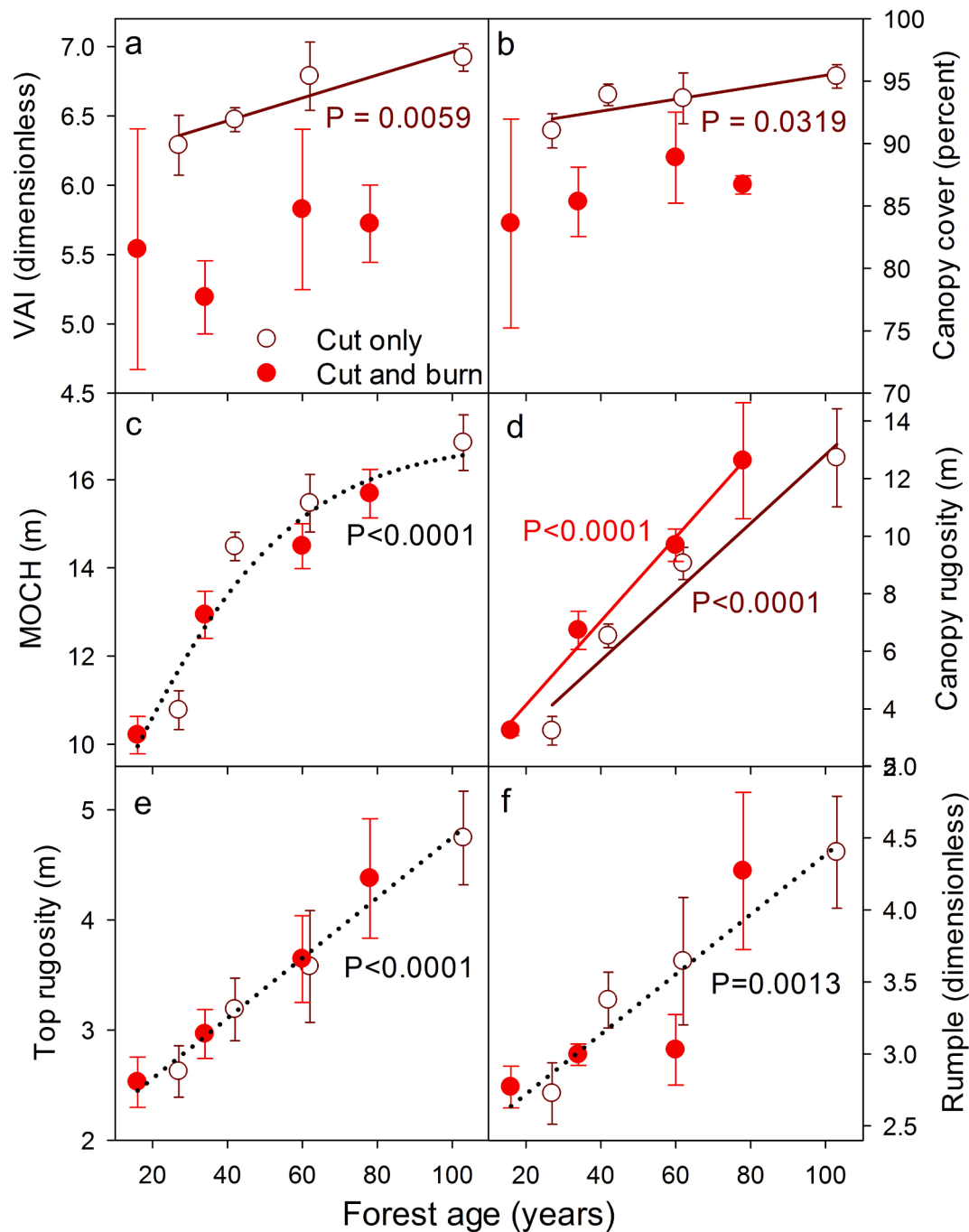


Fig. 5. Vegetation area index (VAI, a), canopy cover (b), mean outer canopy height (c), canopy rugosity (d), top rugosity (e), and rumple (f) in Cut only and Cut and burn forest chronosequences. Dotted lines illustrate significant common trends over time for both forest chronosequences and the solid trendlines indicate significantly different increases over time in Cut only and Cut and burn chronosequences ($P < 0.1$). values Mean ± 1 S.E.

relative to those that were clear-cut only, but differences were quantitatively small and the oldest stands of both chronosequences converged on a similar maximum canopy rugosity value of ~ 13 m. Therefore, while fire modestly influenced the successional trajectories of VAI and canopy cover, the long-term temporal dynamics of structural complexity and height were similar regardless of whether fire occurred at the time of clear-cut harvesting.

3.4. Q4: Synthesis: Structural complexity and disturbance-time interactions across timescales

Focusing on lesser-known patterns of complexity, we combined

results from our disturbance experiments and three additional late-successional stands (>100 yrs-old) to illustrate how canopy rugosity's response to disturbance varies depending on temporal scale, and disturbance source and severity (Fig. 6). Canopy rugosity, a measure more strongly tied to ecosystem functioning in our forested landscape than leaf area or cover (Hardiman et al. 2011), exhibited an s-shaped pattern over nearly 200 years of successional development in the absence of moderate or severe disturbance. Unlike stand-replacement (Fig. 6, red arrow), stem girdling disturbance that eliminated a fraction (~ 45 – 65%) of trees in the century-old forest initially increased or decreased (Fig. 6, orange arrows) – rather than reset – canopy rugosity. Moderate severity disturbance affecting early successional tree species

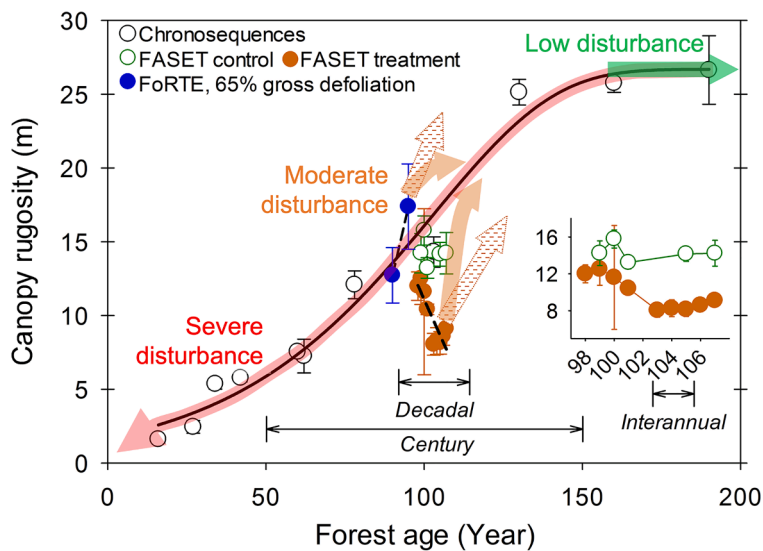


Fig. 6. The temporal dynamics of canopy structural complexity, as canopy rugosity, across the UMBS landscape vary as a function of timescale (horizontal black arrows) and disturbance source/severity (red, orange, and green arrows). In the absence of moderate or severe disturbance, complexity may increase to an asymptotic maximum over successional timescales (green arrow). Intervening moderate severity disturbances may cause complexity to permanently (in the case of state change, shaded orange arrow) or temporarily (solid orange arrow) deviate above or below the smoothed long-term trend. Severe stand-replacing disturbance may fully reset the successional development of complexity (red arrow). The solid (successional) trendline is a 4-parameter sigmoidal Weibull model fitted to chronosequence and late successional stand data ($P < 0.0001$, $r^2_{\text{adjusted}} = 0.97$). Data for three (>100-yr-old) late successional stands are from [Wales et al. \(2020\)](#); FASET and FoRTE data are from this synthesis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

caused a temporary, one-third reduction in canopy rugosity, while 65% gross defoliation, irrespective of species, initially increased canopy rugosity, but the longer-term trajectories are not yet clear. Succession-resetting disturbance reduced structural complexity by an order of magnitude relative to maximum values observed in late successional stands for at least two decades.

4. Discussion

Our findings offer several insights into how disturbance alters temporal patterns of canopy structure in a temperate forest landscape. Our 3-year (FoRTE) stand-scale manipulation of disturbance severity and orientation within the canopy caused anticipated losses in vegetation area and cover, though at levels below treatment targets, and enriched structural complexity at moderate to high levels of gross defoliation (Q1). Conversely, FASET's accelerated succession treatment, implemented at the landscape level, reduced canopy interior structural complexity (Q2). While fire following clear-cut harvesting produced different multi-decadal patterns of LAI and cover, the successional trajectories of canopy complexity and height were quantitatively similar (Q3). Synthesizing observations from these experiments (Q4), we conclude that changes over time in canopy structure following disturbance were dependent on the source and severity of disturbance, and the spatial and temporal scales of manipulation. Different indicators of canopy structure exhibited different post-disturbance temporal dynamics. Notably, vegetation area and cover routinely declined as a result of disturbance, which is broadly consistent with observations from other forests ([Cooper-Ellis et al. 1999](#); [Kashian et al. 2005](#); [Peters et al. 2013](#); [Turner et al. 2016](#)), but the directionality and magnitude of change in indicators of structural complexity varied considerably.

Collectively, our experiments inform a conceptual model (Fig. 6), in which the successional development of structural complexity in the absence of pulse disturbance ([Jentsch and White 2019](#)) is tightly constrained, with intervening low-to-moderate severity disturbances modifying the trajectory of structural complexity. The relatively uniform development of structural complexity over successional timescales, irrespective of disturbance history, may be driven by system-wide optimization of resource acquisition and use ([Fotis and Curtis 2017](#); [Hardiman et al. 2013b](#)). At the leaf- to whole-plant scales, niche partitioning may spatially and temporally constrain individuals' positions and interactions with neighbors, while physiological acclimation and opportunistic growth may ensure stems and leaves are arranged to maximize the capture and optimal use of limiting resources such as light ([Anten 2016](#); [Fotis et al. 2018](#); [Niinemets 2012](#); [Retkute et al. 2015](#);

[Sarlikioti et al. 2011](#)). The ecological consequence of this leaf-to-neighborhood resource optimization, when scaled to the stand and landscape, may be the constrained succession of 3-dimensional vegetation arrangements. While niche partitioning and thus resource-use may intensify as forests age and species diversity increases ([Finke and Snyder 2008](#)), a more temporally constrained pattern of canopy rugosity than diversity at our site ([Scheuermann et al. 2018](#); [Wales et al. 2020](#)) reinforces observations that the two are related but not fully coupled, and complex structures can arise in low diversity forests ([Gough et al. 2020](#); [Hickey et al. 2019](#)). Moreover, canopy rugosity's conserved successional pattern at our relatively tree species-poor site may explain why complexity rather than diversity is more strongly tied to growth-limiting resource use and primary production within our forest landscape ([Scheuermann et al. 2018](#)).

However, disturbances that cause tree mortality alter vegetation arrangements ([Turner et al. 1998](#)) and, thus, appear to redirect these otherwise fixed successional patterns of spatial heterogeneity. Our experiments illustrate that, when these disturbances are moderate in severity, they can either increase or decrease structural complexity, and affect vegetation in different areas of the canopy. For example, in the FASET experiment targeting the tallest trees, structural complexity likely decreased because canopy height declined. Canopy height and structural complexity are closely intertwined, with height constraining the canopy volume with which to build complex vegetation arrangements ([Atkins et al., 2022](#); [Gough et al., 2021b](#)). A gradual recovery in structural complexity may be underway in the FASET forest, however, and could be associated with the stabilization and recent increase in mean outer canopy height. In contrast, FoRTE's disturbance treatments targeted all tree species and multiple size classes and, as a result, diversified rather than reduced canopy height, leading to increases in complexity. That structural complexity may increase, decrease, or remain the same immediately after non-stand replacing disturbance is consistent with observations elsewhere ([Atkins et al. 2020](#); [Fahey et al. 2020](#); [Meigs and Keeton 2018](#); [Meigs et al. 2017](#); [Peterson 2019](#); [Reed et al. 2022](#)), and counter to vegetation area, cover, and quantity measures, which consistently decline following disturbance ([Parker 2020](#)).

Less clear is when and whether disturbance-driven departures from successional trajectories are permanent, signaling a state change, or instead will return to the long-term trendline as the canopy reorganizes. Particularly in younger forests, disturbances that initially reduce the heterogeneity of vegetation distribution could stimulate long-term increases in complexity, for example, by releasing subcanopy vegetation and increasing crown architectural variety ([Willim et al., 2022](#)). Older and more complex forests, however, may respond with less sensitivity to

low-to-moderate severity disturbance (Fahey et al., 2015) when “noncumulative” tree mortality is in balance with regeneration (*sensu*, Bormann and Likens 1979). Understanding which disturbances enhance versus erode structural complexity, and for how long, merits investigation and will require long-term data collection for a number of different disturbance sources and sites (Jucker, 2022; McDowell et al. 2020).

While the response of structural complexity to disturbance is more nuanced than that of leaf area and cover, species diversity indicators respond with similar variability, possibly because of the close relationship between structural and biological complexity. Structurally complex forests contain an array of plant and crown architectures with which to build variable vegetation arrangements (Gough et al. 2020) and, accordingly, disturbances that eliminate or change distributions of species may reduce complexity (Ehbrecht et al. 2017). Our (FASET) landscape-scale analysis that affected early successional tree species illustrated several parallels between structural complexity and diversity. First, the ephemerally high variance around mean canopy rugosity in the third year underscored the large degree of spatial variation within the landscape, mirroring the scale dependencies and considerations of diversity (Turner and Tjorve 2005). Second, in our experiment, interior but not outer canopy complexity declined in response to the accelerated succession disturbance, analogous to the opposing responses of evenness and richness to disturbance in a boreal forest reported by others (Yeboah et al. 2016). Third, canopy complexity’s lagged response to stem girdling demonstrates that, as with diversity, structural changes may not be immediate, and thus short-term observations could result in an incomplete, or even erroneous, interpretation of disturbance response (Pedro et al. 2017). Lastly, observations from our FoRTE study and others emphasize that structural complexity and diversity exhibit variable responses to gradients of disturbance severity. Similar to critiques that the intermediate disturbance hypothesis – positing an increase in diversity at moderate disturbance levels – is too general (Whittaker et al. 2001), our findings reinforce the idea that the effects of disturbance severity on structural complexity cannot be reduced to a single response (Atkins et al. 2020).

Our findings suggest that care should be taken when detecting and interpreting the functional consequences of disturbance from structural complexity measures. Remotely sensed changes in canopy spectrometry and physical structure are routinely used to detect and quantify the location, size, and duration of disturbance from aircraft and spaceborne instrumentation (Senf et al. 2017). These approaches generally use statistical change-detection algorithms to detect losses in vegetation area, cover, and/or changes to greenness (Zhu 2017). Because the directionality of structural complexity’s response to moderate disturbance varies and is dependent upon the indicator of complexity assessed, such indicators may be less useful – given our current limited understanding – to disturbance detection. However, when paired with conventional structural metrics such as canopy cover, which consistently declines following disturbance, structural complexity observations, which are derived from the second statistical moment (variance) of characteristics of canopy structure, could offer insights into functional responses that are not discernible from metrics derived from the mean (first statistical moment) of a canopy characteristic (Cardille et al. 2022). Which structural complexity indicators emerge as useful proxies for ecosystem functioning following disturbance remains a frontier that is increasingly within reach as ground-to-satellite remote sensing of 3-dimensional canopy structure becomes more tractable (Jucker, 2022).

In addition, our findings have implications for the design and application of forest management actions. Increasingly, ecologically-oriented forest management emphasizes the promotion of structural complexity through silvicultural activities, as a way of enhancing ecosystem goods and services (D’Amato and Palik 2021; Fahey et al. 2018). Management treatments that mimic the moderate disturbances imposed in the FoRTE study could increase complexity in targeted ways,

thereby boosting canopy light interception, light-use efficiency, wood production, and carbon sequestration (Atkins et al. 2018b; Fahey et al. 2019). However, our results suggest that the severity and location within the canopy of silvicultural application may produce different structural and, consequently, functional outcomes (Atkins et al. 2020). For example, in our analysis, top-down and bottom-up disturbances had different effects on canopy height and, to some extent, emulated high and low tree diameter thinnings, respectively, targeting different tree size classes. Additionally, our FASET results suggest that the harvest of a single plant functional group could erode forest structural complexity by reducing canopy volume and the crown morphological variation with which to build heterogeneous vegetation arrangements. However, these same results and theoretical expectations of system-wide optimization suggest that the effects of management emulating moderate severity disturbance could be short-lived and have limited impacts on long-term trajectories of complexity and related ecosystem functions. Applying findings such as ours to silvicultural applications will require additional mechanistic understanding of which structural changes also modify ecosystem functions of interest to managers, and for how long.

5. Conclusions

We conclude that structural complexity within our forest landscape developed uniformly over successional timescales but, unlike many conventional measures of structure, complexity responded variably to moderate severity disturbance on short time-scales. This suggests that region-wide increases in moderate severity disturbance from insect pests, pathogens, and extreme weather may present challenges for the prediction and interpretation of future complexity and associated ecosystem functions. Like species diversity, complexity’s most consistent responses occurred at the extreme low and high ends of the disturbance severity continuum, with low disturbance constraining the successional development of complexity and severe disturbance (e.g., from clear-cut harvesting and/or fire) resetting complexity to low levels. The response dynamics that follow moderate disturbance levels were more variable and depended on disturbance severity and source, the measure of complexity examined, and the timing of observations. It is unknown whether and under what circumstances such moderate severity disturbances will permanently redirect the long-term successional dynamics of complexity. Our findings, while specific to our forested landscape, underscore the large degree of variation in how canopy structure responds to different disturbances. Questions remain regarding why, to what extent, and for how long structural complexity changes persist following disturbance and whether such responses are uniform across ecosystems. Advancing understanding in this area will require continuous, multi-decadal measurements of structural complexity for multiple ecosystems and disturbance types, a possibility as the next generation of satellite remote sensing tools launch with the capability of measuring canopy structure, along with diversity (Skidmore et al. 2021), at unprecedented spatio-temporal resolutions.

6. Data and code availability

Lidar-derived canopy structural data are provided here: <https://doi.org/10.5281/zenodo.6452902>. Analysis code and data used in this paper can be accessed via the following repository:

Gough C; Atkins J; Bohrer G; Curtis P; Bond-Lamberty B; Hardiman B; Fahey R; Tallant J; Nave L; Niedermaier K; Hickey L; Clay C (2022): Analysis scripts in support of the manuscript “Disturbance has variable effects on the structural complexity of a temperate forest landscape”. Forecasting Carbon Storage as Eastern Forests Age: Joining Experimental and Modeling Approaches at the UMBS Ameriflux Site, ESS-DIVE repository. Dataset. [ess-dive-c6f3f2c564bcc45-20220413T200325029](https://data.ess-dive.lbl.gov/datasets/ess-dive-c6f3f2c564bcc45-20220413T200325029) accessed via <https://data.ess-dive.lbl.gov/datasets/ess-dive-c6f3f2c>

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CRediT authorship contribution statement

Christopher M. Gough: Conceptualization, Methodology, Formal analysis, Writing – original draft, Supervision, Project administration, Funding acquisition, Writing – review & editing. **Jeff W. Atkins:** Methodology, Software, Investigation, Resources, Data curation, Writing – review & editing. **Robert T. Fahey:** Methodology, Investigation, Resources, Funding acquisition, Writing – review & editing. **Peter S. Curtis:** Supervision, Project administration, Funding acquisition, Writing – review & editing. **Gil Bohrer:** Supervision, Project administration, Funding acquisition, Writing – review & editing. **Brady S. Hardiman:** Supervision, Project administration, Funding acquisition, Writing – review & editing. **Laura J. Hickey:** Resources, Data curation, Writing – review & editing. **Lucas E. Nave:** Supervision, Project administration, Funding acquisition, Writing – review & editing. **Kerstin M. Niedermaier:** Resources, Data curation, Writing – review & editing. **Cameron Clay:** Resources, Data curation, Writing – review & editing. **Jason M. Tallant:** Resources, Data curation, Writing – review & editing. **Ben Bond-Lamberty:** Software, Investigation, Resources, Data curation, Writing – review & editing.

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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