

Effects of forest structural and compositional change on forest microclimates across a gradient of disturbance severity

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ABSTRACT

Forest structural diversity and community composition are key in regulating forest microclimates. When disturbance affects structural diversity or composition, forest microclimates may be altered due to changes in soil temperature, soil water content, and light availability. It is unclear however which structural or compositional components, when changed or to what extent, result in microclimatic change. To address this question, we used data from a large scale, manipulative stem-girdling experiment in northern, lower Michigan—the Forest Resilience and Threshold Experiment (FoRTE). FoRTE follows a factorial design with multiple levels of disturbance severity (0, 45, 65, 85%) based on targeted reductions in gross leaf area index via stem-girdling induced mortality. These disturbance severity treatments are applied in two ways: either as top-down (largest trees are killed) or bottom-up (small to medium trees killed) treatments. We examined how multiple components of structural diversity and community composition changed as a product of disturbance severity and type, and then tested for resulting effects on forest microclimates (light availability, soil temperature, and soil water), using a multivariate, Random Forest framework. We found that measures of community composition (species richness, species evenness, and Shannon-Wiener Diversity Index) and stand structure (basal area, standard deviation of DBH, tree size diversity) declined more following disturbance than did measures of canopy cover, heterogeneity, arrangement, or height. However, when changes in each variable from pre- to post-disturbance, measured as log change, were employed in a multivariate, Random Forest regression framework, structural diversity measures of heterogeneity (rugosity, top rugosity), cover (canopy cover), and arrangement (porosity) were the most influential variables, but with differences among bottom-up and top-down treatments. We found that the death of large trees from disturbance impacts soil temperature, water, and light environments more substantially and uniformly across disturbance gradients than does the death of smaller trees. Our results have implications for both statistical and process-based modeling of forest disturbance.

Introduction

Over large extents—landscape to global scales—microclimates are constrained by latitude and elevation (Geiger et al., 1995; Körner et al., 1983) and by environmental heterogeneity within these physiographic bounds. Abiotic and biotic factors that contribute to environmental heterogeneity—variation in land cover, vegetation, topography, and soils—affect microclimatic components such as light, temperature, and soil moisture (Vanwallegem and Meentemeyer, 2009). In forested

ecosystems specifically, forest structure—including such structural components as aboveground biomass, stand density, leaf area, canopy complexity, canopy cover (J.W. Atkins et al., 2018; Ehbrecht et al., 2021; Fahey et al., 2015; LaRue et al., 2019; Noss, 1990)—substantially contributes to the environmental heterogeneity driving microclimate regulation and variance (Atkins et al., 2015; Chen et al., 1999; Potter et al., 2001; Zuskewert et al., 2014). Functionally, connections between forest structure and microclimate define habitat suitability (Varner and Dearing, 2014), and determine patterns of carbon, water, and nutrient

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cycling (Band et al., 1991). While our baseline understanding of forest structure and microclimate connections has advanced steadily over the past few years (Frenne et al., 2021; Zellweger et al., 2019), our understanding of how forest disturbance alters these connections lags.

Different disturbance agents—e.g., ice storms, pathogens, insect infestations—can affect different forest structural or compositional components, resulting in divergent structural outcomes (Atkins et al., 2020). For example, ice storms may erode the upper canopy (Fahey et al., 2020), low intensity forest fires may primarily kill subcanopy vegetation (Armour et al., 1984), and species-specific pathogens or insects may increase the number and area of canopy gaps (McCarthy, 2001). It is however unclear which structural components, when altered by disturbance, exert the strongest controls over subsequent microclimate changes. To answer this question, it is necessary to link forest structure changes in response to disturbance and then link that change to concomitant changes in the magnitude and variance of relevant micrometeorological attributes, including soil moisture, soil temperature, and the canopy light environment. Manipulative experiments offer a tractable means to explore structural outcomes from disturbance and their connections to forest microclimates as naturally occurring disturbances are random in space, time, and magnitude, and rarely occur in opportune study locations with pre-existing data and infrastructure.

Here we focus on one such experimental manipulation, the Forest Resilience and Threshold Experiment (FoRTE), established in 2018 in northern, lower Michigan (Atkins et al., 2021; Gough et al., 2021). FoRTE uses stem-girdling to mimic phloem-disruption at four disturbance severity levels, 0, 45, 65, and 85% based on targeted reductions in leaf area. Early findings from FoRTE, two years post-disturbance, show more structurally complex areas of the forest exhibited a loss of resistance in belowground functions (i.e., soil respiration) with increasing levels of disturbance severity relative to less complex areas, while above-ground functions in more complex forests were more resistant (i.e., above-ground wood net primary productivity and maximum photosynthetic rates) relative to less complex forests (Gough et al., 2021; Niedermaier et al., 2022). The strong correlation between pre-disturbance forest structure and functional resistance suggests that carbon (C) cycling responses are influenced by structural change, which results in a cascade of biotic and abiotic (including microclimatic) change. Additionally, time since disturbance is potentially an important consideration. At shorter time scales, canopy cover and leaf area may exert dominant controls, being the primary factors affected initially by disturbance. As a forest recovers, canopy cover and leaf area may return to pre-disturbance levels, but forest structure and arrangement could be altered such that canopy layering, complexity, and arrangement may be different from pre-disturbance values.

Using data pre- and post-disturbance data from FoRTE, we ask the following questions:

- Q1) Which structural and compositional components change the most in response to phloem-disrupting disturbance two-years post-disturbance after controlling for disturbance severity and disturbance type?
- Q2) Which structural and compositional components altered by disturbance are most strongly correlated with the post-disturbance magnitude and variance of abiotic microclimatic processes—soil temperature, soil moisture, and canopy light interception?

2. Methods

2.1. Field site and experimental description

FoRTE is a modeling and manipulative field experiment located at the University of Michigan Biological Station (UMBS) in northern, lower Michigan, USA (45.56 N, – 84.67 W) testing the effects of disturbance

severity and disturbance type on temperate forest carbon cycling dynamics. At UMBS the annual air temperature is 5.5 °C and mean annual precipitation is 817 mm (Gough et al., 2013). UMBS is comprised of ~100-year-old middle successional forests with the upper-canopy dominated by bigtooth and trembling aspen (*Populus grandidentata* and *P. tremuloides*, respectively) and paper birch (*Betula papyrifera*). These early successional tree species established following widespread harvesting and fire in the region in the early twentieth century and are now rapidly declining (Gough et al., 2013), 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*).

FoRTE employs a fully factorial experimental design with various disturbance severity levels of 0, 45, 65, and 85%, respectively, (based on targeted reductions in gross leaf area index via stem-girdling induced tree mortality), each paired with either top-down or bottom-up disturbance treatments (where trees are girdled sequentially by either increasing (i.e. bottom-up) or decreasing (i.e. top-down) diameter-at-breast height (DBH) starting with the smallest (>8 cm DBH) or largest tree, respectively, until targeted disturbance thresholds are achieved) (Atkins et al., 2021; Gough et al., 2020; Grigri et al., 2020) (Fig. 1).

Each replicate is located within a unique landscape ecosystem, collectively representative of secondary forests in the Great Lakes region of North America and yet substantially varied from each other in plant community composition, forest structure, and net primary productivity (Gough et al., 2020; Hardiman et al., 2011) due to unique climate, soils, biota, and landforms (Pearsall and others 1995) and shared disturbance history (Scheuermann et al., 2018).

2.2. Defining structural and compositional diversity and change

To address Q1 we evaluated the change in components of structural and compositional diversity defined by the hierarchy established by Franklin (1988) and Noss (1990). We constrained the universe of variables considered based on a priori understanding of which structural and compositional components are associated with observed microclimate patterns and processes (Abd Latif and Blackburn, 2010; Heithecker and Halpern, 2006; Ma et al., 2010; Parker et al., 2004) (See Table S1 for detailed descriptions of all variables outlined below as well as referenced literature). To evaluate change, we used the relative change for each variable between 2018 (pre-disturbance) and 2020 (post-disturbance) at the plot level ($n = 30$) calculated as follows:

$$\hat{S}_i = \ln \left(\frac{S_{i2018}}{S_{i2020}} \right) \quad (1)$$

Where $\hat{S}_i$ is the log change for a given structural or compositional index. Log change is a normalized, symmetric, and additive indicator of relative change (Törnqvist et al., 1985) which accounts for differences among the units and starting values of structural and compositional variables while also providing the direction of change—negative for a decrease, positive for an increase of a given index.

2.3. Structural diversity

Our definition of structural diversity includes two elements. First, stand structure, defined as the horizontal and vertical distribution of stand components—specifically tree heights and diameters (Helms, 1998). We quantified stand structure using plot level estimates of the standard deviation of diameter-at-breast-height (DBH) measurements (σ_{DBH}), canopy tree Gini coefficient (a measure of size inequality in tree diameters), basal area, and tree size diversity index (H_d)—where the Shannon-Wiener Diversity equation is used to quantify the proportion of basal area distributed among 5 cm DBH size classes (Buongiorno et al., 1994). Each of these variables were calculated for live trees only. Second, we examined canopy structural complexity metrics derived from

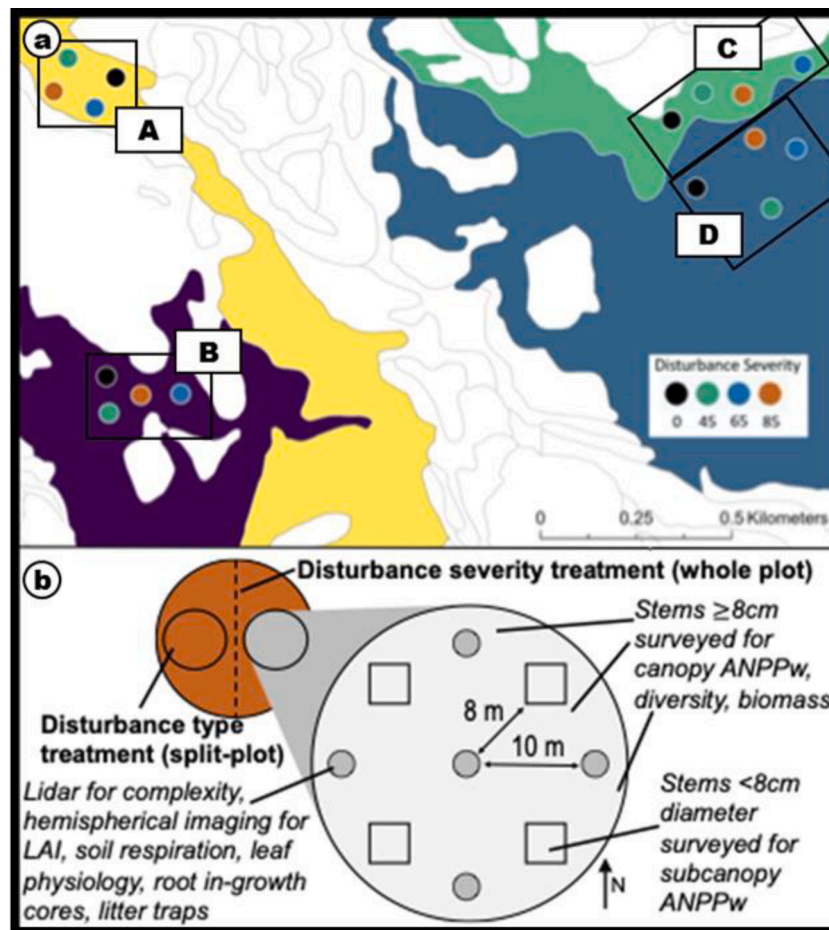


Fig. 1. (a) Map showing the distribution of plots in relation to landform types (*)—colors indicate assigned severity levels. Plot replicates are grouped (A, B, C, D); (b) Subplot diagram showing position of nested subplots for sampling and arrangement of subplots within the plot (orange).

terrestrial, portable canopy lidar data (Hardiman et al., 2011; Parker and Russ, 2004) using version 2.0.2 of the R package *forestr* (J.W. Atkins et al., 2018). These metrics include: 1) canopy cover (CC), the proportion of canopy planar area covered by leaf area (Onaindia et al., 2004); 2) canopy rugosity (R_C), the horizontal and vertical variance of canopy elements (Gough et al., 2020); 3) top rugosity (R_T) (Parker et al., 2004); 4) foliar height diversity (FHD) (MacArthur and MacArthur, 1961) a measure of canopy layering; 5) the effective number of layers (ENL) (Ehbrecht et al., 2017), another measure of canopy layering; 6) canopy porosity (P_C), the proportion occupied to unoccupied canopy space; 7) clumping index (Ma et al., 2018), a measure of canopy arrangement; 8) mean canopy height (H); 9) maximum canopy height (H_{Max}); 10) mean outer canopy height (MOCH); 11) lidar determined distributional heights, common across lidar instruments, that describe the percentile height of canopy density (p10, p25, p50, p75, p90). Leaf area variables were explicitly excluded from our analysis as the disturbance levels in FoRTE are based on targeted reductions in leaf area (See Appendix Table A1 for full descriptions).

2.4. Compositional diversity

We estimated community composition using measures of biodiversity, specifically defined in terms of the relative abundance and distribution of species within the forest (Simberloff, 1999)—as opposed to genetic or ecosystem biodiversity. We quantified biodiversity as species richness (S), species evenness (E), and Shannon-Wiener Index (H).

2.5. Forest microclimatology

We considered micrometeorological variables such as soil temperature (T_{Soil} ; °C), soil water content (VWC;%), the standard deviation of each (σT_{Soil} , σVWC), and as a proxy for the canopy light environment, canopy light absorption ($faPAR$, $\mu mol m^{-2} s^{-1}$). In situ T_{Soil} and VWC were concurrently measured twice a month during the growing season at five locations in each subplot in 2018 and 2020. T_{Soil} was measured to 7 cm depth with a LICOR-6400 thermocouple probe (LI-COR Inc, Lincoln, NE, USA) and VWC was measured to 20 cm depth with a CS620 soil moisture probe (Campbell Scientific Inc., Logan, UT, USA). To minimize confounding diurnal effects, T_{Soil} and VWC measurements were not taken within 48 h of a rainfall event. $faPAR$ was measured once for each subplot during the peak of the growing season (July) for 2018, and 2020, using a handheld ceptometer (Decagon Devices; Pullman, WA). Approximately 40 distributed, below-canopy PAR readings were taken during clear sky conditions within each sampled subplot. These values were then related to coincident open-sky, above-canopy measurements— $faPAR$ is calculated as the ratio of below- to above-canopy PAR and approximates the amount of light absorbed by the forest canopy. When open-sky measurements were not available, tower-based PAR readings from the nearby (within 2 km of each plot) UMBS AmeriFlux tower (UMB) were used. Tower PAR measurements were corrected using a calibration curve.

2.6. Structural connections to forest microclimatology via random forest regression

To answer Q2, we used a multivariate, Random Forest regression modeling approach. We specifically sought to test the impact of changes in stand, structural, and compositional diversity on the 2020 (post-disturbance) growing season average of each micrometeorological variable (T_{Soil} , VWC, σT_{Soil} , σVWC , faPAR). Random forest regression models were created in R 4.1 (R Core Team, 2022) to evaluate relationships between structural and micrometeorological change using the *randomForest* (Liaw and Wiener, 2002) and *ranger* (Wright et al., 2022) packages in R, augmented with validation functions from the *rfUtilities* package (Evans and Cushman, 2009). While Random Forest is generally insensitive to multicollinearity, model performance is often improved by removing colinear and multicollinear variables (Murphy et al. 2010). We first assessed collinearity using the *spatialEco* package in R (Evans et al., 2022), testing for pairwise collinear correlations among all candidate variables, removing strongly colinear variables from further analysis, including basal area and Gini Index. We then tested all remaining variables for multicollinearity using the *multi.collinear()* function in *rfUtilities* that uses QR decomposition and permutation ($n = 1000$) to test for the presence of multicollinearity. No variables were found to be multicollinear.

Next, for model selection, we split our data into bottom-up and top-down treatments and created RF models for each micrometeorological variable. Final models were developed using the R package *ranger* (Wright et al., 2022) with 501 trees and importance scaling based on permutation (Altmann et al., 2010) which corrects for feature bias through repeated permutation of the outcome vector ($n = 1000$) to estimate the distribution of measured importance, additionally creating a significance statistic, the permutation importance value or *p-value*. Then, for each model, we removed all variables with negative importance values and *p-values* greater than 0.1. For validation purposes, we used a Jackknife resampling approach whereby a Jackknife estimator is built by aggregating parameter estimates through leave-one-out resampling (i.e., $n = n - 1$). For each model we report model R^2 (i.e., the amount of explained variation, based on out-of-bag or OOB data and reported as “variance explained” in text below), prediction root mean square error (RMSE), and out-of-bag (OOB) prediction error (i.e., Mean Square Error, MSE). We also report statistical parameters from the Jackknife resampling validation including median Jackknife R^2 , RMSE, and prediction error.

3. Results

3.1. Structural component change from disturbance (Q1)

While we observed changes in structural diversity following disturbance within treatment and disturbance severity combinations, broad, generalizable patterns of structural change were limited to changes in stand structure and community composition (Fig. 2; Table A2). Basal area (BA), Shannon-Weiner Index (H), Gini coefficient, and variance in tree diameter-at-breast-height (σDBH) each of which decreased with higher levels of disturbance severity in both top-down and bottom-up treatments. Measures of community composition declined more precipitously (as much as log change values of -4) in bottom-up treatments, but overall showed the most change as compared to other variables (Fig. 2). Measures of canopy height showed mixed results between treatments and among disturbance severities. Percentile heights (i.e., p25, p50, p75) showed both increases and decreases among experimental combinations, though noticeable increases were observed in the 45% disturbance severity plots regardless of treatment. *MOCH* generally increased for all disturbance severity and treatment combinations. Canopy complexity also exhibited mixed effects, with canopy rugosity (R_C) generally increasing at higher disturbance severity levels for the bottom-up treatment while the effective number of layers (ENL) increases for all disturbance severity and treatment combinations (Fig. 2).

Correlation analysis showed that community composition and stand structural variables were more strongly correlated among top-down treatments than in bottom-up treatments (Fig. 3); while measures of canopy height, arrangement and heterogeneity were broadly more negatively correlated in the bottom-up treatment (Fig. 3).

3.2. Connecting structure to microclimatology (Q2)

3.2.1. Soil temperature

Based on random forest regression models, structural components, rather than compositional explained greater variation in T_{Soil} patterns in both the bottom-up and top-down treatments. In the bottom-up treatment, T_{Soil} was described by a combined model of (in order of variable importance; Fig. A3) changes in canopy cover ($\widehat{CC}$) and structural complexity ($\widehat{R_C}$) explained 45% of the observed variance (i.e., model R^2 on OOB error of 0.28). Soil temperature increased with increases in canopy rugosity and reductions in canopy cover (Fig. A5). In the top-down treatment, patterns of T_{Soil} were best described by a model

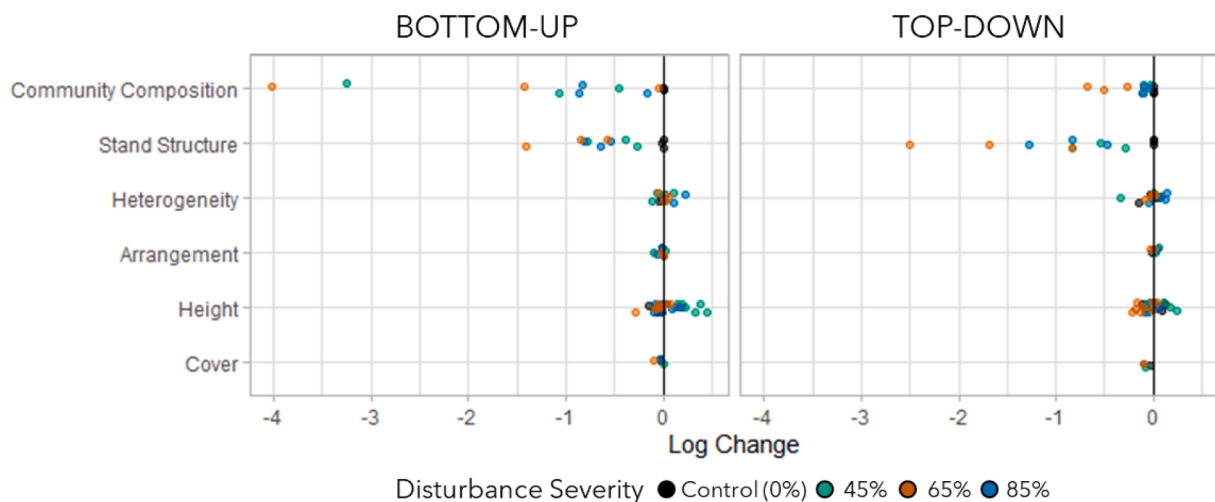


Fig. 2. Log change by structural diversity category (see Fig. 2; Table A1 for further information) by treatment. Colors indicate the targeted disturbance severity. Negative values indicate reductions from pre-disturbance (2018) to post-disturbance (2020).

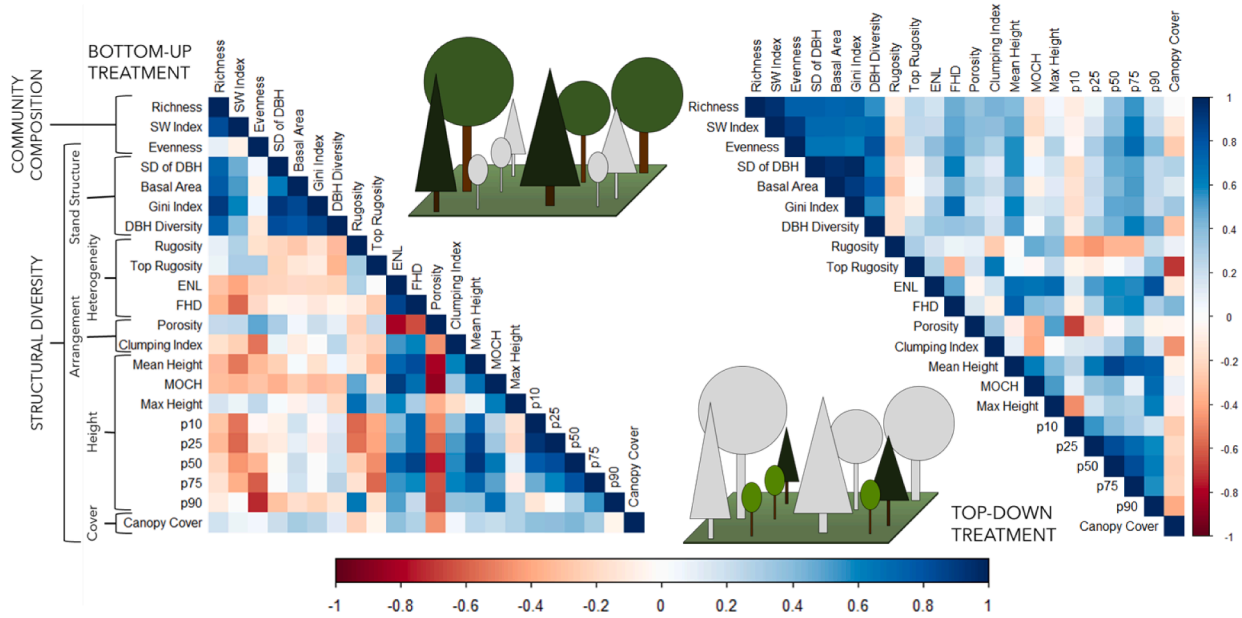


Fig. 3. Correlation matrices (Pearson's r) for log change of each community and structural variable, by Bottom-Up and Top-Down treatments. Inset conceptual diagrams show which trees were girdled (indicated as greyed out) for each treatment.

including changes in canopy cover and structural complexity—specifically top rugosity ($\widehat{R}_T$, $\widehat{CC}$), explaining 45% of the observed variance (Table 2; Fig. A7). Increases in T_{Soil} were correlated with structural complexity, though this time with increases in R_T which describes the complexity of the outer canopy surface and decreases in FHD which describes internal forest layering, as well as correlated again with reductions in canopy cover (Fig. A8).

3.2.2. Volumetric water content

Mean VWC increased at higher disturbance severities in bottom-up treatments, but for top-down treatments, only the variance increased at higher disturbance severities (Fig. 4). We observed that σVWC patterns in bottom-up treatments were well fit with a model including parameters structural complexity ($\widehat{R}_T$) and canopy height ($\widehat{p75}$), explaining 23% of the variance (Fig. A10). Soil water variance showed a parabolic relationship with canopy height and structural complexity (Fig. A11). VWC regimes in top-down treatments were best described by a model including on structural diversity, specifically only top rugosity ($\widehat{R}_T$), explaining 12% of the observed variance (Fig. A9) though a higher OOB error rate (1.56) than any other significant model. However, for

σVWC in top-down treatments, while the model included only measures of stand structure, in addition to top rugosity ($\widehat{R}_T$), the model additionally included porosity ($\widehat{P}_C$)—a measure of the proportion of the canopy occupied by vegetation—explaining 26% of the observed variance. VWC peaked at moderate values of each structural variable but declined at higher values (Fig. A13).

3.2.3. Light environment

We found that for the canopy light environment, as inferred from estimates of the fraction of absorbed photosynthetically active radiation ($faPAR$), a model including only changes in canopy cover ($\widehat{CC}$) in the top-down treatment to be significant, explaining 23% of the variance. No relationship was found for bottom-up treatments. Across both treatments, $faPAR$ decreases with increasing disturbance severity (Fig. 4).

4. Discussion

We show that some, but not all, forest structural and compositional diversity components changed from their pre-disturbance values two

Table 2

Model regression table with micrometeorological variable, treatment (bottom-up, top-down), model variables from random forest model selection process including model R^2 , root mean square error (RMSE), and out-of-bag (OOB) prediction error or mean square error (MSE); as well as Jackknife resampling statistics—with the exception of models that only retained on variable, thus not allowing for resampling analysis, indicated by an asterisk (*).

		Model Results	Model Results			Jackknife Resampling		
Variable	Treatment	Model Variables	Model R ²	RMSE	OOB Prediction error (MSE)	R ²	RMSE	Prediction error (MSE)
Soil Temp. (T _{Soil} , °C)	Bottom-Up	$\widehat{CC}, \widehat{R}_C$	0.45	0.53	0.28	0.39	0.57	0.33
Soil Temp. (T _{Soil} , °C)	Top-Down	$\widehat{CC}, \widehat{R}_T, \widehat{FHD}$	0.45	0.72	0.52	0.42	0.76	0.56
σSoil Temp. (T _{Soil} , °C)	Bottom-Up	$\widehat{CC}, \widehat{R}_C$	0.27	0.66	0.43	0.23	0.68	0.46
σSoil Temp. (T _{Soil} , °C)	Top-Down	—	—	—	—	—	—	—
Volumetric Water Content (VWC,%)	Bottom-Up	—	—	—	—	—	—	—
Volumetric Water Content (VWC,%)*	Top-Down	$\widehat{R}_T$	0.12	1.56	2.19	—	—	—
σ Volumetric Water Content (VWC,%)	Bottom-Up	$\widehat{R}_T, \widehat{p75}$	0.23	0.54	0.29	0.22	0.56	0.31
σ Volumetric Water Content (VWC,%)	Top-Down	$\widehat{R}_T, \widehat{P}_C$	0.26	0.53	0.28	0.19	0.55	0.31
faPAR (μmol m ^{−2} s ^{−1})	Bottom-Up	—	—	—	—	—	—	—
faPAR (μmol m ^{−2} s ^{−1})	Top-Down	$\widehat{CC}$	0.23	0.10	0.009	—	—	—

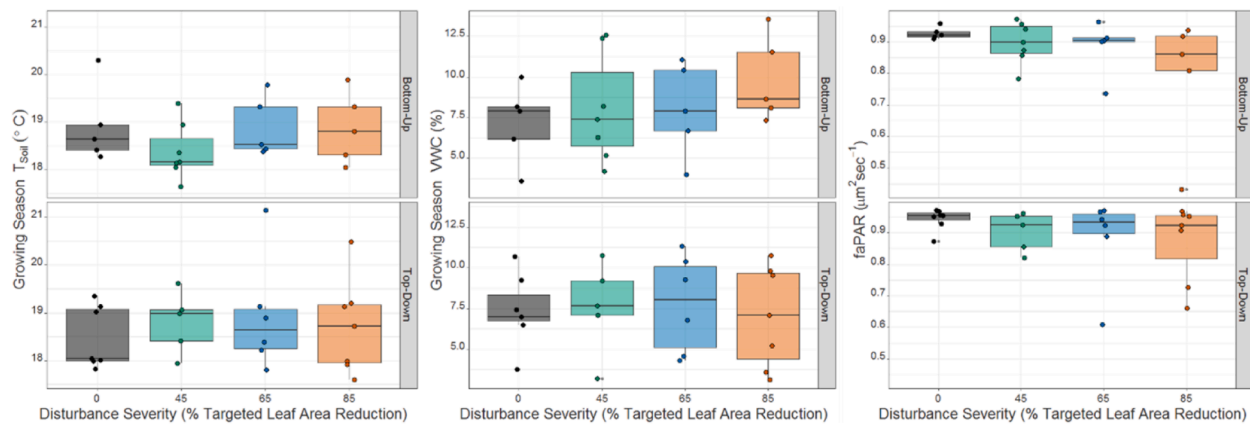


Fig. 4. Soil temperature (°C), volumetric water content (%), and the fraction of photosynthetically absorbed radiation ($\mu\text{mol m}^{-2} \text{s}^{-1}$) for 2020 (2-years post disturbance) by disturbance severity (0% black, 45% green, 65% blue, 85% orange), and treatment (bottom-up, top-down).

years after the establishment of a manipulative, stem-girdling experiment. We found by connecting the amount of structural and compositional change to post-disturbance patterns of soil temperature, soil water, and light, we could isolate which structural and compositional components were most influential in controlling specific forest microclimate attributes—however based on our analysis only structural diversity measures of height, arrangement, cover, and heterogeneity were influential. We found that almost ubiquitously, top-down disturbance treatments—where the largest trees were killed (Fig. 2)—affected forest microclimates, though bottom-up disturbance treatments—where only the smallest trees were killed—had mixed effects, isolated generally to only changes in the variance of soil temperature and water regimes. Specifically, we found that structural changes resulted in effects on soil temperature regimes in disturbed plots as evidenced by model inclusion of structural diversity components describing structural complexity and canopy cover. We found that patterns of soil temperature were well described in both top-down and bottom-up treatments, however for variance in soil temperature, we found observable patterns only for bottom-up treatments. The magnitude of soil water availability was notably affected only in top-down treatments where the largest trees were killed, while no observable relationships among candidate variables were found for bottom-up treatments. We observed that the variance of soil water availability in both top-down and bottom-up treatments could be described using models with structural diversity components. We found only canopy cover could describe the canopy light environment, but only in top-down treatments.

We observed that measures of community composition and stand structure changed more with increasing disturbance severity. Community composition measures such as species richness, evenness, and diversity indices (Shannon-Weiner) decreased more noticeably in the bottom-up treatments, while stand structural measures decreased in both treatments (with some notable decreases at the 85% severity level in top-down treatments: Fig. 3). Removal of the smallest trees in the forest (i.e., bottom-up treatments) reduces both the number of species and overall diversity rather notably as these smaller trees are typically late and mid successional species (e.g., pine, oak, maple) which tend to be more numerous and diverse. The top-down treatment—removing the largest trees—primarily targets early successional species (e.g., aspen, birch), thus not affecting community composition as dramatically (Gough et al. 2008; Hardiman et al., 2011). Stand structural measures decreased with increasing disturbance severity across treatment as expected. Given previous work, it is reasonable to assume that a stronger effect on complexity measures as a function of disturbance severity would have been observed—with greater disturbance severity more strongly affecting complexity (Stuart-Haëntjens et al., 2015)—time since disturbance may be a key consideration here. The experimental design of FoRTE allows observation of structural diversity change as the

impacts of disturbance unfold. Unlike disturbance agents such as wind or ice storms which create pulsed, one-time disturbance events where resulting structural change occurs during the disturbance, stem-girdling results in mortality over a protracted timeframe (Edwards and Ross-Todd, 1979). Often, girdled trees will continue to leaf-out for several more years following girdling, though overall leaf area will diminish steadily (Gough et al., 2013). It is possible that the lack of evidence supporting microclimatic effects due to changes in community composition and stand structure in our analysis could be attributed to a lag effect—i.e., it may simply take longer than two years for these changes to affect microclimates, while other structural diversity metrics are capable of capturing changing dynamics more rapidly. The unique perspective offered by FoRTE, with pre-disturbance plus annual measures of structural change following, helps to illustrate the mechanisms underlying functional outcomes from disturbance.

We show that changes in structural diversity following disturbance well describe observed patterns of some, but not all forest microclimatic components (i.e., soil temperature, soil water content, and light absorption). No measures of community composition or stand structure were included as selected variables, despite those categories exhibiting greater overall change from pre- to post-disturbance state. Rather, measures of canopy heterogeneity, cover, arrangement, and height were found to be more important in determining and describing patterns of microclimate change. Changes in canopy structural complexity as either R_C or R_T and canopy cover were identified most often as the most important parameters, with each appearing in three out of ten possible relationships. Of note, while four out of the six observed relationships (Table 2) were best described by multivariate models, in two instances—VWC and f_{aPAR} in top-down treatments—only changes in either top rugosity or canopy cover were retained in the model. Additionally canopy cover was included in three of the seven observed relationships and top rugosity in five of the seven. Previous studies (Atkins et al., 2020) of low to moderate severity disturbance effects on forest structure have not indicated canopy cover as a component notably affected by disturbances; however, many post-disturbance structural observations occur at times after the forest has begun to recover. Leaf area and canopy cover (CC) likely return to pre-disturbance levels faster than other structural diversity measures. Measures of canopy layering, complexity, and related factors may either increase, decrease, or return to pre-disturbance levels, but do so on longer time scales. High severity disturbances with high mortality often decimate canopy cover and leaf area, resulting in successional reversion or fundamental state changes—e.g., forests to grasslands or deserts. In these cases, microclimate effects are substantial—in time, space, and magnitude (Hardwick et al., 2015). Canopy cover is thus a key explanatory variable in this context. Canopy cover can be remotely sensed by many different types of sensors, both passive and active (Korhonen et al., 2011; Atkins et al., 2020),

across scales from local (e.g., hemispherical cameras, canopy analyzers), to regional (drone- or airplane-based sensors), to global (spaceborne instruments such as Landsat, GEDI, ICESat-2). Canopy cover can also be estimated using traditional forestry methods such as a densiometer. While we do show that the inclusion of measures such as R_C , R_T increase our ability to describe process outcomes, these structural parameters can only be inferred from lidar or structure-from-motion data, potentially limiting their application currently. The ability to map change using canopy cover alone is non-trivial and useful in situations where lidar data are unavailable, thus limiting the derivation of such structural parameters. However, for areas where lidar data are available, we will be able to moderately to substantially increase our ability to monitor and attribute microclimatic change. While this work focuses on identifying the relationship between structural change and microclimate processes, our validation analysis shows that predictions informed by data on structural are possible, however more data, monitoring, and analyses are needed.

The assessment of structural mechanisms driving changes to the forests microclimates has profound implication for understanding and modeling the earth system. For example, understanding how disturbances will impact ecosystem processes such as soil respiration (R_S)—the largest efflux of carbon from terrestrial ecosystems (Bond-Lamberty et al., 2018; Lei et al., 2021). R_S is among the most important ecosystem functions directly influenced by soil temperature and moisture. Therefore, assessing the aboveground structural mechanisms driving changes to the soil microclimate can aid in better understanding how disturbances will impact this globally important flux. An assessment of R_S in FoRTE showed that significant declines with increasing disturbance severity were driven by continued suppression of carbohydrate supply to the roots, but there was no difference between top-down and bottom-up treatments in the first two years (Mathes et al. *in review*). However, as changes to canopy structural metrics—particularly canopy cover—become more pronounced, differences in R_S between disturbance types may emerge (Mathes et al. *in review*). For example, as canopy gaps in the top-down disturbance continue to grow, rising soil temperatures could increase rate of heterotrophic contributions to respiration, suggesting that the soil microclimate, mediated by canopy structural changes, will become an important driver of R_S recovery.

Importantly though, we only investigated microclimate during the growing season. Basal area could be a strong predictor of microclimate variation at annual time steps because canopy cover is meaningless in the winter for broadleaved trees (Latimer and Zuckerberg, 2017). Chen et al. (1999) summarized several forest structural components that influence microclimatic conditions, with a particular emphasis on the effects of fragmentation. For example, summertime temperatures generally decrease away from forest edges (albeit with an increase in humidity), although these effects have been difficult to predict (Saunders et al., 1998). Similarly, forests with less canopy cover tend to experience greater variability with higher maximum temperatures and lower minimum temperatures (Chen et al., 1999; Clinton, 2003) with greater amplitudes near the center of canopy gaps (Ritter et al., 2005). Ecologically mediated effects of forest structure and edges on microclimate are of growing interest due to increased rates of forest fragmentation associated with worldwide increases in deforestation (Wade et al., 2003). These efforts must also be informed by measurements and analyses conducted during non-growing season and transitional periods, in both higher latitudes where snowfall and snowpack play a key role in determining microclimates (Broxton et al., 2021) and lower latitudes where snowfall plays little to no role.

4.1. Community composition and the role of biodiversity

Species diversity is often positively correlated with both the rate and variability of many ecosystem functions (Hooper et al., 2005), and therefore functional stability (Balvanera et al., 2006; May 1974; Peralta et al., 2014). However, in regulating forest microclimates following

disturbance, we find little evidence for the influence of community variables. Much of our understanding of this relationship comes from studies of models (Ives and Carpenter, 2007), mesocosms (Downing et al., 2014), and grasslands (Stuart-Haëntjens et al., 2018) with comparatively less consideration given to forested ecosystems (Balvanera et al., 2006; Gough et al., 2020; Musavi et al., 2017). Our understanding of biodiversity and functional stability relationships in forests is limited primarily to inferences made from research connecting community composition to production stability (Jucker et al., 2014; Silva Pedro et al., 2016) showing that mixed forests tend to be more functionally stable than monocultures to effects from disturbance (Jactel et al., 2018). Here we show that changes in community composition do not directly affect microclimates within two years of a disturbance. While further work will hopefully contextualize these relationships, over space and through time, we posit there may be connections here to tree species specific water use strategies that will emerge. Forests in the Great Lakes have notable populations of maples and oaks, species with varying water-use strategies with maples tending to be more conservative, closing their stomata in response to stress more readily than oaks (Matheny et al., 2014). These differences extend below ground as well, with maples and oaks differing in rooting depth strategies resulting in lateral root interactions driving water sourcing and ultimately the spatiotemporality of soil water (Agee et al., 2021).

4.2. Time and future divergence

Our study focused only on the first two years of change following a stem-gridling event, but senescence can vary by species or individual with mortality taking upwards of three or more years for some trees following stem-girdling (Gough et al., 2013). Therefore, any observed structural changes are likely to increase in the future, with further separation among disturbance severities and treatment.

We also expect the influence of community compositional and stand structural change to emerge and be magnified over time as well. The normalized difference approach we employed in this study does not consider the pre-disturbance forest structural attributes such as complexity, biomass, or any other measure, but rather focuses on the relative change or effect size from pre- to post-disturbance. This normalized approach centers the amount of change as the independent variable. It is possible that a more detailed consideration of the pre-disturbance state is necessary in connecting which structural components influence specific abiotic processes. It may be that more complex forests have more stable microclimates than their less complex counterparts, with complexity converging greater resistance.

5. Conclusions

We show that forest structural and compositional change following disturbance can be correlated with forest microclimatic response and that a multivariate framework considering both structural and compositional change can identify patterns of response. We also show that the same severity of disturbance, depending on whether smaller or larger trees are affected, can have different structural outcomes, and subsequently different microclimate ramifications. Modeling efforts focusing on effects of disturbance should consider how a disturbance unfolds in addition to the severity of disturbance.

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.

Data availability

Data are freely available, linked to and described in text and

statement.

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