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Coupled structure-function responses to disturbance: High structural complexity resistance supports primary production resistance

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University

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Abstract

The capacity of forests to resist structural change and retain material legacies—the biotic and abiotic resources that persist through disturbance—is crucial to sustaining ecosystem functioning after disturbance. However, the role of forest structure as both a material legacy and feature supporting carbon (C) cycling stability following disturbance has not been widely investigated. We used a large-scale disturbance manipulation to ask whether LiDAR-derived canopy structures as material legacies drive 3-year responses of NPP to a range of disturbance severity levels. As part of the Forest Resilience Threshold Experiment (FoRTE) in northern Michigan, USA we simulated phloem-disrupting disturbances at a range of severities and two disturbance types. We quantified the legacies of forest structure using two approaches: one measured change in structure and primary production from pre- to post-disturbance and the second estimated resistance as log transformed ratios of control and treatment values. We found that total aboveground wood net primary production ($ANPP_w$) remained similar across disturbance severities as remnant trees rapidly increased rates of primary production. Experiment-wide, disturbance had limited effects on change in mean structural complexity values; however, high variance underscored large differences in the magnitude and direction of complexity's response at the plot-scale. Plot-scale structural complexity, but not VAI, resistance strongly predicted $ANPP_w$ resistance while temporal VAI and structural complexity changes did not. We conclude that the presence of material legacies in the form of forest structure may affect primary production stability following disturbance, and that how legacies are quantified may affect the interpretation of disturbance response.

Vita

Kerstin Niedermaier was born on November 30th, 1995 in Cleveland, Ohio. She graduated from Shaker Heights High School in Shaker Heights, Ohio with an International Baccalaureate Diploma in 2014. Afterwards, she attended the University of Virginia as an Echol's scholar, where she graduated with distinction with dual degrees in Biology and Anthropology in 2018. Her published research includes "Timing is everything: dichogamy and pollen germinability underlie variation in autonomous selfing among populations".

Introduction

Forests of the upper Great Lakes region have been strong carbon (C) sinks for over a century (Pan et al. 2011), but partial disturbances from pests, pathogens, and extreme weather threaten to diminish their capacity to sequester C (Running 2008, Seidl et al. 2014a, Hicke et al. 2011). These partial disturbances are increasing in spatial extent in the region (Cohen et al. 2016), restructuring forests in ways that differ from historical stand-replacing disturbances. Unlike severe disturbance, partial or moderate severity disturbances may cause patchy, species-specific tree mortality or eliminate entire plant functional groups and, consequently, dramatically reshape forest structure while producing gradients of disturbance severity across forest landscapes (Atkins et al. 2020). Yet, the degree to which these resulting changes in forest structure correlate with C cycling responses to partial disturbance, including net primary production (NPP), is unclear (Fahey et al. 2016, Grigri et al. 2020, Gough et al. 2020).

Conceptual and analytical frameworks for interpreting how disturbance affects forest structure and function include two complementary ecological constructs, that of “material legacies” (*sensu* Johnstone et al. 2016) and “ecosystem stability” (*sensu* Hillebrand et al. 2018). The term “material legacy” represents the ecological memory of an environment and encompasses biotic and abiotic resources that are retained through disturbance and may support compositional and functional recovery (Johnstone et al. 2016, Royo et al. 2010, Franklin et al. 2000). Studies of material legacies have emphasized surviving tree species’ abundances and vegetation spatial arrangement (Seidl et al. 2014b, Turner et al. 1998, Meigs and Keeton 2018, Engelken et al. 2019); coarse downed and standing woody debris (Engelken et al. 2019, Meigs and Keeton 2018, Taboada et al. 2018); and soil seed bank and seed persistence (Johnstone et al. 2016, Turner et al. 1998, Harris et al. 2021). These material legacies are sometimes calculated as the change in mass or abundance of a resource following disturbance, with some disturbances reducing (e.g., number of live stems) and others increasing (e.g., downed woody debris) resources in response to disturbance (Taboada et al. 2018). Concurrently, complementary ecosystem stability literature provides guidance on defining and characterizing structural and functional responses to

disturbance (Mathes et al. 2021). Among the metrics of ecosystem stability, “resistance” describes the direction and magnitude of structural and functional changes that immediately follow disturbance (Radchuck et al. 2019, Hillebrand et al. 2018), and is calculated as the log ratio of pre-post or control-treatment responses to disturbance (Mathes et al. 2021). In the same way that temporal change in pools of materials or structures is used to quantify the presence of material legacies, we recognize the similarities within this stability framework to provide the opportunity to quantify legacies in a novel way, as *resistant* materials or structures. Unifying the concepts and analytical frameworks of material legacies and stability is an emphasis on ecosystem change dynamics and a common goal of advancing understanding and interpretation of responses to disturbance.

It is well known that compensatory growth by the release of legacy subcanopy trees after disturbance maintains functional stability (Fahey et al. 2016, Stuart-Haëntjens et al. 2015, Grigri et al. 2020), but changes in forest structure that accompany this growth response may be equally important legacies that shape ecosystem functional stability. As subcanopy trees increase production to make up for losses in canopy production after disturbance, the forest structures that remain after disturbance change as well. These changes in the forest structure that result from the reshuffling in canopy strata contributions may play an important role in maintaining high levels of NPP, measured as high resistance, after disturbance. As it stands, studies of material legacies do not consider the role of remnant forest structure in maintaining or predicting functional stability. These remnant forest structures refer to stand-to-landscape scale structural features that remain intact after a disturbance. Examples of canopy structures of interest include leaf and vegetation area index (L/VAI) and complexity as canopy rugosity, which have previously established ties to NPP (Reich et al. 2012, LaRue et al. 2019, Hardiman et al. 2011). Structural legacies such as structural complexity can thus drive either positive or negative resistance, whereas conventionally understood material legacies, which are often depleted immediately after disturbance, may be unlikely to confer positive resistance.

In an effort to relate these two ecological concepts, we used a large-scale disturbance manipulation to ask: do canopy structures as material legacies mediate 3-year above ground wood net

primary production (ANPP_w) responses to disturbance, including resistance (*sensu* Mathes et al. 2021)? Our analysis is part of the Forest Resilience Threshold Experiment (FoRTE), which used stem-girdling to attain 0%, 45%, 65%, and 85% gross defoliation (i.e., disturbance severity) levels and two disturbance types, one targeting large canopy trees and one targeting smaller canopy trees (Fig. 2). We focused on two canopy structural measures that are strongly coupled with ANPP_w at our site and elsewhere, vegetation area index (VAI) and canopy rugosity (Hardiman et al. 2011, Gough et al. 2019, Fotis et al. 2018). VAI is a single, dimensionless value that quantifies the layers of vegetation per unit ground area. Canopy rugosity—a measure of complexity that scales with height—integrates horizontal and vertical variability in vegetation distribution (Hardiman et al. 2011). These biomass-dependent canopy structural measures are sensitive to disturbance (Atkins et al. 2020) and tied to ecosystem functioning (Gough et al. 2019), and thus meet the defining criteria of a material legacy (*sensu* Johnstone et al. 2016). Our specific objectives were to evaluate: 1) the separate contributions of the subcanopy and upper canopy to ANPP_w after disturbance; 2) how VAI and canopy rugosity respond to different disturbance severities and treatment types; and 3) whether canopy structural and ANPP_w changes and resistances are correlated. We hypothesized that: there would be a significant rise in subcanopy ANPP_w paired with a decline in upper canopy ANPP_w as the time-since-disturbance progressed; VAI would be more sensitive to disturbance than canopy rugosity (Fahey et al. 2016, Stuart-Haëntjens et al. 2015); and, as a result, canopy rugosity would be more closely coupled to changes and resistances in ANPP_w (Hardiman et al. 2013b, Gough et al. 2020).

Methods

Study Site

Our study is part of the Forest Resilience Threshold Experiment (FoRTE) at the University of Michigan Biological Station (UMBS) in the northern lower peninsula of Michigan, USA (45.56° N, 84.68° W). Mean annual temperature was 7.2°C and mean annual precipitation is 75.44 cm in 2021

(NOAA, 2022, "Climate at a Glance"). The forests at our site are primarily 100-year-old secondary forests positioned on a gently sloping glacial outwash landscape. The upper canopy is composed of naturally declining early successional species: bigtooth and trembling aspen (*Populus grandidentata* and *P. tremuloides*) and paper birch (*Betula papyrifera*). Ascendent later successional species include red oak (*Quercus rubra*), eastern white pine (*Pinus strobus*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*). The subcanopy is primarily composed of red maple, red oak, American beech, sugar maple, eastern white pine, serviceberry (*Amelanchier spp.*), red pine (*Pinus resinosa*), striped maple (*Acer pennsylvanicum*), and balsam fir (*Abies balsamea*). Throughout, we categorize forest strata as: upper canopy as trees > 8 cm diameter at breast height (DBH) and subcanopy as trees 1- 8 cm DBH. Prior to the initiation of experimental treatment, upper canopy leaf area in each subplot was estimated using site or region-specific equations relating DBH to leaf area.

FORTE is a replicated experimental manipulation of disturbance severity and source. Within a replicate, there are four 0.5-ha whole-plots, which were randomly assigned a disturbance severity of 0%, 45%, 65%, or 85% gross defoliation based on previously established allometries. Whole-plots were then bisected from north to south into two split-plots, which were designated either a top-down or bottom-up treatment type. In the top-down treatment type, simulated disturbance targeted the largest upper canopy trees, while in the bottom-up treatment type, the smallest upper canopy trees were targeted (Fig. 2). Within split-plots, 0.1 ha circular subplots with a 5 m treatment buffer around its perimeter were established and used as the experimental unit throughout. In total, there are 32 subplots across 4 replicates (Fig. 1A).

Treatment replicates are nested within four distinct "land ecosystem types" that have been categorized by unique soil, biota, landform, and climate (Pearsall et al. 1995), and which are broadly representative of dominant ecosystems in the region (Nave et al. 2019; Fig. 1A). While each of the land ecosystem types share disturbance histories and overlapping tree species, the community composition, structural complexity, and net primary production in each replicate differ (Scheuermann et al 2018; Hardiman et al 2011).

To simulate a phloem-disrupting disturbance, we stem-girdled ~3,600 canopy trees experiment-wide in May, 2019. For the top-down treatment, the largest upper canopy trees were selected first for stem girdling until the total targeted gross leaf area was reached; conversely, in the bottom-up treatment the smallest upper canopy (> 8 cm) trees were girdled first to achieve the targeted gross leaf area (Fig. 2). Stem-girdled trees were scored at 1 m height with a chainsaw and a 10 cm-wide strip of bark removed with a pry bar. Trees were girdled irrespective of tree species to simulate indiscriminate disturbances from generalist insect defoliators and phloem feeders. Three years after disturbance, subplots represent disturbed forests with a range of structures and composition.

Aboveground Wood Net Primary Production

Subcanopy, upper canopy, and total aboveground wood net primary production (ANPP_w) were calculated using project protocols detailed by Grigri et al. (2020) and Atkins et al. (2021). Our approach used repeated measurements of DBH to infer the woody biomass increment from one year to the next. In the spring of 2018, all upper canopy and subcanopy trees were censused and identified to the species level. Dendrometer bands were installed at 1.3 m height on ~25% of all (girdled and non-girdled) upper canopy trees (n = 666) in the summer of 2018. Dendrometer bands were fitted atop a thin, mechanically shaved band of outer bark to ensure an even and snug fit. The bands are made of 1.27 cm-wide steel tape with a 5.08 cm stainless steel spring and stickers indicating the change in circumference of each tree. Each year, dendrometer bands were read at least once in summer and the following autumn, when stem growth has paused for the dormant season (Gough et al. 2009).

Daily species-specific relative growth rates (RGR, cm day⁻¹) were estimated for each subplot (Grigri et al. 2020). When there was no relationship between RGR and DBH ($p > 0.05$), a mean subplot and species-specific RGR value was applied to un-banded trees to estimate their annual DBH increment. When subplot-level RGR varied by DBH ($p < 0.05$), RGR of the unbanded trees was modeled using regression equations that adjust for the effect of diameter.

Once the annual DBH increment of growth was estimated separately for all banded and unbanded upper canopy trees, site-specific allometries were used to calculate aboveground wood biomass (kg) (Gough et al. 2008, Cooper 1981). Annual aboveground wood biomass increments of the upper canopy were then used to estimate ANPP_w (kg C ha⁻¹ year⁻¹) by scaling the sum of woody biomass growth per subplot to the hectare and multiplying by 0.48, the site-specific C fraction, to convert biomass to C mass (Gough et al. 2008).

In the subcanopy, annual DBH measurements were used to measure diameter growth. Species-level censuses were conducted in 2019 in one quarter of each subplot (0.025 ha) to estimate stem density of the subcanopy and four 2x2 m vegetation sampling areas were established in each subplot (Fig. 1B). Within vegetation sampling areas, two individuals were tagged for repeated DBH measurements. In instances where there were fewer than two subcanopy class trees within a vegetation sampling area, the subcanopy tree nearest to the center of the vegetation sampling area was selected and measured instead. Repeated DBH measurements of the tagged subcanopy trees in the summer and autumn of each year were used to calculate annual increment of growth. Subcanopy woody biomass was calculated using annual growth increment and site-specific allometries, accounting for subcanopy stem-density in each subplot.

Total subplot ANPP_w was calculated as the sum of upper canopy and subcanopy ANPP_w with uncertainty calculated as the standard error of mean annual ANPP_w among subplots (Gough et al. 2008).

Forest Structures

We estimated canopy structural metrics using Light Detection and Ranging (LiDAR) technology. A portable canopy LiDAR (PCL) was used in the summers of 2018-2021 to map horizontal and vertical vegetation arrangement in each subplot. The PCL consists of a metal frame that is worn at 1 m above ground level, mounted with a laser with a maximum pulse frequency of 2,000 Hz (Riegl LD90 3100 VHS; Riegl USA, Inc., Orlando, Florida). Measurements were taken in each subplot in two perpendicular 40 m transects: one running north-south and one running east-west. Structural metrics were derived from the two-dimensional hit-grids using *forestr* in R (Atkins et al. 2018). Canopy structural traits captured by

LiDAR included mean outer canopy height (MOCH), canopy rugosity, cover fraction (the proportion of area occupied by vegetation), rumple (a measure of surface roughness captured by the outer canopy surface area relative to the ground surface area (Parker et al. 2004)), and VAI. Other structural metrics analyzed were subcanopy and canopy biomass, derived from annual incremental measurements of DBH described above, and species diversity derived using Shannon's index. For full mathematical derivations of structural metrics, we refer readers to Atkins et al. (2018).

Structural and primary production resistance and changes

We used two complementary approaches to evaluate the correspondence between structure and ANPP_w following disturbance. The first compared subplot changes (δ) over time as a means of calculating the presence of material legacies. For VAI, canopy rugosity, and ANPP_w, mean subplot values in 2018 or 2019 (ANPP_w only) were subtracted from those of 2021. Positive resistance and δ values signal a net increase in material legacies or ANPP_w following disturbance, while negative values indicate the net loss of material legacies. A second approach compared the normalized resistance values calculated as the log response ratio of control versus treatment VAI, canopy rugosity, or ANPP_w (Mathes et al. 2021).

Statistical Analysis

For analysis of changes in ANPP_w across disturbance severity, years and canopy strata, we used a time-series split plot analysis of variance (ANOVA). We used this model for subcanopy, upper canopy, and total ANPP_w analyses, respectively. ANPP_w was log transformed to meet assumption of normality across all canopy strata. Levene's Test was used to test for homogeneity of variance; assumptions of equal variance were met in the upper canopy, but not in the subcanopy, where variance increased with increasing disturbance severity. Pairwise comparisons of ANPP_w were conducted using Fisher's least significant difference across time and disturbance severity. A significance level of 0.05 was assumed for all analyses.

In order to determine which structural legacies remained intact after disturbance, we compared change in VAI and canopy rugosity to the control subplots across all disturbance severities and types using a two-way ANOVA. Assumptions of normality and equal variance were checked using a Shapiro-Wilkes test and Levene's test, respectively. Using the same model structure, we compared VAI and upper canopy resistance across disturbance severities and types to control subplot resistance (0).

Before analysis of relationships of individual structural metrics and $ANPP_w$, we conducted a multiple linear regression with all of the structural metrics derived from LiDAR data collection. The full model included resistance values for canopy and subcanopy biomass, species diversity (as Shannon's index), mean outer canopy height (MOCH), canopy rugosity, cover fraction, rumple, and VAI. Variables were tested for collinearity using a correlation matrix and multicollinearity using a variance inflation factor test (VIF), where values greater than 5 were considered to be multicollinear. Collinear variables, cover fraction resistance and canopy biomass resistance, were removed from the model. All remaining variables met assumptions of normality and equal variance according to a Shapiro-Wilkes test and visual inspection of residuals, respectively. We selected a model using a step-Akaike Information Criterion (AIC) to determine the best fit model ranking. After ranking model fit, we also calculated the corrected AIC score (AICc) due to the small sample size.

We conducted simple linear regressions of canopy rugosity and VAI resistance versus $ANPP_w$ resistance to determine significance of relationships. An analysis of covariance (ANCOVA) was performed to test for interactions between disturbance severity and type and replicate. Assumptions of normality and homogeneity were conducted using visual inspection of plots of residuals.

All statistical analyses were conducted using R software (v4.0.2, R Core Team 2020) using *MASS* (v7.3.51.6, Venables and Ripley 2002), *MuMIn* (v1.46.0, Barton 2022), and *agricolae* (v1.3-3, de Mendiburu 2020) packages. Raw data for this project are available in the FoRTE data package (FoRTE Project Data, <https://fortexperiment.github.io/fortedata/>).

Results

Aboveground Wood Net Primary Production

Sustained levels of ANPP_w in the upper canopy and concurrent increases in subcanopy ANPP_w with rising disturbance severity maintained total ANPP_w over the 3-year period, even at the highest disturbance severity and across both top-down and bottom-up treatment types (Fig. 3). Upper canopy ANPP_w did not differ among disturbance severity levels or treatment type ($p > 0.05$, Table S1). However, variability in ANPP_w at the subplot scale increased in the upper canopy ranging from 871 - 3921 kgC ha⁻¹ year⁻¹ in 2019 to 790 - 4642 kgC ha⁻¹ year⁻¹ in 2021 (Fig. 3A). On average, the upper canopy contributed 95% of total ANPP_w in 2019 and 82% of total ANPP_w in 2021. At the same time, subcanopy ANPP_w increased significantly with rising disturbance severity over time (Fig. 3B, Table S1; $p < 0.05$). Mean subcanopy ANPP_w at the 85% disturbance severity level was 127 kgC ha⁻¹ year⁻¹ in 2019 and 777 kgC ha⁻¹ year⁻¹ in 2021, an increase of 511%. Furthermore, in 2021 the contribution of the subcanopy to total ANPP_w increased with disturbance severity, averaging 5.9%, 16.5%, 23.24%, and 26.5% of total ANPP_w in the control, 45%, 65%, and 85% gross defoliation levels, respectively. There was also increasing variability in the subcanopy at the subplot scale; in 2019, subcanopy ANPP_w ranged from 4 - 409 kgC ha⁻¹ year⁻¹, while in 2021, subcanopy ANPP_w ranged from 10 - 2419 kgC ha⁻¹ year⁻¹. As a result of sustained ANPP_w in the upper canopy and increased production in the subcanopy, there was no significant effect of disturbance severity or treatment type on total ANPP_w (Fig. 3C; $p > 0.05$). When subcanopy and upper canopy ANPP_w values were combined, there was no significant difference in mean ANPP_w by disturbance severity or type. These findings suggest total and stratum-specific ANPP_w displayed high resistance to increasing disturbance severity in the first three years, with subcanopy material legacies playing a proportionally larger role at higher disturbance severities.

Canopy structural responses to disturbance

Disturbance severity had a significant effect on mean change in VAI over time and VAI resistance relative to the control. Between the initiation of the disturbance and 2021, there was a significant decrease in VAI, at 65% ($p = 0.02$) and 85% ($p = 0.005$) disturbance severities when compared to the temporal change in the control (Fig. 4A). Mean VAI resistance at 45% and 85% disturbance severity and across top-down and bottom up treatments was -0.19 ± 0.04 , while at 65%, VAI resistance was significantly lower at -0.30 ± 0.12 ($p = 0.04$; Fig. 4B).

Neither disturbance severity nor treatment type had an effect on mean change in canopy rugosity over time or canopy rugosity. There was no significant difference relative to the control between canopy rugosity in 2018 and canopy rugosity in 2021 across all disturbance severities ($p = 0.07$) and types ($p = 0.08$, Fig. 4C). At the same time, mean canopy rugosity resistance was 0.08 ± 0.09 across all disturbance treatments and types. There were no significant effects of disturbance severity or type on mean rugosity resistance ($p > 0.05$, Fig. 4D). These findings demonstrate that, experiment-wide, VAI declined overall, both over time and relative to the control while canopy rugosity remained stable. Additionally, when disturbance effects on canopy structure were evaluated as normalized resistance, VAI overall displayed relatively low resistance and canopy rugosity neutral resistance to the disturbance treatments.

Structure-production resistance and change relationships

Structure-ANPP_w relationships differed for canopy rugosity and VAI, depending upon whether disturbance responses were expressed as a plot-level changes over time or log ratio treatment and control resistance values. Neither change in plot-scale VAI (Adj. $R^2 = -0.03$, $p = 0.98$) nor change in canopy rugosity (Adj. $R^2 = -0.01$, $p = 0.37$) between 2018 and 2021 corresponded with temporal changes in ANPP_w. Canopy rugosity resistance was a strong, positive predictor of ANPP_w resistance (Adj. $R^2 = 0.56$, $p < 0.001$), while VAI resistance was not correlated with changes in wood primary production resistance (Adj. $R^2 = 0.02$, $p = 0.23$). When determining the best fit model for predicting ANPP_w resistance, rugosity resistance alone was the most appropriate explanatory variable (AIC = - 57.94, AICc = 13.370; Table S2).

These findings indicate that resistance of structural complexity alone was the strongest predictor of primary production resistance.

Discussion

Three years after stem-girdling, total ANPP_w exhibited complete resistance to disturbance, including at the highest disturbance severity level, despite significant losses of VAI. As time progressed, co-occurring growth responses of legacy subcanopy and upper canopy trees fully compensated for progressive defoliation, and the magnitude of subcanopy response was proportional to the severity of disturbance (O1). Experiment-wide, mean VAI declined in response to some disturbance treatments, exhibiting relatively low resistance to partial disturbance, while canopy rugosity means and resistance values remained stable (O2); however, large variances indicate high plot-to-plot variation. At the plot-scale, resistances of canopy rugosity and ANPP_w, were strongly correlated, irrespective of disturbance treatment (O3). Together, our findings indicate that at least three aspects of forest structure contributed to high total ANPP_w resistance in the first three years following disturbance: sustained upper canopy ANPP_w; a positive subcanopy ANPP_w response to increasing disturbance severity; and greater ANPP_w resistance tied to high resistance of canopy rugosity.

The contributions of legacy subcanopy and upper canopy trees to total ANPP_w increased with disturbance severity over time and fully offset the declining growth and eventual mortality of stem-girdled trees. This sustained production by healthy (i.e., ungirdled) upper canopy trees three years following disturbance is contrary to our initial hypothesis that upper canopy tree production would decline in year three. High growth rates in the third year after disturbance differed from high first-year responses, during which both girdled and ungirdled trees exhibited comparable radial stem growth (Grigri et al. 2020, Fig. 3A), a phenomenon associated with the accumulation of non-structural carbohydrates above the girdle following phloem-disruption (Regier et al. 2010, Mei et al. 2014). At the same time, we observed a substantial, compensatory rise in subcanopy ANPP_w production (Fig. 3B), likely stimulated by a multi-year increase in canopy gap formation and increased light availability, especially at the highest

severities (Campbell et al. 2009, Fahey et al. 2016, Stuart-Haëntjens et al. 2015, Muscolo et al. 2014, Hanson and Lorimer 2007). The subcanopy ANPP_w response intensified over time, highlighting a lagged response between disturbance and the subcanopy's growth response. High variation as the disturbance unfolded and with increasing disturbance severity, especially in the subcanopy, indicate wide-ranging responses to disturbance that were not explained by our findings.

Material legacies summarizing forest structures exhibited different degrees of change and resistance following disturbance. At the highest disturbance severities (65% and 85% gross defoliation), VAI declined, as expected, in response to our treatments targeting different gross defoliation levels, similar to observed responses to disturbance elsewhere (Kashian et al. 2005, Peters et al. 2013). The resulting negative change over time and reduction relative to the control in VAI forced broad declines in vegetation quantity across disturbance treatment subplots (Fig. 4A, 4B). This temporal decline of VAI is in line with conventional understandings of material legacies, namely, that disturbance precipitates a net *loss* of pooled individuals or structures immediately following disturbance. For canopy rugosity, however, temporal increases and positive resistance values at the subplot level were balanced in almost equal numbers with subplots exhibiting temporal declines and negative resistance values, irrespective of disturbance severity or treatment type (Fig. 4C). As a result, mean canopy rugosity experiment-wide changed insignificantly, but exhibited high variability at the smaller spatial scale (Fig. 5C). Our findings that disturbance exerts variable effects on canopy structural complexity are congruent with those reported elsewhere (Atkins et al. 2020, Meigs and Keeton 2018, Peterson 2019), further demonstrating that disturbance may either erode or enhance complexity. Furthermore, our findings suggest that quantifying material legacies as change from pre- to post-disturbance is comparable to normalized resistance ratios when assessing experiment-wide responses to disturbance.

Wood net primary production's resistance to disturbance was directly coupled with the resistance of canopy rugosity but not VAI, indicating small spatial scale responses of structural complexity to disturbance strongly predicted the response of a key ecosystem function. Of the six LiDAR-derived structural metrics included in our analysis, canopy rugosity resistance was the only driver of ANPP_w

resistance (Fig. 5, Table S2). Previous work has shown positive relationships between wood or total NPP and leaf area index (LAI) (Scheuermann et al. 2017), canopy rugosity (Hardiman et al. 2011, Fotis et al. 2018, Gough et al. 2019, Gough et al. 2021a), tree density and size (Seidl et al. 2012), and species diversity (Pedro et al. 2015); however, our analysis is among the first to show that the normalized disturbance responses (i.e., resistances) of complexity and primary production parallel one another. The significance of this finding is three-fold. First, it supports theoretical expectations (Mathes et al. 2021) that the use of normalized log ratios provides a more sensitive test of disturbance response than pre- to post- comparisons because the relativized (treatment:control) response eliminates variability associated with difference in response magnitudes of the variable of interest (Hillebrand et al. 2018). That is not to say that measurements of change over time are inconsequential; instead, capturing change from pre- to post-disturbance of structures and matter is still an important means by which legacies of disturbance can be quantified. Secondly, and related, change metrics incorporate temporal variability that is not driven solely by disturbance, whereas normalized resistance metrics generated by comparing treatment and control responses account for year-to-year variation explained by other factors such as climate (Mathes et al. 2021). Third, in application, our results suggest that forests that naturally accumulate or are actively managed to enhance structural complexity are more likely to sustain, or even increase, their rates of primary production following disturbance. Moreover, such indices of structural complexity may provide a useful guide for forecasting functional resistance in advance of disturbance.

Conclusion

We conclude that forests with high resistance to losses in structural complexity may be more functionally resistant to moderate-to-severe slow-acting disturbances. This functional resistance is highlighted by the strong positive relationship between rugosity resistance and ANPP_w resistance. However, when quantified as temporal change, a similar relationship between structure and function was not found, emphasizing the value of normalized metrics of change for quantifying the effects of material legacies. Furthermore, an intact subcanopy, a product of high structural complexity, may be critical for

compensatory growth to offset C losses in real-time as upper canopy trees senesce (Fahey et al. 2016, Stuart-Haëntjens et al. 2015). This slowly-unfolding disturbance emphasizes the high capacity of forests to reallocate resources to offset production losses and maintain functional stability as disturbances progress over time. As such, our findings reiterate that management for structurally complex forests could lead to greater ecosystem stability after a disturbance (Evans & Perschel 2008, D'Amato et al. 2011, Puettmann et al. 2009, D'Amato & Palik 2021).

Finally, our analysis suggests that an expanded definition of “material legacies” is warranted, one that accounts for the possibility of an increase in pooled biotic or abiotic materials or functionally relevant features such as complexity. As it is currently defined, material legacies are, by nature, materials that existed before and persisted through disturbance. Our findings, along with emerging findings in the field (Taboada et al. 2018), demonstrate that certain structural material legacies can be generated entirely by the onset of disturbance, as in the case of canopy rugosity. Such a broader inclusion would parallel recent extensions of stability theory and analysis, which acknowledge the potential for negative and positive functional resistance (Mathes et al. 2021, Hillebrand et al. 2018.), for example, in the case of higher primary production following disturbance (Stuart-Haentjens et al. 2015, Williams et al. 2017). Finally, the use of stability metrics such as resistance for quantifying and understanding material legacies of disturbance connects two ecologically complementary frameworks in a way that could prove invaluable for understanding structure-function relationships both in forest ecosystems as well as other systems more broadly.

Figures

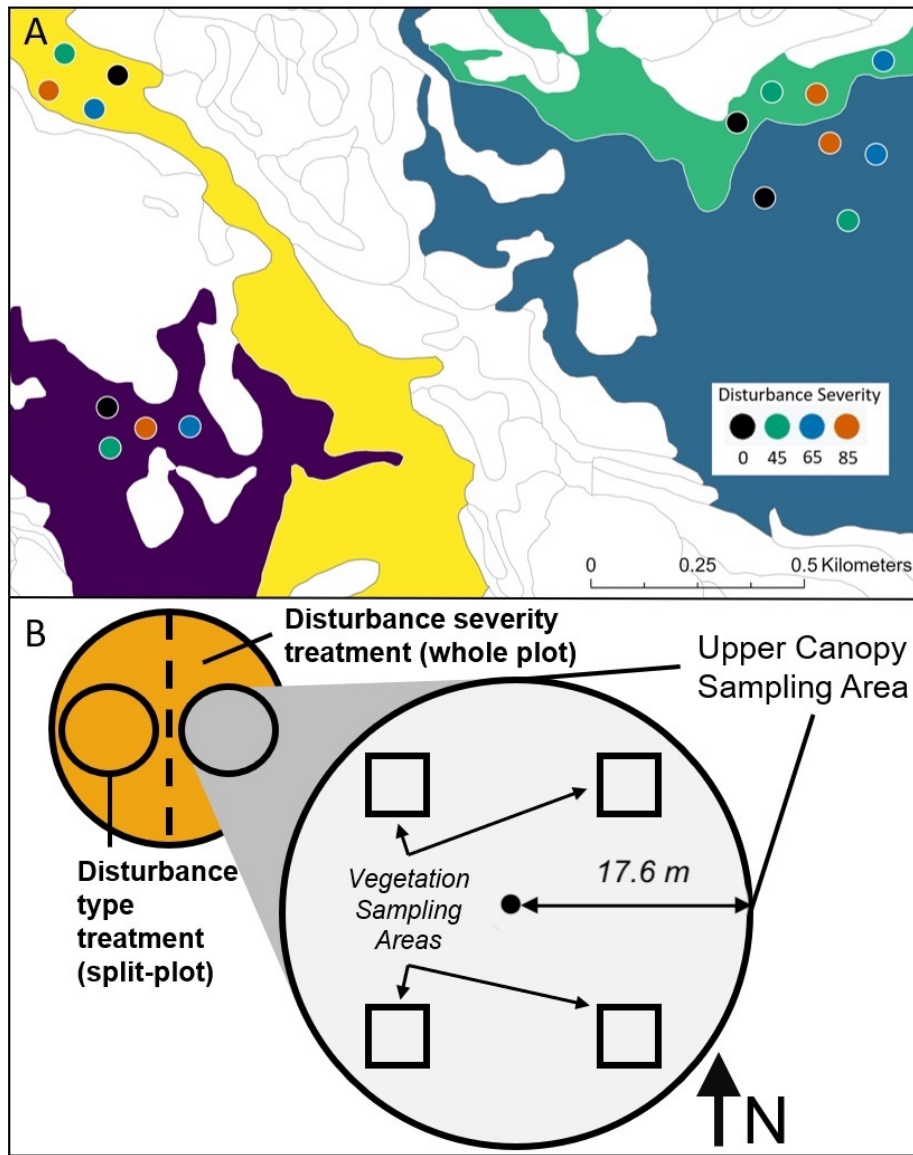
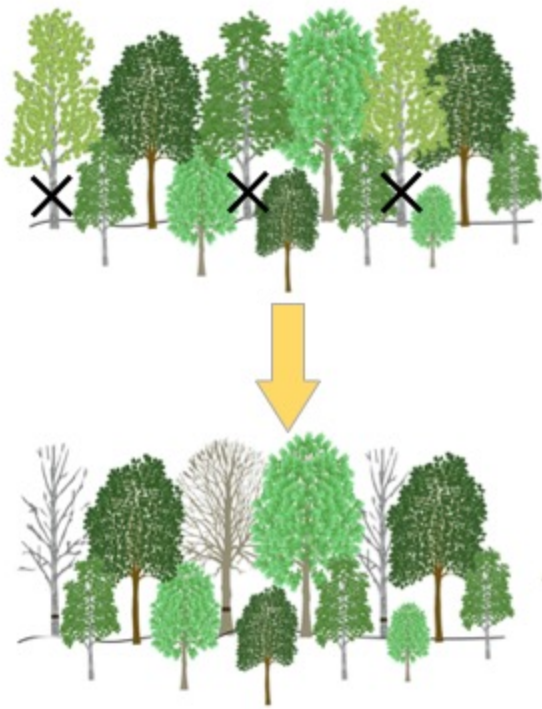


Figure 1: Map of Forest Threshold Resilience Experiment (FoRTE) replicates (A) and split-plot design (B). Replicates, which are used as experimental blocks, represent four different land ecosystem types and are designated by color with non-experimental land left white. Within each replicate, there are four randomly assigned disturbance severities representing 0%, 45%, 65%, and 85% gross defoliation, which are designated by color (A). Each plot is likewise bisected into two subplots, with each half randomly assigned either top-down or bottom-up disturbance type (B). The subplot is used as the experimental unit throughout the experiment.

A. Top-Down



B. Bottom-Up

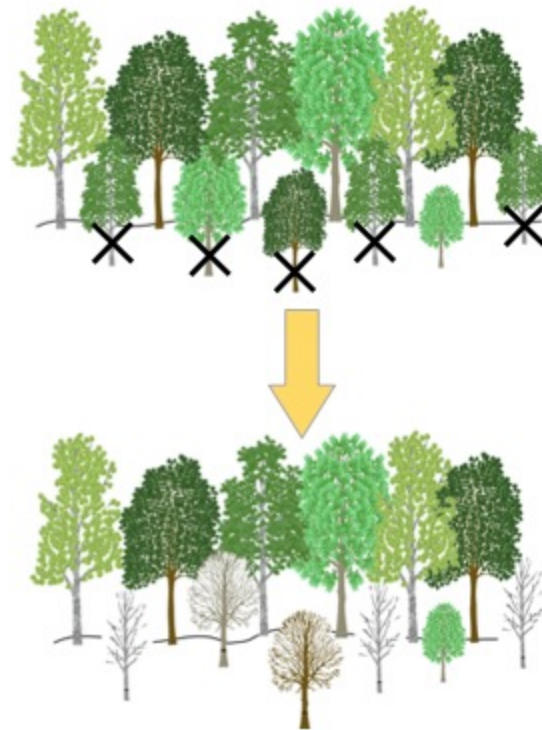


Figure 2: A representation of the two treatment types used in each subplot. In the top-down treatment type, the largest upper canopy trees (> 8 cm) were girdled until the designated disturbance severity target (either 0%, 45%, 65%, or 85% gross defoliation) was reached (A). In the bottom-up treatment type, the smallest upper canopy trees (> 8 cm) were girdled until the designated disturbance severity target was reached (B). The bottom half of the figure illustrates the predicted remnant forest structure three years after disturbance initiation.

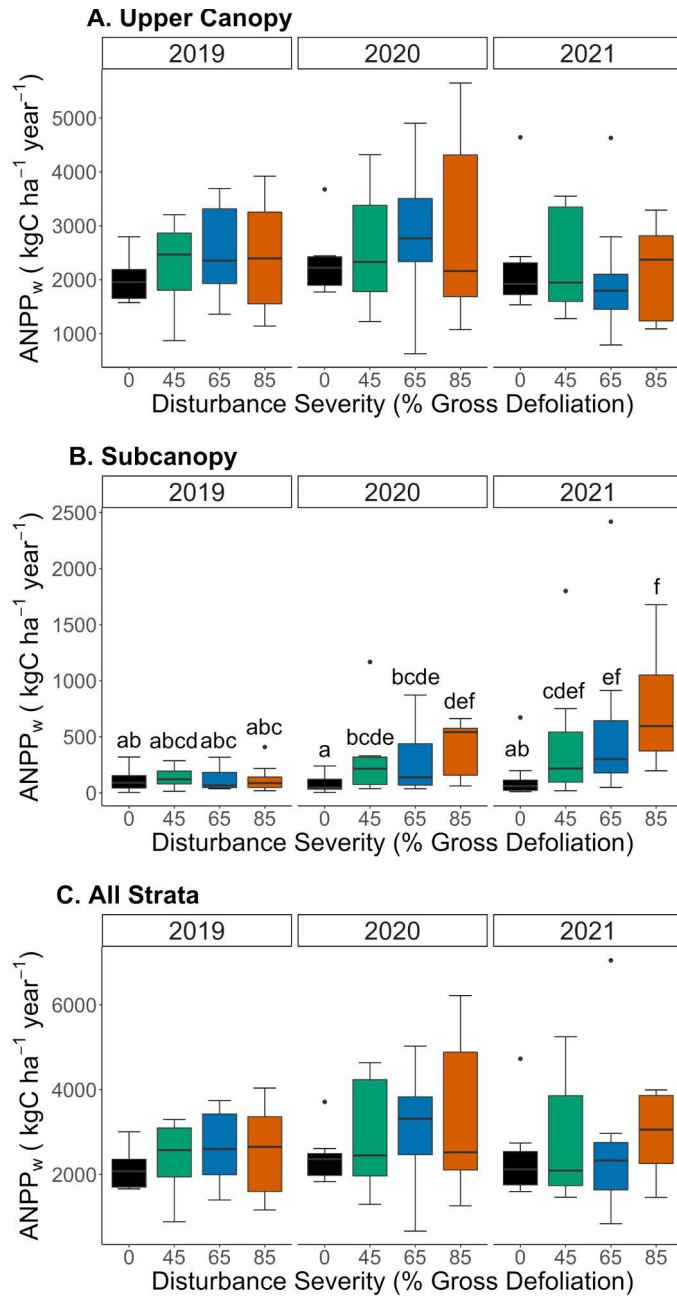


Figure 3: Box plots representing aboveground wood net primary production (ANPP_w) in the upper canopy (A.), subcanopy (B.), and sum of both upper canopy and subcanopy (C.). Middle horizontal lines represent the median ANPP_w, boxes represent the interquartile ranges, and the whiskers represent the maximum and minimum subplot values for ANPP_w. Colored boxes represent disturbance severity, or percent gross defoliation, which is repeated in each stratum for years 2019-2021. Non-overlapping letters in panel B. indicate significant pairwise differences between disturbance severities ($p < 0.05$). In the upper canopy and both strata combined, there was no significant effect of disturbance severity (A., C.)

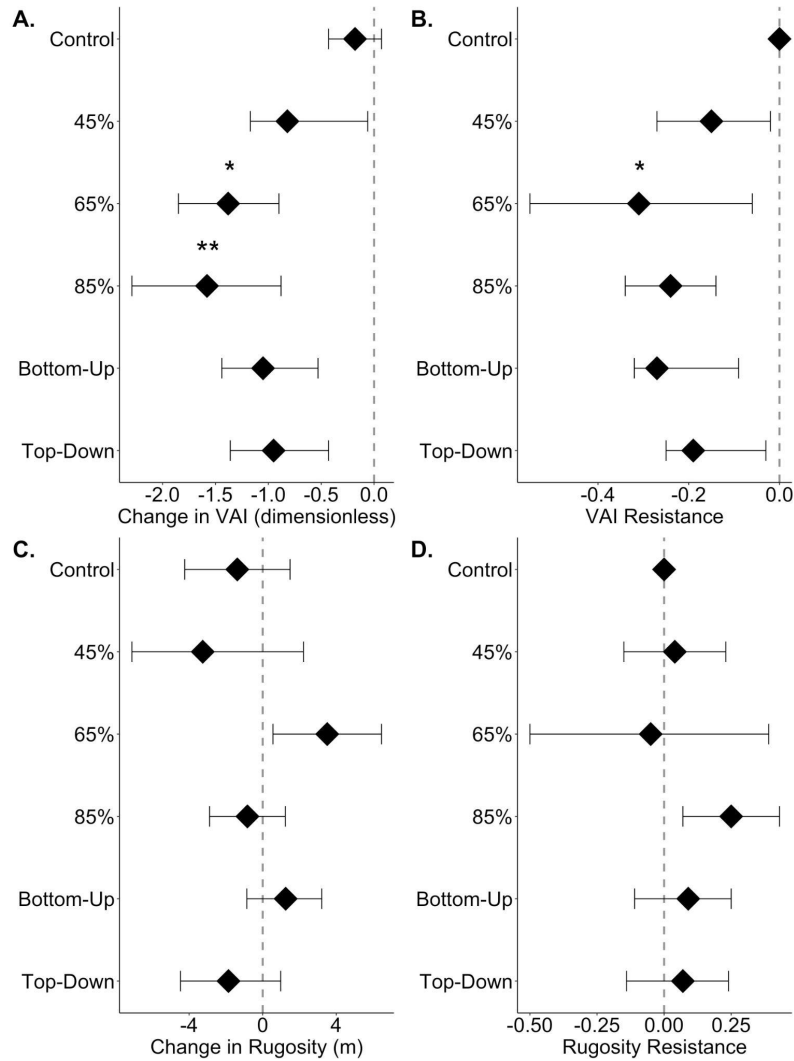


Figure 4: Comparisons of mean vegetation area index (VAI) from 2018 to 2021 (A.) and mean canopy rugosity from 2018 to 2021 (B.) by disturbance severity and type. Comparisons of VAI resistance to VAI resistance in the control (C.) and rugosity resistance to rugosity resistance in the control (D.) where resistance is calculated as the log response of each subplot divided by its corresponding control plot by disturbance severity and type. Bars represent 95% confidence intervals. Significant differences from the control plots are indicated by a single star ($p < 0.05$) or two stars ($p < 0.01$). In panels A and C vertical lines at 0.0 indicate no change over time and in panels B and D vertical lines at 0.0 indicate resistance values equal to the control.

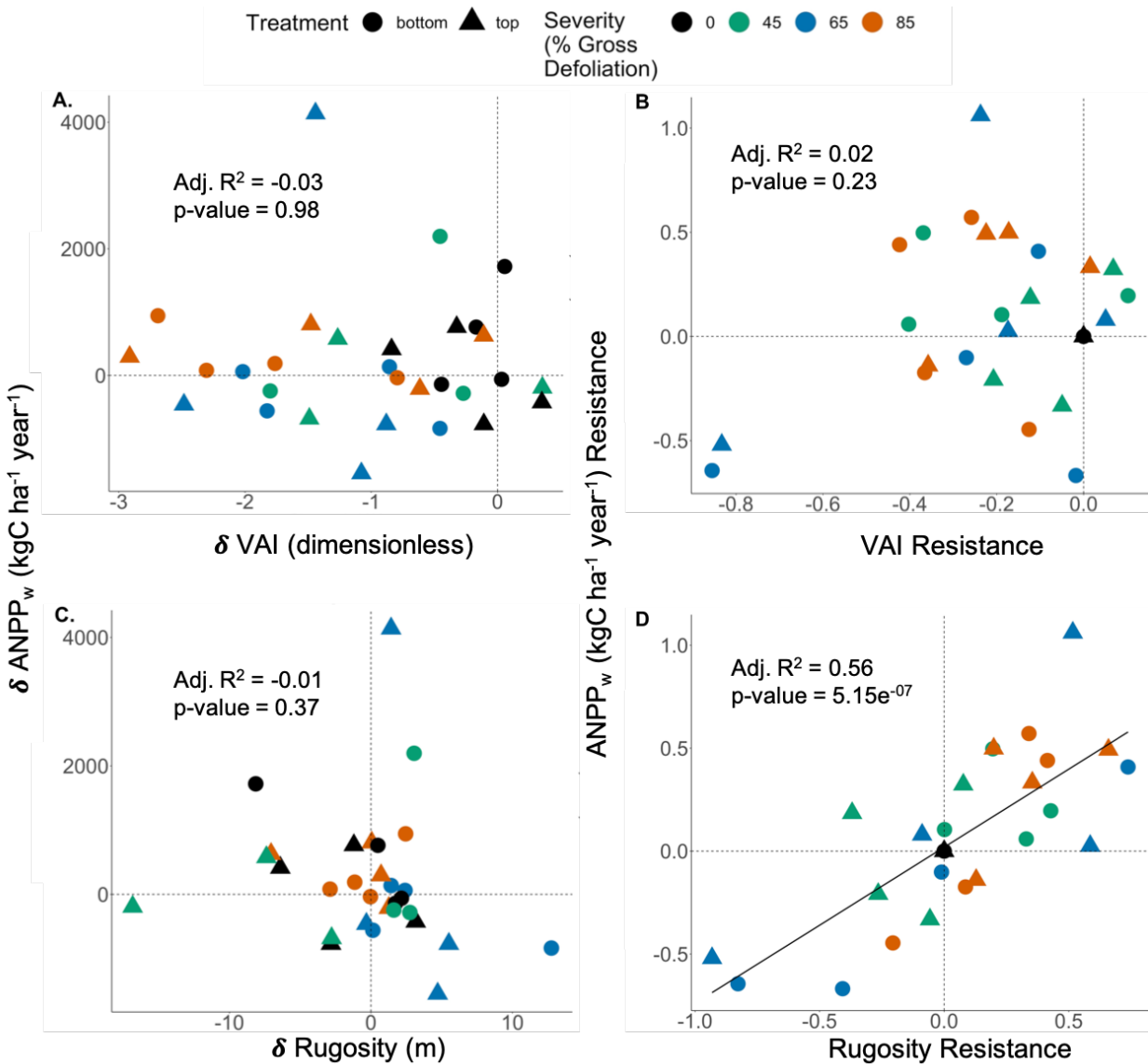


Figure 5: Linear regressions relating change in vegetation area index (VAI) to change in aboveground wood net primary production (ANPP_w) (A.); VAI resistance to ANPP_w resistance (B.); change in canopy rugosity to change in ANPP_w (C.); and rugosity resistance to ANPP_w resistance (D.). A solid trendline is included when a significant relationship is present ($p < 0.05$). In panels A. and C., where changes in structural metrics over time are shown, a decrease in structural metric ($x < 0$) over time represents structures that existed before disturbance that remain 3 years after, while an increase in structural metric ($x > 0$) over time represents structures that were generated by disturbance. In panels B. and D., where structural resistance is shown, a decrease in structural metric relative to the control ($x < 0$) is designated as net negative resistance, while an increase in structural resistance ($x > 0$) is designated as net positive resistance.

Appendix 1:

Table S1: Split-plot mixed ANOVA model structure and statistical parameters used to compare aboveground woody net primary production ($ANPP_w$) in the subcanopy (diameter at breast height (DBH) 1 - 8 cm), upper canopy (DBH > 8 cm), and total (subcanopy + upper canopy). The effects of disturbance severity (randomized within a replicate) and disturbance type (randomized within a disturbance level) are tested against separate B and A error terms, respectively. Replicate is used as a blocking factor.

	<i>Source of Variation</i>	<i>df</i>	<i>SS</i>	<i>MSE</i>	<i>F</i>	<i>p-value</i>
Subcanopy $ANPP_w$	Replicate	3	25.23	8.411		
	Year	2	16.540	8.270	29.03	< 0.001
	Error A (replicate x year):	6	1.709	0.285		
	Treatment	1	0.051	0.0515	0.063	0.807
	Treatment x Year	2	0.108	0.054	0.067	0.936
	Error B (replicate x treatment x year)	9	7.313	0.8125		
	Severity	3	27.262	9.087	6.919	< 0.001
	Year x Severity	6	9.983	1.664	1.267	0.288
	Severity x Treatment	3	2.930	0.977	0.744	0.531
	Year x Severity x Treatment	6	0.324	0.054	0.041	0.100
	Residuals	54				
	Total	95				
Canopy $ANPP_w$	Replicate	3	5.504	1.835		
	Year	2	0.560	0.280	3.763	0.087

Error A (replicate x year):	6	0.447	0.074		
Treatment	1	9.329e ⁻⁵	9.329e ⁻⁵	4.850e ⁻⁴	0.983
Treatment x Year	2	3.831e ⁻²	1.916e ⁻²	0.100	0.906
Error B (replicate x treatment x year)	9	1.731	0.192		
Severity	3	5.561e ⁻²	1.854e ⁻²	0.120	0.948
Year x Severity	6	3.540e ⁻¹	5.899e ⁻²	0.382	0.887
Severity x Treatment	3	1.009	0.336	2.180	0.101
Year x Severity x Treatment	6	8.160e ⁻²	1.360e ⁻²	0.088	0.997
Residuals	54				
Total	95				

Total ANPP _w	Replicate	3	7.089	2.363		
	Year	2	0.319	0.160	1.605	0.277
	Error A (replicate x year):	6	0.597	0.099		
	Treatment	1	0.003	0.003	0.016	0.903
	Treatment x Year	2	0.027	0.014	0.079	0.924
	Error B (replicate x treatment x year)	9	1.548	0.172		
	Severity	3	0.400	0.133	0.946	0.425
	Year x Severity	6	0.192	0.032	0.227	0.966

Severity x Treatment	3	1.055	0.352	2.495	0.070
Year x Severity x Treatment	6	0.067	0.011	0.079	0.100
Residuals	54				
Total	95				

Table S2: Summary of AIC and AICc linear model selection. Variables of interest included resistance of subcanopy biomass (R_{SB}), resistance of Shannon's Index of diversity ($R_{diversity}$), resistance of mean outer canopy height (R_{MOCH}), resistance of rugosity ($R_{rugosity}$), resistance of rumple (R_{rumple}), and resistance of vegetation area index (R_{VAI}). Models displayed include the full model, an intermediate model, and the best fit model, respectively. Final models were selected from candidates below the significance level ($\alpha = 0.01$) and the lowest AICc score.

<i>Variables</i>	<i>Adj. R²</i>	<i>F Statistic</i>	<i>p-value</i>	<i>AIC</i>	<i>AICc</i>
R_{SB} , $R_{diversity}$, R_{MOCH} , $R_{rugosity}$, R_{rumple} , R_{VAI}	0.4728	4.438	< 0.01	-50.27	29.436
$R_{diversity}$, R_{MOCH} , $R_{rugosity}$, R_{rumple}	0.5273	7.413	< 0.001	-54.22	20.830
$R_{rugosity}$	0.551	29.23	< 0.0001	-57.94	13.370

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