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**FOREST STRUCTURAL COMPLEXITY AND NET PRIMARY PRODUCTION
RESILIENCE ACROSS A GRADIENT OF DISTURBANCE IN A GREAT LAKES
ECOSYSTEM**

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

by

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Abstract

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By Lisa T. Haber

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Major Advisor: Christopher M. Gough, PhD, Department of Biology

The globally important forest carbon (C) sink is susceptible to disturbance, which modifies physical and biological structure of forests. In this study, we examined the linkage between disturbance severity and ecosystem biological and physical structural change, and implications for NPP within an experimentally disturbed forest in northern Michigan, USA. We found that while biological structure did not change in response to disturbance, three of four physical structural measures increased or were unimodally related to disturbance severity 10 years after disturbance. Physical structural shifts mediated by disturbance were not found to directly influence processes coupled with NPP. However, decadal changes in the spatial aggregation index of Clark and Evans, though not a function of disturbance severity, were found to predict canopy light uptake, leaf physiological variability, and relative NPP within plots. We conclude that ecosystem structural shifts across disturbance severity continua are variable and differ in their relationship to NPP resilience.

Introduction

Forests are a large terrestrial carbon (C) sink, absorbing 1.1 ± 0.8 Pg C annually (Pan et al., 2011) and mitigating human CO₂ emissions (Ciais et al., 2013). Even as forests provide this and other crucial ecosystem services, their future as a robust C sink is in question as changing disturbance regimes broadly modify the structure, distribution, and function of forests (Dixon et al., 1994; Hicke et al., 2012; Reyer et al., 2015; Seidl, Rammer, & Spies, 2014). The ecological consequences of severe, stand-replacing disturbances such as clear cut harvests, intense wildfires and extreme weather are well-understood, broadly observed to reset succession, and transition the forest to a temporary C source (Ghimire et al., 2015; C. Zhang et al., 2015). However, moderate severity disturbances such as insect or pathogen outbreaks and age-related senescence – affecting a subset of canopy trees – may instead enhance forest C uptake to a point by redistributing and making more efficient the use of growth-limiting resources (Gough et al., 2013). With disturbance on the rise globally, understanding how ecosystem structure and production shift along continua of disturbance severity is key to filling a fundamental knowledge gap in disturbance ecology, and to informing management and modeling of the carbon cycle (Amiro et al., 2010).

Disturbance is broadly understood to separately modify ecosystem structure and production (Mooney and Godron, 1983; Kimmins, 1997), but the directionality and extent of change, and relationship between structure and production along disturbance continua is a long-standing, unresolved topic of fundamental importance to ecology. For decades, ecologists have studied the role of moderate or intermediate disturbance in maintaining species diversity, but with no clear consensus reached (Miller, Roxburgh, & Shea, 2011). The much-debated intermediate disturbance hypothesis (Connell, 1978; Grime, 1973) postulated a unimodal,

“hump-backed” relationship between species diversity and disturbance frequency or intensity in which moderate severity disturbance increases – to a point – diversity. Some recent scholarship has questioned the real-world applicability of this paradigm (Fox, 2013; Mackey & Currie, 2001) despite its long lineage in community ecology and mixed empirical support (Huston, 2014; Mayor et al., 2015). Whether such a structural shift broadly occurs in nature following disturbance has important functional implications because biological structure, often described using metrics of biodiversity, exerts strong controls on productivity in a wide array of terrestrial and aquatic ecosystems (Cardinale et al., 2011; Spehn, Joshi, Schmid, Diemer, & Körner, 2000; Tilman, Wedin, & Knops, 1996). Positive diversity-productivity relationships are observed across multiple ecosystem types, including forests (Castro-Izaguirre et al., 2016; Forrester & Smith, 2012; Liang et al., 2016; Paquette & Messier, 2011; Zhang, Chen, & Reich, 2012). Similarly, linkages between physical structure and disturbance, and implications of these for production are not known, despite recently established relationships between canopy physical complexity and primary production (Fahey, Fotis, & Woods, 2015; Gough, Vogel, Hardiman, & Curtis, 2010; Hardiman et al., 2013; Hardiman, Bohrer, Gough, Vogel, & Curtis, 2011; Lei, Wang, & Peng, 2009; Tait & Schiel, 2011; Zenner, Peck, Lähde, & Laiho, 2012). However, a universal relationship between structural complexity and productivity is not at all clear; in a study of European monocultural forest stands, increased tree size (diameter) inequality was found to negatively relate to stand productivity (Bourdier et al., 2016), while yet another study found a neutral relationship between structural complexity and productivity in forests (Long & Shaw, 2010).

Disturbance-induced shifts in biological and physical forest structure may give rise to corresponding shifts in plant physiological responses through enhanced spatial heterogeneity of

the light environment, including through the formation of canopy gaps (Canham, 1984, 1988; Pickett & White, 1985), which alter light availability to understory plants. Forest structural changes following disturbance can promote the release and rapid growth of subcanopy trees, sustaining productivity following a moderate severity disturbance (Stuart-Haëntjens, Curtis, Fahey, Vogel, & Gough, 2015). Leaf-level physiological responses to gradients in light availability and environmental stress depend on physical as well as biological canopy structure (Niinemets, 2007), indicating that shifts in both kinds of structure may have important implications for leaf physiological responses following disturbance.

This study builds on prior investigations of biogeochemical cycling and disturbance at the University of Michigan Biological Station (UMBS) in the Upper Great Lakes ecoregion. In 2008, a 39-hectare (large-scale) experimental forest disturbance was initiated in which all mature aspen (*Populus*) and birch (*Betula*) trees were stem girdled and allowed to die over subsequent seasons. Prior work at this experimental site has pointed to high forest production resilience along a disturbance severity continuum, but with the supporting mechanisms unresolved (Gough et al., 2013; Nave et al., 2011; Stuart-Haëntjens et al., 2015). We utilize a broad gradient of disturbance severity to ask: (1) How do physical and biological structure change along a continuum of disturbance severity?; (2) Do changes in physical and biological structure force shifts in light distribution and variability, and consequently leaf physiology and morphology?; and (3) Are disturbance-driven changes in physical and biological structure coupled with patterns of primary production? Using ecological theory and prior observations as *a priori* guides, we postulated that structural and primary production shifts along the disturbance severity continuum would proceed along one of three possible trajectories: linear (Hicke et al., 2012), unimodal (e.g. Connell, 1978), or threshold (Stuart-Haëntjens et al., 2015). We hypothesized that with

increasing disturbance severity, as structural and resource homogenization occurs, an increase in subcanopy light availability would reduce leaf photosynthetic trait variability within canopies (Niinemets, 2007).

Methods

Site and experiment description

This study was part of the Forest Accelerated Succession Experiment (FASET), located at the University of Michigan Biological Station (UMBS) in northern Lower Michigan (45°35.5' N, 84°43' W). The site is a regionally-representative mixed northern hardwood forest that regrew following clearcutting and fire in the late 19th and early 20th centuries (Gough, Vogel, Harrold, George, & Curtis, 2007). Prior to experimental disturbance, the canopy was dominated by early successional aspen (*Populus grandidentata* and *tremuloides*) and birch (*Betula papyrifera*). Since the disturbance, northern red oak (*Quercus rubra*) and red maple (*Acer rubrum*) have gained canopy dominance, with eastern white pine (*Pinus strobus*), American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), striped maple (*Acer pensylvanicum*) and subcanopy shrub species in the genus *Amelanchier* (serviceberry) making up the remainder of abundant woody species (Fahey et al., 2016).

The FASET study was initiated in May 2008 to examine C cycling processes following a moderate severity disturbance caused by age-related senescence of aspen and birch (Nave et al., 2011). The treatment involved stem girdling all aspen and birch trees within a 39 hectare area, accelerating the transition from early to middle stages of ecological succession in advance of that which is occurring region-wide (Wolter & White, 2002). Our study builds on a considerable body of work from FASET demonstrating surprising forest productive resilience to disturbance (Gough et al., 2013; Nave et al., 2011; Stuart-Haëntjens et al., 2015), and extends the upper continuum of disturbance severity to focus on the mechanistic implications of structure for primary production ten years following the disturbance treatment. Specifically, we examine structure, light distribution, leaf physiological, and primary production change across a

continuum of 37 to 86% basal area loss, relating biological and physical structural features to mechanisms underlying primary production across this gradient of disturbance severity. Our 1 ha study area was gridded into 25 plots of 20 m x 20 m each. This area had been stem mapped in 2007 (pre-disturbance) and we used the varying pre-disturbance fraction of aspen and birch basal area within plots as the post-disturbance gradient in basal area loss, or disturbance severity. In 2015 and 2016, we remapped 60% of the hectare (or 15 of the original 25 plots), focusing on the extremes of the basal area loss continuum (Figure 1).

Our measurements within each plot were intended to examine whether and why physical and biological structure, modified – or not – by disturbance, affects processes shaping primary production resistance to disturbance. To characterize post-disturbance alteration in forest structure and function, we captured both mean and variance shifts for key structural and biological variables between 2007 and 2015 or 2016. Structure, characterized by presence of and spatial relationships among species and stem sizes, was linked to function in terms of leaf-level physiology and, ultimately, aboveground biomass increment. While shifts in central tendency of plot-level variables shed light on the direction and magnitude of disturbance-driven structural and biological changes, variability in structural and functional attributes as well as biological diversity may explain apparent resilience (or lack thereof) to disturbance within plots.

Stem mapping

Detailed stem mapping was conducted before and after experimental disturbance to assess changes in biological and physical structure of plots. In 2007, prior to the experiment, the location, diameter, and species of stems with a diameter at breast height (DBH) ≥ 1 were recorded within the 1 ha study area, with a total stem count of 2,621 (Figure 1). During summer

2015 and 2016, we resurveyed 15 plots with high pre-disturbance aspen and birch to extend the continuum of disturbance severity well beyond the ~60% mortality primary production threshold examined previously at our site (Stuart-Haentjens et al., 2015). We used a laser rangefinder (TruPulse 360R, Laser Technology Inc., Colorado, USA) to identify the polar coordinate of each stem relative to plot center, recording azimuth angle to the nearest ± 1 degree and distance to an accuracy of ± 30 cm. The polar coordinates of each tree were then converted to a Cartesian coordinates system.

Aboveground wood net primary production ($ANPP_w$)

To evaluate how forest growth changed across the continuum of disturbance severity, we estimated aboveground wood net primary production ($ANPP_w$) as total plot wood biomass increment between the summer of 2007 (pre-disturbance) and summers 2015 or 2016 (seven or eight years post-disturbance, respectively). All live, including ingrown, and dead trees with a $DBH \geq 1$ cm were identified to species and their DBH recorded. We estimated wood mass from site-specific allometric equations, deriving wood mass increment, or $ANPP_w$, from the change in live stocks between 2007 and 2015 or 2016, and converting dry mass to C mass using site- and species-specific carbon densities (Gough, Vogel, Schmid, Su, & Curtis, 2008).

Leaf area index

We assessed leaf area index (LAI) recovery following disturbance during peak leaf-on conditions in 2016 through optical imaging of the forest canopy within each of our 15 plots. Hemispherical skyward-facing images at plot center were taken at 1 m above the forest floor under diffuse light using a leveled camera with a 180° fisheye lens. Images were registered using

ImageJ (Version 1.51; Schneider et al., 2012) software, and estimates of LAI were derived using Gap Light Analyzer (Version 2.0; Frazer et al., 1999) software with MINIMUM thresholding applied, as this algorithm is suitable for canopies with gaps (Inoue, Yamamoto, & Mizoue, 2011).

The fraction of photosynthetically active radiation absorbed by canopies

To evaluate whether decade-long shifts in canopy structure altered light interception and distribution, we quantified the fraction of photosynthetically active radiation (fPAR) absorbed by canopies in each plot during 2016. We used an AccuPAR LP-80 ceptometer (Decagon Devices Inc, Pullman, Washington, USA) to measure ground-level PAR along a 2 m x 2 m gridded 400 m² area within each plot for a total of 100 distributed PAR measurements. Concurrent above-canopy PAR measurements were obtained from an Apogee SQ-110 quantum sensor (Apogee Instruments Inc., Logan, Utah, USA) positioned on a nearby (< 200 m) meteorological tower, and ground-level data were matched to the closest (≤ 5 min) above-canopy PAR datum. Measurements were attempted under clear sky conditions between the hours of 11:30 am and 4:00 pm from mid-July to early August, 2016, but intermittent cloud cover forced the omission of 1 to 32 % of total PAR measurements within 9 of the 15 plots as above-canopy and ground-level cloud effects could not be simultaneously registered. The mean and variance of fPAR was computed for each plot.

Leaf physiology and morphology

We examined whether differences in light environment across the disturbance continuum corresponded with variation in leaf physiology and morphology. Our approach aimed to

characterize the broad trait variability within a plot owing to differences in species and light environment. To achieve this goal, leaves at 1 m and 3 m canopy height were sampled for physiology and morphology in 1 m² quadrats positioned at 0, 2, 4, and 6 m along the four cardinal axes, for a total of 13 quadrats. Two leaves, irrespective of species, that intercepted the vertical axis at the center of the quadrat were selected for measurements; if no leaves intercepted this axis, then the two leaves that came closest to doing so within the bounds of the quadrat were selected. When the leaves of woody species were absent from a quadrat, bracken fern (*Pteridium aquilinum*), a prominent subcanopy species, was sampled if present. Though up to 26 leaves per plot could be sampled using our protocol, actual sample size varied from a minimum of 6 to a maximum of 20 leaves because of vegetation gaps.

We measured maximum photosynthetic capacity (A_{\max}) and quantum yield using a LI-6400XT Portable Photosynthesis System (LI-COR Incorporated, Lincoln, Nebraska, USA). A_{\max} was determined as the maximum rate at which light-saturated ($2000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) leaves assimilated carbon dioxide per meter squared of leaf tissue per second ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Five light-saturated measurements were made per leaf once internal CO_2 assimilation stabilized, and were averaged to yield a single value for A_{\max} . Apparent quantum yield of photosynthesis (q) values were obtained for 1 m leaves through light response curve model fitting. Sampled leaves were subjected to increasing light intensity over a range from 0 to $2000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ under fully controlled CO_2 and humidity conditions, and CO_2 assimilation was measured once stabilized at each of 10 set points. Although modeled light response curve fits were attempted for all 97 leaves collected at 1 m height, 8 of the leaves' models failed to converge on a closed solution; thus, we present q results derived from 79 statistically significant ($\alpha = 0.05$) curves. Light response curves were generated using R Statistical Software (R Core Team 2017).

We characterized leaf morphology as leaf dry mass per area (LMA), a commonly measured leaf trait useful in distinguishing shade- from sun-adapted leaves, and one which is sensitive to disturbance-driven changes in subcanopy light regime (Poorter, Niinemets, Poorter, Wright, & Villar, 2009). Individual leaf area was determined using a LI-3100C Area Meter (LI-COR Incorporated, Lincoln, Nebraska, USA). Pine needles and deciduous broadleaf specimens were each included in analysis and scanned at the appropriate resolution (0.1 mm² and 1 mm², respectively). Leaves were subsequently dried at 60°C for 48 hours, then weighed to calculate LMA.

Physical and biological structure

We computed a suite of physical and biological structural metrics for each plot before and after disturbance to evaluate whether the stem girdling treatment shifted structure across the disturbance severity continuum. Our analysis incorporates several structural variables with demonstrated connections to ecosystem disturbance (Lei et al., 2009; Bourdier et al., 2016; Dănescu et al., 2016; Table 1). For physical structure, we derived four conventional spatial and non-spatial metrics of horizontal structure (McElhinny, Gibbons, Brack, & Bauhus, 2005; Pommerening, 2002; Szmyt, 2014). Two spatially agnostic measures were: the coefficient of variation of stem diameter (CV DBH), a relative measure of variability in stem sizes within plots; and the Gini coefficient of DBH (G), a dimensionless measure of stem size inequality. Two spatially explicit structural metrics were: the diameter differentiation index (T_d), a nearest-neighbor metric equal to the average stem size difference between neighboring trees; and the aggregation index of Clark and Evans (R), with $R = 1$ indicating a completely random distribution of stems (a Poisson process), $R > 1$ a tendency towards regularity in stem

arrangement, and $R < 1$ a clustered pattern in stems. To account for edge effects between adjacent plots that might influence clumping patterns of stems, the Donnelly correction (Donnelly, 1978) was applied to the Clark and Evans index computation. Two biological structural measures were derived: the non-spatial Shannon species diversity index (H) and a nearest neighbor spatial metric, the species mingling index (M). Only live stems at the time of remeasurement (in 2015 or 2016) were included in the derivation of biological structural indices, and we used pre- and post-disturbance values to compute the change (Δ) in each metric. All indices were computed using R Statistical Software.

Statistical analysis

To evaluate relationships between disturbance severity and structure, and resulting impacts on light availability, plant physiology and morphology, and primary production, we conducted a series of linear regression analyses sequentially relating these parameters to one another. Our analyses evaluated the support for three disturbance severity-response hypotheses grounded in prior observations: a linear null model (Hicke et al., 2012); a unimodal quadratic relationship adhering to the intermediate disturbance hypothesis (Connell, 1978); and a threshold model reflecting an abrupt state change (Stuart-Haëntjens et al., 2015). All three model fits were attempted and the model that had significance at $\alpha = 0.10$ with the highest adjusted r-squared value was chosen. Linear and non-linear modeling was conducted using SigmaPlot (Systat Software Inc., San Jose, California, USA).

Postulating that variance in light availability and, consequently physiology and morphology peaks at moderate disturbance severity levels, we examined fPAR and leaf physiology and morphology for declining variability with increasing disturbance severity. We employed the Levene's test to compare subplot (i.e. individual sampled leaves') variances in

LMA, A_{\max} and q values across plots along the disturbance severity continuum as well as the Breusch-Pagan test to assess consistent variances (i.e. plot-level coefficient of variation) of those parameters at a gross (plot-level) scale. p -values for both tests are reported and the significance level was again set at $\alpha = 0.10$. This analysis was conducted using R Statistical Software.

Results

Disturbance severity and forest production

To establish continuity in the response of primary production to rising disturbance severity among studies at our site (Gough et al., 2013; Stuart-Haëntjens et al., 2015), we examined trends in LAI and ANPP_w across plots following disturbance. Consistent with prior results from our site (Stuart-Haëntjens et al., 2015), we found wood NPP declined with rising disturbance severity, and plot level ANPP_w declined beyond ~60% basal area mortality (Table 2). We observed a significant linear decline in canopy LAI and ANPP_w with rising disturbance severity ($p = 0.02$, Adj. $r^2 = 0.29$; $p < 0.001$, Adj. $r^2 = 0.57$), and a corresponding linear increase in subcanopy contribution to production ($p < 0.0001$, Adj. $r^2 = 0.76$, Figure 2). These findings reinforce previous site results showing primary production declines following the mortality of more than half of all canopy trees while extending the basal area mortality continuum by 17%.

Canopy light interception and disturbance severity

We observed a non-linear relationship between canopy light interception and disturbance severity, with fPAR beginning to decline when basal area senescence exceeded ~50%. Our model selection suggested canopy fPAR decreased nonlinearly, exhibiting a mild unimodal relationship with rising disturbance severity ($p = 0.04$, Adj. $r^2 = 0.31$, Figure 3). Though primary production declined linearly and fPAR non-linearly, the disturbance severity at which each began to decline was similar (roughly 50% basal area loss for mean fPAR and 60% for relative ANPP_w).

Physical and biological structure

We observed a significant shift in physical, but not biological, structure across the disturbance severity continuum. Three of four physical structure measures, none of which were correlated with disturbance severity before the experiment, experienced significant changes (Δ) with rising disturbance severity (Figure 4 a, b, c, d). The coefficient of variation in DBH exhibited a marginally significant decline with rising disturbance severity ($p = 0.10$, Adj. $r^2 = 0.13$), while spatially explicit ΔT_d showed a more significant decline ($p = 0.02$, Adj. $r^2 = 0.31$). ΔG followed a unimodal trend across the disturbance severity continuum, with lower DBH inequalities at low and high disturbance severities and peak values between 50-60% basal area senesced ($p = 0.08$, Adj. $r^2 = 0.23$), roughly corresponding with the disturbance level at which light and primary production began to decline. The shift in Clark and Evans' aggregation index (ΔR) did not exhibit a significant relationship with disturbance severity in our model tests (linear model result: $p = 0.84$, Adj. $r^2 = -0.07$). Taken together, our findings suggest that increasing disturbance severity homogenized or made more uniform the arrangement of vegetation. In contrast, both biological structure measures, the species mingling and Shannon's diversity index, did not change in response to rising disturbance severity (linear model results: $p = 0.26$, Adj. $r^2 = 0.03$; $p = 0.91$, Adj. $r^2 = -0.08$, respectively).

Leaf morphology and physiology across disturbance severity

Mean plot-level LMA (including deciduous broadleaf and evergreen needleleaf species) did not exhibit any trend across the disturbance severity continuum, nor did either of the leaf physiological parameters examined (A_{\max} and q). However, leaf physiological and morphological variance patterns across the disturbance continuum were suggestive of narrowing variability in photosynthetic, but not morphological, characteristics as disturbance severity increased.

Levene's test for equality of variances in A_{\max} values across plots provided strong evidence for heteroscedasticity ($p < 0.001$; Figure 5 b, c), though the Breusch-Pagan test failed to reject the null hypothesis of homoscedasticity across CV A_{\max} values for all plots at $\alpha = 0.10$ ($p = 0.18$). For the quantum yield of photosynthesis, both Levene's and Breusch-Pagan tests suggest nearly significant heteroscedasticity across the disturbance severity continuum, though both tests failed to reach significance ($p = 0.11$ and $p = 0.11$, respectively). In contrast, leaf morphology was not significantly variable across the continuum of disturbance severity (Figure 5 a). These results suggest a lessening of occupied leaf photosynthetic trait space at higher levels of disturbance severity, and coincide with progressive homogenization of physical structure in more severely disturbed plots.

Synthesis: disturbance-structure-primary production interactions

We examined whether decade-long physical structural changes – shaped by or independent of disturbance – linked to primary production through an interrelated chain of relationships coupling structure with fPAR, leaf physiology, and ANPP_w. We focus on two physical structural metrics: the Gini index of DBH (ΔG), exhibiting a significant change with rising disturbance severity, and the Clark and Evans' aggregation index (ΔR), which did not change with disturbance but was significantly unimodally related to primary production ($p = 0.07$, Adj. $r^2 = 0.25$, Figure 6 h). Even though ΔG followed a unimodal distribution across the disturbance continuum, this measure of physical structure exhibited no relationship with canopy light interception, A_{\max} variability, or primary production (Figure 6 b, c, d). These findings suggest that, although disturbance severity shifted stem diameter distributions, this structural change had no bearing on processes regulating ecosystem function. In contrast, ΔR was

unaffected by disturbance but negatively related to canopy light capture and leaf physiology ($p = 0.04$, Adj. $r^2 = 0.24$; $p = 0.04$, Adj. $r^2 = 0.24$, respectively, Figure 6 f, g), suggesting a mechanistic relationship – irrespective of disturbance – with primary production. For this metric, primary production was greatest in plots exhibiting little change in R , which measures the tendency of stems towards clustering or orderliness over the 10-year period. These findings indicate that while ΔR was not related to disturbance, decade-long shifts toward a more heterogeneous, clumped stem arrangement (negative ΔR) were related to increased light capture (higher $fPAR$) as well as more variable leaf-level physiology (larger $CV A_{max}$) within plots. In contrast, increased randomization of stem arrangement (positive ΔR) predicted lower $fPAR$ and $CV A_{max}$.

Discussion:

We found across a continuum of disturbance severity spanning 37 to 86% basal area loss that physical, but not biological, structure changed linearly or unimodally, and that the directionality of primary production was linked with decade-long structural changes that occurred independent of disturbance. Contrary to our expectations, biological structure, expressed in both spatially explicit and spatially agnostic metrics, exhibited no change with increasing disturbance severity, while physical structure declined when expressed as CV DBH, Gini index, and the spatially explicit diameter differentiation index. However, none of these disturbance-related structural changes corresponded with leaf physiological parameters or with primary production within plots. Our results show that the directionality of physical structure change over time does correlate with primary production, but in our study these relationships were not prompted by disturbance-driven changes.

The effect of disturbance on ecosystem structure was mixed, with increasing severity causing shifts in three of four physical structural parameters but no change in either of two biological structural variables, suggesting that a nuanced and cross-disciplinary perspective of structure-disturbance severity relationships is essential. Both the coefficient of variation of DBH and the diameter differentiation index declined linearly across the disturbance gradient, while the Gini index of DBH shifted unimodally in response to rising disturbance severity. Variability in tree diameter was found to be a frequently measured attribute of stand structural complexity and predictive of forest functioning in a recent literature review (McElhinny et al., 2005), suggesting that diminished horizontal structural variation could have impacts on ecological processes such as primary production that are linked to physical structure of forests. However, we found that decade-long change in a different horizontal structural metric, unmediated by disturbance, was

linked to production. Changes in the aggregation index of Clark and Evans did not exhibit a pattern across the disturbance severity continuum but were found to relate to the decadal trajectory of primary production. In contrast to physical forest structure, biological diversity did not shift in response to disturbance. One longstanding, though still controversial (Fox, 2013; Huston, 2014; Mackey & Currie, 2001), conceptual linkage between disturbance and biodiversity is the intermediate disturbance hypothesis (IDH), which states that species richness or diversity will be maximized at intermediate disturbance frequency or intensity. Our results indicate that while biodiversity shifts did not display the unimodal response predicted by the IDH, other forms of ecosystem complexity – physical structural shifts – did exhibit such a pattern. Two “hump-backed” relationships, one in which physical structural shifts peaked at moderate disturbance severity, and another in which relative primary production peaked at intermediate values of structural change following disturbance, are suggestive of an IDH-like disturbance-complexity relationship. Based on our findings here, we argue for an expanded rather than a narrowed conception and application of the IDH, with inclusion of a much broader range of biological and physical complexity measures considered.

Though disturbance-related changes in physical structure were not related to primary production, we found physical structural change, expressed as stem aggregation, unaffected by disturbance corresponded with decadal changes in wood NPP. Previous studies have indicated that fine-scale horizontal structure of forest stands can have important implications for primary production (Antonarakis, Saatchi, Chazdon, & Moorcroft, 2011; Silva Pedro, Rammer, & Seidl, 2017) and that plant stem clumping in particular can result in decreased production through diminished belowground resource uptake (De Boeck, Nijs, Lemmens, & Ceulemans, 2006). Our analysis showed that greatest relative $ANPP_w$ occurred in plots with the lowest 10-year change in

stem aggregation ($\Delta R = 0$, Figure 6 h), with plots tending either towards a more clumped stem arrangement ($\Delta R < 0$) or a more ordered pattern ($\Delta R > 0$) experiencing the lowest relative primary production. Recent work has shown that the impacts of species composition and horizontal forest structure, including variation of tree diameter, on forest NPP shift depending on stand age, with composition enhancing productivity at earlier life stages and horizontal structure positively impacting NPP at later developmental stages (Silva Pedro et al., 2017). Our analysis suggests that processes other than disturbance, namely 10-year successional dynamics within the forest or random environmental variation through time, are pushing functionally relevant horizontal structural change within these experimental plots.

The degree of stem aggregation, though not mediated by disturbance severity, altered resource acquisition within plots and contributed to a reduction in canopy light interception and homogenization of leaf physiological capacity. Plot-level increases in the aggregation index of Clark and Evans, $\Delta R > 0$, corresponded with the lowest mean plot fPAR values. This finding indicates that shifting away from a clumped, heterogeneously arranged horizontal vegetation structure towards a more uniform stem distribution reduced canopy light interception. Leaf level physiological variability, expressed as CV A_{\max} , also exhibited a negative linear relationship with increasing stem aggregation. Variance in the maximum photosynthetic rate of leaves was lowest in plots that experienced shifts toward a more uniform stem distribution, or $\Delta R > 0$, indicating that increased spatial homogeneity of plots drove increased homogeneity of plant physiology. Homogenization of stem distribution appears to have driven homogenization of the subcanopy light environment (although with marginal significance, $p = 0.11$), leading to more homogeneous leaf level physiology. Although our analysis revealed a unimodal relationship with production

declining as vegetation structure becomes more clumped or uniform, reduced ANPP_w of more heterogeneous vegetation structure was driven by a single plot (Figure 6 h).

Conclusions:

We have demonstrated that decade-long forest structural changes are important to trajectories of primary production, but not in ways directly mediated by disturbance. Contrary to expectations informed by ecological theory, biological structural metrics showed no pattern of change in response to disturbance severity at our site. Among the four physical structural metrics we investigated, three responded either linearly or unimodally to rising disturbance, though none of these structural changes was found to relate to processes coupled with primary production. Plot-level shifts in the fourth physical structural metric, the aggregation index of Clark and Evans, did not respond to disturbance but were predictive of canopy light capture, variance in leaf physiology, and ANPP_w. Two relationships involving horizontal structural change were suggestive of the IDH, one in which moderate disturbance severities caused peak increase in stem size inequalities and another in which intermediate shifts in stem aggregation predicted the greatest relative net primary production, suggesting that this theoretical framework may have applicability across a broader range of forest structural parameters beyond biological diversity. Future work should more rigorously investigate potential mechanistic pathways connecting physical forest structure, functional change, and primary production.

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Appendix:

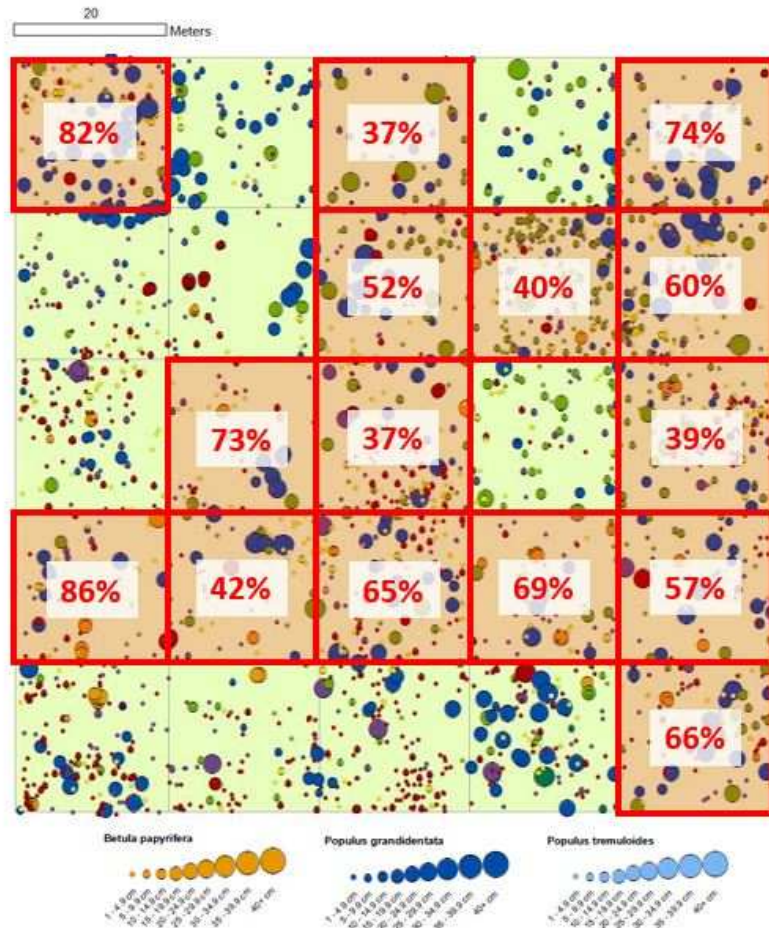


Figure 1. Stem map of the FASET hectare in 2007 illustrating relative stem sizes (via circle diameter) and distribution. Pre-disturbance aspen and birch basal area (orange and blue circles) is highlighted and the 15 plots resurveyed in 2015-16 are shown in red, including the percentage of tree basal area within the plot comprised of aspen and birch.

Table 1. Physical and biological structure metrics computed in this study. Either the original citation of the metric or a representative publication describing its use in an ecological context is provided, excluding the coefficient of variation.

Index	Computation	Explanation of variables
Shannon's diversity index, H (Shannon & Weaver, 1964)	$H = - \sum_{i=1}^S p_i \ln(p_i)$	S : total number of species in the community p_i : proportion of S made up of the i th species n : number of nearest neighboring trees analyzed per individual (4)
Species mingling index, M (Pommerening, Gonçalves, & Rodríguez-Soalleiro, 2011)	$M = \sum_{k=1}^n \frac{k}{n} m_k = \frac{1}{N} \sum_{i=1}^N M_i$	k : number of nearest neighbors that are conspecific trees m_k : number of trees having each possible value of the ratio $\frac{k}{n}$ N : total number of trees
Gini coefficient, G (Bourdier et al., 2016)	$Gini = 2 \frac{\sum_{i=1}^n i g_i}{nG} - \frac{n+1}{n}$	g_i : DBH of tree i G : sum of all tree diameters n : total number of trees
Coefficient of variation, CV	$CV = \frac{\sigma}{\mu} \times 100\%$	σ : standard deviation μ : sample mean
Diameter differentiation index, T_d (Pommerening, 2002)	$T_{ij} = 1 - \frac{\min(DBH_i, DBH_j)}{\max(DBH_i, DBH_j)};$ $T_i \in [0, 1]$	T_{ij} : diameter differentiation for the i th reference tree and its nearest neighbor j ($j = 1, 2, \text{ or } 3$)
Clark and Evans' aggregation index, R (Clark & Evans, 1954)	$R = \frac{\bar{r}_{obs}}{E(r)}, \text{ where } E(r) = \frac{1}{2 \times \sqrt{\frac{N}{A}}};$ $R \in [0, 2.1419]$	\bar{r}_{obs} : mean observed distance from trees to their nearest neighbors $E(r)$: mean nearest neighbor distance in a Poisson forest with N total trees and area of A

Table 2. Relative aboveground woody net primary production (ANPP_w) estimates for experimental plots for the interval from summer 2007 (pre-disturbance) to summer 2015 or 2016 (post-disturbance). Biomass (kg C) increment was derived from stem growth measurements and site- and species-specific allometries. Relative ANPP_w (plot-level fraction of mean) was obtained by dividing each plot's biomass increment by the mean increment across all 15 plots, in order to allow for meaningful comparison across plots with heterogeneous pre-disturbance biomass.

Plot ID	Fraction of Basal Area Loss (dimensionless)	Biomass Increment (kg C)	Relative ANPP_w (dimensionless)
B16	0.37	1467.53	0.424
B60	0.374	1397.91	0.356
B64	0.389	1107.06	0.074
B40	0.395	1159.94	0.126
B80	0.418	1525.04	0.480
B38	0.516	1008.15	-0.022
B86	0.572	1046.48	0.015
B42	0.596	1632.12	0.584
B82	0.649	1027.58	-0.003
B108	0.662	972.34	-0.056
B84	0.69	556.84	-0.460
B58	0.725	601.82	-0.416
B20	0.744	834.57	-0.190
B12	0.819	780.17	-0.243
B78	0.856	340.68	-0.669

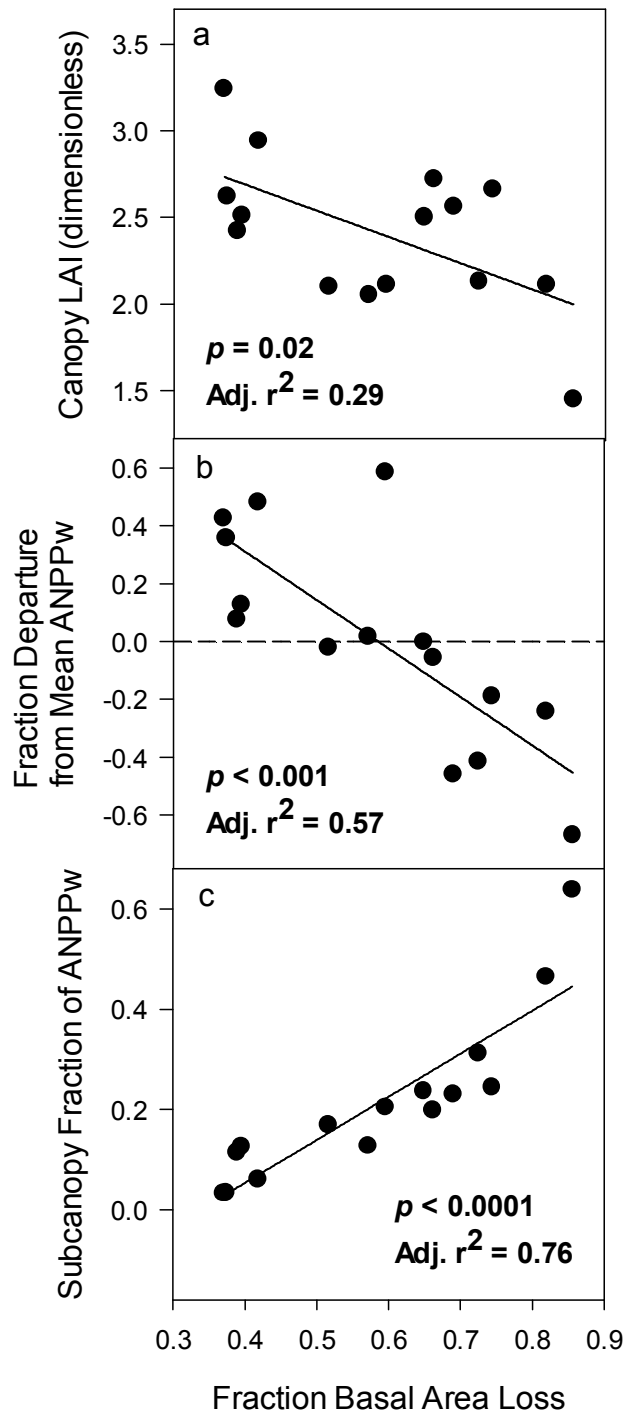


Figure 2. Productivity relationships with disturbance (expressed as fraction of basal area lost following disturbance). (a) Canopy leaf area index (LAI) declined linearly with rising disturbance severity, expressed as fraction of tree basal area lost. (b) The plot-level fraction departure from mean ANPP_w across all plots also declined linearly and became consistently negative past a fractional basal area loss of approximately 0.60, roughly the previously determined threshold of disturbance severity up to which

plots had been found to be resilient (Stuart-Haëntjens et al., 2015). Additionally, (c) the subcanopy fraction of ANPP_w increased linearly across disturbance severity.

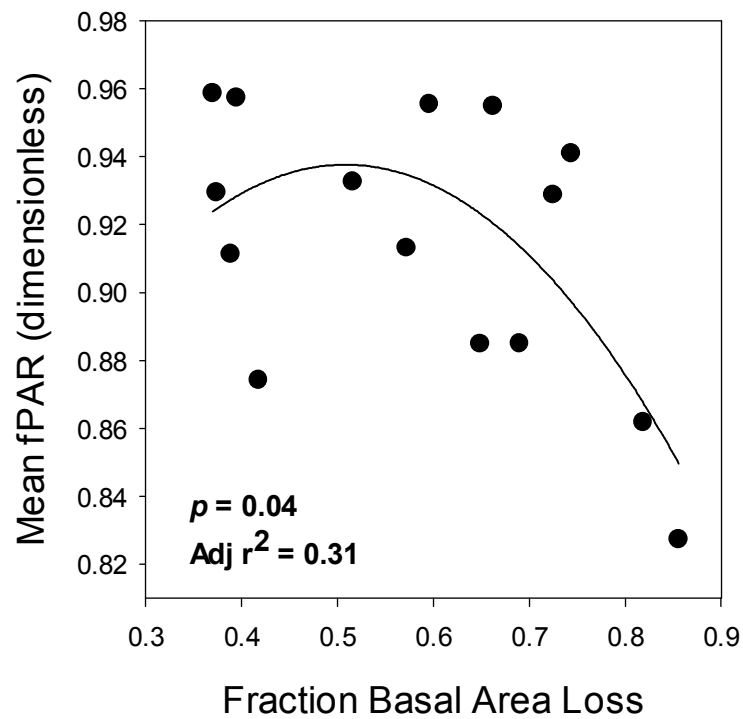


Figure 3. The fraction of photosynthetically active radiation (fPAR) absorbed by the canopy, averaged over 100 individual plot-level measurements, exhibited a unimodal quadratic relationship with rising disturbance severity (expressed as fraction of basal area lost). Beyond a fraction of lost basal area equal to 0.49, the slope of the function becomes negative, indicating a decline in plot-level light capture.

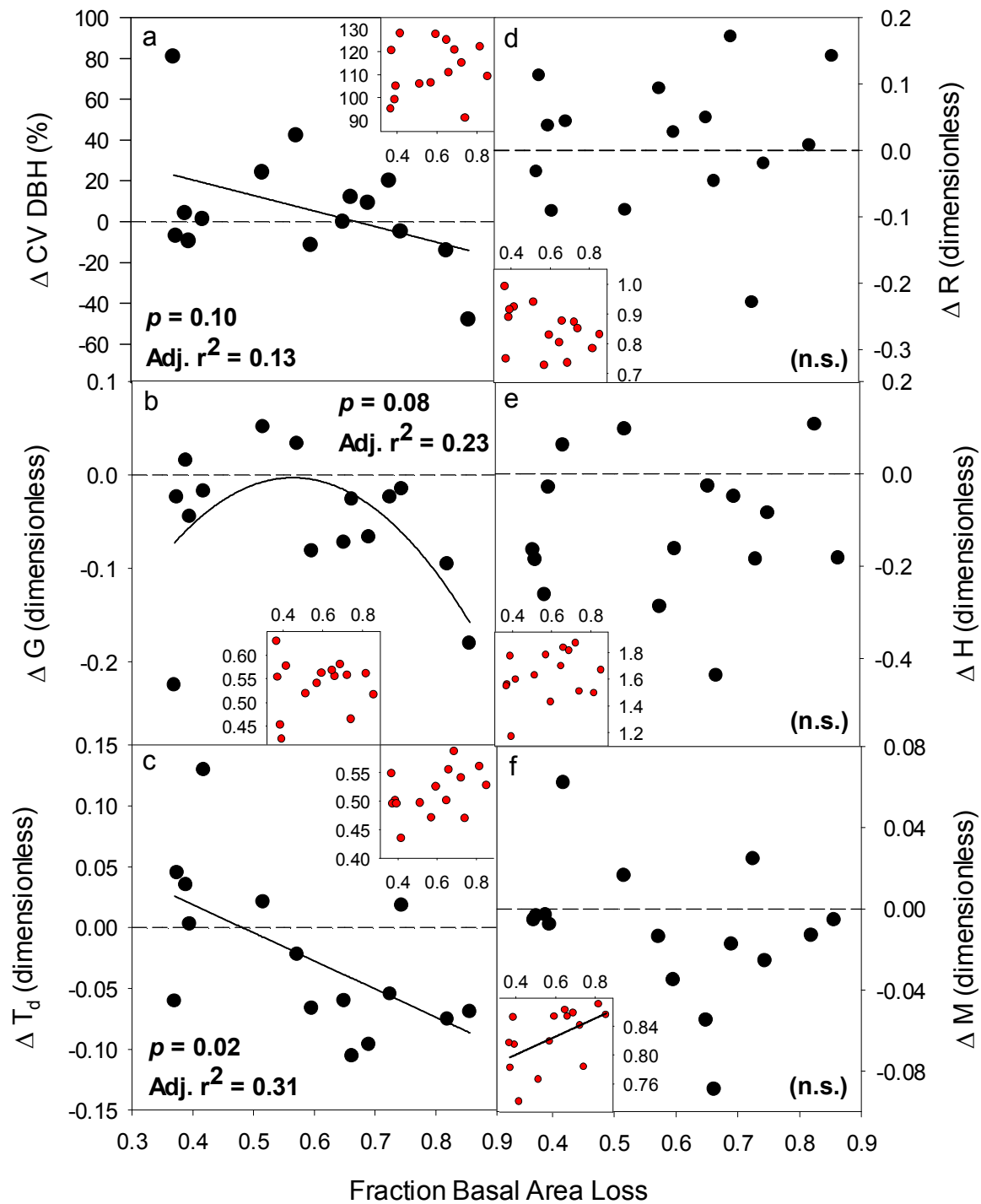


Figure 4. Physical (a, b, c, d) and biological (e, f) structural shifts (Δ) across the disturbance continuum (expressed as fraction of basal area lost). Inset graphs with red circles show the values for each metric in 2007 (pre-disturbance). Three of four shifts in physical structural indices (the coefficient of variation of DBH, CV DBH; the Gini coefficient of DBH, G; and the diameter differentiation index, T_d ; but not the Clark and Evan's aggregation index, R) exhibited a relationship with disturbance severity, whereas shifts

in biological structure (the Shannon's diversity index, H , and the species mingling index, M) did not (n.s.). The only significant trend in 2007 across the aspen and birch basal area gradient (i.e. the post-disturbance basal area loss gradient) was a positive linear relationship for M ($p = 0.05$, Adj. $r^2 = 0.21$).

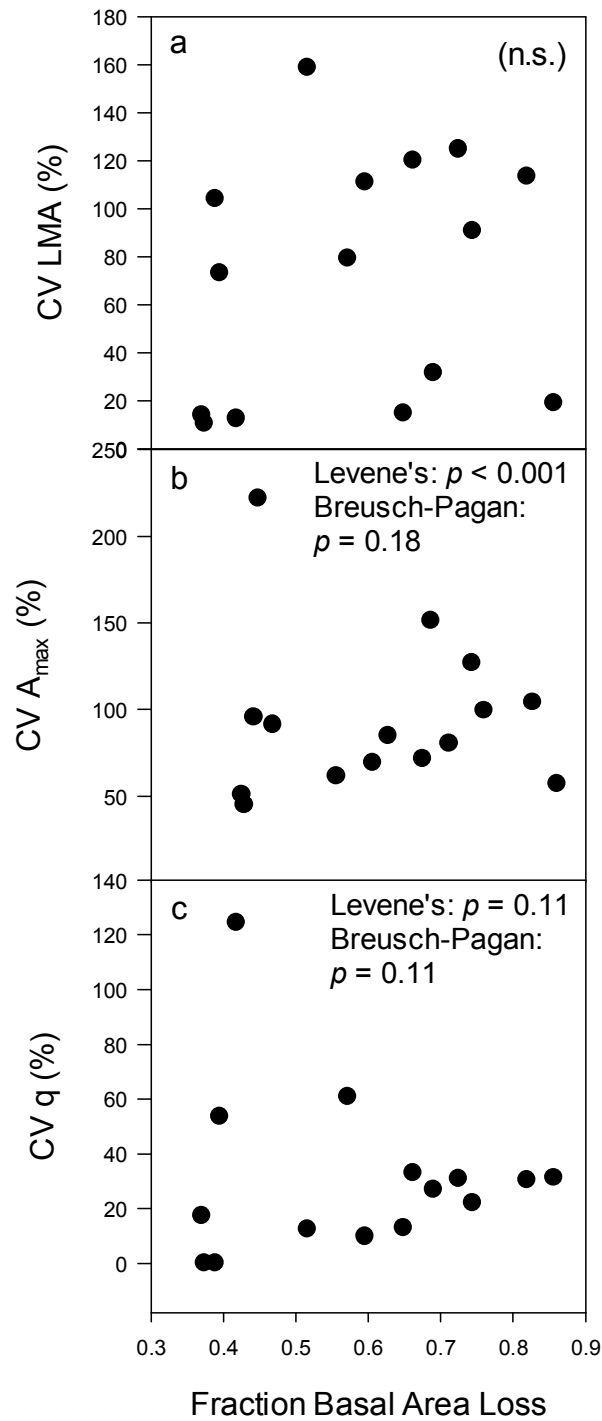


Figure 5. Morphological (a) and physiological (b, c) variability in leaves across the disturbance gradient, expressed as relative within-plot variability (CV). While LMA variability across all sampled leaves showed no pattern with rising disturbance severity, plot-level variance in maximum photosynthetic capacity (A_{\max}) and quantum yield of photosynthesis (q) lessened with rising disturbance severity as assessed by both the Levene's test for equality of variances in physiological values across plots, and the studentized Breusch-Pagan test for heteroscedasticity.

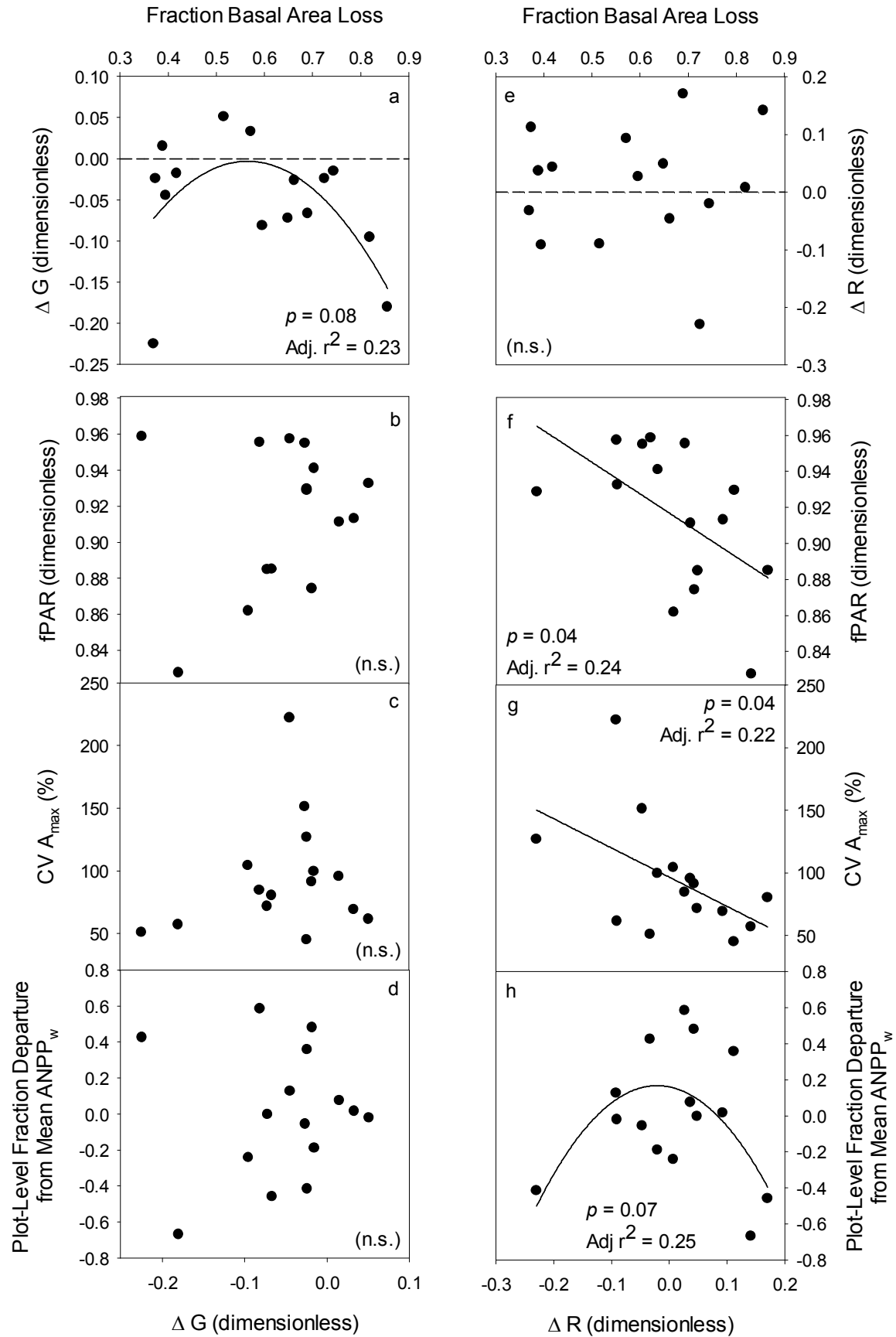


Figure 6. Synthesis of disturbance-structure-function relationships for shifts in two physical structural metrics: the Gini index of DBH (ΔG , left panel, a-d) and the aggregation index of Clark and Evans (ΔR , right panel, e-h). The topmost graphs contrast these structural shifts across the disturbance severity gradient (fraction of basal area lost), with ΔG responding unimodally to rising disturbance severity while ΔR showed no response. Successive graphs examine how canopy light capture (mean fPAR), variance in leaf-level physiology ($CV A_{max}$), and net primary production ($ANPP_w$) respond to each of these structural shifts, with no significant relationships found for ΔG and these variables but patterns in response to ΔR apparent.