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FOREST STRUCTURE, DIVERSITY, AND PRIMARY PRODUCTION IN RELATION TO DISTURBANCE SEVERITY

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Key words: disturbance severity, primary production, biodiversity, complexity, structure, function

Abstract

1. Differential disturbance severity effects on forest vegetation structure, species diversity, and net primary production (NPP) have been long theorized and observed. Here, we examined these factors concurrently to explore the potential for a mechanistic pathway linking disturbance severity, changes in light environment, leaf functional response, and wood NPP in a temperate hardwood forest.
2. Using a suite of measurements spanning an experimental gradient of tree mortality, we evaluated the direction and magnitude of change in vegetation structural and diversity indexes in relation to wood NPP. Informed by prior observations, we hypothesized that forest structural and species diversity changes and wood NPP would exhibit either a linear, unimodal, or threshold response in relation to disturbance severity. We expected increasing disturbance severity would progressively shift subcanopy light availability and leaf traits, thereby coupling structural and species diversity changes with primary production.

- 49 3. Linear or unimodal changes in three of four vegetation structural indexes were observed
50 across the gradient in disturbance severity. However, disturbance-related changes in
51 vegetation structure were not consistently correlated with shifts in light environment, leaf
52 traits, and wood NPP. Species diversity indexes did not change in response to rising
53 disturbance severity.
- 54 4. We conclude that, in our study system, the sensitivity of wood NPP to rising disturbance
55 severity is generally tied to changing vegetation structure but not species diversity.
56 Changes in vegetation structure are inconsistently coupled with light environment and
57 leaf traits, resulting in mixed support for our hypothesized cascade linking disturbance
58 severity to wood NPP.

59

60 **Introduction**

61 Disturbances modify forest structure (Fig. 1) and, in doing so, may alter core ecosystem
62 functions, including net primary production (NPP). Effects of disturbance severity on indexes
63 describing forest tree species diversity and vegetation structure and, separately, on NPP have
64 been long theorized and observed (Clements, 1916; Pickett & White, 1985). However, these
65 effects have rarely been examined together despite evidence of forest structure-function coupling
66 in a number of ecological contexts (Scheuermann, Nave, Fahey, Nadelhoffer, & Gough, 2018;
67 Silva Pedro, Rammer, & Seidl, 2017). Joint investigation of forest structure-function
68 relationships is timely as the range of disturbance severities present on temperate forest
69 landscapes expands and, consequently, broadly reshapes plant species diversity and vegetation
70 structure (Seidl et al., 2017; Turner, 2010) and NPP (Stuart-Haëntjens, Curtis, Fahey, Vogel, &
71 Gough, 2015), sometimes in surprising ways (Curtis & Gough, 2018). This widespread
72 broadening of disturbance severity is caused by a recent proliferation of low to medium severity
73 disturbances -- those that result in partial rather than complete tree mortality -- from insect pests,
74 pathogens, and extreme weather, which in many temperate regions are outpacing increases in
75 severe stand-replacing disturbances (Cohen et al., 2016). Concurrent observations of changes in
76 tree species diversity, vegetation structure, and NPP across a range of disturbance severities thus
77 provide an opportunity to examine an understudied structure-function linkage (Fahey et al.,
78 2016; Hardiman, Bohrer, Gough, Vogel, & Curtis, 2011).

79 Though rooted in different theoretical foundations, separate studies of tree species
80 diversity, vegetation structure, and NPP suggest a similar array of responses to variable
81 disturbance severities, implying that structural and functional changes across disturbance
82 continua may be linked. Unimodal (Connell, 1978), linear (Hicke et al., 2012), and threshold
83 (Tilman et al., 2001) trends in species diversity, vegetation structure, and NPP have been
84 observed across disturbance severity gradients. For species diversity, inconsistent patterns across
85 disturbance severity and frequency gradients have garnered considerable attention and are a
86 source of ongoing debate (c.f. Fox, 2013; Huston, 2014), though very high levels of disturbance
87 tend to consistently drive down diversity (Alroy, 2017; Bendix, Wiley Jr., & Commons, 2017).
88 Vegetation structure indexes summarizing tree distribution and dimensional heterogeneity
89 exhibit similarly variable patterns of change across disturbance severity gradients (Hardiman et
90 al., 2013; Sagara et al., 2018). The range of NPP responses to disturbance severity is less studied
91 (Curtis & Gough, 2018), but observations of aquatic and terrestrial ecosystems together with
92 model predictions suggest unimodal, linear, and threshold responses may occur in nature (Amiro
93 et al., 2010; Stuart-Haëntjens et al., 2015), pointing to the possibility of parallel changes in forest
94 structure and production after disturbance.

95 Synchronous and mechanistically coupled changes in species diversity, vegetation
96 structure and NPP across disturbance severity gradients could arise through a cascade of
97 interrelated disturbance-driven shifts in forest structure, resource availability and distribution,
98 and leaf functional traits (Fig. 2). In this framework, disturbance reshapes species diversity and
99 vegetation structure, features closely linked with growth-limiting resource availability and
100 variability within canopies (Halpern & Spies, 1995). The collective production of maturing
101 forests approaching middle stages of succession may be especially poised to benefit from
102 moderate levels of disturbance that reallocate resources from senescent, short-lived species to
103 longer-lived successors with limited resources (Odum, 1969). Resource (e.g. light) quantity and
104 variability within canopies, both of which may increase when moderate severity disturbance
105 augments species diversity and vegetation structural heterogeneity (Ishii & Asano, 2010; Sercu
106 et al., 2017), ostensibly drive corresponding changes in leaf physiological or other functional
107 traits that may in turn affect ecosystem-scale carbon fixation (Fotis & Curtis, 2017). Though
108 linkages between any two contiguous segments of this cascade -- for example, resource
109 environment and plant physiological response -- are established, the presence of a continuous

110 chain of cause and effect that links disturbance severity with ecosystem structure and NPP has
111 not been investigated.

112 Here, we examined whether wood NPP of forest plots spanning an experimental
113 disturbance severity gradient responded to changes in tree species diversity and vegetation
114 structure over a subsequent 9-year period. We also evaluated whether forest structure-function
115 coupling in this context occurred through intermediary shifts in patterns of light availability and
116 variability and concurrent changes in leaf physiological and morphological properties. Prior
117 work at our site, the University of Michigan Biological Station (UMBS), focused separately on
118 vegetation structure or production change following disturbance (Gough et al., 2013; Sagara et
119 al., 2018). In the present study we asked: (Q1) How did species diversity and vegetation structure
120 change along a continuum of disturbance severity?; (Q2) were disturbance-driven changes in
121 species diversity and vegetation structure correlated with availability and variability of
122 understory light, with implications for leaf physiological and morphological traits?; and (Q3)
123 were changes in species diversity and vegetation structure related to wood NPP, and was this
124 relationship modulated by concomitant shifts in light environment and leaf traits? Drawing from
125 plant physiological, community, and ecosystem ecology principles, our goal is to advance
126 understanding of forest structure-function relationships across disturbance severity continua.

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128

129 **Materials and Methods**

130

131 *Site and experiment description*

132 This study was part of the Forest Accelerated Succession Experiment (FASET) at the University
133 of Michigan Biological Station (UMBS) in northern Lower Michigan (45°35.5' N, 84°43' W).
134 FASET was initiated in 2008 to examine biogeochemical, including carbon (C) cycling,
135 processes following disturbance caused by age-related senescence of aspen and birch (Nave et
136 al., 2011). The treatment involved stem girdling all aspen (*Populus grandidentata* Michx. and
137 *tremuloides* Michx.) and birch (*Betula papyrifera* Marshall) trees within a 39 hectare area,
138 accelerating the transition from early to middle succession in advance of that which is occurring
139 region-wide (Wolter & White, 2002). Prior to the experimental disturbance in 2008, the canopy
140 was dominated by early successional aspen and birch, which broadly colonized the upper Great

141 Lakes region following widespread clear-cut harvesting and fire at the turn of the 20th century
142 (Gough, Vogel, Harrold, George, & Curtis, 2007). Since our experimental stem girdling,
143 northern red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.) have gained canopy
144 dominance, with eastern white pine (*Pinus strobus* L.), American beech (*Fagus grandifolia*
145 Ehrh.), sugar maple (*Acer saccharum* Marshall), striped maple (*Acer pensylvanicum* L.) and
146 subcanopy shrub species in the genus *Amelanchier* (serviceberry) making up the remainder of
147 abundant woody species (Fahey et al., 2016).

148 Our data collection centered on twice stem mapped 20 m x 20 m plots within a
149 contiguous hectare of the FASET manipulation that spanned a disturbance severity gradient,
150 expressed as the plot-level percentage of tree basal area killed by girdling, from 37 to 86 %
151 (Supplemental Fig. 1, Supplemental Table 1). The fraction of basal area lost within a plot was
152 identical to the fraction of basal area comprised of aspen and birch, which varied across plots due
153 to small-scale, and putatively random, variation in these species' abundances. Prior to the
154 experiment in 2007 and then again after manipulation-induced tree mortality in 2015 or 2016, the
155 spatial location of each tree stem was mapped via laser rangefinder (TruPulse 360R laser
156 rangefinder, Laser Technology Inc., Colorado, USA), and the diameter at breast height (DBH)
157 and species identification were recorded for 1,589 woody stems with a DBH \geq 1 cm in 15 of 25
158 plots. These plots were selected based on their high pre-disturbance aspen and birch abundance,
159 thereby extending the continuum of disturbance severity beyond 60 % tree mortality, the
160 disturbance threshold at our site beyond which production steeply declined (Stuart-Haëntjens et
161 al., 2015). Stem map data were used to derive a suite of plot tree species diversity and structural
162 measures as well as the annual change in live wood biomass (NPP) over the intervening 8- or 9-
163 year period. Additionally, we paired stem map data with light and leaf trait information, the
164 methods of which are detailed below.

165

166 *Species diversity and vegetation structure indices*

167 From stem maps, we computed plot-scale tree species diversity and vegetation structure metrics
168 before (2007) and after (2015 or 2016) disturbance across the continuum of severity (Table 1).
169 Our analysis incorporated several related but distinct species diversity and vegetation structure
170 variables with demonstrated sensitivity to disturbance and impacts on productivity (Bourdier et
171 al., 2016; Dănescu, Albrecht, & Bauhus, 2016). We categorized measures describing physical

172 attributes -- irrespective of tree species identity -- as “vegetation structure,” in contrast to those
173 which quantified species diversity in either a spatially explicit or agnostic way.

174 For vegetation structure, we derived two spatial and two non-spatial metrics
175 (Pommerening, 2002; Szmyt, 2014; Table 1). Because spatial arrangement of stems, irrespective
176 of tree species, may have implications for productivity (Pacala & Deutschman, 1995; Williams,
177 Paquette, Cavender-Bares, Messier, & Reich, 2017), we included two metrics that contain tree
178 location information in addition to two that capture size difference. The spatially agnostic
179 measures were: the coefficient of variation of stem diameter (CV DBH), a relative measure of
180 variability in stem sizes within plots; and the Gini coefficient of DBH (G), a dimensionless
181 measure of stem size inequality. The spatially explicit structural metrics were: the diameter
182 differentiation index (T_d), a nearest-neighbor metric expressing the average stem size difference
183 between neighboring trees; and the aggregation index of Clark and Evans (R), with $R = 1$
184 indicating a completely random distribution of stems (a Poisson process), $R > 1$ a tendency
185 towards regular spacing among stems, and $R < 1$ a clustered spatial pattern in stem locations. To
186 account for edge effects between adjacent plots that might influence clumping patterns of stems,
187 the Donnelly correction (Donnelly, 1978) was applied to the Clark and Evans index computation.
188 Two tree species diversity measures were derived: the non-spatial Shannon species diversity
189 index (H) and a nearest neighbor spatial metric, the species mingling index (M). Only stems that
190 were alive in 2007 and/or at the time of re-measurement (in 2015 or 2016) were included in the
191 derivation of these indexes, all of which were computed using R statistical software (R Core
192 Team, 2017).

194 *Aboveground wood net primary production*

195 We derived 8- or 9-year aboveground wood NPP across the disturbance severity gradient from
196 total plot live wood mass increment between 2007 and 2015 or 2016. We first estimated plot
197 wood mass before and after disturbance for all live stems with $DBH \geq 1$ cm using region-
198 specific allometric equations relating DBH to wood mass (Perala & Alban, 1994), and then
199 divided this total increment by the number of intervening years to obtain an annual production
200 value. To compare relative responses to disturbance of plot wood NPP, irrespective of initial
201 production, we report the difference in individual plot wood NPP from the 15-plot mean wood
202 NPP. This difference is expressed as plot fraction of departure from mean wood NPP (hereafter,

203 NPP_{dep}), and was calculated by dividing the wood NPP of each plot by mean wood NPP,
204 quantity minus one.

205

206 *Leaf area index*

207 We assessed peak leaf area index (LAI) in 2016 through optical imaging of the canopy.
208 Hemispherical skyward-facing images at plot centers were taken at 1 m above the forest floor
209 under diffuse light using a leveled camera with a 180° fisheye lens. Images were registered using
210 ImageJ (Version 1.51; Schneider, Rasband, & Eliceiri, 2012), and estimates of LAI were derived
211 using Gap Light Analyzer (Version 2.0; Frazer, Canham, & Lertzman, 1999) software with
212 MINIMUM thresholding applied, as this algorithm is suitable for canopies with gaps (Inoue,
213 Yamamoto, & Mizoue, 2011).

214

215 *The fraction of photosynthetically active radiation absorbed by canopies*

216 To evaluate whether changes in species diversity and vegetation structure corresponded with
217 canopy light interception, we quantified the fraction of photosynthetically active radiation
218 (fPAR) absorbed by the canopies of each plot at peak LAI in 2016. We used an AccuPAR LP-80
219 ceptometer (Decagon Devices Inc, Pullman, Washington, USA) to measure ground-level PAR
220 along a 2 m x 2 m gridded 400 m² area within each plot for a total of 100 measurements.
221 Concurrent above-canopy PAR measurements were obtained from an Apogee SQ-110 quantum
222 sensor (Apogee Instruments Inc., Logan, Utah, USA) positioned on a nearby (< 200 m)
223 meteorological tower, and ground and above-canopy PAR matched to the closest (≤ 5 min)
224 datum for the derivation of fPAR. Measurements were attempted under clear sky conditions
225 between the hours of 11:30 am and 4:00 pm from mid-July to early August, 2016, but
226 intermittent cloud cover in 9 plots forced the omission of 1 to 32 % of total PAR measurements
227 in these plots.

228

229 *Leaf physiology and morphology*

230 We examined the means and variability of leaf physiological and morphological characteristics
231 across the disturbance severity continuum during peak leaf out (mid-July to mid-August) in
232 2016. To capture representative variation along vertical and horizontal canopy axes, we
233 established 1 m² quadrats at 0, 2, 4, and 6 m from the center of our plots along the four cardinal

234 axes. Two leaves, irrespective of species, that came closest to intercepting the vertical axis at the
235 center of the quadrat at 1 m and 3 m canopy height were selected for measurements. When the
236 leaves of woody species were absent from a quadrat, bracken fern (*Pteridium aquilinum* L.), the
237 most prominent subcanopy herbaceous species, was sampled if present. Though up to 26 leaves
238 per plot could be sampled using our protocol, actual sample size varied from a minimum of 6 to
239 a maximum of 20 leaves because of vegetation gaps.

240 For each sampled leaf, we measured photosynthetic capacity of light-saturated leaves
241 (A_{sat}) and apparent quantum yield using a LI-6400XT Portable Photosynthesis System (LI-COR
242 Incorporated, Lincoln, Nebraska, USA). A_{sat} was the stable maximum rate at which light-
243 saturated ($2000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) leaves assimilated carbon dioxide ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$).
244 Apparent quantum yield of photosynthesis (q) values were obtained for 1 m leaves through light
245 response curve model fitting using R code for nonlinear least squares regression of a
246 nonrectangular hyperbola (Heberling & Fridley, 2013). Our models used 10 measurements for
247 fitting curves and derived q with the following parameters: incoming PAR, photosynthetic rate
248 (A_{net}), maximum photosynthetic rate (A_{max}), daytime dark respiration rate (A_{net} at PAR = 0), and
249 a dimensionless curve convexity parameter. Although modeled light response curve fits were
250 attempted for all 97 leaves collected at 1 m height, 18 of the leaves' models failed to converge on
251 a closed solution; thus, we present q results derived from 79 statistically significant ($\alpha = 0.05$)
252 curves.

253 We characterized leaf morphology as leaf mass per area (LMA), a commonly measured
254 leaf trait useful in distinguishing shade- from sun-adapted leaves, and one which is sensitive to
255 disturbance-driven changes in subcanopy light regime (Poorter, Niinemets, Poorter, Wright, &
256 Villar, 2009). Individual leaf area was determined using a LI-3100C Area Meter (LI-COR
257 Incorporated, Lincoln, Nebraska, USA). Pine needles and deciduous broadleaf specimens were
258 each included in analysis and scanned at the appropriate resolution (0.1 mm^2 and 1 mm^2 ,
259 respectively). Leaves were subsequently dried at $60 \text{ }^\circ\text{C}$ for 48 hours, then weighed to calculate
260 leaf mass per area.

261

262 *Statistical analysis*

263 To evaluate whether disturbance severity shifts species diversity and vegetation structure, and
264 consequently initiates a cascade of changes in fPAR, leaf physiology and morphology, and
265 ultimately wood NPP, we conducted a series of regression analyses based on *a priori*
266 expectations of the cause-and-effect order and shape of these relationships. For all response
267 variables, we evaluated three disturbance severity-response relationships grounded in prior
268 published observations: a linear null model (Hicke et al., 2012); a unimodal quadratic
269 relationship adhering to the intermediate disturbance hypothesis (Connell, 1978); and, a
270 threshold model reflecting an abrupt non-linear transition or break point (Stuart-Haëntjens et al.,
271 2015). All three model fits were attempted and the model that had significance at $\alpha = 0.10$ with
272 the lowest Akaike Information Criterion corrected for small sample size (AICc) value was
273 chosen. To enable comparison across models and to guard against inflation of explanatory
274 power, we report the Adjusted r^2 value for each selected model. A synthesis of disturbance-
275 structure-function relationships was conducted to determine whether the postulated ordered
276 cascade of effects -- with disturbance shifting vegetation structure and species diversity, light
277 capture, leaf physiology, and finally NPP -- was supported statistically (Fig. 2). Linear and non-
278 linear modeling and AICc computation was conducted using SigmaPlot 13.0 (Systat Software
279 Inc., San Jose, California, USA). In addition, we employed the Levene's test for equality of
280 variance in fPAR, LMA, A_{sat} and q values across the disturbance severity continuum using R.

281

282

283 **Results**

284

285 *Disturbance severity and aboveground wood net primary production*

286 Establishing continuity across studies, our observations of declining LAI and plot-level fraction
287 of departure from mean wood NPP (NPP_{dep}) with increasing tree basal area mortality (Fig. 3a, b)
288 were consistent with those previously observed for our site (Stuart-Haëntjens et al., 2015), while
289 extending the upper limit of disturbance severity by nearly 20 %. Comparable to nearby plots
290 (Stuart-Haëntjens et al., 2015), we found NPP_{dep} declined when basal area mortality exceeded
291 approximately 60 % (Figure 3b). In contrast to the non-linear threshold response observed by
292 Stuart-Haëntjens et al. (2015) at 4 or 5 years following disturbance, at 8 or 9 years post-
293 disturbance we observed a linear decline in canopy LAI and NPP_{dep} as basal area losses (i.e., as

294 disturbance severity) increased ($p = 0.02$, Adj. $r^2 = 0.29$, AICc = -24.3; $p < 0.001$, Adj. $r^2 = 0.57$,
295 AICc = -37.1).

296

297 *Study Q1: Species diversity and vegetation structure*

298 We observed significant but variable changes in most vegetation structural but not species
299 diversity measures across the disturbance severity continuum. Three of four vegetation structure
300 metrics, none of which correlated with aspen and birch basal area across plots before the
301 experiment, exhibited significant changes (Δ) with rising disturbance severity (Figure 4a-d). The
302 coefficient of variation in DBH declined weakly and linearly with rising disturbance severity (p
303 = 0.10, Adj. $r^2 = 0.13$; AICc = 104.8), while spatially explicit ΔT_d showed a stronger linear
304 decline ($p = 0.02$, Adj. $r^2 = 0.31$; AICc = -81.8). ΔG followed a weakly unimodal trend across the
305 disturbance severity gradient, with lower DBH inequalities (i.e., greater homogeneity) occurring
306 at low and high disturbance severities and peak values between 50 - 60 % basal area senesced (p
307 = 0.08, Adj. $r^2 = 0.23$; AICc = -73.4), corresponding with the disturbance level at which NPP_{dep}
308 began to decline. The shift in Clark and Evans' aggregation index (ΔR) did not exhibit a
309 significant relationship with disturbance severity (linear model: $p = 0.84$, Adj. $r^2 = -0.07$, AICc =
310 -61.2). Neither species diversity measure, the Shannon's diversity or the spatially-explicit species
311 mingling index (Fig. 4e, f), changed across the disturbance severity gradient (linear model
312 results: $p = 0.91$, $p = 0.26$, respectively).

313

314 *Study Q2: Canopy light interception, leaf morphology, and physiology*

315 We observed a significant negative linear relationship between canopy light interception and
316 disturbance severity ($p = 0.06$, Adj. $r^2 = 0.18$, AICc = -93.6, Fig. 5), mirroring the trend in
317 declining NPP_{dep} (Fig. 3b) with rising disturbance. Variance in fPAR (expressed as CV fPAR)
318 exhibited no significant relationship with disturbance severity when tested for linear, unimodal,
319 or threshold model fits ($p = 0.14$, $p = 0.13$, and $p = 0.31$, respectively), although evidence of non-
320 constant variance was found in fPAR measurements across the disturbance severity continuum
321 via the Levene's test ($p < 0.001$, Table 2).

322 Rising disturbance severity reduced the spatial variability of some physiological but not
323 morphological leaf traits and had no effect on mean values at the plot scale. Mean plot LMA
324 (including deciduous broadleaf and evergreen needleleaf species) did not exhibit a significant
325 pattern of change across the disturbance severity continuum, nor did either leaf physiological
326 parameter examined (A_{sat} and q , data not shown). However, coefficients of variation (CV) for
327 A_{sat} , q , and LMA declined at high disturbance severities, with maximal values occurring below
328 50 % basal area loss. Levene's test for equality of variances provided strong evidence for
329 heteroscedasticity in A_{sat} values across plots ($p < 0.001$, Table 2), though not for the apparent
330 quantum yield of photosynthesis (q ; $p = 0.11$) or for LMA ($p = 0.28$).

331

332 *Study Q3: Cascading disturbance-structure-production interactions*

333 We examined whether changes over time in forest structure – shaped by or independent of
334 disturbance – are linked to wood NPP through an interrelated cascade of relationships coupling
335 structure with fPAR, leaf physiology, and NPP_{dep} . We focus on two vegetation structure metrics:
336 the Gini index of DBH (ΔG), exhibiting a significant change with rising disturbance severity ($p =$
337 0.08 , Adj. $r^2 = 0.23$, AICc = -73.4), and the Clark and Evans' aggregation index (ΔR), which did
338 not change with disturbance but was significantly unimodally related to NPP_{dep} ($p = 0.07$, Adj. r^2
339 $= 0.25$, AICc = -26.1 , Fig. 6). Even though ΔG followed a unimodal distribution across the
340 disturbance continuum, this measure of vegetation structure exhibited no relationship with fPAR,
341 CV A_{sat} , or wood NPP_{dep} , resulting in a broken chain between disturbance-driven changes in
342 stem diameter distribution and downstream mechanisms hypothesized to affect NPP. In contrast,
343 ΔR was unrelated to disturbance severity, but its change over the 8 to 9-yr study period was
344 correlated via negative linear, unimodal, and positive linear models with all four intermediary
345 variables (mean and CV fPAR, mean and CV A_{sat}) in our hypothetical mechanistic pathway
346 (Figs. 2 and 6) and directly with NPP_{dep} .

347

348

349 **Discussion**

350 We found forest structural indexes describing vegetation structure but not species diversity
351 changed across a disturbance severity gradient spanning 37 to 86 % tree basal area loss, but that
352 wood NPP was not related to forest structural shifts mediated by disturbance. Most of the
353 vegetation structural indexes that we examined declined at high disturbance severities and,
354 contrary to some prior results (Buckling, Kassen, Bell, & Rainey, 2000; Budke, Jarenkow, & de
355 Oliveira-Filho, 2010), species diversity indexes exhibited no change with increasing disturbance
356 severity. Disturbance-driven changes in vegetation structure, though prevalent, were not linked
357 with wood NPP. Instead, we found changes over time in the Clark and Evans' aggregation index
358 -- the only vegetation structural index unrelated to disturbance severity -- correlated with wood
359 NPP, indicating forest plots trending toward structural uniformity, independent of disturbance,
360 had lower production.

361 Similar to the mixed relationships broadly reported in the literature (Hughes, Byrnes,
362 Kimbro, & Stachowicz, 2007; Mackey & Currie, 2001), we found the effect of disturbance
363 severity on forest structure measures was mixed, with unimodal or linear responses in three of
364 four vegetation structure measures but no pattern of effects on tree species diversity. The decline
365 of three different vegetation structural measures at high levels of disturbance severity points to a
366 multifaceted increase in vegetation structural uniformity at high levels of disturbance. Consistent
367 with our findings, moderate disturbance severity may increase vegetation structural
368 heterogeneity (Seidl, Rammer, & Spies, 2014) but such responses are variable (Biswas & Mallik,
369 2010) possibly because of differences in pre-disturbance material legacies, community
370 composition, successional stage, and vegetation distribution (Dietze & Matthes, 2014). Though
371 we observed no relationship between species diversity indexes and disturbance severity, our null
372 findings are aligned with recent observations (Hughes et al., 2007; Mackey & Currie, 2001).
373 Ecological theory -- including the intermediate disturbance hypothesis (IDH) -- posits peak
374 species diversity in the moderate or intermediate range of disturbance frequency and intensity
375 (Connell, 1978; Huston, 2014), but, as with vegetation structure, empirical support for a
376 universal unimodal relationship is mixed (Mackey & Currie, 2001). In our forest ecosystem,
377 vegetation structure may show greater sensitivity to changing disturbance severity because tree
378 species diversity was already low prior to disturbance (mean tree species richness = 7.4).
379 Additionally, at our study site within FASET, the loss of a single plant functional type (fast-
380 growing, short-lived early successional trees) – simulating successional change region-wide –

381 was consistent across the entire manipulation. Taken together, the mixed significance and shape
382 of forest structure-disturbance severity relationships that we observed reinforce the importance
383 of applying system-dependent context to the interpretation of ecological theory (Huston, 2014).

384 Disturbance severity modified the subcanopy light environment and exerted mixed
385 effects on leaf traits. Deeper canopy light penetration is widely observed at higher disturbance
386 severities (Fauset et al., 2017; Turton & Siegenthaler, 2004) as is increased light spatial
387 homogeneity as canopies become more uniformly open (Chazdon & Fetcher, 1984). We
388 incorrectly anticipated that at high disturbance severities, a more homogenous and enriched
389 subcanopy light environment would consistently augment leaf trait uniformity and promote sun-
390 leaf physiology and morphology. Significantly different variances in plot-level fPAR across the
391 disturbance continuum, despite a concomitant decline in fPAR at high disturbance severity, may
392 explain why leaf morphology and one of two leaf physiological parameters (q , but not A_{sat})
393 remained steady with rising disturbance severity. Underlying our expectation of co-varying light
394 environment and leaf trait properties are observations linking growth-limiting resource
395 availability and variability across topographic, successional, and disturbance gradients with the
396 means and variability of plant traits (Herben, Klimešová, & Chytrý, 2018; Wilfahrt, 2018).
397 Moreover, earlier observations from our experimental site showed significant changes in
398 subcanopy leaf trait profiles 4 years after disturbance (Stuart-Haëntjens et al., 2015). Our results
399 instead show that changes in subcanopy light environment and leaf traits 9 years after
400 disturbance were not proportional to tree mortality, suggesting that leaf physiological and
401 morphological traits may have returned to their pre-disturbance means, indicative of functional
402 resilience (Hillebrand et al., 2017).

403 Despite strong pair-wise relationships between many variables, we did not observe a
404 continuous mechanistic cascade coupling disturbance severity with NPP. Though an
405 interconnected cause-and-effect chain was not detected, bivariate relationships along our
406 proposed cascade are supported by prior observations linking: disturbance severity and forest
407 structure (Sousa, 1984); vegetation structure and light environment (Ishii & Asano, 2010); light
408 environment and leaf physiology and morphology (Niinemets, 2010); and leaf physiology and
409 morphology and primary production (Chapin, 2003). We may not have observed a mechanistic
410 linkage joining vegetation structure and production because relationships within every segment

411 of the hypothesized cascade (e.g., disturbance severity vs. vegetation structure, Fig. 2) were often
412 not significant or only weakly significant and, accordingly, unlikely to carry forward to NPP
413 (Fig. 6). Both our small sample size of 15 plots and the inherent variability within our study
414 ecosystem yielded uncertainty in our analysis, and we caution that strong evidence for or against
415 relationships among variables was not consistently detected. We also may not have captured the
416 most functionally important mediating processes – in our case, light environment and leaf
417 physiological and morphological traits – connecting vegetation structure and wood NPP.
418 However, prior work from our site (Stuart-Haëntjens et al., 2015) and other forests (Atkins,
419 Fahey, Hardiman, & Gough, 2018) demonstrates that light is a growth-limiting resource tied to
420 species diversity and vegetation structure and, separately, that leaf photosynthetic traits can be
421 predictors of ecosystem level production (Wang et al., 2015). Our inconclusive findings bolster
422 recent pleas for manipulative experiments aimed at identifying the mechanisms linking
423 ecosystem structure and function following disturbance (Hillebrand et al., 2017; Hooper et al.,
424 2005).

425 Though disturbance-shaped vegetation structure was not coupled with wood NPP,
426 changes in stem arrangement over time – independent of disturbance – had effects on primary
427 production. Wood NPP was greatest when the Clark and Evans stem aggregation index was
428 stable over time ($\Delta R = 0$), with plots trending toward a more clumped stem arrangement ($\Delta R <$
429 0) or a more ordered pattern ($\Delta R > 0$) exhibiting the lowest relative NPP_{dep} . A tendency toward
430 more ordered or uniform stem arrangements corresponded with less canopy light absorbed and
431 reduced variability in A_{sat} . Vegetation structure, even when not altered by recent disturbance, can
432 exert a strong influence over production (Hardiman et al., 2011). However, numerous unresolved
433 questions center on understanding which vegetation structural features are most closely tied to
434 production and whether they change over time and across ecosystems. The principal vegetation
435 structural determinant of forest production may change as ecosystem development unfolds over
436 decades to centuries (Silva Pedro et al., 2017) and may differ among plant functional types
437 (Scheuermann et al., 2018). Additionally, the successional context of ecosystems – in our study
438 case, a forest in transition from early- to middle-stages – differentially influences the production
439 response to disturbance. Our findings would likely not have been the same in a fast-growing,
440 early successional forest, nor in an old growth forest with fewer subcanopy trees poised to
441 benefit from disturbance-mediated release. Advancing understanding of structure-function

442 relationships will require nuanced consideration of the way vegetation structural and species
443 diversity attributes are shaped and, in turn, shape production, with attention to multiple scales of
444 organization and time required to understand the breadth of patterns found in nature.

445

446 **Conclusions**

447 Determining how and why disturbance -- which is increasing in frequency and extent globally --
448 will modify forest ecosystem structure and functioning remains a grand challenge because of the
449 complexity, variability, and dynamic nature of these core ecosystem properties. Our results,
450 though mixed, suggest that several interrelated linkages exist in our study ecosystem between
451 disturbance severity, vegetation structure (but not species diversity), subcanopy light
452 environment and leaf traits, and NPP. However, our findings also reveal a lack of complete
453 continuity linking disturbance to structure and functional change through the mediating effects of
454 changing resource environment and leaf physiology and morphology. We conclude that
455 additional investigation of multiple ecosystems at various stages of development is needed to
456 identify which structural changes owing to disturbance affect core ecosystem functions such as
457 primary production.

458

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465 2007 stem maps (including that featured in Supplemental Figure 1).

466

467 **Authors' Contributions**

468 L.T.H., R.T.F., and C.M.G. designed the current study; W.S.C. designed and directed 2007
469 study; L.T.H., N.C.P., and S.B.W. collected 2015-2016 data; L.T.H. processed data, performed

470 statistical analyses, and wrote manuscript draft; B.S.H. provided analytical expertise and
471 guidance; all authors contributed substantially to revisions.

472

473 **Data Accessibility**

474 Raw data for all analyses from 2007 and 2015-2016, as well as code used to run structural
475 analyses, are available through the Figshare digital repository: 10.6084/m9.figshare.11935197

476

477 **Conflict of Interest Statement**

478 The authors have no conflicts of interest to declare.

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Figure Legends and Tables:

Figure 1. Our study system is a northern temperate mixed hardwood forest where experimental disturbance has altered vegetation structure, including the creation of deep canopy gaps.

Figure 2. Hypothesized sequence of mechanistic linkages coupling disturbance severity and net primary production. Boxes illustrate ecological variables while arrows represent relationships between variables. Citations indicate example prior studies where these bivariate relationships have been supported: (1) Connell, 1978; (2) Sousa, 1984; (3) Sercu et al., 2017; (4) Canham, Finzi, Pacala, & Burbank, 1994; (5) Ishii & Asano, 2010; (6) Parker & Brown, 2000; (7) Ellsworth & Reich, 1993; (8) Niinemets, 2010; (9) Rozendaal, Hurtado, & Poorter, 2006; (10) Santiago & Wright, 2007; (11) Chapin, 2003; (12) Nicotra et al., 2010.

Table 1. Vegetation structural and species diversity 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, 1949)	$H = - \sum_{i=1}^S p_i \ln(p_i)$	S : total number of species in the community p_i : proportion of S made up of the i th species

Species mingling index,
 M
 (Pommerening,
 Gonçalves, & Rodríguez-
 Soalleiro, 2011)

$$M = \sum_{k=1}^n \frac{k}{n} m_k = \frac{1}{N} \sum_{i=1}^N M_i$$

n : number of nearest neighboring
 trees analyzed per individual (4)
 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

Figure 3. Leaf area index (a, LAI) and fraction of departure from mean wood NPP (b, NPP_{dep}) in relation to disturbance severity expressed as the fraction of basal area loss.

Figure 4. Vegetation structure and species diversity changes (Δ) across a disturbance severity continuum expressed as fraction of basal area loss. Vegetation structure indices: the coefficient of variation of DBH (a, CV DBH), the Gini coefficient of DBH (b, G), the diameter differentiation index (c, T_d), and the Clark and Evan’s aggregation index (d, R). Diversity indices: the Shannon’s diversity index (e, H) and the species mingling index (f, M).

Figure 5. The fraction of photosynthetically active radiation (fPAR) absorbed by the canopy in relation to disturbance severity expressed as the fraction basal area loss. Means +/- 1 S.E.

Table 2. Statistical test results for means and equality of variance (Levene’s test) for canopy light interception (fPAR) and leaf physiological (maximum rate of light-saturated photosynthesis, A_{sat} ; apparent quantum yield of photosynthesis, q) and morphological (LMA) parameters. Significance was determined at $\alpha = 0.10$ for all tests, and significant p -values are shown in bold. Where no significant fit was found among candidate linear, unimodal, and threshold relationships, p -values for linear models are reported.

	Light	Physiology & Morphology		
	fPAR	LMA	A_{sat}	q
Mean vs. Disturbance Severity	$p = 0.04$ (unimodal)	$p = 0.69$	$p = 0.29$	$p = 0.29$
Levene’s test	$p < 0.001$	$p = 0.28$	$p < 0.001$	$p = 0.11$

Figure 6. Illustration of an interconnected disturbance-structure-function cascade for two vegetation structural metrics: the aggregation index of Clark and Evans (ΔR) and the Gini index

of DBH (ΔG). ΔR , though not correlated with disturbance severity, exhibited either unimodal or linear) relationships with all five downstream variables tested. In contrast, ΔG , though related unimodally to disturbance severity, did not relate to canopy light capture (fPAR), leaf-level physiology (A_{sat}), or fraction of departure from mean wood net primary production (NPP). To enable direct comparison of different models across this proposed mechanistic pathway, adjusted r^2 values are provided for each variable linkage, and models were selected based on the lowest Akaike Information Criterion correction for small sample size (AICc) scores. p -values and AICc scores are provided in Supplementary Table 2. Only one threshold relationship was retained across variables tested.

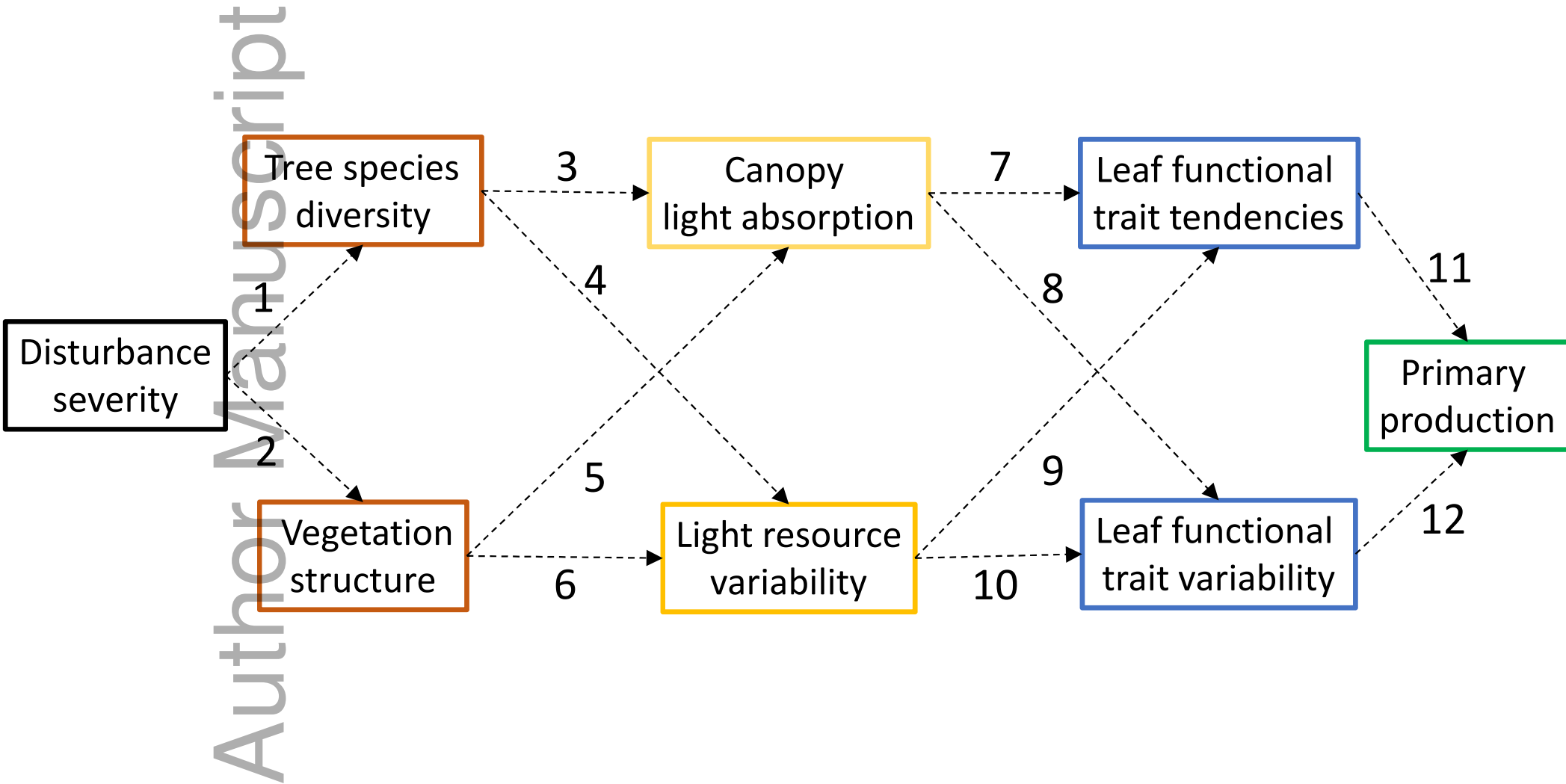
Supplemental Figure Legends and Tables

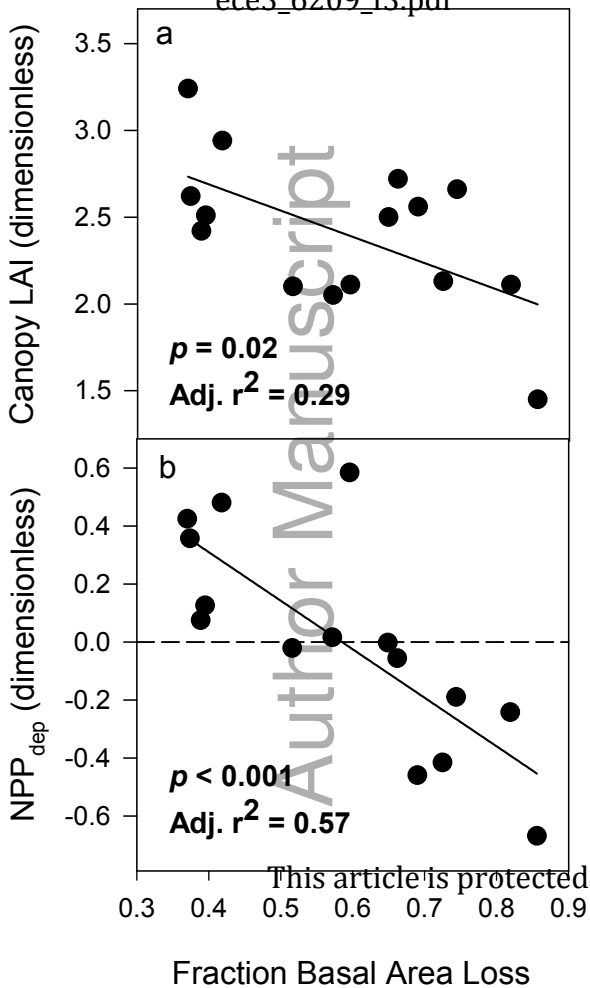
Supplemental Figure 1. 2007 stem map of a (100 m x 100 m) 1-ha Forest Accelerated Succession Experiment stand illustrating stem size class (via circle diameter, ranging from 1 cm to 40+ cm DBH) and spatial distribution. Prior to disturbance, there was ample coverage by aspen (blue) and birch (orange), which were targeted for girdling and subsequently lost. The remainder of pre-disturbance species were white pine (green), red maple (red), red oak (light purple), serviceberry (yellow), and lesser representation by striped maple (pink) and American beech (dark purple).

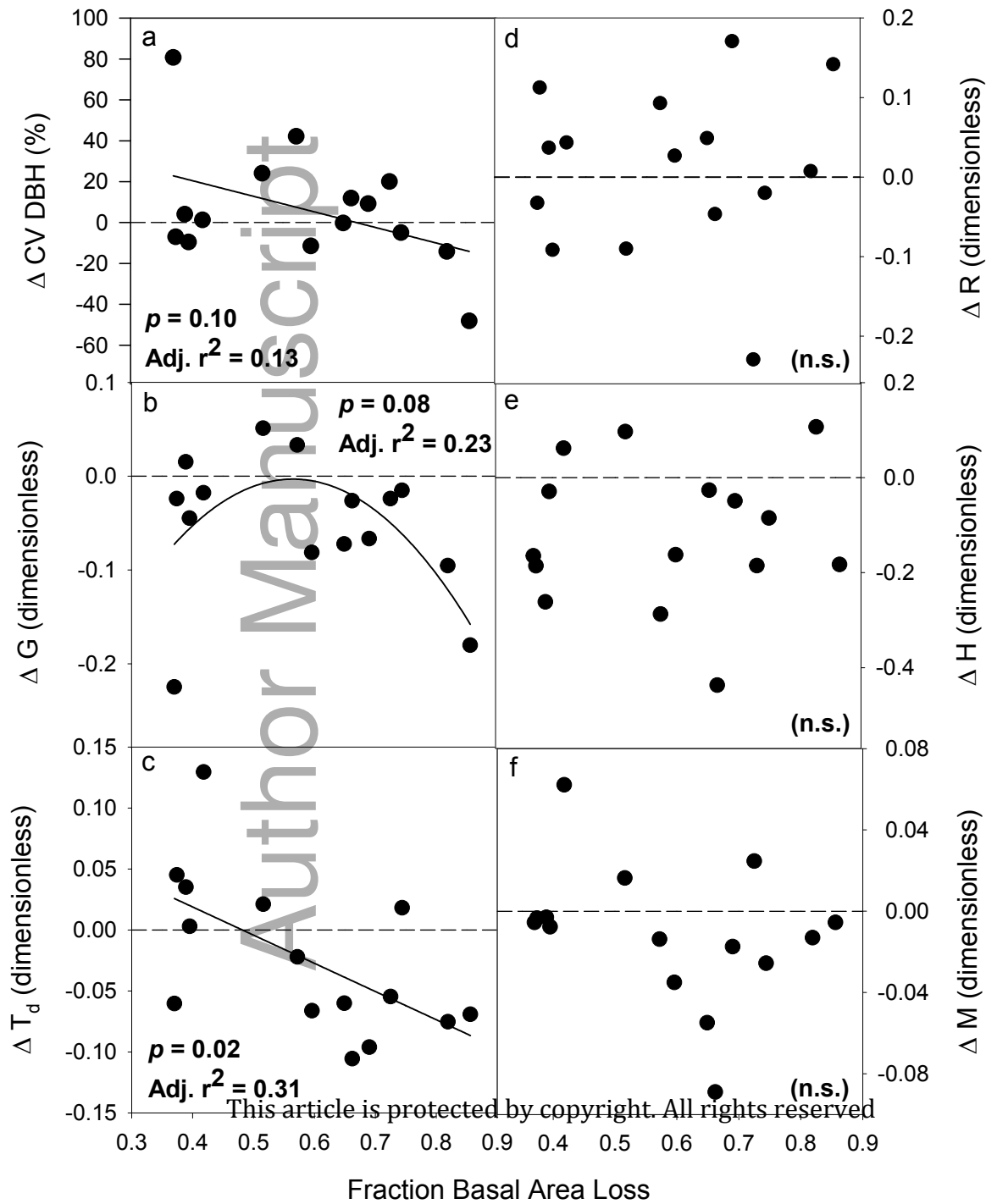


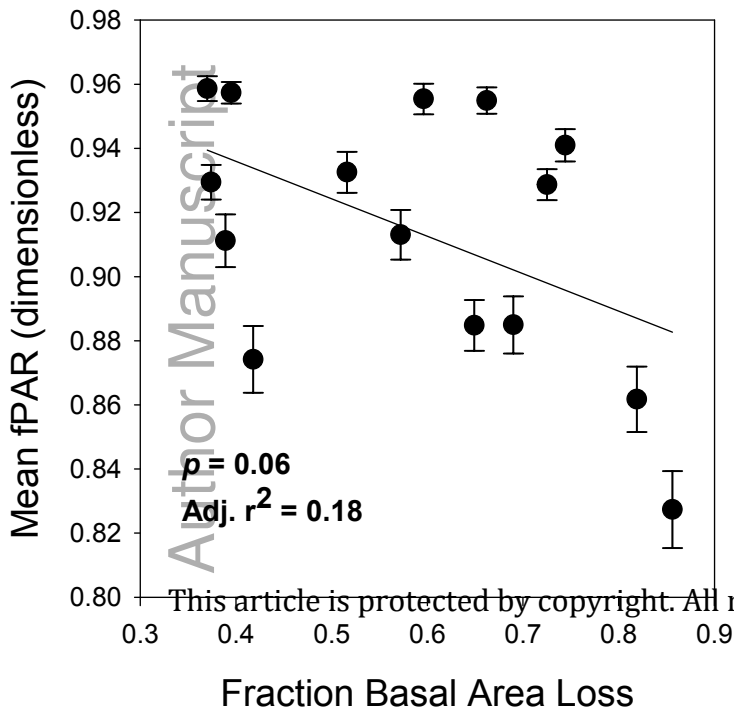
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AU









- ← Negative linear
- ← Positive linear
- ← Unimodal
- ← Threshold
- ← Not Significant

