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12 Running head: Succession, disturbance, carbon cycling

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Disturbance-accelerated succession increases the production of a temperate forest

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43 **Abstract:**

44 Many secondary deciduous forests of eastern North America are approaching a transition in

45 which mature early successional trees are declining, resulting in an uncertain future for this

46 century-long carbon (C) sink. We initiated the Forest Accelerated Succession Experiment

47 (FASET) at the University of Michigan Biological Station to examine the patterns and

48 mechanisms underlying forest C cycling following the stem girdling-induced mortality of >6,700

49 early successional *Populus spp.* (aspen) and *Betula papyrifera* (paper birch). Meteorological flux

50 tower-based C cycling observations from the 33-ha treatment forest have been paired with those

51 from a nearby unmanipulated forest since 2008. Following over a decade of observations, we

52 revisit our core hypothesis: that net ecosystem production (NEP) would increase following the

53 transition to mid-late successional species dominance due to increased canopy structural

54 complexity. Supporting our hypothesis, NEP was stable, briefly declined, and then increased

55 relative to the control in the decade following disturbance; however, increasing NEP was not

56 associated with rising structural complexity but rather with a rapid 1-year recovery of total leaf

57 area index as mid-late successional *Acer*, *Quercus*, and *Pinus* assumed canopy dominance. The

58 transition to mid-late successional species dominance improved carbon-use efficiency (CUE =

59   NEP/gross primary production) as ecosystem respiration declined. Similar soil respiration rates

60   in control and treatment forests, along with species differences in leaf physiology and the rising

61   relative growth rates of mid-late successional species in the treatment forest, suggest changes in

62   aboveground plant respiration and growth were primarily responsible for increases in NEP. We

63   conclude that deciduous forests transitioning from early to middle succession are capable of

64   sustained or increased NEP, even when experiencing extensive tree mortality. This adds to

65   mounting evidence that aging deciduous forests in the region will function as C sinks for decades

66   to come.

67

68   Key words: disturbance, succession, carbon, production, leaf area index, structural complexity,

69   forests, stability, resistance, AmeriFlux

70   1.   Introduction

71   In North America's temperate deciduous forests, the concurrent transition to mid-late

72   successional species composition and increased frequency and extent of moderate-severity

73   disturbances (Cohen et al. 2016; Kautz et al. 2017; Kosiba et al. 2018; Stueve et al. 2011) may

74   threaten the sustainability of this globally significant century-long carbon (C) sink (Birdsey et al.

75   2006; Pan et al. 2011a; Williams et al. 2016). Following widespread clear-cut harvesting and

76   agricultural abandonment over a century ago, forest regrowth in the eastern half of the continent

77   has sustained C sequestration in plant biomass and soils (Pan et al. 2011b). Now, as vast areas of

78   early successional tree species reach maturity and begin to decline (Gough et al. 2016),

79   significant community compositional and structural changes are underway as mid-late

80   successional species assume canopy dominance. At the same time, stand-replacing disturbances

81   in the region are becoming less common and instead trending toward more frequent partial

82   canopy defoliation and tree mortality from wind and ice, insects, pathogens, and age-related

83   senescence. These patchy disturbances may accelerate succession (Abrams and Scott 1989),

84   advancing compositional and structural changes that would otherwise require decades to unfold

85   (Atkins et al. 2020; Franklin et al. 2007; Hanson and Lorimer 2007). This region-wide ecological

86   intersection of shifting disturbance regime amid a rapid successional transition raises questions

87   about future forest C sequestration and the mechanistic pathways leading to its stability or

88   decline (Goetz et al. 2012).

89   Although disturbance-succession interactions have long transcended ecological

90   disciplines (sensu Whittaker 1956) and served as guiding tenets of ecosystem management

91   (Coates and Burton 1997), theory and observations offer conflicting views on how forecasted

92   changes in forest composition and structure will affect ecosystem C balance, or net ecosystem

93   production (NEP) (Tang et al. 2017). Defining NEP as the annual balance of ecosystem-wide

94   photosynthetic C uptake or gross primary production (GPP) minus C losses from ecosystem

95   respiration (ER), theorists hypothesized a half-century ago that the maturation and subsequent

96   mortality of early successional trees would drive down NEP by reducing photosynthetic surface

97   area and, therefore, GPP, and increasing ER as detritus-fueled heterotrophic respiration increased

98   (Odum 1969). However, space-for-time substitution or chronosequence studies applying eddy-

99   covariance or modern inventory approaches suggest the magnitude of these age-related declines

100   in NEP may be less than theorized (Besnard et al. 2018; Curtis and Gough 2018; Gough et al.

101   2016; Luyssaert et al. 2008). Moreover, low-to-moderate severity disturbances may accelerate

102   succession, expediting, rather than rewinding, the development of compositional and structural

103   features associated with older forests (Abrams and Scott 1989). Disturbance-mediated

104   successional advancement may liberate growth-limiting resources and foster the development of

105   canopy structural features associated with improved growth and resource-use efficiency, thereby

106   offsetting declines in production from tree mortality (Hardiman et al. 2013b). For example,

107   structural complexity, defined as the spatial heterogeneity of leaf area distribution within a

108   canopy, increases as forests age and in response to some forms of disturbance, and is associated

109   with higher rates of net primary production (Gough et al. 2019).

110   Few studies continuously track NEP as disturbance and succession-related compositional

111   and structural changes unfold and resolve. Yet, long-term uninterrupted ecosystem-scale

112   measurements, particularly when paired with controls, are crucial to advancing fundamental

113   understanding of what drives NEP during and following ecologically dynamic periods; such

114   knowledge cannot be acquired from short-term or chronosequence based approaches (Hicke et

115   al. 2012). These foundational ecological knowledge gaps are relevant to many unresolved forest

116   C management questions. For example, should forest managers cultivate an early or mid-late

117   successional stand structure to maximize C sequestration? What disturbances should be

118   minimized or fostered through management to sustain forest C sequestration?

119   The Forest Accelerated Succession Experiment (FASET) was initiated in 2008 with the

120   primary goal of quantifying C exchange processes throughout a successional shift from a

121   maturing early successional *Populus-Betula* (aspen-birch) to middle successional *Acer-Pinus-*

122   *Quercus* forest. Secondarily, the experiment evaluated C cycling responses to a moderate-

123   severity disturbance resulting in the mortality of one-third (by stem basal area) of all canopy

124   trees. Observations from the first four years of the experiment (summarized in Fig. 1) revealed

125   that, counter to our hypothesis, NEP was sustained at higher-than-expected levels despite

126   temporary declines in LAI of ~40% (Gough et al. 2013; Stuart-Haentjens et al. 2015) as rapidly

127   retranslocated nitrogen (Nave et al. 2011a; Nave et al. 2014) enhanced the physiological

128   competency and compensating growth of healthy vegetation (Fahey et al. 2016). In addition,

129   increases in heterotrophic respiration fueled by the influx of detritus were lower and more

130   gradual than anticipated, and not large enough to transition the treatment forest from C sink to

131   source (Schmid et al. 2016).

132   Here, following more than a decade of observations, we reassess the core hypothesis of

133   the FASET study (Gough et al. 2013): when fully transitioned to mid-late successional species

134   dominance, NEP in the treatment forest will exceed that of the unmanipulated, control forest. In

135   support of open science best practices (Nilsen et al. 2020), we include in Supplemental

136   Information the 2006 FASET proposal narrative detailing the project, focusing here on the first

137   objective and hypothesis (Supplemental Information, "FASET Proposal"). Briefly, we posited

138   that the treatment forest would gain structural complexity over time as aspen and birch mortality

139   gave rise to a patchy multi-layered canopy, and that this enhanced canopy structural complexity

140   would drive greater resource-use efficiency (Atkins et al. 2020; Atkins et al. 2018b; Hardiman et

141   al. 2013a) and, consequently, higher production (Gough et al. 2019; Hardiman et al. 2013b).

142

143   2. Methods

144   2.1. Study site and experimental overview

145   Our study is hosted by the University of Michigan Biological Station (UMBS), in northern

146   Michigan, USA (45°35'N 84°43'W). The mean annual temperature at the site is 5.5^{o}C and mean

147   annual precipitation is 817 mm (1942-2003). Prior to experimental disturbance, early

148   successional species, i.e., bigtooth aspen (*Populus grandidentata*), trembling aspen (*Populus*

149   *tremuloides*), and white birch (*Betula papyrifera*), were dominant components of the forest

150 canopy, representing 39% of stand basal area (Gough et al. 2010). In the years before the

151 experiment, mid-late successional northern red oak (*Quercus rubra*), eastern white pine (*Pinus*

152 *strobus),* sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and American beech (*Fagus*

153 *grandifolia*) were gaining dominance as early-successional aspen and birch stem mortality rates

154 averaged ~4% annually (Gough et al. 2013; Gough et al. 2010). Prior to the experiment, forest

155 structural features were similar in control and treatment forests, with the density of trees $\geq$8 cm

156 diameter at breast height (DBH) 700-800 ha^{-1}, basal area ~25 m^2 ha^{-1}, and leaf area index (LAI)

157 averaging ~4.5, but slightly higher in the treatment forest. Although several decades older, our

158 study site falls near typical or median conditions for upland forests across the region in growth

159 rate, physiography and soils as detailed in Nave et al. (2017).

160 Broadly, we initiated the Forest Accelerated Succession Experiment (FASET) to identify

161 how disturbance, succession, and ongoing climate change affect C fluxes in aging mixed

162 temperate forests (see Nave et al. 2011a). In May 2008, we stem girdled >6,700 aspen and birch

163 trees within four separate treatment areas totaling 39 ha, thereby accelerating the transition to a

164 canopy composition and structure that approximates longer-term changes projected for forests

165 regionally (Nave et al. 2011a), while enabling investigation of moderate-severity disturbance

166 response (Gough et al. 2013; Stuart-Haentjens et al. 2015). Tree status surveys conducted three

167 years following treatment indicated that 97% of girdled trees were dead or partially defoliated,

168 but with spatially variable basal area mortality of 6 to 69% among sampling plots (described

169 below). This experimental disturbance, including the patchy distribution of mortality, is similar

170 in severity to moderate disturbances from wind and ice events, insects, and pathogens that result

171 in partial canopy defoliation (Amiro et al. 2010; Franklin et al. 2007), but note that structural

172 (Atkins et al. 2020) and functional (Dietze and Matthes 2014) responses may vary substantially

173 among disturbances. Experimental defoliation from girdling was compounded by patchy forest

174 tent caterpillar (*Malacosoma disstria*) herbivory in 2010 (Gough et al. 2013); this disturbance

175 affected the control forest as well as the experimentally manipulated forest.

176 Paired C cycling measurements were collected within separate meteorological flux tower

177 footprints from 2008 through 2019, in both the control and treatment forests (Fig. 2). Ground-

178 based measurements were conducted in 8 pairs of ecologically similar 0.1-ha control and

179 treatment plots, selected in advance of the 2008 girdling to encompass the ranges of plant

180 community composition and LAI levels present prior to disturbance (Nave et al. 2011a). Paired

181 plots are a subset of 81 control and 22 treatment plots nested within the footprints of separate

182 control (US-UMB) and treatment (US-UMd) meteorological towers operating within the

183 AmeriFlux Core Site network (Pastorello et al. 2020), each measuring the net ecosystem CO_2

184 exchange (NEE) between forest and atmosphere. The US-UMd treatment tower, operating since

185 mid-2007, is located to the east of the main 33-ha treatment area. Three additional 2-ha treatment

186 replicate plots spanning a productivity gradient and located outside of the US-UMd tower

187 footprint (Sagara et al. 2018) are not included in the current analysis. The control tower was

188 established in 1997 in unmanipulated forest 1.5 km to the west, the ecology and biogeochemistry

189 of which are described in a series of early studies (Bovard et al. 2005; Curtis et al. 2002; Curtis

190 et al. 2005; Gough et al. 2008a; Schmid et al. 2003). Surrounding each tower is a circular 1.1-ha

191 plot and, radiating from the tower base, smaller 0.1-ha plots are arrayed at 100-m intervals along

192 transects extending 1000 m and 300 m in control and treatment forests, respectively.

193

194   2.2. Leaf area index

195 We estimated the LAI of dominant tree species within the treatment and control forests from

196 repeated collections of leaf litterfall within each of the 8 paired plots from 2007 through 2019.

197 Leaf litter was removed from three litter traps (0.264 m^2) per 0.1-ha plot and 20 litter traps per

198 1.1-ha plot weekly during leaf fall and monthly during other seasons, pooled by plot, separated

199 by species, dried, and weighed. LAI was calculated from species- and site-specific litterfall mass

200 and specific leaf area (SLA) values (Gough et al. 2010). We assumed that deciduous species

201 shed their leaves annually, and that evergreens *Pinus strobus* and *Pinus resinosa* replaced their

202 leaves over the course of two years.

203

204   2.3. Net ecosystem CO_2 exchange, gross primary production, and ecosystem respiration

205 We used eddy-covariance (EC) flux and meteorological data from each of the two sites to derive

206 ecosystem C fluxes. For the control (US-UMB, Gough et al. 2021a) and treatment (U-UMd

207 Gough et al. 2021b) sites, data were processed following a standard EC flux processing protocol

208 (Rebmann et al. 2012). Data were collected at 10 Hz, using a 3-D ultrasonic anemometer

209 (CSAT3, Campbell Scientific, Logan, UT) and gas analyzer (LI-6262 until 2008, then LI-7000,

210 LI-COR Biosciences, Lincoln, NE) at heights of 46 m (US-UMB) and 32 m (US-UMd). Full

211 instrument lists and instrument operation notes for the sites are available from the sites' pages in

212   AmeriFlux. Spikes in 10 Hz data were removed: observations above or below a reasonable range

213   removed, as well as values that were more than 6 standard deviations greater than a 2-minute

214   moving average, and values marked as bad by each sensors' data quality variable, were removed

215   and replaced by NaN. Despiked 10 Hz data were processed into 30-minute averages and fluxes

216   (covariances). 30-minute periods that included less than 50% of the 10 Hz data were removed

217   and marked as missing observations. These were exceptionally rare and occurred less than 1% of

218   the time.

219   NEE was calculated by adding the observed EC flux of C to the half-hourly rate of

220   change of C concentration within the canopy (SC, change of carbon storage), with positive

221   values indicating a net C flux from atmosphere to forest. SC was measured by sampling CO_2

222   concentration within the subcanopy, using an additional closed path gas analyzer (LI 6262, Li-

223   COR Biosciences, Lincoln, NE) and sampling air from intakes at multiple elevations under the

224   tower top. Flux data during periods of low turbulent mixing was filtered using the u*-filter

225   threshold approach, with the threshold values calculated seasonally following Reichstein et al.

226   (2005). Filtered nighttime NEE observations were assumed to be observations of ecosystem

227   respiration (ER). Seasonal ER observations were used to train an automated neural network

228   (ANN) model using time of day, air temperature, vapor pressure deficit, soil temperature, and

229   soil moisture as inputs (Lasslop et al. 2010). The exact setup of the ANN models we used is

230   described in Morin et al. (2014a). For all ANN models, we used 50% of the data for training,

231   25% for evaluation and 50% for validation of the ensemble's goodness-of-fit. We used the

232   ensemble mean of the best 10% of 1000 ANN models to predict ER during the day, and during

233   nighttime observation gaps.

234   To calculate gross primary productivity (GPP), we assumed that during the growing

235   season, GPP = (observed NEE – modeled ER). In the winters and nighttime, we assumed GPP =

236   0. We used ANN models similar to those used for ER to model GPP for the purpose of gap

237   filling where NEE observations were missing in the daytimes of each growing season. The ANN

238   models for GPP used air temperature, incoming PAR, relative humidity, vapor pressure deficit,

239   sensible and latent heat fluxes, and soil moisture as input variables. Before running the ANN

240   models for GPP and ER, we gap filled the input variables used by these models. Specifically,

241   meteorological variables other than fluxes and soil moisture were gap filled using values

242   measured at the same time in the adjacent site (i.e., US-UMB data to gap fill US-UMd, and vice

243   versa). If data were missing from both sites, ANN inputs were gap filled using a bi-linear

244   interpolation between the observations before and after the gap as well as between observations

245   in the same time of day in the day before and after the gap. Fluxes used as ANN input, i.e.,

246   sensible and latent heat fluxes, were gap filled using seasonal ANN models with air temperature,

247   humidity, VPD, soil moisture, and time of day as inputs. Finally, after we had full seasonal

248   predictions of ER and GPP, we gap filled NEE (as gap-filled GPP + gap-filled ER), summing

249   half-hourly values during a calendar year to produce annual net ecosystem production (NEP).

250   To estimate uncertainty of the observation, we followed the approach of Richardson et al.

251   (2006), calculating a compounding error distribution for daytime and nighttime data at each

252   season in each year. We used the distribution of the ANN prediction members within the

253   ensemble around the deviation from the observation in the validation dataset to estimate the

254   uncertainty of the gap-filled data (Morin et al. 2014b). We simulated an ensemble of 1000

255   members of the observed and gap-filled data with added random error (drawn from the

256   corresponding distribution, based on data type, day or night, and season/year), and estimated the

257   error of the total C accumulation from the standard deviation of the ensemble.

258

259   2.4. Canopy structure from LiDAR

260   We characterized multiple aspects of canopy structure in each of the 8 paired control and

261   treatment plots using a ground-based Portable Canopy LiDAR (PCL) system. The design,

262   operation, and validation of this system is described in Parker et al. (2004). The system has been

263   used previously at our site to relate canopy structure to net primary production (Hardiman et al.

264   2011; Hardiman et al. 2013b) and to investigate initial (2008-2011) canopy structural changes

265   following tree mortality (Hardiman et al. 2013a). The PCL is based on an upward looking, near-

266   infrared pulsed-laser operating at up to 2000 Hz (model LD90-3100VHS-FLP, Riegl USA, Inc.,

267   Orlando, FL, USA). Our system was mounted on a custom-built frame worn by operators while

268   walking along transects that passed through the center of each plot. We binned the raw data

269   horizontally and vertically into 1-m^2 grids for structural analysis, and derived estimates of

270   canopy structure using the R package *forestr* (Atkins et al. 2018a).

271   We restrict our analysis to canopy structural measures significantly correlated with forest

272   production (Gough et al. 2019): mean canopy height (m); vegetation area index (VAI;

273   dimensionless, includes leaf and woody biomass); canopy rugosity (m, vertical and horizontal

274 vegetation density and distribution variability); top rugosity (m, outer canopy surface vegetation
275 density and distribution variability); rumple (dimensionless, ratio of canopy outer surface area to
276 ground surface area); and canopy cover (%, ratio of bins returning lidar hits to the total bin
277 number). Three of these measures – canopy rugosity, top rugosity, and rumple – summarize
278 stand-scale complexity, describing different but related aspects of canopy physical structural
279 heterogeneity (Gough et al. 2020). We refer readers to Atkins et al. (2018a; 2018b) for in-depth
280 descriptions and mathematical derivations of each structural measure.
281
282   2.5. Wood biomass relative growth rate
283 We estimated the annual relative growth rates (RGR) of aboveground wood biomass from
284 repeated measurements of tree stem diameter and allometric biomass equations. For most years,
285 we measured the diameter at breast height (DBH) annually of a subsample of the total tree
286 population with DBH ≥ 8 cm in control (n = 700 of 8860) and treatment (n = 383 of 2500)
287 forests using custom-built band dendrometers. In 2001, 2006, and 2011, RGRs were derived
288 from complete censuses of all stems with DBH ≥ 8 cm using tape measures. We inferred the
289 aboveground wood biomass in each of 81 control and 22 treatment plots (Fig. 2) using species-
290 and site- or region-specific allometric equations that relate DBH to aboveground wood biomass
291 (Gough et al. 2008b). Mean annual RGRs for individual stems of each species within a treatment
292 were calculated from the incremental change in total aboveground wood biomass from one year
293 to the next divided by the starting biomass.
294
295   2.6. Leaf gas exchange
296 In 1999, we measured leaf level gas exchange of the most abundant canopy dominant species
297 prior to disturbance, which, at the time, constituted a mix of early (aspen and birch) and mid-late
298 (red maple and red oak) successional species. Leaf CO_2 assimilation (A) versus intercellular CO_2
299 concentration (C_i) or A/C_i curves were constructed using a LI-COR 6400 (Vogel and Curtis
300 1995) with a (mean ± S.D.) cuvette temperature of 28.2 °C ± 0.57°C, relative humidity 45% ±
301 4.9%, and a saturating photosynthetically active radiation of 1800 µmol m^2 s^{-1}. The maximum
302 rate of carboxylation (V_{cmax}) and maximum rate of electron transport (J_{max}) were calculated using
303 the Farquhar C3 photosynthesis equation (1980), and light-saturated net CO_2 assimilation (A_{sat})
304 and stomatal conductance (g_s) reported for ambient CO_2 concentrations at the time of 380 ppm.

305　For dark respiration (R_d), we sampled leaves without the actinic light source two hours before

306　sunrise at leaf temperatures of 18.6°C ± 0.2°C.

307

308　　2.7. Statistical analysis

309　Our statistical analyses were guided by our core objective of examining and relating control and

310　treatment C fluxes, LAI, and canopy structure over the decade-plus study period. For LAI and

311　soil respiration, derived from repeated measures within paired plots, we used time-series

312　ANOVA followed by pairwise (LSD) comparisons of control and treatment means within a year.

313　In the case of unreplicated meteorologically derived C fluxes, we tested the hypothesis that

314　annual NEP increases over the long-term in the treatment forest (Fig. 1) by applying linear and

315　2- and 3-piecewise regression, retaining the model with the highest adjusted r^2 to account for

316　overfitting. Because lidar-based measurements of canopy structure were staggered and not

317　conducted annually and RGR measurements were not paired between treatments, we examined

318　temporal changes using linear regression, fitting separate models to control and treatment forests

319　when slopes and/or intercepts had non-overlapping 95 % confidence intervals. All statistical

320　analyses applied an α of 0.05. In figures throughout, green circles illustrate control and orange

321　squares represent treatment forest data. SAS (V94) or Sigmaplot (V14.0) software was used for

322　statistical analyses; code, files, and data to reproduce all results shown here are archived at

323　https://figshare.com/s/a6aa55b2468828594b47.

324

325　3.　Results

326　　3.1. Leaf area index

327　Following an initial decline, treatment forest total LAI recovered to control levels as mid-late

328　successional tree species rapidly replaced diminishing aspen and birch LAI (Fig. 3; Appendix

329　S1: Fig. S2). Total LAI was significantly greater in the treatment forest relative to the control the

330　year before and the year of girdling, but was significantly lower in 2010, two years after girdling.

331　This reduction in treatment forest total LAI was caused by the rapid loss of aspen and birch LAI

332　(of ~1 unit) from 2009 to 2010. The reduction was short-lived, however, with mid-late

333　successional maple, oak, and pine LAI increasing by nearly 2 units in the following year, 2011.

334　From 2011 through 2019, total LAI was similar in control and treatment forests, but leaf area

335　contributions from early and mid-late successional species differed. Aspen and birch leaf areas

336 were eliminated from the treatment forest three years after girdling, while the LAI of early

337 successional species stabilized at ~1 unit in the control forest for the remainder of the

338 observation period. Maple, oak, and pine were the only constituents of treatment forest LAI

339 beginning in 2011, and thereafter mid-late successional species' LAI exceeded that of the control

340 forest.

341

342 3.2. Annual net ecosystem production, carbon use efficiency, and soil respiration

343 Following a half-decade of high interannual variation exhibiting no mean temporal trend, annual

344 NEP in the treatment forest increased significantly (Fig. 4). Change-point regression analysis of

345 time-series identified co-occurring but different directional changes over time in control and

346 treatment forest NEP. Control forest NEP increased significantly from ~2 to 3 Mg C ha^{-1} yr^{-1}

347 between 2008 and 2013, after which NEP was relatively stable, averaging 3 Mg C ha^{-1} yr^{-1}.

348 Conversely, treatment forest NEP varied interannually by ~1.5 Mg C ha^{-1} yr^{-1} in the first six

349 years following girdling without exhibiting mean changes over time, averaging 3 Mg C ha^{-1} yr^{-1}

350 during this period. After 2014, treatment forest annual NEP sharply increased, ranging from ~3

351 to ~5 Mg C ha^{-1} yr^{-1} from 2014 through 2019 and averaging ~5 Mg C ha^{-1} yr^{-1} during the last

352 three years of this period.

353 When relative treatment effects (as percent difference from control) were considered to

354 minimize the interannual variation from other sources, change-point regression yielded three

355 segments, reflecting the dynamic relationship between NEP in control and treatment forests. In

356 the first 4 years, a zero (non-significant) slope indicated control and treatment forest NEP

357 paralleled one another, with treatment forest NEP averaging 66% greater than that of the control.

358 This period of stability was followed by a steep 2-year decline in relative NEP and, thereafter, a

359 6-year positive slope during which the treatment forest recovered its relatively higher NEP,

360 exceeding the control by 100% in the final year (2019).

361 Annual NEP in control and treatment forests closely paralleled carbon-use efficiency

362 (CUE). Following a variable period in the treatment forest, from 2008 to 2014, during which

363 annual CUE reached a low of ~0.2 twice, mean annual CUE increased abruptly to ~0.4 for the

364 next five years. Control forest CUE was similarly variable over time, from ~0.1 to 0.3, but failed

365 to reach the sustained high levels exhibited by the treatment forest.

366   Rising CUE in the treatment forest was associated with decreased ecosystem respiration
367   (Appendix S1: Fig. S3B) and stable soil respiration (Fig. 5) and annual GPP (Appendix S1: Fig.
368   S3A), suggesting that increases in NEP were supported by a reduction in aboveground
369   respiration. Ecosystem respiration rather than GPP drove interannual variation in CUE
370   (Appendix S1: Fig. S3), with a drop in annual respiratory flux in the treatment forest coinciding
371   with the period of peak CUE, from 2015 to 2019. Mean soil respiration, the largest component of
372   ecosystem respiration at our site (Curtis et al. 2005), was significantly lower in the treatment
373   forest during 3 of the first 4 years following girdling, but recovered and did not differ from the
374   control thereafter.
375
376   3.3. Wood biomass relative growth rates by successional cohort
377   The trajectories of early and mid-late successional cohort RGRs differed in control and treatment
378   forests (Fig. 6). In the control forest, early successional species RGR declined by half over a 19-
379   yr period (P<0.0001), while mid-late successional species RGR displayed no long-term trend. In
380   contrast, early successional species RGR declined rapidly to nearly zero within two years of stem
381   girdling in the treatment forest (P=0.003), while the RGR of mid-late successional species
382   steadily climbed, doubling over the course of a decade (P<0.0001).
383
384   3.4. Leaf physiology of dominant canopy species
385   Leaf physiological properties differed between dominant canopy trees from early and mid-late
386   successional cohorts (Table 1). Red maple, which constituted the largest fraction of LAI in the
387   treatment forest (Appendix S1: Fig. S1), exhibited lower photosynthetic functioning and lower
388   dark respiration than other species. With the exception of stomatal conductance, which was
389   highest in aspen, the leaf physiological properties of red oak were similar to those of aspen and
390   birch.
391
392   3.5. Canopy structure changes over time
393   Changes in canopy structure over time varied depending on the treatment and structural
394   characteristic, with canopy cover and height decreasing in both control and treatment forests and
395   complexity declining only in the treatment forest (Fig. 7). Over a 10-yr period, mean canopy
396   height declined 1.5 m, VAI fell 1.5 units, and canopy cover diminished ~15% in both control and

397   treatment forests. Structural complexity measures, canopy rugosity and top rugosity, declined 4

398   m and 1.5 m, respectively, in the treatment forest only, while remaining unchanged in the

399   control. Neither the control nor treatment forest exhibited significant changes over time in

400   rumple.

401

402   3.6. Coupled compositional, structural and NEP change

403   Higher annual NEP and CUE were associated with successional changes leading to lower

404   structural complexity and greater dominance of mid-late successional species (Fig. 8). While the

405   transition from early to mid-late successional species dominance was accelerated and complete

406   in the treatment forest, the control site exhibited a similar but more incremental change in canopy

407   composition. When control and treatment forests were considered members of the same

408   successional continuum (as visualized in Fig. 8), we found that the doubling of mid-late

409   successional species LAI correlated with a more than two-fold increase in annual NEP and CUE.

410   Conversely, a halving of structural complexity (as canopy rugosity) as succession advanced

411   correlated with a comparable increase in annual NEP. These findings indicate that naturally

412   occurring (control) and accelerated (treatment) succession to mid-late successional species

413   dominance, rather than progressive increases in complexity, drove increases in NEP over the

414   decade-plus observation period.

415

416   4.   Discussion

417   4.1. Experimental efficacy: Successional changes in composition and structure

418   Regrowing temperate deciduous forests of eastern North America are broadly approaching the

419   century mark in age (Gough et al. 2016) and compositionally shifting to communities comprised

420   of mid-late successional species, including the *Acer spp.* and *Quercus spp.* assemblages that our

421   experiment promoted (Bose et al. 2017; Frelich and Reich 1995; Goring et al. 2016; Wolter and

422   White 2002). Our aspen and birch stem girdling resulted in complete mortality within three

423   years, accelerating the transition to an ecosystem that compositionally and, to some degree,

424   structurally resembles such emergent mid-successional forests. This disturbance-mediated

425   accelerated succession is similar to that which may follow naturally occurring moderate-severity

426   disturbances (Abrams and Scott 1989; Allen et al. 2012). Also consistent with other forests in the

427   region (Parker et al. 2004), we observed a reduction in canopy height and cover as the tallest,

428 early successional species declined and gaps formed in the previously closed-canopy forest

429 (Foster et al. 1997). Counter to some prior observations and our hypothesis, however, accelerated

430 succession reduced rather than increased complexity measures (Hardiman et al. 2013b; Hickey et

431 al. 2019; Scheuermann et al. 2018; Wales et al. 2020).

432   Unlike the slower pace of succession that occurs in the absence of disturbance, stem

433 girdling prompted the relatively rapid, synchronized decline of tall *Populus spp.*, uniformly –

434 even if temporarily – compressing canopy height and thus reducing structural complexity

435 (Gough et al. 2020). In the control and other naturally aging forests, the gradual, patchy decline

436 of early successional species and co-incident ascension of mid-late species may have helped

437 maintain canopy height and provided the crown architectural variety associated with structurally

438 complex canopies (Curtis and Gough 2018; Fahey et al. 2019; Van Pelt et al. 2016). Lastly, in

439 control and treatment forests, opposing trends in total (litter-trap based) leaf area and (lidar-

440 derived) VAI may have arisen because compensatory leaf production was rapid as early

441 successional species declined, stabilizing total LAI (Foster et al. 1997), while the deterioration of

442 intact standing woody debris represented in declining VAI was more gradual (Schmid et al.

443 2016). From these patterns of compositional and structural change, we conclude that stem

444 girdling successfully expedited the transition to mid-late successional communities and gave rise

445 to structural features associated with aging forests, with one notable exception: structural

446 complexity decreased rather than increased.

447   With succession and disturbance intertwined in our experiment and in nature, the three-

448 year pace of aspen and birch decline, along with the degree and distribution of mortality in the

449 treatment forest, were similar to the timing and severity of naturally occurring disturbances

450 (Flower and Gonzalez-Meler 2015; Hicke et al. 2012). Experiment-wide, ephemeral mean LAI

451 declines of ~40 % in the treatment forest are within the range reported for disturbances from

452 insects and pathogens, and also fire, wind, and ice (Battles et al. 2017; Cohen et al. 2016;

453 Townsend et al. 2012). Similar to insect pests and pathogens (Hicke et al. 2012), girdled trees'

454 growth declined over a period of several years, slower than that following wind, fire, or felling,

455 and may have been particularly gradual because of aspen's large pool of non-structural

456 carbohydrates and intertwined clonal root system (Grigri et al. 2020; Landhausser and Lieffers

457 2002). Our targeted elimination of two tree genera is also representative of boring insect and

458 pathogen host specificity (Kautz et al. 2017; Kosiba et al. 2018; Lovett et al. 2006), but differs

459   from generalists and defoliators such as the gypsy moth (*Lymantria dispar*). The uneven

460   distribution of aspen and birch resulted in patchy mortality across the treated landscape, with

461   (0.1-ha) plot gross basal area losses of 6 to 69 % (Stuart-Haentjens et al. 2015). Consequently,

462   spatially variable mortality produced a landscape mosaic with different degrees and dimensions

463   of gap formation (Stuart-Haentjens et al. 2015), a signature of host-specific disturbances and

464   extreme weather events that cause uneven distributions of tree mortality (Atkins et al. 2020;

465   Turner 2010). While noting these similarities between FASET and naturally-occurring

466   disturbances, we stress that the timing, distribution, and host-specificity of disturbance may lead

467   to ecologically important variation in canopy structure (Atkins et al. 2020) and C cycling-related

468   processes (Dietze and Matthes 2014).

469   The dynamic compositional and structural reorganization of the treatment forest

470   following stem girdling underscores the benefit of continuous observations—crucially, paired

471   with a control forest—for interpreting NEP responses to an abrupt successional transition

472   catalyzed by moderate-severity disturbance. Opportunistic observational studies have greatly

473   advanced understanding of the ecological consequences of disturbance-succession interactions,

474   but, in the absence of a control, disentangling the effects of disturbance from other equally potent

475   drivers of interannual variation in C fluxes cannot be done unambiguously. For example, we

476   observed parallel initial declines in control and treatment forest NEP, indicating that stem

477   girdling was not exclusively responsible for a downward trend that, without an unmanipulated

478   reference, would appear to align entirely with our hypothesis and theoretical expectations of

479   declining production immediately after disturbance (Fig. 1, Anderegg et al. 2016). Instead,

480   common control and treatment NEP responses to climate variability, which accounts for

481   interannual variation of >100% at our site (Gough et al. 2008a), and a widespread early-season

482   gypsy moth outbreak in 2010 likely drove initial parallel changes in production (Gough et al.

483   2013). Thus, we echo previous calls for ecologists to take care in drawing inferences from

484   observational results with uncertain controls (Johnson and Miyanishi 2008).

485   In our study, the rapidity of compositional, structural, and NEP change also highlights

486   how either longer-interval, space-for-time substitutions (i.e., chronosequences) or infrequent data

487   collection may fail to detect the ecosystem changes that are especially dynamic following

488   disturbance, and which may foreshadow long-term change (Hillebrand et al. 2018; Seidl et al.

489   2014). For example, our observations revealed how a rapid, yet enduring, 2-unit increase in late

490 successional species LAI sustained NEP when a third of canopy trees were abruptly lost to

491 disturbance. These findings and others (Chang et al. 2019) pointing to the particularly dynamic

492 nature of ecosystem change following disturbance reinforce the mechanistic value of high-

493 frequency, continuous observations.

494

495 4.2. Confronting the core Forest Accelerated Succession Experiment hypothesis with

496 observations

497 Revisiting our hypothesis (Fig. 1) following more than a decade of observations, we found

498 support for long-term increases in NEP after a brief decline relative to the control, with

499 increasing production associated with the rising prominence of mid-late successional species

500 rather than increasing structural complexity. Treatment forest NEP briefly declined below that of

501 the control forest in the fifth year after stem girdling and three years after total LAI reached a

502 low point, suggesting canopy physiology (i.e., as observed by lower CUE) rather than leaf

503 quantity temporarily drove down production. The subsequent rise in treatment forest NEP is

504 consistent with observations of century-old deciduous forests naturally transitioning to middle

505 succession that have shown NEP may remain stable or increase as compositional and structural

506 changes unfold (Beamesderfer et al. 2020a; Brzostek et al. 2014; Dragoni et al. 2011; Finzi et al.

507 2020; Froelich et al. 2015; Keenan et al. 2013; Urbanski et al. 2007). Paralleling our results, an

508 increase in annual NEP in Harvard Forest's mixed deciduous forests was associated with the

509 emergent canopy dominance of mid-late successional species, including *Quercus rubra* (Finzi et

510 al. 2020). More broadly, canopy composition is implicated as a primary determinant of temperate

511 forest NEP in comparative studies controlling for variability in climate and soils (Beamesderfer

512 et al. 2020b; Tamrakar et al. 2018).

513 While our analysis did not elucidate the full mechanistic pathway leading to increasing

514 long-term NEP in the treatment forest, it suggests several interrelated plant-to-canopy

515 compositional and physiological changes are responsible. The accelerated succession treatment

516 expedited the mortality of already declining century-old aspen and birch, rapidly advancing the

517 dominance of mid-late successional species with higher relative growth rates. By comparison, in

518 the control forest, mid-late successional relative growth rates stagnated over nearly two decades

519 while the growth of early successional species gradually declined. A canopy compositional

520 transition from aspen and birch to red oak and red maple in the treatment forest did not

521 negatively affect relative growth rates, even though the photosynthetic competency of red maple,

522 the most prominent species by LAI, is less than that of other canopy dominant species. Given its

523 dominance, red maple's lower leaf dark respiration rate could explain why ecosystem respiration

524 declined even though soil respiration, overwhelmingly the largest source of respiratory CO_2, did

525 not differ between control and treatment forests. Rather than increasing NEP by enhancing

526 canopy complexity as we hypothesized, the mortality of slowly growing aspen and birch appears

527 to have competitively "released" more vigorous mid-late successional species, akin to a

528 moderate canopy thinning that enhances access to growth-limiting resources (Campbell et al.

529 2009; Hou et al. 2016; Matsushita et al. 2015).

530 Recognizing that an indefinite rise in treatment forest NEP is not sustainable, two future

531 trajectories seem ecologically plausible: stabilization at the current rate or a gradual decline to

532 control levels. The growth stimulating effects of increased availability of limiting resources

533 following the decline or removal of competing vegetation may be short-lived (Kweon and

534 Comeau 2019). For example, NEP in the treatment forest could stabilize or decline as available

535 N, which increased significantly following stem girdling, returns to levels comparable to those

536 observed in the control forest (Nave et al. 2011a). However, periodic, low-intensity elimination

537 of plant competition through natural or facilitated disturbances, which are increasing in the

538 region (Cohen et al. 2016), could reinvigorate growth and sustain ecosystem scale production

539 (Lu et al. 2016). Whether NEP remains elevated relative to the control forest could depend on the

540 successional dynamics of N cycling in the compositionally shifted and N-limited treatment forest

541 and the degree of retention as N capital contained in detritus is slowly mineralized and reclaimed

542 by plant biomass or, instead, leached or emitted in gaseous form (Rastetter et al. 2020).

543 Our observations thus far leave several additional questions unanswered. For example,

544 with only four years of available N data collection, we do not know whether compositional

545 changes in the treatment forest permanently modified N cycling rates or availability (Nave et al.

546 2014). Similarly, species level differences in transpiration emerged in the first few years

547 following disturbance as soil water availability changed (Matheny et al. 2014). These differences

548 varied based on the hydraulic traits of different species (Matheny et al. 2017), and may affect

549 long-term NEP by altering the physiology and composition of the canopy. While our present

550 analysis does not directly address heterotrophic respiration, stable total soil respiration rates,

551 recent reductions in ER, and lower-than-expected coarse woody debris respiration rates of ~1 to

552   2 Mg C ha^{-1} yr^{-1} six years following stem girdling (Schmid et al. 2016) suggest respiratory CO_2

553   produced from the decomposition of legacy C is not enough to offset increasing production.

554   However, with tree mortality supplying a large influx of detritus, the future extent of detritus-C

555   retention (e.g., in soils) and lagged detritus-fueled heterotrophic respiration could affect net C

556   balance for decades to come (Clark et al. 2018; Harmon et al. 2011; Mosier et al. 2017).

557

558   4.3. Application and conclusions

559   We conclude that aging deciduous forests transitioning from early to middle succession have the

560   potential to sustain high levels of NEP well into the future, and that production may be sustained,

561   or even enhanced, by disturbance regimes that cause low-to-moderate levels of mortality,

562   although changing frequency and increasing interactivity among disturbances introduces

563   uncertainty into future trajectories. A decade ago, with a paucity of empirical data, theory (Odum

564   1969) implied that the maturing of regrown secondary forests would erode the terrestrial C sink

565   of eastern North America (Birdsey et al. 2006). However, our results and mounting evidence

566   elsewhere (e.g., Besnard et al. 2018; Williams et al. 2014) strongly suggest otherwise, leading us

567   to conclude that forest management practices encouraging reversion to a young forest age

568   structure are not the only option for active management to promote and enhance the region's

569   terrestrial C sink (Keith et al. 2014). Our century-old study forest, which is more advanced in age

570   than most of the region's deciduous forests (Gough et al. 2016), exhibited increased rates of

571   carbon sequestration (as NEP) when actively transitioned from early to middle succession.

572   Conservation of these aging forests and management using silvicultural strategies that emulate

573   moderate-severity disturbance (e.g., multi-cohort management approaches; Hanson and Lorimer

574   2007) is likely to preserve, or even enhance, the region's terrestrial C sink while supplying

575   additional ecosystem goods and services associated with older forests (Bauhus et al. 2009).

576   In addition, our decade-long study demonstrates that forests are capable of substantial

577   resistance and rapid recovery following moderate-severity disturbance, providing preliminary

578   guidance for forest managers contemplating disturbance avoidance and recovery strategies. By

579   departing from theory (Buma 2015; Ellison et al. 2005), our observations show that disturbance

580   may alter structure and composition considerably without inflicting a commensurate change in

581   functioning, illustrating the capacity of internal ecosystem constituents to rapidly adjust to

582   stabilize whole-ecosystem function. Although ecosystem processes may remain stable across a

583 range of severities (Stuart-Haentjens et al. 2015), the inherent or cultivated stand features that
584 confer functional stability are largely unknown (Seidl et al. 2016). Therefore, our findings may
585 not translate directly to dissimilar ecosystems or disturbance types that force changes in
586 composition and structure over longer or shorter timescales, affect different species or plant
587 functional groups, or are compounding or frequent. As disturbances increase and diversify, C-
588 focused managers should prioritize the mitigation of functionally detrimental disturbances
589 (Hurteau et al. 2013), a consideration that requires much greater understanding of how forests
590 will respond to a burgeoning variety of disturbance sources, severities, and frequencies.

591

599

600 Supporting Information: Additional supporting information may be found online at: [link to be
601 added in production]

602

603 Open Research: Site instrumentation, meteorological data, soil moisture, fluxes and plot-level
604 leaf area are available through AmeriFlux for sites US-UMB (Gough et al. 2021a,
605 https://doi.org/10.17190/AMF/1246107) and US-UMd (Gough et al. 2021b,
606 https://doi.org/10.17190/AMF/1246134). Additional data presented in figures, along with code
607 for statistical analysis, are available via Figshare (Gough 2021,
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936

937 Table 1. Gas exchange parameters for canopy dominant tree species comprising early and mid-

938 late successional cohorts in control and treatment forests, 1999. Letter differences indicate least

939 significant differences (LSD), α=0.1. Values are in μmol m^{-2} s^{-1} except g_s which is in mol m^{-2} s^{-1}.

940 Means $\pm$ 1 S.E.

Successional cohort	Species	A_{sat}	g_s	R_d	V_{cmax}	J_{max}
Early	*Populus grandidentata* (n=4)	20.9[b]	0.35[c]	-0.66[ab]	71.4[b]	137.9[b]
		(1.2)	(0.02)	(0.09)	(4.4)	(7.4)
	Betula papyrifera (n=3-5)	17.0[b]	0.27[b]	-0.73[b]	58.5[ab]	123.2[b]
		(1.6)	(0.03)	(0.17)	(8.0)	(16.5)

Mid-late	*Quercus rubra* (n=4)	13.6[b]	0.21[b]	-0.77[b]	62.6[b]	128.3[b]
		(2.5)	(0.04)	(0.05)	(6.8)	(14.3)
	Acer rubrum (n=8)	9.2[a]	0.09[a]	-0.40[a]	47.3[a]	68.5[a]
		(0.6)	(0.01)	(0.07)	(3.5)	(7.2)

941   A_{sat}-Light-saturated leaf CO_2 assimilation, g_s-leaf stomatal conductance, R_d-dark respiration,

942   V_{cmax}-maximum rate of carboxylation, J_{max}-the maximum rate of electron transport

943   Figure legends

944   Fig. 1. Hypothesized and observed (%), 2007/8-2011, differences between control and treatment

945   annual net ecosystem production (NEP) and nitrogen (N) availability following initiation via

946   stem girdling of the Forest Accelerated Succession Experiment (FASET) in 2008. Observed leaf

947   area index (LAI) is also illustrated. We hypothesized that aspen and birch mortality would

948   increase N availability, and temporarily reduce NEP. Prior published observations point to an

949   initial increase in N availability, while illustrating relative NEP stability despite temporary

950   declines in LAI. Here, we test the hypothesis that decade-long advancement to a more

951   structurally complex, middle successional canopy would increase NEP. Orange symbols

952   summarize results from a series of publications describing initial (4-yr) FASET treatment

953   responses in net primary and ecosystem production (Gough et al. 2013; Stuart-Haentjens et al.

954   2015), respiration (Schmid et al. 2016), canopy structure and composition (Fahey et al. 2016;

955   Hardiman et al. 2013a), and nitrogen cycling (Nave et al. 2011a; Nave et al. 2014).

956

957   Fig. 2. Map of control and treatment areas, inventory and paired plots, and meteorological flux

958   tower locations for the Forest Accelerated Succession Experiment (FASET) at the University of

959   Michigan Biological Station. The stippled treatment areas include the primary 33-ha semi-

960   circular plot positioned within the treatment flux tower footprint and three separate 2-ha replicate

961   plots to the west. Control and treatment footprints contain a total of 81 and 22 inventory plots,

962   respectively, including a 1-ha plot at the base of each tower and 0.1-ha plots spaced 100-m apart

963   along transects that radiate from the base of each tower. The eight paired 0.1-ha control and

964   treatment plots sharing filled and open symbols, respectively, are a subset of inventory plots with

965   similar pre-treatment leaf area indexes and tree canopy compositions.

966

967   Fig. 3. Observed annual changes in control and treatment forest total LAI (A) and the LAI of

968   early (*Populus* & *Betula*) and mid-late (*Acer*, *Quercus* & *Pinus*) successional species (B), 2007-

969   2019. Stars denote pairwise significance within years, $\alpha = 0.05$. Means $\pm$ 1 S.E.

970

971   Fig. 4. The absolute (A) and relative differences in annual net ecosystem production (NEP, B)

972   and absolute carbon use efficiency (CUE = NEP/GPP, C) of control and treatment forests, 2008-

973   2019. Green solid (control) and orange dotted (treatment) lines in "A" illustrate segmented

974   regression lines and break-points, all of which are significant, P<0.0001. For "B", the orange

975   dashed trendline is P<0.0001, except for the first non-significant (2008-2011) segment. Estimate

976    $\pm$ uncertainty.

977

978   Fig. 5. Mean soil respiration in control and treatment forests, 2009-2017. Stars denote pairwise

979   significance within years, $\alpha = 0.05$. Means $\pm$ 1 S.E.

980

981   Fig. 6. Wood biomass relative growth rates per year (yr^{-1}) for early successional (*Populus*,

982   *Betula*) and mid-late successional (*Acer*, *Quercus*, *Pinus*) species in control (A, 1999-2017) and

983   treatment (B, 2007-2017)) plots. Means $\pm$ 1 S.E.

984

985   Fig. 7. Lidar-derived estimates of canopy structure for control and treatment forests, and their

986   trendlines, 2008-2019. All regressions are $P < 0.05$. Means $\pm$ 1 S.E.

987

988   Fig. 8. Annual net ecosystem production (NEP) of control and treatment forests in relation to

989   mid-late successional species leaf area index (LAI, A) and canopy rugosity, a measure of

990   structural complexity (B), along with the relationship between carbon-use efficiency (NEP/GPP)

991   and mid-late successional species LAI (C). Accelerated succession increased mid-late

992   successional species LAI (Fig. 2) and decreased canopy rugosity (Fig. 5). Means $\pm$ 1 S.E.
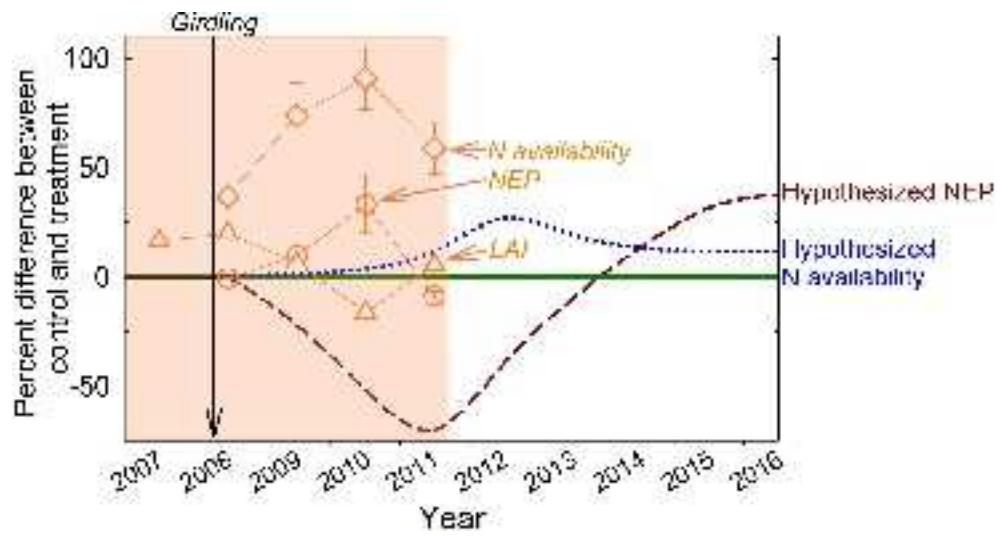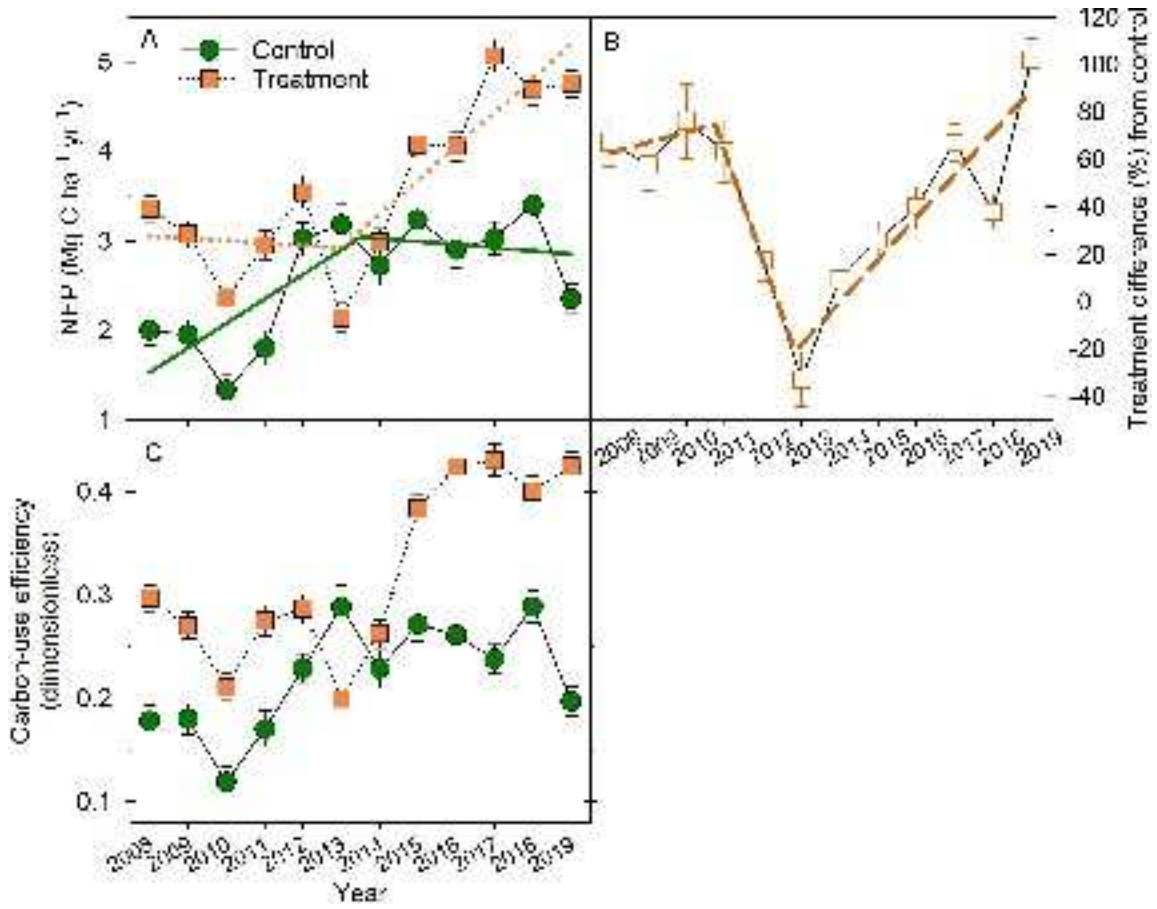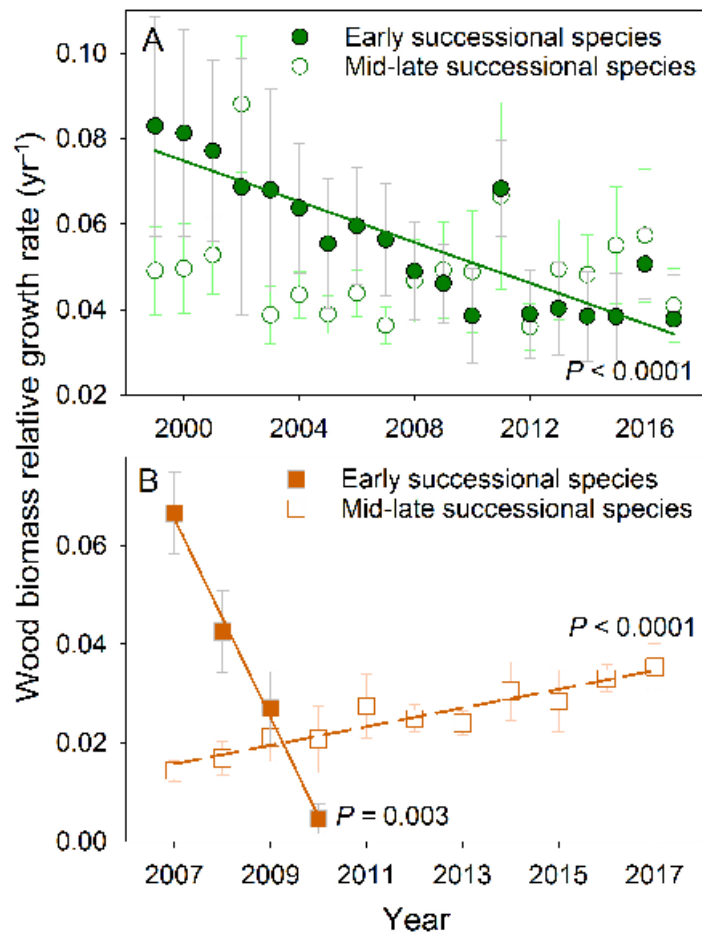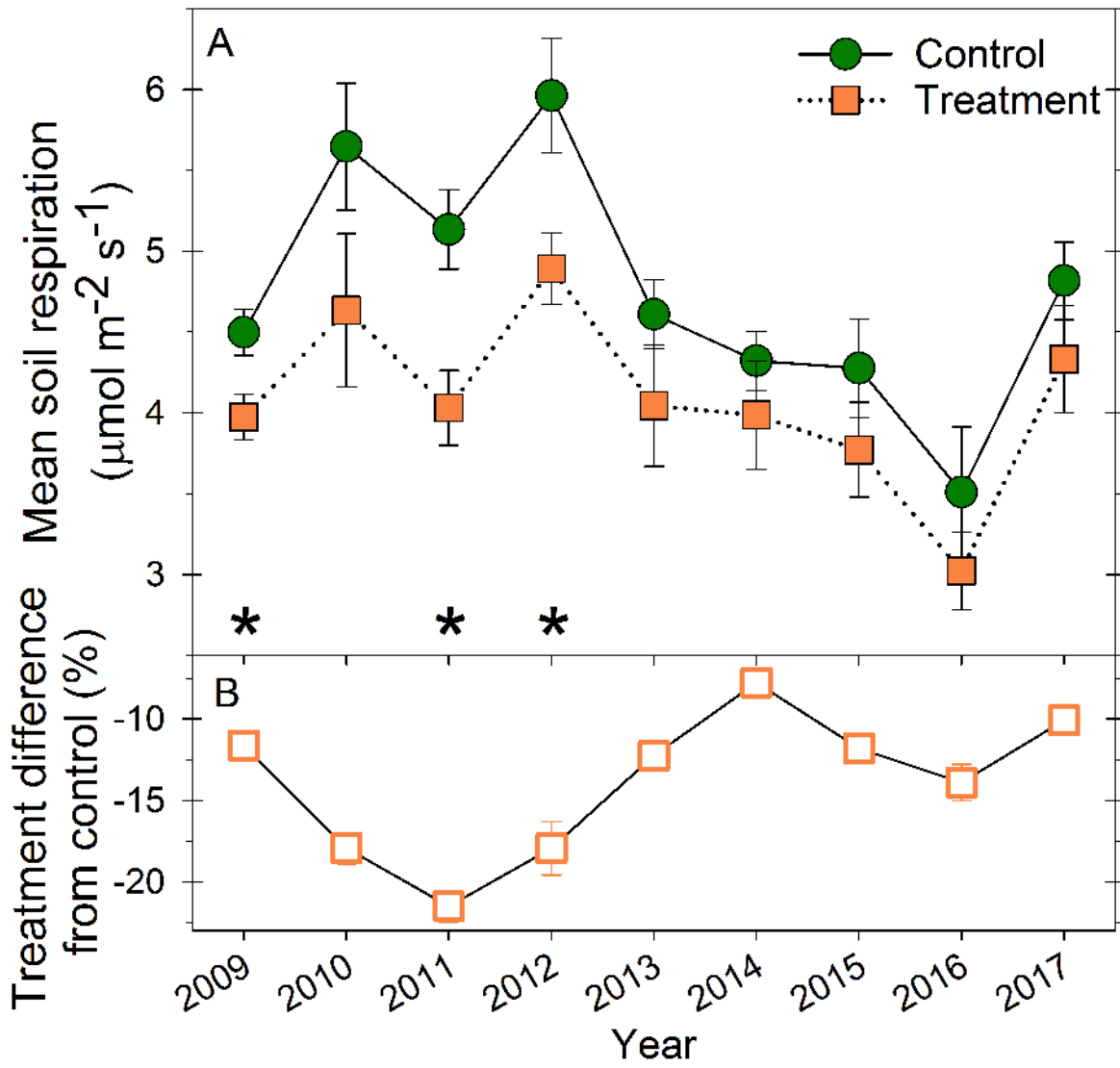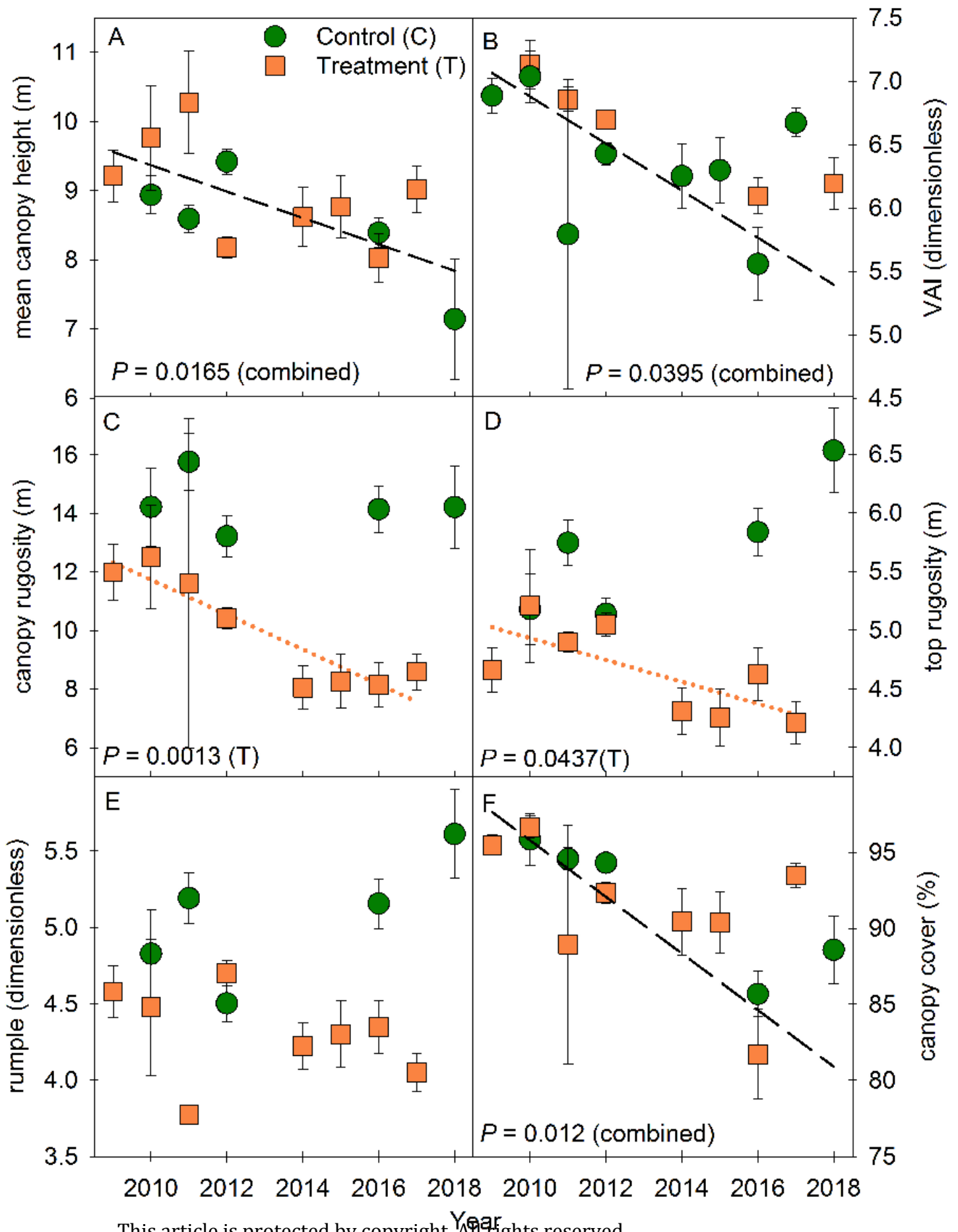
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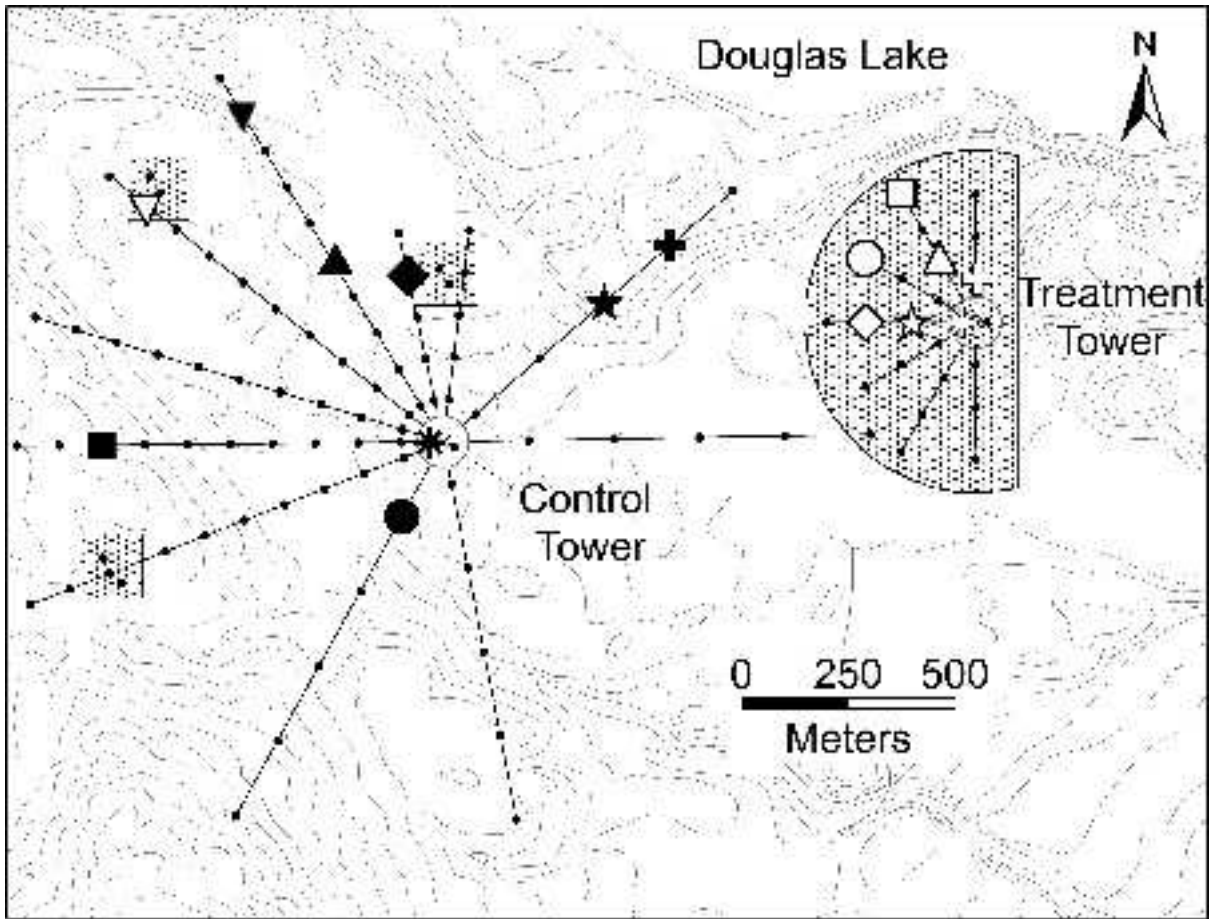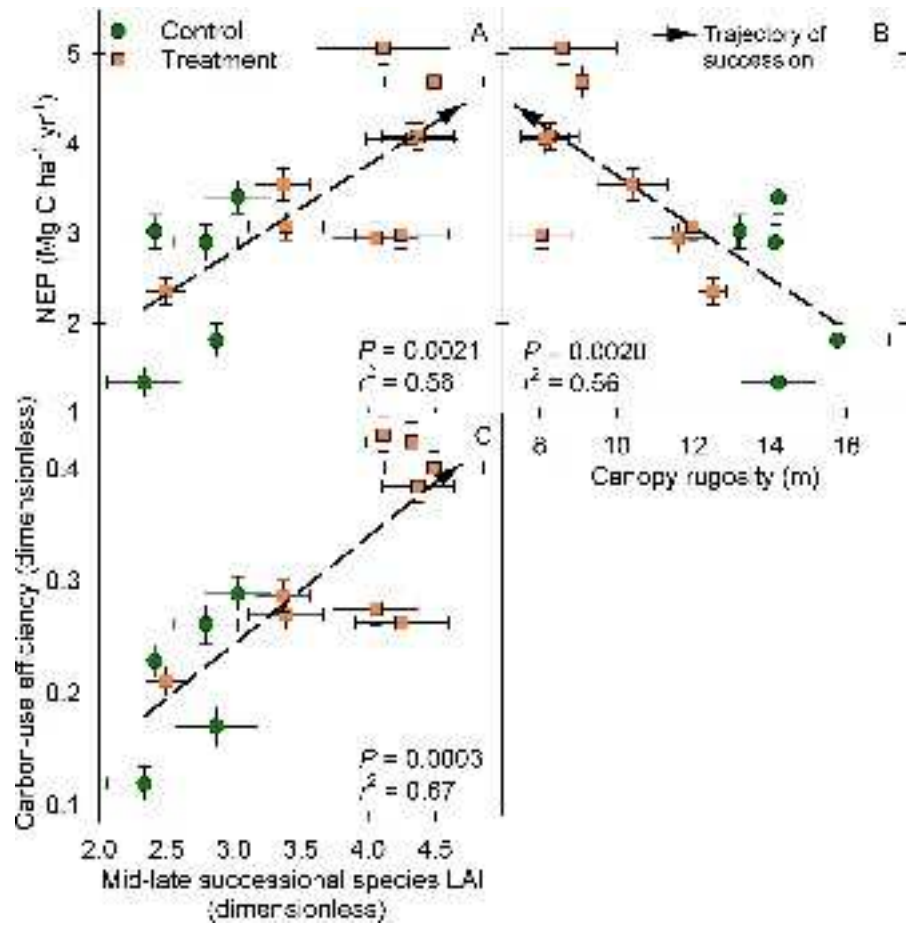
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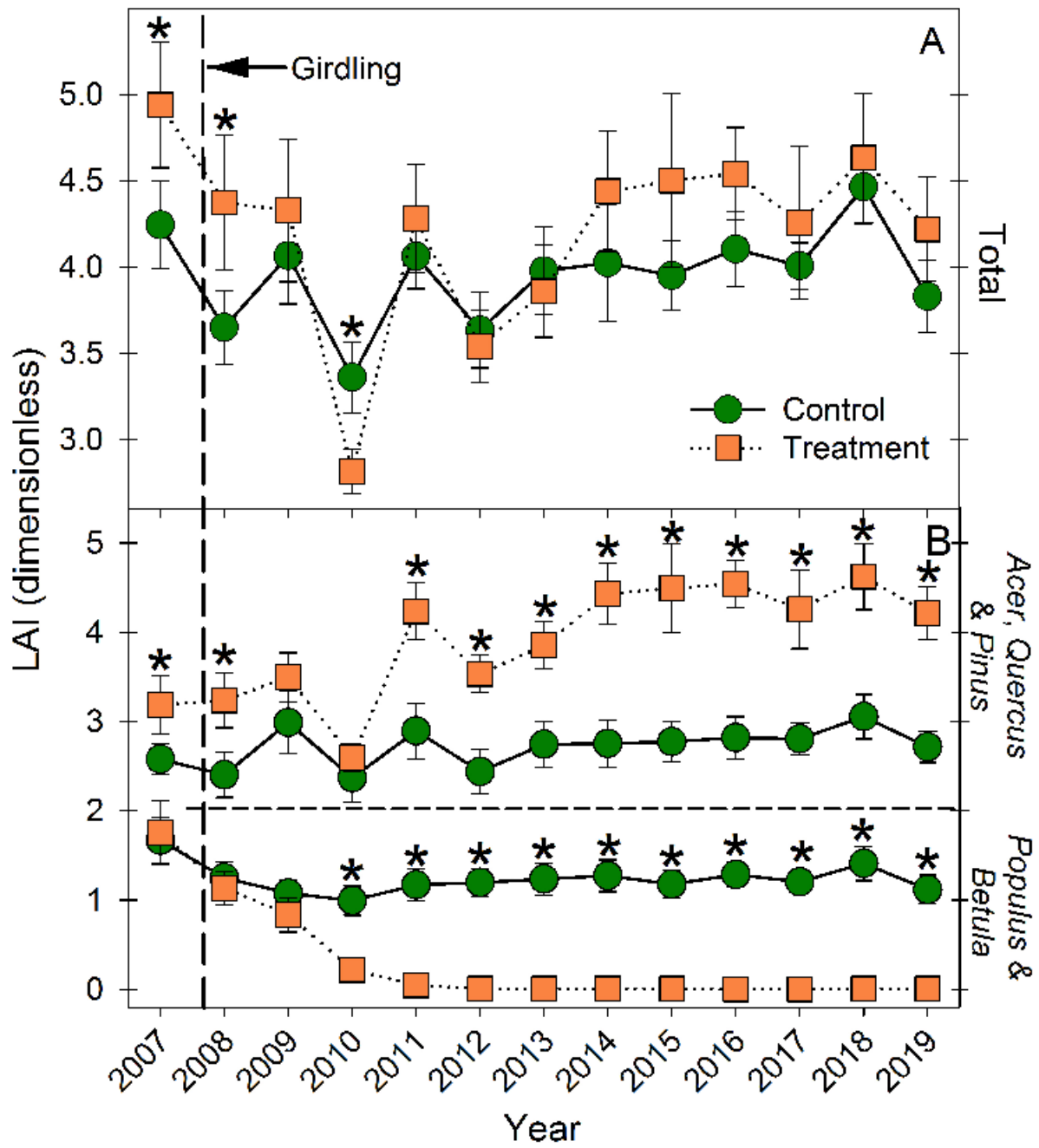
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