



Disturbance-accelerated succession increases the production of a temperate forest

CHRISTOPHER M. GOUGH ,^{1,9} GIL BOHRER,² BRADY S. HARDIMAN,³ LUCAS E. NAVE,⁴ CHRISTOPH S. VOGEL,⁴
JEFF W. ATKINS ,¹ BEN BOND-LAMBERTY,⁵ ROBERT T. FAHEY,⁶ ALEXANDER T. FOTIS,⁷ MAXIM S. GRIGRI,¹
LISA T. HABER,¹ YANG JU,² CALLIE L. KLEINKE,² KAYLA C. MATHES,¹ KNUTE J. NADELHOFFER,⁸
ELLEN STUART-HAËNTJENS,¹ AND PETER S. CURTIS⁷

¹Department of Biology, Virginia Commonwealth University, Box 842012, 1000 West Cary Street, Richmond, Virginia 23284 USA

²Department of Civil, Environmental and Geodetic Engineering, Ohio State University, 2070 Neil Avenue, Columbus, Ohio 43210 USA

³Forestry and Natural Resources and Environmental and Ecological Engineering, Purdue University, West Lafayette, Indiana 47907 USA

⁴Biological Station and Department of Ecology and Evolutionary Biology, University of Michigan, Pellston, Michigan 49769 USA

⁵Joint Global Change Research Institute, Pacific Northwest National Laboratory, 5825 University Research Court, College Park, Maryland 20740 USA

⁶Department of Natural Resources and the Environment, Center for Environmental Sciences and Engineering, University of Connecticut, 1376 Storrs Road, Storrs, Connecticut 06269 USA

⁷Department of Evolution, Ecology, and Organismal Biology, Ohio State University, 318 W 12th Avenue, Columbus, Ohio 43210 USA

⁸Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109 USA

Citation: Gough, C. M., G. Bohrer, B. S. Hardiman, L. E. Nave, C. S. Vogel, J. W. Atkins, B. Bond-Lamberty, R. T. Fahey, A. T. Fotis, M. S. Grigri, L. T. Haber, Y. Ju, C. L. Kleinke, K. C. Mathes, K. J. Nadelhoffer, E. Stuart-Haëntjens, and P. S. Curtis. 2021. Disturbance-accelerated succession increases the production of a temperate forest. *Ecological Applications* 31(7):e02417. 10.1002/eap.2417

Abstract. Many secondary deciduous forests of eastern North America are approaching a transition in which mature early-successional trees are declining, resulting in an uncertain future for this century-long carbon (C) sink. We initiated the Forest Accelerated Succession Experiment (FASET) at the University of Michigan Biological Station to examine the patterns and mechanisms underlying forest C cycling following the stem girdling-induced mortality of >6,700 early-successional *Populus* spp. (aspen) and *Betula papyrifera* (paper birch). Meteorological flux tower-based C cycling observations from the 33-ha treatment forest have been paired with those from a nearby unmanipulated forest since 2008. Following over a decade of observations, we revisit our core hypothesis: that net ecosystem production (NEP) would increase following the transition to mid-late-successional species dominance due to increased canopy structural complexity. Supporting our hypothesis, NEP was stable, briefly declined, and then increased relative to the control in the decade following disturbance; however, increasing NEP was not associated with rising structural complexity but rather with a rapid 1-yr recovery of total leaf area index as mid-late-successional *Acer*, *Quercus*, and *Pinus* assumed canopy dominance. The transition to mid-late-successional species dominance improved carbon-use efficiency (CUE = NEP/gross primary production) as ecosystem respiration declined. Similar soil respiration rates in control and treatment forests, along with species differences in leaf physiology and the rising relative growth rates of mid-late-successional species in the treatment forest, suggest changes in aboveground plant respiration and growth were primarily responsible for increases in NEP. We conclude that deciduous forests transitioning from early to middle succession are capable of sustained or increased NEP, even when experiencing extensive tree mortality. This adds to mounting evidence that aging deciduous forests in the region will function as C sinks for decades to come.

Key words: AmeriFlux; carbon; disturbance; forests; leaf area index; production; resistance; stability; structural complexity; succession.

INTRODUCTION

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

composition and increased frequency and extent of moderate-severity disturbances (Stueve et al. 2011, Cohen et al. 2016, Kautz et al. 2017, Kosiba et al. 2018) may threaten the sustainability of this globally significant century-long carbon (C) sink (Birdsey et al. 2006, Pan et al. 2011b, Williams et al. 2016). Following widespread clear-cut harvesting and agricultural abandonment over a century ago, forest regrowth in the eastern

Manuscript received 14 December 2020; revised 19 February 2021; accepted 22 March 2021; final version received 13 July 2021. Corresponding Editor: Yude Pan.

⁹E-mail: cmgough@vcu.edu

half of the continent has sustained C sequestration in plant biomass and soils (Pan et al. 2011a). Now, as vast areas of early-successional tree species reach maturity and begin to decline (Gough et al. 2016), significant community compositional and structural changes are underway as mid-late-successional species assume canopy dominance. At the same time, stand-replacing disturbances in the region are becoming less common and instead trending toward more frequent partial canopy defoliation and tree mortality from wind and ice, insects, pathogens, and age-related senescence. These patchy disturbances may accelerate succession (Abrams and Scott 1989), advancing compositional and structural changes that would otherwise require decades to unfold (Franklin et al. 2007, Hanson and Lorimer 2007, Atkins et al. 2020). This region-wide ecological intersection of shifting disturbance regime amid a rapid successional transition raises questions about future forest C sequestration and the mechanistic pathways leading to its stability or decline (Goetz et al. 2012).

Although disturbance–succession interactions have long transcended ecological disciplines (sensu Whittaker 1956) and served as guiding tenets of ecosystem management (Coates and Burton 1997), theory and observations offer conflicting views on how forecasted changes in forest composition and structure will affect ecosystem C balance, or net ecosystem production (NEP; Tang et al. 2017). Defining NEP as the annual balance of ecosystem-wide photosynthetic C uptake or gross primary production (GPP) minus C losses from ecosystem respiration (ER), theorists hypothesized a half-century ago that the maturation and subsequent mortality of early-successional trees would drive down NEP by reducing photosynthetic surface area and, therefore, GPP, and increasing ER as detritus-fueled heterotrophic respiration increased (Odum 1969). However, space-for-time substitution or chronosequence studies applying eddy-covariance or modern inventory approaches suggest the magnitude of these age-related declines in NEP may be less than theorized (Luyssaert et al. 2008, Gough et al. 2016, Besnard et al. 2018, Curtis and Gough 2018). Moreover, low-to-moderate-severity disturbances may accelerate succession, expediting, rather than rewinding, the development of compositional and structural features associated with older forests (Abrams and Scott 1989). Disturbance-mediated successional advancement may liberate growth-limiting resources and foster the development of canopy structural features associated with improved growth and resource-use efficiency, thereby offsetting declines in production from tree mortality (Hardiman et al. 2013b). For example, structural complexity, defined as the spatial heterogeneity of leaf area distribution within a canopy, increases as forests age and in response to some forms of disturbance, and is associated with higher rates of net primary production (Gough et al. 2019).

Few studies continuously track NEP as disturbance and succession-related compositional and structural changes unfold and resolve. Yet, long-term uninterrupted

ecosystem-scale measurements, particularly when paired with controls, are crucial to advancing fundamental understanding of what drives NEP during and following ecologically dynamic periods; such knowledge cannot be acquired from short-term or chronosequence-based approaches (Hicke et al. 2012). These foundational ecological knowledge gaps are relevant to many unresolved forest C management questions. For example, should forest managers cultivate an early or mid-late-successional stand structure to maximize C sequestration? What disturbances should be minimized or fostered through management to sustain forest C sequestration?

The Forest Accelerated Succession Experiment (FASET) was initiated in 2008 with the primary goal of quantifying C exchange processes throughout a successional shift from a maturing early-successional *Populus–Betula* (aspen–birch) to middle-successional *Acer–Pinus–Quercus* forest. Secondly, the experiment evaluated C cycling responses to a moderate-severity disturbance resulting in the mortality of one-third (by stem basal area) of all canopy trees. Observations from the first four years of the experiment (summarized in Fig. 1) revealed that, counter to our hypothesis, NEP was sustained at higher-than-expected levels despite temporary declines in LAI of ~40% (Gough et al. 2013, Stuart-Haentjens et al. 2015) as rapidly retranslocated nitrogen (Nave et al. 2011a, 2014) enhanced the physiological competency and compensating growth of healthy vegetation (Fahey et al. 2016). In addition, increases in heterotrophic respiration fueled by the influx of detritus were lower and more gradual than anticipated, and not large enough to transition the treatment forest from C sink to source (Schmid et al. 2016).

Here, following more than a decade of observations, we reassess the core hypothesis of the FASET study (Gough et al. 2013): when fully transitioned to mid-late-successional species dominance, NEP in the treatment forest will exceed that of the unmanipulated, control forest. In support of open science best practices (Nielsen et al. 2020), we include in Supplemental Information the 2006 FASET proposal narrative detailing the project, focusing here on the first objective and hypothesis (Supplemental Information: FASET Proposal). Briefly, we posited that the treatment forest would gain structural complexity over time as aspen and birch mortality gave rise to a patchy multi-layered canopy, and that this enhanced canopy structural complexity would drive greater resource-use efficiency (Hardiman et al. 2013a, Atkins et al. 2018b, 2020) and, consequently, higher production (Hardiman et al. 2013b, Gough et al. 2019).

METHODS

Study site and experimental overview

Our study is hosted by the University of Michigan Biological Station (UMBS), in northern Michigan, USA (45°35' N 84°43' W). The mean annual temperature at

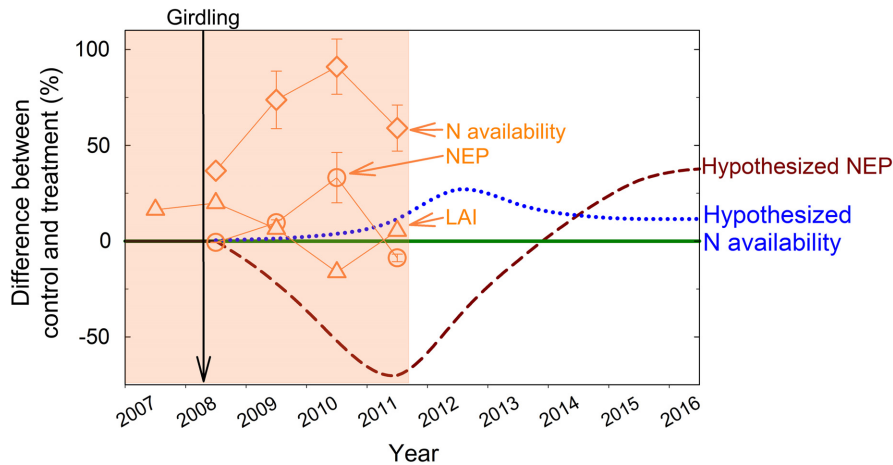


FIG. 1. Hypothesized and observed (%), 2007/8–2011, differences between control and treatment annual net ecosystem production (NEP) and nitrogen (N) availability following initiation via stem girdling of the Forest Accelerated Succession Experiment (FASET) in 2008. Observed leaf area index (LAI) is also illustrated. We hypothesized that aspen and birch mortality would increase N availability, and temporarily reduce NEP. Prior published observations point to an initial increase in N availability, while illustrating relative NEP stability despite temporary declines in LAI. Here, we test the hypothesis that decade-long advancement to a more structurally complex, middle-successional canopy would increase NEP. Orange symbols summarize results from a series of publications describing initial (4-yr) FASET treatment responses in net primary and ecosystem production (Gough et al. 2013, Stuart-Haentjens et al. 2015), respiration (Schmid et al. 2016), canopy structure and composition (Hardiman et al. 2013a, Fahey et al. 2016), and nitrogen cycling (Nave et al. 2011a, 2014).

the site is 5.5°C and mean annual precipitation is 817 mm (1942–2003). Prior to experimental disturbance, early-successional species, i.e., bigtooth aspen (*Populus grandidentata*), trembling aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*), were dominant components of the forest canopy, representing 39% of stand basal area (Gough et al. 2010). In the years before the experiment, mid-late-successional northern red oak (*Quercus rubra*), eastern white pine (*Pinus strobus*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), and American beech (*Fagus grandifolia*) were gaining dominance as early-successional aspen and birch stem mortality rates averaged ~4% annually (Gough et al. 2010, Gough et al. 2013). Prior to the experiment, forest structural features were similar in control and treatment forests, with the density of trees ≥ 8 cm diameter at breast height (DBH) 700–800 ha⁻¹, basal area ~25 m²/ha, and leaf area index (LAI) averaging ~4.5, but slightly higher in the treatment forest. Although several decades older, our study site falls near typical or median conditions for upland forests across the region in growth rate, physiology and soils as detailed in Nave et al. (2017).

Broadly, we initiated the Forest Accelerated Succession Experiment (FASET) to identify how disturbance, succession, and ongoing climate change affect C fluxes in aging mixed temperate forests (see Nave et al. 2011a). In May 2008, we stem-girdled >6,700 aspen and birch trees within four separate treatment areas totaling 39 ha, thereby accelerating the transition to a canopy composition and structure that approximates longer-term changes projected for forests regionally (Nave et al. 2011a), while enabling investigation of

moderate-severity disturbance response (Gough et al. 2013, Stuart-Haentjens et al. 2015). Tree status surveys conducted three years following treatment indicated that 97% of girdled trees were dead or partially defoliated, but with spatially variable basal area mortality of 6–69% among sampling plots. This experimental disturbance, including the patchy distribution of mortality, is similar in severity to moderate disturbances from wind and ice events, insects, and pathogens that result in partial canopy defoliation (Franklin et al. 2007, Amiro et al. 2010), but note that structural (Atkins et al. 2020) and functional (Dietze and Matthes 2014) responses may vary substantially among disturbances. Experimental defoliation from girdling was compounded by patchy forest tent caterpillar (*Malacosoma disstria*) herbivory in 2010 (Gough et al. 2013); this disturbance affected the control forest as well as the experimentally manipulated forest.

Paired C cycling measurements were collected within separate meteorological flux tower footprints from 2008 through 2019, in both the control and treatment forests (Fig. 2). Ground-based measurements were conducted in eight pairs of ecologically similar 0.1-ha control and treatment plots, selected in advance of the 2008 girdling to encompass the ranges of plant community composition and LAI levels present prior to disturbance (Nave et al. 2011a). Paired plots are a subset of 81 control and 22 treatment plots nested within the footprints of separate control (US-UMB) and treatment (US-UMd) meteorological towers operating within the AmeriFlux Core Site network (Pastorello et al. 2020), each measuring the net ecosystem CO₂ exchange (NEE) between forest and

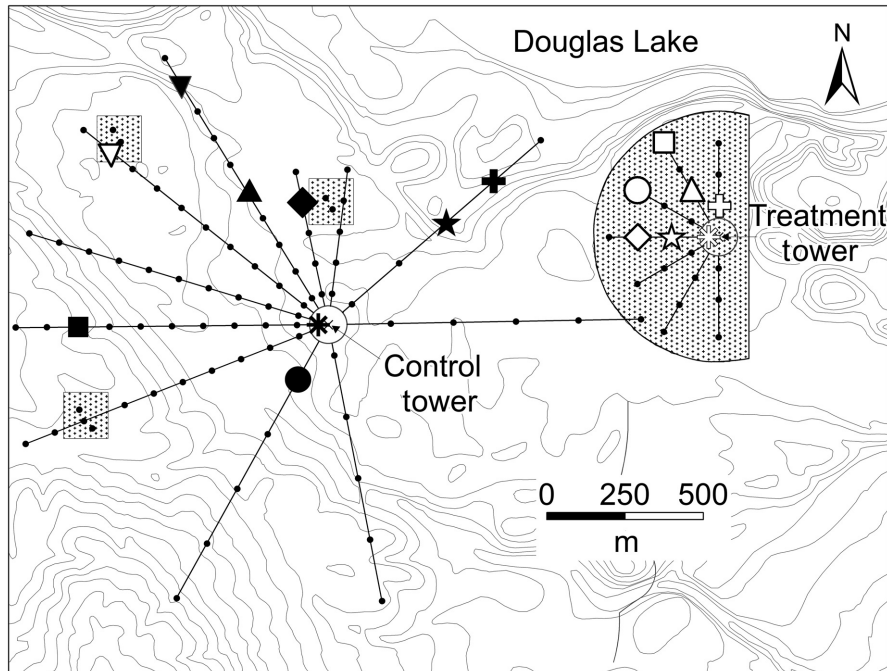


FIG. 2. Map of control and treatment areas, inventory and paired plots, and meteorological flux tower locations for the Forest Accelerated Succession Experiment (FASET) at the University of Michigan Biological Station. The stippled treatment areas include the primary 33-ha semi-circular plot positioned within the treatment flux tower footprint and three separate 2-ha replicate plots to the west. Control and treatment footprints contain a total of 81 and 22 inventory plots, respectively, including a 1-ha plot at the base of each tower and 0.1-ha plots spaced 100 m apart along transects that radiate from the base of each tower. The eight paired 0.1-ha control and treatment plots sharing filled and open symbols, respectively, are a subset of inventory plots with similar pre-treatment leaf area indexes and tree canopy compositions.

atmosphere. The US-UMd treatment tower, operating since mid-2007, is located to the east of the main 33-ha treatment area. Three additional 2-ha treatment replicate plots spanning a productivity gradient and located outside of the US-UMd tower footprint (Sagara et al. 2018) are not included in the current analysis. The control tower was established in 1997 in unmanipulated forest 1.5 km to the west, the ecology and biogeochemistry of which are described in a series of early studies (Curtis et al. 2002, Schmid et al. 2003, Bovard et al. 2005, Curtis et al. 2005, Gough et al. 2008a). Surrounding each tower is a circular 1.1-ha plot and, radiating from the tower base, smaller 0.1-ha plots are arrayed at 100-m intervals along transects extending 1,000 m and 300 m in control and treatment forests, respectively.

Leaf area index

We estimated the LAI of dominant tree species within the treatment and control forests from repeated collections of leaf litterfall within each of the eight paired plots from 2007 through 2019. Leaf litter was removed from three litter traps (0.264 m²) per 0.1-ha plot and 20 litter traps per 1.1-ha plot weekly during leaf fall and monthly during other seasons, pooled by plot, separated by species, dried, and weighed. LAI was calculated from species- and site-specific litterfall mass and specific leaf

area (SLA) values (Gough et al. 2010). We assumed that deciduous species shed their leaves annually, and that evergreens *Pinus strobus* and *Pinus resinosa* replaced their leaves over the course of two years.

Net ecosystem CO₂ exchange, gross primary production, and ecosystem respiration

We used eddy-covariance (EC) flux and meteorological data from each of the two sites to derive ecosystem C fluxes. For the control (US-UMB, Gough et al. 2021a) and treatment (U-UMd, Gough et al. 2021b) sites, data were processed following a standard EC flux processing protocol (Rebmann et al. 2012). Data were collected at 10 Hz, using a three-dimensional ultrasonic anemometer (CSAT3; Campbell Scientific, Logan, Utah, USA) and gas analyzer (LI-6262 until 2008, then LI-7000; LI-COR Biosciences, Lincoln, Nebraska, USA) at heights of 46 m (US-UMB) and 32 m (US-UMd). Full instrument lists and instrument operation notes for the sites are available from the sites' pages in AmeriFlux. Spikes in 10 Hz data were removed: observations above or below a reasonable range removed, as well as values that were more than 6 standard deviations greater than a 2-minute moving average, and values marked as bad by each sensors' data quality variable, were removed and replaced by NaN. Despiked 10 Hz data were processed into 30-

minute averages and fluxes (covariances). The 30-minute periods that included less than 50% of the 10 Hz data were removed and marked as missing observations. These were exceptionally rare and occurred less than 1% of the time.

NEE was calculated by adding the observed EC flux of C to the half-hourly rate of change of C concentration within the canopy (SC, change of carbon storage), with positive values indicating a net C flux from atmosphere to forest. SC was measured by sampling CO₂ concentration within the subcanopy, using an additional closed path gas analyzer (LI 6262; Li-COR Biosciences) and sampling air from intakes at multiple elevations under the tower top. Flux data during periods of low turbulent mixing was filtered using the u^* -filter threshold approach, with the threshold values calculated seasonally following Reichstein et al. (2005). Filtered nighttime NEE observations were assumed to be observations of ecosystem respiration (ER). Seasonal ER observations were used to train an automated neural network (ANN) model using time of day, air temperature, vapor pressure deficit, soil temperature, and soil moisture as inputs (Lasslop et al. 2010). The exact setup of the ANN models we used is described in Morin et al. (2014a). For all ANN models, we used 50% of the data for training, 25% for evaluation and 50% for validation of the ensemble's goodness-of-fit. We used the ensemble mean of the best 10% of 1000 ANN models to predict ER during the day, and during nighttime observation gaps.

To calculate gross primary productivity (GPP), we assumed that during the growing season, $GPP = (\text{observed NEE} - \text{modeled ER})$. In the winters and nighttime, we assumed $GPP = 0$. We used ANN models similar to those used for ER to model GPP for the purpose of gap filling where NEE observations were missing in the daytimes of each growing season. The ANN models for GPP used air temperature, incoming PAR, relative humidity, vapor pressure deficit, sensible and latent heat fluxes, and soil moisture as input variables. Before running the ANN models for GPP and ER, we gap filled the input variables used by these models. Specifically, meteorological variables other than fluxes and soil moisture were gap filled using values measured at the same time in the adjacent site (i.e., US-UMB data to gap fill US-UMd, and vice versa). If data were missing from both sites, ANN inputs were gap filled using a bi-linear interpolation between the observations before and after the gap as well as between observations in the same time of day in the day before and after the gap. Fluxes used as ANN input, i.e., sensible and latent heat fluxes, were gap filled using seasonal ANN models with air temperature, humidity, VPD, soil moisture, and time of day as inputs. Finally, after we had full seasonal predictions of ER and GPP, we gap filled NEE (as gap-filled $GPP + \text{gap-filled ER}$), summing half-hourly values during a calendar year to produce annual net ecosystem production (NEP).

To estimate uncertainty of the observation, we followed the approach of Richardson et al. (2006), calculating a compounding error distribution for daytime and nighttime data at each season in each year. We used the distribution of the ANN prediction members within the ensemble around the deviation from the observation in the validation dataset to estimate the uncertainty of the gap-filled data (Morin et al. 2014b). We simulated an ensemble of 1,000 members of the observed and gap-filled data with added random error (drawn from the corresponding distribution, based on data type, day or night, and season/year), and estimated the error of the total C accumulation from the standard deviation of the ensemble.

Canopy structure from LiDAR

We characterized multiple aspects of canopy structure in each of the eight paired control and treatment plots using a ground-based Portable Canopy LiDAR (PCL) system. The design, operation, and validation of this system is described in Parker et al. (2004). The system has been used previously at our site to relate canopy structure to net primary production (Hardiman et al. 2011, 2013b) and to investigate initial (2008–2011) canopy structural changes following tree mortality (Hardiman et al. 2013a). The PCL is based on an upward looking, near-infrared pulsed-laser operating at up to 2,000 Hz (model LD90-3100VHS-FLP; Riegl USA, Inc., Orlando, Florida, USA). Our system was mounted on a custom-built frame worn by operators while walking along transects that passed through the center of each plot. We binned the raw data horizontally and vertically into 1-m² grids for structural analysis, and derived estimates of canopy structure using the R package *forestR* (Atkins et al. 2018a).

We restrict our analysis to canopy structural measures significantly correlated with forest production (Gough et al. 2019): mean canopy height (m); vegetation area index (VAI; dimensionless, includes leaf and woody biomass); canopy rugosity (m, vertical and horizontal vegetation density and distribution variability); top rugosity (m, outer canopy surface vegetation density and distribution variability); rumple (dimensionless, ratio of canopy outer surface area to ground surface area); and canopy cover (%; ratio of bins returning lidar hits to the total bin number). Three of these measures—canopy rugosity, top rugosity, and rumple—summarize stand-scale complexity, describing different but related aspects of canopy physical structural heterogeneity (Gough et al. 2020). We refer readers to Atkins et al. (2018a, b) for in-depth descriptions and mathematical derivations of each structural measure.

Wood biomass relative growth rate

We estimated the annual relative growth rates (RGR) of aboveground wood biomass from repeated

measurements of tree stem diameter and allometric biomass equations. For most years, we measured the diameter at breast height (DBH) annually of a subsample of the total tree population with $DBH \geq 8$ cm in control ($n = 700$ of 8,860) and treatment ($n = 383$ of 2,500) forests using custom-built band dendrometers. In 2001, 2006, and 2011, RGRs were derived from complete censuses of all stems with $DBH \geq 8$ cm using tape measures. We inferred the aboveground wood biomass in each of 81 control and 22 treatment plots (Fig. 2) using species- and site- or region-specific allometric equations that relate DBH to aboveground wood biomass (Gough et al. 2008b). Mean annual RGRs for individual stems of each species within a treatment were calculated from the incremental change in total aboveground wood biomass from one year to the next divided by the starting biomass.

Leaf gas exchange

In 1999, we measured leaf level gas exchange of the most abundant canopy dominant species prior to disturbance, which, at the time, constituted a mix of early- (aspen and birch) and mid-late (red maple and red oak)-successional species. Leaf CO_2 assimilation (A) vs. intercellular CO_2 concentration (C_i) or A/C_i curves were constructed using a LI-COR 6400 (Vogel and Curtis 1995) with a (mean \pm SD) cuvette temperature of $28.2^\circ \pm 0.57^\circ C$, relative humidity $45\% \pm 4.9\%$, and a saturating photosynthetically active radiation of $1,800 \mu mol \cdot m^{-2} \cdot s^{-1}$. The maximum rate of carboxylation (V_{cmax}) and maximum rate of electron transport (J_{max}) were calculated using the Farquhar C3 photosynthesis equation (1980), and light-saturated net CO_2 assimilation (A_{sat}) and stomatal conductance (g_s) reported for ambient CO_2 concentrations at the time of 380 ppm. For dark respiration (R_d), we sampled leaves without the actinic light source two hours before sunrise at leaf temperatures of $18.6^\circ \pm 0.2^\circ C$.

Statistical analysis

Our statistical analyses were guided by our core objective of examining and relating control and treatment C fluxes, LAI, and canopy structure over the decade-plus study period. For LAI and soil respiration, derived from repeated measures within paired plots, we used time-series ANOVA followed by pairwise (LSD) comparisons of control and treatment means within a year. In the case of unreplicated meteorologically derived C fluxes, we tested the hypothesis that annual NEP increases over the long-term in the treatment forest (Fig. 1) by applying linear and two- and three-piecewise regression, retaining the model with the highest adjusted r^2 to account for overfitting. Because lidar-based measurements of canopy structure were staggered and not conducted annually and RGR measurements were not paired between treatments, we examined temporal changes

using linear regression, fitting separate models to control and treatment forests when slopes and/or intercepts had non-overlapping 95% confidence intervals. All statistical analyses applied an α of 0.05. In figures throughout, green circles illustrate control and orange squares represent treatment forest data. SAS (V94) or Sigmaplot (V14.0) software was used for statistical analyses; code, files, and data to reproduce all results shown here are archived at <https://figshare.com/s/a6aa55b2468828594b47>.

RESULTS

Leaf area index

Following an initial decline, treatment forest total LAI recovered to control levels as mid-late-successional tree species rapidly replaced diminishing aspen and birch LAI (Fig. 3; Appendix S1; Fig. S2). Total LAI was significantly greater in the treatment forest relative to the control the year before and the year of girdling, but was significantly lower in 2010, two years after girdling. This reduction in treatment forest total LAI was caused by the rapid loss of aspen and birch LAI (of ~ 1 unit) from 2009 to 2010. The reduction was short-lived, however, with mid-late-successional maple, oak, and pine LAI increasing by nearly two units in the following year, 2011. From 2011 through 2019, total LAI was similar in control and treatment forests, but leaf area contributions from early- and mid-late-successional species differed. Aspen and birch leaf areas were eliminated from the treatment forest three years after girdling, while the LAI of early-successional species stabilized at ~ 1 unit in the control forest for the remainder of the observation period. Maple, oak, and pine were the only constituents of treatment forest LAI beginning in 2011, and thereafter mid-late-successional species' LAI exceeded that of the control forest.

Annual net ecosystem production, carbon use efficiency, and soil respiration

Following a half-decade of high interannual variation exhibiting no mean temporal trend, annual NEP in the treatment forest increased significantly (Fig. 4). Change-point regression analysis of time-series identified co-occurring but different directional changes over time in control and treatment forest NEP. Control forest NEP increased significantly from ~ 2 to $3 \text{ Mg C} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ between 2008 and 2013, after which NEP was relatively stable, averaging $3 \text{ Mg C} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$. Conversely, treatment forest NEP varied interannually by $\sim 1.5 \text{ Mg C} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ in the first six years following girdling without exhibiting mean changes over time, averaging $3 \text{ Mg C} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ during this period. After 2014, treatment forest annual NEP sharply increased, ranging from ~ 3 to $\sim 5 \text{ Mg C} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ from 2014 through 2019 and averaging $\sim 5 \text{ Mg C} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ during the last three years of this period.

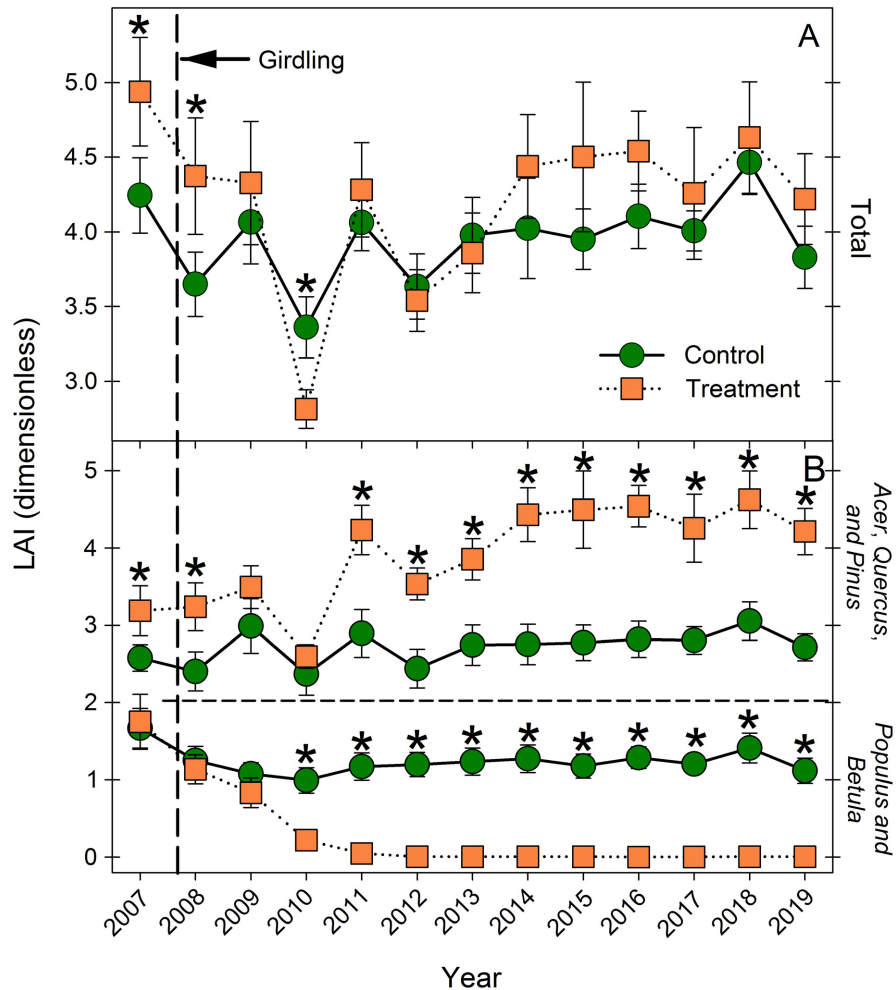


FIG. 3. Observed annual changes in control and treatment (A) forest total LAI and (B) the LAI of early (*Populus* and *Betula*) and mid-late (*Acer*, *Quercus*, and *Pinus*)-successional species, 2007–2019. Stars denote pairwise significance within years, $\alpha = 0.05$. Values are means \pm SE.

When relative treatment effects (as percent difference from control) were considered to minimize the interannual variation from other sources, change-point regression yielded three segments, reflecting the dynamic relationship between NEP in control and treatment forests. In the first 4 yr, a zero (non-significant) slope indicated control and treatment forest NEP paralleled one another, with treatment forest NEP averaging 66% greater than that of the control. This period of stability was followed by a steep 2-yr decline in relative NEP and, thereafter, a 6-yr positive slope during which the treatment forest recovered its relatively higher NEP, exceeding the control by 100% in the final year (2019).

Annual NEP in control and treatment forests closely paralleled carbon-use efficiency (CUE). Following a variable period in the treatment forest, from 2008 to 2014, during which annual CUE reached a low of ~ 0.2

twice, mean annual CUE increased abruptly to ~ 0.4 for the next five years. Control forest CUE was similarly variable over time, from ~ 0.1 to 0.3 , but failed to reach the sustained high levels exhibited by the treatment forest.

Rising CUE in the treatment forest was associated with decreased ecosystem respiration (Appendix S1: Fig. S3B) and stable soil respiration (Fig. 5) and annual GPP (Appendix S1: Fig. S3A), suggesting that increases in NEP were supported by a reduction in aboveground respiration. Ecosystem respiration rather than GPP drove interannual variation in CUE (Appendix S1: Fig. S3), with a drop in annual respiratory flux in the treatment forest coinciding with the period of peak CUE, from 2015 to 2019. Mean soil respiration, the largest component of ecosystem respiration at our site (Curtis et al. 2005), was significantly lower in the treatment forest during three of the first four years following

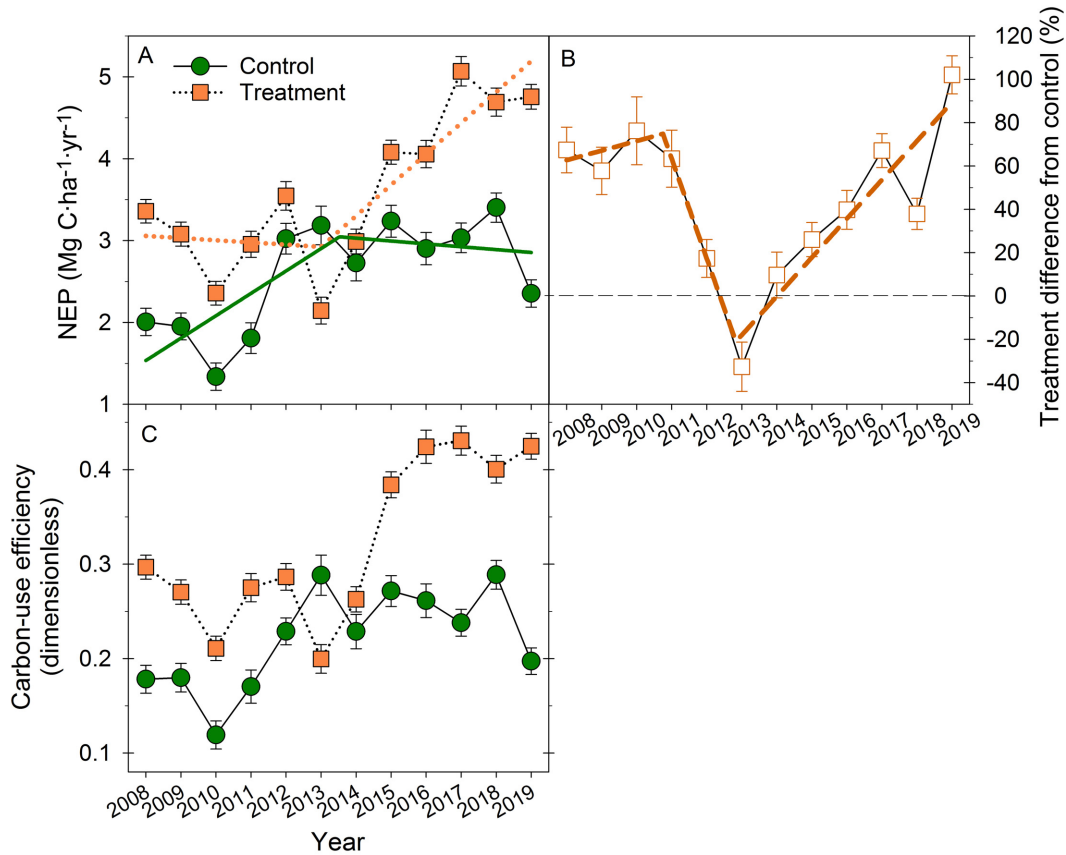


FIG. 4. The (A) absolute and (B) relative differences in annual net ecosystem production (NEP) and (C) absolute carbon use efficiency (CUE = NEP/GPP) of control and treatment forests, 2008–2019. Green solid (control) and orange dotted (treatment) lines in panel A illustrate segmented regression lines and break-points, all of which are significant, $P < 0.0001$. For panel B, the orange dashed trend line is $P < 0.0001$, except for the first non-significant (2008–2011) segment. Values are estimate \pm uncertainty.

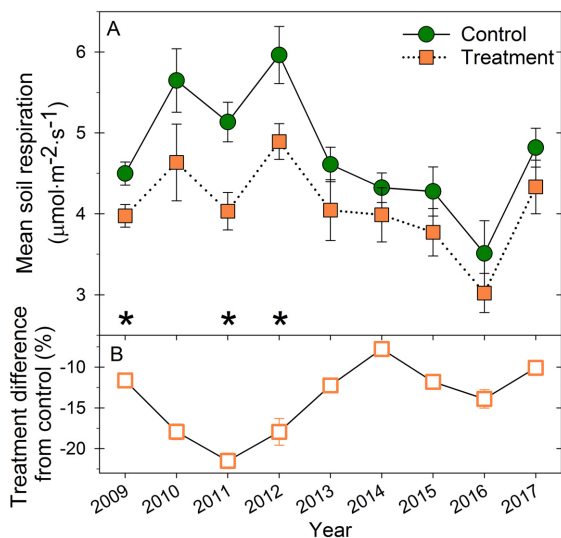


FIG. 5. Mean soil respiration in control and treatment forests, 2009–2017. Stars denote pairwise significance within years, $\alpha = 0.05$. Values are means \pm SE.

girdling, but recovered and did not differ from the control thereafter.

Wood biomass relative growth rates by successional cohort

The trajectories of early and mid-late-successional cohort RGRs differed in control and treatment forests (Fig. 6). In the control forest, early-successional species RGR declined by half over a 19-yr period ($P < 0.0001$), while mid-late-successional species RGR displayed no long-term trend. In contrast, early-successional species RGR declined rapidly to nearly zero within two years of stem girdling in the treatment forest ($P = 0.003$), while the RGR of mid-late-successional species steadily climbed, doubling over the course of a decade ($P < 0.0001$).

Leaf physiology of dominant canopy species

Leaf physiological properties differed between dominant canopy trees from early and mid-late-successional cohorts (Table 1). Red maple, which constituted the

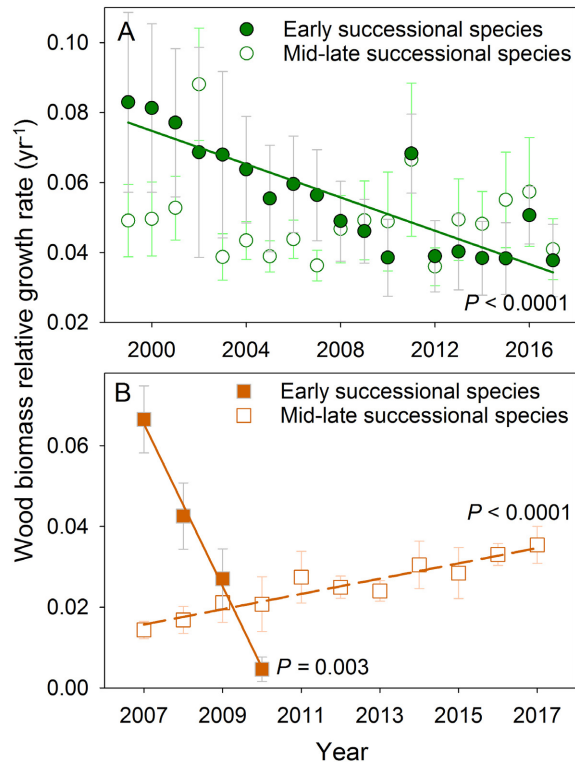


FIG. 6. Wood biomass relative growth rates per year (yr^{-1}) for early-successional (*Populus*, *Betula*) and mid-late-successional (*Acer*, *Quercus*, *Pinus*) species in (A) control (1999–2017) and (B) treatment (2007–2017) plots. Values are means \pm SE.

largest fraction of LAI in the treatment forest (Appendix S1: Fig. S1), exhibited lower photosynthetic functioning and lower dark respiration than other species. With the exception of stomatal conductance, which was highest in aspen, the leaf physiological properties of red oak were similar to those of aspen and birch.

Canopy structure changes over time

Changes in canopy structure over time varied depending on the treatment and structural characteristic, with canopy

cover and height decreasing in both control and treatment forests and complexity declining only in the treatment forest (Fig. 7). Over a 10-yr period, mean canopy height declined 1.5 m, VAI fell 1.5 units, and canopy cover diminished $\sim 15\%$ in both control and treatment forests. Structural complexity measures, canopy rugosity and top rugosity, declined 4 m and 1.5 m, respectively, in the treatment forest only, while remaining unchanged in the control. Neither the control nor treatment forest exhibited significant changes over time in rumple.

Coupled compositional, structural and NEP change

Higher annual NEP and CUE were associated with successional changes leading to lower structural complexity and greater dominance of mid-late-successional species (Fig. 8). While the transition from early to mid-late-successional species dominance was accelerated and complete in the treatment forest, the control site exhibited a similar but more incremental change in canopy composition. When control and treatment forests were considered members of the same successional continuum (as visualized in Fig. 8), we found that the doubling of mid-late-successional species LAI correlated with a more than two-fold increase in annual NEP and CUE. Conversely, a halving of structural complexity (as canopy rugosity) as succession advanced correlated with a comparable increase in annual NEP. These findings indicate that naturally occurring (control) and accelerated (treatment) succession to mid-late-successional species dominance, rather than progressive increases in complexity, drove increases in NEP over the decade-plus observation period.

DISCUSSION

Experimental efficacy: Successional changes in composition and structure

Regrowing temperate deciduous forests of eastern North America are broadly approaching the century mark in age (Gough et al. 2016) and compositionally shifting to communities comprised of mid-late-successional species, including the *Acer* spp. and *Quercus*

TABLE 1. Gas exchange parameters for canopy dominant tree species comprising early and mid-late-successional cohorts in control and treatment forests, 1999.

Cohort and species	A_{sat}	g_s	R_d	V_{cmax}	J_{max}
Early					
<i>Populus grandidentata</i> ($n = 4$)	20.9 ^b (1.2)	0.35 ^c (0.02)	-0.66 ^{ab} (0.09)	71.4 ^b (4.4)	137.9 ^b (7.4)
<i>Betula papyrifera</i> ($n = 3-5$)	17.0 ^b (1.6)	0.27 ^b (0.03)	-0.73 ^b (0.17)	58.5 ^{ab} (8.0)	123.2 ^b (16.5)
Mid-late					
<i>Quercus rubra</i> ($n = 4$)	13.6 ^b (2.5)	0.21 ^b (0.04)	-0.77 ^b (0.05)	62.6 ^b (6.8)	128.3 ^b (14.3)
<i>Acer rubrum</i> ($n = 8$)	9.2 ^a (0.6)	0.09 ^a (0.01)	-0.40 ^a (0.07)	47.3 ^a (3.5)	68.5 ^a (7.2)

Notes: A_{sat} , light-saturated leaf CO_2 assimilation; g_s , leaf stomatal conductance; R_d , dark respiration; V_{cmax} , maximum rate of carboxylation; J_{max} , the maximum rate of electron transport. Letter differences indicate least significant differences (LSD), $\alpha = 0.1$. Values are in $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ except for g_s , which is in $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Values are means \pm SE.

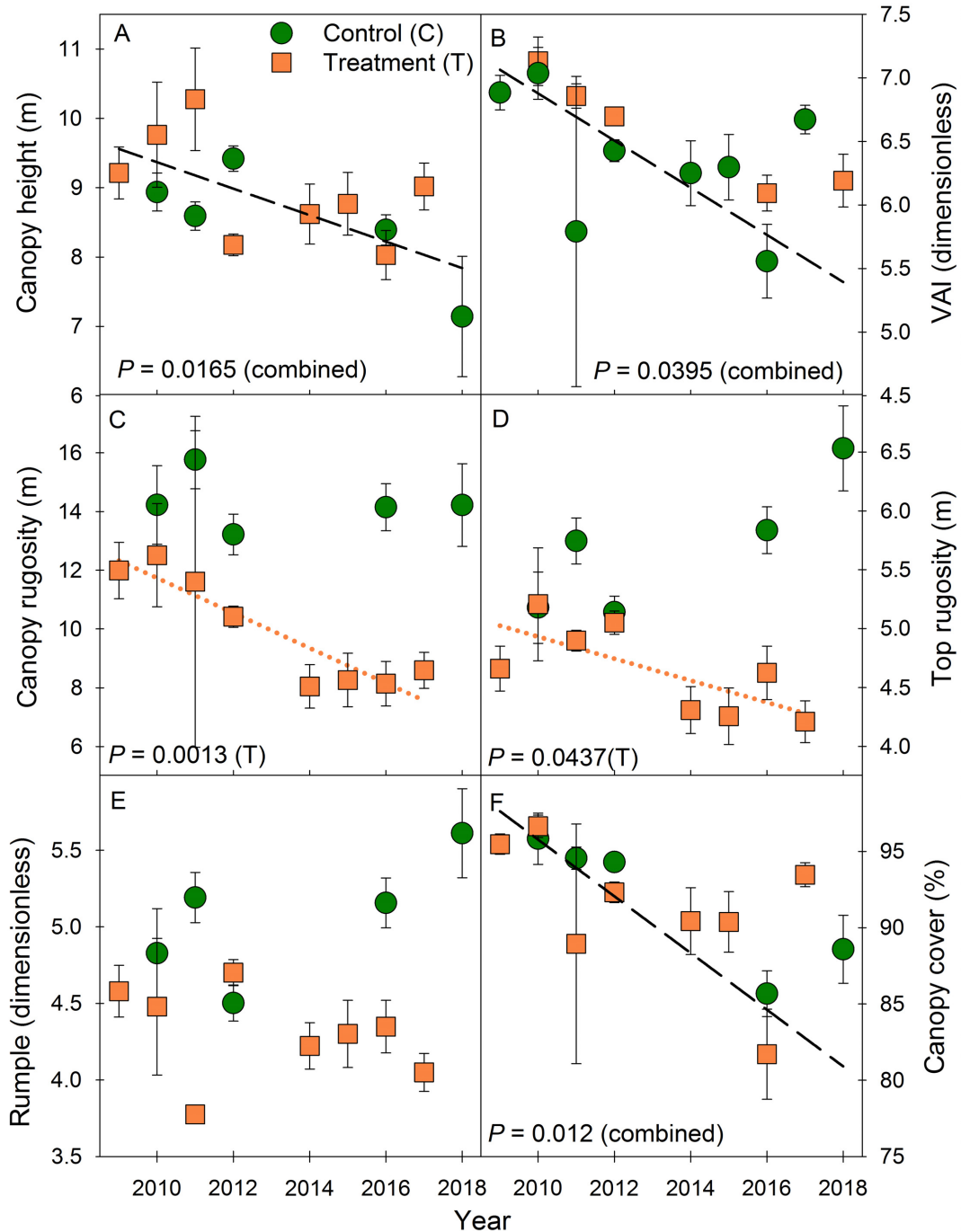


FIG. 7. Lidar-derived estimates of canopy structure for control and treatment forests, and their trend lines, 2008–2019. All regressions are $P < 0.05$. Values are means \pm SE.

spp. assemblages that our experiment promoted (Frelich and Reich 1995, Wolter and White 2002, Goring et al. 2016, Bose et al. 2017). Our aspen and birch stem girdling resulted in complete mortality within three years, accelerating the transition to an ecosystem that compositionally and, to some degree, structurally resembles such emergent mid-successional forests. This

disturbance-mediated accelerated succession is similar to that which may follow naturally occurring moderate-severity disturbances (Abrams and Scott 1989, Allen et al. 2012). Also consistent with other forests in the region (Parker et al. 2004), we observed a reduction in canopy height and cover as the tallest, early-successional species declined and gaps formed in the previously

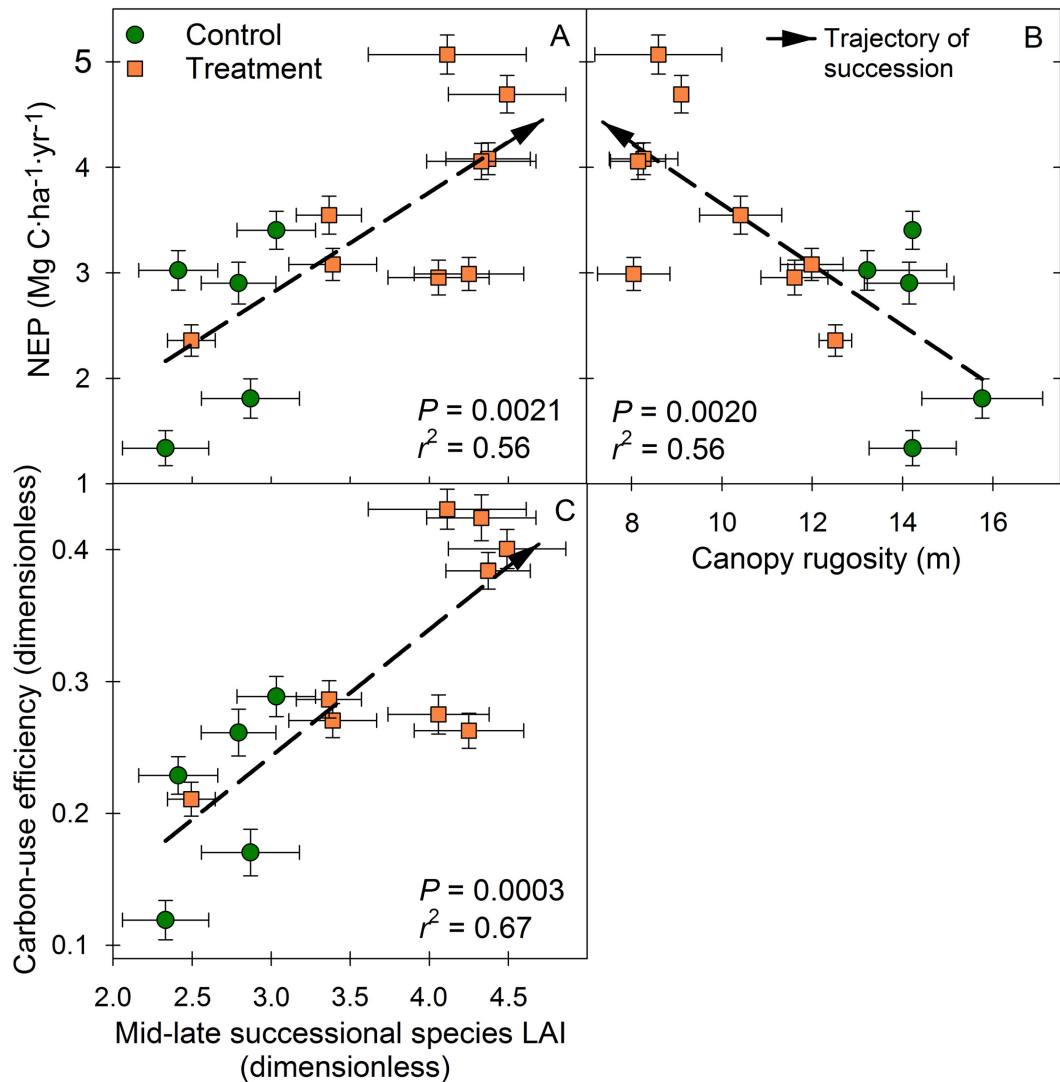


FIG. 8. Annual net ecosystem production (NEP) of control and treatment forests in relation to mid-late-successional species (A) leaf area index (LAI) and (B) canopy rugosity, a measure of structural complexity, along with (C) the relationship between carbon-use efficiency (NEP/GPP) and mid-late-successional species LAI. Accelerated succession increased mid-late-successional species LAI (Fig. 2) and decreased canopy rugosity (Fig. 5). Values are means \pm SE.

closed-canopy forest (Foster et al. 1997). Counter to some prior observations and our hypothesis, however, accelerated succession reduced rather than increased complexity measures (Hardiman et al. 2013b, Scheuermann et al. 2018, Hickey et al. 2019, Wales et al. 2020).

Unlike the slower pace of succession that occurs in the absence of disturbance, stem girdling prompted the relatively rapid, synchronized decline of tall *Populus* spp., uniformly, even if temporarily, compressing canopy height and thus reducing structural complexity (Gough et al. 2020). In the control and other naturally aging forests, the gradual, patchy decline of early-successional species and coincident ascension of mid-late-successional species may have helped maintain canopy

height and provided the crown architectural variety associated with structurally complex canopies (Van Pelt et al. 2016, Curtis and Gough 2018, Fahey et al. 2019). Last, in control and treatment forests, opposing trends in total (litter-trap based) leaf area and (lidar-derived) VAI may have arisen because compensatory leaf production was rapid as early-successional species declined, stabilizing total LAI (Foster et al. 1997), while the deterioration of intact standing woody debris represented in declining VAI was more gradual (Schmid et al. 2016). From these patterns of compositional and structural change, we conclude that stem girdling successfully expedited the transition to mid-late-successional communities and gave rise to structural features associated

with aging forests, with one notable exception: structural complexity decreased rather than increased.

With succession and disturbance intertwined in our experiment and in nature, the three-year pace of aspen and birch decline, along with the degree and distribution of mortality in the treatment forest, were similar to the timing and severity of naturally occurring disturbances (Hicke et al. 2012, Flower and Gonzalez-Meler 2015). Experiment-wide, ephemeral mean LAI declines of ~40% in the treatment forest are within the range reported for disturbances from insects and pathogens, and also fire, wind, and ice (Townsend et al. 2012, Cohen et al. 2016, Battles et al. 2017). Similar to insect pests and pathogens (Hicke et al. 2012), girdled trees' growth declined over a period of several years, slower than that following wind, fire, or felling, and may have been particularly gradual because of aspen's large pool of non-structural carbohydrates and intertwined clonal root system (Landhausser and Lieffers 2002, Grigri et al. 2020). Our targeted elimination of two tree genera is also representative of boring insect and pathogen host specificity (Lovett et al. 2006, Kautz et al. 2017, Kosiba et al. 2018), but differs from generalists and defoliators such as the gypsy moth (*Lymantria dispar*). The uneven distribution of aspen and birch resulted in patchy mortality across the treated landscape, with (0.1-ha) plot gross basal area losses of 6–69% (Stuart-Haentjens et al. 2015). Consequently, spatially variable mortality produced a landscape mosaic with different degrees and dimensions of gap formation (Stuart-Haentjens et al. 2015), a signature of host-specific disturbances and extreme weather events that cause uneven distributions of tree mortality (Turner 2010, Atkins et al. 2020). While noting these similarities between FASET and naturally occurring disturbances, we stress that the timing, distribution, and host specificity of disturbance may lead to ecologically important variation in canopy structure (Atkins et al. 2020) and C cycling-related processes (Dietze and Matthes 2014).

The dynamic compositional and structural reorganization of the treatment forest following stem girdling underscores the benefit of continuous observations, crucially, paired with a control forest, for interpreting NEP responses to an abrupt successional transition catalyzed by moderate-severity disturbance. Opportunistic observational studies have greatly advanced understanding of the ecological consequences of disturbance-succession interactions, but, in the absence of a control, disentangling the effects of disturbance from other equally potent drivers of interannual variation in C fluxes cannot be done unambiguously. For example, we observed parallel initial declines in control and treatment forest NEP, indicating that stem girdling was not exclusively responsible for a downward trend that, without an unmanipulated reference, would appear to align entirely with our hypothesis and theoretical expectations of declining production immediately after disturbance (Fig. 1; Anderegg et al. 2016). Instead, common control and treatment

NEP responses to climate variability, which accounts for interannual variation of >100% at our site (Gough et al. 2008a), and a widespread early-season gypsy moth outbreak in 2010 likely drove initial parallel changes in production (Gough et al. 2013). Thus, we echo previous calls for ecologists to take care in drawing inferences from observational results with uncertain controls (Johnson and Miyanishi 2008).

In our study, the rapidity of compositional, structural, and NEP change also highlights how either longer-interval, space-for-time substitutions (i.e., chronosequences) or infrequent data collection may fail to detect the ecosystem changes that are especially dynamic following disturbance, and which may foreshadow long-term change (Seidl et al. 2014, Hillebrand et al. 2018). For example, our observations revealed how a rapid, yet enduring, 2-unit increase in late-successional species LAI sustained NEP when a third of canopy trees were abruptly lost to disturbance. These findings and others (Chang et al. 2019) pointing to the particularly dynamic nature of ecosystem change following disturbance reinforce the mechanistic value of high-frequency, continuous observations.

Confronting the core forest accelerated succession experiment hypothesis with observations

Revisiting our hypothesis (Fig. 1) following more than a decade of observations, we found support for long-term increases in NEP after a brief decline relative to the control, with increasing production associated with the rising prominence of mid-late-successional species rather than increasing structural complexity. Treatment forest NEP briefly declined below that of the control forest in the fifth year after stem girdling and three years after total LAI reached a low point, suggesting canopy physiology (i.e., as observed by lower CUE) rather than leaf quantity temporarily drove down production. The subsequent rise in treatment forest NEP is consistent with observations of century-old deciduous forests naturally transitioning to middle succession that have shown NEP may remain stable or increase as compositional and structural changes unfold (Urbanski et al. 2007, Dragoni et al. 2011, Keenan et al. 2013, Brzostek et al. 2014, Froelich et al. 2015, Beamesderfer et al. 2020a, Finzi et al. 2020). Paralleling our results, an increase in annual NEP in Harvard Forest's mixed deciduous forests was associated with the emergent canopy dominance of mid-late-successional species, including *Quercus rubra* (Finzi et al. 2020). More broadly, canopy composition is implicated as a primary determinant of temperate forest NEP in comparative studies controlling for variability in climate and soils (Tamrakar et al. 2018, Beamesderfer et al. 2020b).

While our analysis did not elucidate the full mechanistic pathway leading to increasing long-term NEP in the treatment forest, it suggests several interrelated plant-to-canopy compositional and physiological changes are

responsible. The accelerated succession treatment expedited the mortality of already declining century-old aspen and birch, rapidly advancing the dominance of mid-late-successional species with higher relative growth rates. By comparison, in the control forest, mid-late-successional relative growth rates stagnated over nearly two decades while the growth of early-successional species gradually declined. A canopy compositional transition from aspen and birch to red oak and red maple in the treatment forest did not negatively affect relative growth rates, even though the photosynthetic competency of red maple, the most prominent species by LAI, is less than that of other canopy dominant species. Given its dominance, red maple's lower leaf dark respiration rate could explain why ecosystem respiration declined even though soil respiration, overwhelmingly the largest source of respiratory CO₂, did not differ between control and treatment forests. Rather than increasing NEP by enhancing canopy complexity as we hypothesized, the mortality of slowly growing aspen and birch appears to have competitively "released" more vigorous mid-late-successional species, akin to a moderate canopy thinning that enhances access to growth-limiting resources (Campbell et al. 2009, Matsushita et al. 2015, Hou et al. 2016).

Recognizing that an indefinite rise in treatment forest NEP is not sustainable, two future trajectories seem ecologically plausible: stabilization at the current rate or a gradual decline to control levels. The growth stimulating effects of increased availability of limiting resources following the decline or removal of competing vegetation may be short-lived (Kweon and Comeau 2019). For example, NEP in the treatment forest could stabilize or decline as available N, which increased significantly following stem girdling, returns to levels comparable to those observed in the control forest (Nave et al. 2011a). However, periodic, low-intensity elimination of plant competition through natural or facilitated disturbances, which are increasing in the region (Cohen et al. 2016), could reinvigorate growth and sustain ecosystem scale production (Lu et al. 2016). Whether NEP remains elevated relative to the control forest could depend on the successional dynamics of N cycling in the compositionally shifted and N-limited treatment forest and the degree of retention as N capital contained in detritus is slowly mineralized and reclaimed by plant biomass or, instead, leached or emitted in gaseous form (Rastetter et al. 2021).

Our observations thus far leave several additional questions unanswered. For example, with only four years of available N data collection, we do not know whether compositional changes in the treatment forest permanently modified N cycling rates or availability (Nave et al. 2014). Similarly, species level differences in transpiration emerged in the first few years following disturbance as soil water availability changed (Matheny et al. 2014). These differences varied based on the hydraulic traits of different species (Matheny et al. 2017), and may

affect long-term NEP by altering the physiology and composition of the canopy. While our present analysis does not directly address heterotrophic respiration, stable total soil respiration rates, recent reductions in ER, and lower-than-expected coarse woody debris respiration rates of ~1–2 Mg C·ha⁻¹·yr⁻¹ six years following stem girdling (Schmid et al. 2016) suggest respiratory CO₂ produced from the decomposition of legacy C is not enough to offset increasing production. However, with tree mortality supplying a large influx of detritus, the future extent of detritus-C retention (e.g., in soils) and lagged detritus-fueled heterotrophic respiration could affect net C balance for decades to come (Harmon et al. 2011, Mosier et al. 2017, Clark et al. 2018).

Application and conclusions

We conclude that aging deciduous forests transitioning from early to middle succession have the potential to sustain high levels of NEP well into the future, and that production may be sustained, or even enhanced, by disturbance regimes that cause low-to-moderate levels of mortality, although changing frequency and increasing interactivity among disturbances introduces uncertainty into future trajectories. A decade ago, with a paucity of empirical data, theory (Odum 1969) implied that the maturing of regrown secondary forests would erode the terrestrial C sink of eastern North America (Birdsey et al. 2006). However, our results and mounting evidence elsewhere (e.g., Williams et al. 2014, Besnard et al. 2018) strongly suggest otherwise, leading us to conclude that forest management practices encouraging reversion to a young forest age structure are not the only option for active management to promote and enhance the region's terrestrial C sink (Keith et al. 2014). Our century-old study forest, which is more advanced in age than most of the region's deciduous forests (Gough et al. 2016), exhibited increased rates of carbon sequestration (as NEP) when actively transitioned from early to middle succession. Conservation of these aging forests and management using silvicultural strategies that emulate moderate-severity disturbance (e.g., multi-cohort management approaches; Hanson and Lorimer 2007) is likely to preserve, or even enhance, the region's terrestrial C sink while supplying additional ecosystem goods and services associated with older forests (Bauhus et al. 2009).

In addition, our decade-long study demonstrates that forests are capable of substantial resistance and rapid recovery following moderate-severity disturbance, providing preliminary guidance for forest managers contemplating disturbance avoidance and recovery strategies. By departing from theory (Ellison et al. 2005, Buma 2015), our observations show that disturbance may alter structure and composition considerably without inflicting a commensurate change in functioning, illustrating the capacity of internal ecosystem constituents to rapidly adjust to stabilize whole-ecosystem function. Although ecosystem processes may remain stable across a range of

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

ACKNOWLEDGMENTS

We appreciate the comments of two peer reviewers and the Subject Matter Editor, Yude Pan. This work was supported by the National Science Foundation Division of Environmental Biology, Awards 1655095 (C. M. Gough, B. Bond-Lamberty) and 1856319 (K. J. Nadelhoffer, L. E. Nave, C. M. Gough) and by the Department of Energy AmeriFlux Core Site support to US-UMB and US-UMd sites. We thank the University of Michigan Biological Station for hosting our work, decades of staff, students, technicians, and visiting researchers for contributing to it, and Resident Biologists Bob Vande Kopple and Adam Schubel for their support.

LITERATURE CITED

- Abrams, M. D., and M. L. Scott. 1989. Disturbance-mediated accelerated succession in 2 Michigan forest types. *Forest Science* 35:42–49.
- Allen, M. S., V. Thapa, J. R. Arevalo, and M. W. Palmer. 2012. Windstorm damage and forest recovery: Accelerated succession, stand structure, and spatial pattern over 25 years in two Minnesota forests. *Plant Ecology* 213:1833–1842.
- Amiro, B. D., et al. 2010. Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *Journal of Geophysical Research: Biogeosciences* 115:G00K02.
- Anderegg, W. R. L., et al. 2016. When a tree dies in the forest: Scaling climate-driven tree mortality to ecosystem water and carbon fluxes. *Ecosystems* 19:1133–1147.
- Atkins, J. W., et al. 2020. Application of multidimensional structural characterization to detect and describe moderate forest disturbance. *Ecosphere* 11:e03156.
- Atkins, J. W., G. Bohrer, R. T. Fahey, B. S. Hardiman, T. H. Morin, A. E. L. Stovall, N. Zimmerman, and C. M. Gough. 2018a. Quantifying vegetation and canopy structural complexity from terrestrial lidar data using the forestR package. *Methods in Ecology and Evolution* 9:2057–2066.
- Atkins, J. W., R. T. Fahey, B. H. Hardiman, and C. M. Gough. 2018b. Forest canopy structural complexity and light absorption relationships at the subcontinental scale. *Journal of Geophysical Research: Biogeosciences* 123:1387–1405.
- Battles, J. J., N. L. Cleavitt, D. S. Saah, B. T. Poling, and T. J. Fahey. 2017. Ecological impact of a microburst windstorm in a northern hardwood forest. *Canadian Journal of Forest Research* 47:1695–1701.
- Bauhus, J., K. Puettmann, and C. Messier. 2009. Silviculture for old-growth attributes. *Forest Ecology and Management* 258:525–537.
- Beamesderfer, E. R., M. A. Arain, M. Khomik, and J. J. Brodeur. 2020a. The impact of seasonal and annual climate variations on the carbon uptake capacity of a deciduous forest within the great lakes region of Canada. *Journal of Geophysical Research: Biogeosciences* 125:e2019JG005389.
- Beamesderfer, E. R., M. A. Arain, M. Khomik, J. J. Brodeur, and B. M. Burns. 2020b. Response of carbon and water fluxes to meteorological and phenological variability in two eastern North American forests of similar age but contrasting species composition—a multiyear comparison. *Biogeosciences* 17:3563–3587.
- Besnard, S., et al. 2018. Quantifying the effect of forest age in annual net forest carbon balance. *Environmental Research Letters* 13:124018.
- Birdsey, R. A., K. Pregitzer, and A. Lucier. 2006. Forest carbon management in the United States: 1600–2100. *Journal of Environmental Quality* 35:1461–1469.
- Bose, A. K., A. Weiskittel, and R. G. Wagner. 2017. A three decade assessment of climate-associated changes in forest composition across the north-eastern USA. *Journal of Applied Ecology* 54:1592–1604.
- Bovard, B. D., P. S. Curtis, C. S. Vogel, H. B. Su, and H. P. Schmid. 2005. Environmental controls on sap flow in a northern hardwood forest. *Tree Physiology* 25:31–38.
- Brzostek, E. R., D. Dragoni, H. P. Schmid, A. F. Rahman, D. Sims, C. A. Wayson, D. J. Johnson, and R. P. Phillips. 2014. Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests. *Global Change Biology* 20:2531–2539.
- Buma, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere* 6:70.
- Campbell, J., G. Alberti, J. Martin, and B. E. Law. 2009. Carbon dynamics of a ponderosa pine plantation following a thinning treatment in the northern Sierra Nevada. *Forest Ecology and Management* 257:453–463.
- Chang, C. C., et al. 2019. Testing conceptual models of early plant succession across a disturbance gradient. *Journal of Ecology* 107:517–530.
- Clark, K. L., H. J. Renninger, N. Skowronski, M. Gallagher, and K. V. R. Schafer. 2018. Decadal-scale reduction in forest net ecosystem production following insect defoliation contrasts with short-term impacts of prescribed fires. *Forests* 9:145.
- Coates, K. D., and P. J. Burton. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. *Forest Ecology and Management* 99:337–354.
- Cohen, W. B., Z. Yang, S. V. Stehman, T. A. Schroeder, D. M. Bell, J. G. Masek, C. Huang, and G. W. Meigs. 2016. Forest disturbance across the conterminous United States from 1985–2012: The emerging dominance of forest decline. *Forest Ecology and Management* 360:242–252.
- Curtis, P. S., and C. M. Gough. 2018. Forest aging, disturbance and the carbon cycle. *New Phytologist* 219:1188–1193.
- Curtis, P. S., P. J. Hanson, P. Bolstad, C. Barford, J. C. Randolph, H. P. Schmid, and K. B. Wilson. 2002. Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agricultural and Forest Meteorology* 113:3–19.
- Curtis, P. S., C. S. Vogel, C. M. Gough, H. P. Schmid, H. B. Su, and B. D. Bovard. 2005. Respiratory carbon losses and the carbon-use efficiency of a northern hardwood forest, 1999–2003. *New Phytologist* 167:437–455.
- Dietze, M. C., and J. H. Matthes. 2014. A general ecophysiological framework for modelling the impact of pests and pathogens on forest ecosystems. *Ecology Letters* 17:1418–1426.
- Dragoni, D., H. P. Schmid, C. A. Wayson, H. Potter, C. S. B. Grimmond, and J. C. Randolph. 2011. Evidence of increased

- net ecosystem productivity associated with a longer vegetated season in a deciduous forest in south-central Indiana, USA. *Global Change Biology* 17:886–897.
- Ellison, A. M., et al. 2005. Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3:479–486.
- Fahey, R. T., et al. 2019. Defining a spectrum of integrative trait-based vegetation canopy structural types. *Ecology Letters* 22:2049–2059.
- Fahey, R. T., E. J. Stuart-Haentjens, C. M. Gough, A. De La Cruz, E. Stockton, C. S. Vogel, and P. S. Curtis. 2016. Evaluating forest subcanopy response to moderate severity disturbance and contribution to ecosystem-level productivity and resilience. *Forest Ecology and Management* 376:135–147.
- Farquhar, G. D., S. V. Caemmerer, and J. A. Berry. 1980. A biochemical-model of photosynthetic CO₂ assimilation in leaves of C-3 species. *Planta* 149:78–90.
- Finzi, A. C., et al. 2020. Carbon budget of the harvard forest long-term ecological research site: pattern, process, and response to global change. *Ecological Monographs* 90: e01423.
- Flower, C. E., and M. A. Gonzalez-Meler. 2015. Responses of temperate forest productivity to insect and pathogen disturbances. Pages 547–569 in S. S. Merchant, editor. *Annual review of plant biology*. Volume 66. Annual Reviews, Palo Alto, California, USA.
- Foster, D. R., J. D. Aber, J. M. Melillo, R. D. Bowden, and F. A. Bazzaz. 1997. Forest response to disturbance and anthropogenic stress. *BioScience* 47:437–445.
- Franklin, J. F., R. J. Mitchell, and B. J. Palik. 2007. Natural disturbance and stand development principles for ecological forestry. General Technical Report NRS-19. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, Pennsylvania, USA.
- Frelich, L. E., and P. B. Reich. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecological Monographs* 65:325–346.
- Froelich, N., H. Croft, J. M. Chen, A. Gonsamo, and R. M. Staebler. 2015. Trends of carbon fluxes and climate over a mixed temperate-boreal transition forest in southern Ontario, Canada. *Agricultural and Forest Meteorology* 211:72–84.
- Goetz, S. J., et al. 2012. Observations and assessment of forest carbon dynamics following disturbance in North America. *Journal of Geophysical Research: Biogeosciences* 117:G02022.
- Goring, S. J., et al. 2016. Novel and lost forests in the upper Midwestern United States, from new estimates of settlement-era composition, stem density, and biomass. *PLoS ONE* 11:34.
- Gough, C. 2021. Gough et al._NEP a decade following accelerated succession. Figshare. Dataset. <https://doi.org/10.6084/m9.figshare.13286666.v1>
- Gough, C. M., J. W. Atkins, R. T. Fahey, and B. S. Hardiman. 2019. High rates of primary production in structurally complex forests. *Ecology* 100:e02864.
- Gough, C. M., J. W. Atkins, R. T. Fahey, B. S. Hardiman, and E. A. LaRue. 2020. Community and structural constraints on the complexity of eastern North American forests. *Global Ecology and Biogeography* 29:2107–2118.
- Gough, C., G. Bohrer, and P. Curtis. 2021a. AmeriFlux US-UMB University of Michigan Biological Station, Version 16-5, AmeriFlux AMP, (Dataset). <https://doi.org/10.17190/AMF/1246107>
- Gough, C., G. Bohrer, and P. Curtis. 2021b. AmeriFlux US-UMd UMBS Disturbance, Version 10-5, AmeriFlux AMP, (Dataset). <https://doi.org/10.17190/AMF/1246134>
- Gough, C. M., P. S. Curtis, B. S. Hardiman, C. M. Scheuermann, and B. Bond-Lamberty. 2016. Disturbance, complexity, and succession of net ecosystem production in North America's temperate deciduous forests. *Ecosphere* 7: e01375.
- Gough, C. M., B. S. Hardiman, L. E. Nave, G. Bohrer, K. D. Maurer, C. S. Vogel, K. J. Nadelhoffer, and P. S. Curtis. 2013. Sustained carbon uptake and storage following moderate disturbance in a great lakes forest. *Ecological Applications* 23:1202–1215.
- Gough, C. M., C. S. Vogel, B. Hardiman, and P. S. Curtis. 2010. Wood net primary production resilience in an unmanaged forest transitioning from early to middle succession. *Forest Ecology and Management* 260:36–41.
- Gough, C. M., C. S. Vogel, H. P. Schmid, and P. S. Curtis. 2008a. Controls on annual forest carbon storage: Lessons from the past and predictions for the future. *BioScience* 58:609–622.
- Gough, C. M., C. S. Vogel, H. P. Schmid, H. B. Su, and P. S. Curtis. 2008b. Multi-year convergence of biometric and meteorological estimates of forest carbon storage. *Agricultural and Forest Meteorology* 148:158–170.
- Grigri, M. S., J. W. Atkins, C. Vogel, B. Bond-Lamberty, and C. M. Gough. 2020. Aboveground wood production is sustained in the first growing season after phloem-disrupting disturbance. *Forests* 11:1306.
- Hanson, J. J., and C. G. Lorimer. 2007. Forest structure and light regimes following moderate wind storms: implications for multi-cohort management. *Ecological Applications* 17:1325–1340.
- Hardiman, B. S., G. Bohrer, C. M. Gough, and P. S. Curtis. 2013a. Canopy structural changes following widespread mortality of canopy dominant trees. *Forests* 4:537–552.
- Hardiman, B. S., G. Bohrer, C. M. Gough, C. S. Vogel, and P. S. Curtis. 2011. The role of canopy structural complexity in wood net primary production of a maturing northern deciduous forest. *Ecology* 92:1818–1827.
- Hardiman, B. S., C. M. Gough, A. Halperin, K. L. Hofmeister, L. E. Nave, G. Bohrer, and P. S. Curtis. 2013b. Maintaining high rates of carbon storage in old forests: A mechanism linking canopy structure to forest function. *Forest Ecology and Management* 298:111–119.
- Harmon, M. E., B. Bond-Lamberty, J. W. Tang, and R. Vargas. 2011. Heterotrophic respiration in disturbed forests: A review with examples from North America. *Journal of Geophysical Research: Biogeosciences* 116:G00K04.
- Hicke, J. A., et al. 2012. Effects of biotic disturbances on forest carbon cycling in the United States and Canada. *Global Change Biology* 18:7–34.
- Hickey, L. J., J. Atkins, R. T. Fahey, M. R. Kreider, S. B. Wales, and C. M. Gough. 2019. Contrasting development of canopy structure and primary production in planted and naturally regenerated red pine forests. *Forests* 10:566.
- Hillebrand, H., S. Langenheder, K. Lebet, E. Lindstrom, O. Ostman, and M. Striebel. 2018. Decomposing multiple dimensions of stability in global change experiments. *Ecology Letters* 21:21–30.
- Hou, L., Z. Li, C. L. Luo, L. L. Bai, and N. N. Dong. 2016. Optimization forest thinning measures for carbon budget in a mixed pine-oak stand of the qingling mountains, China: A case study. *Forests* 7:16.
- Hurteau, M. D., B. A. Hungate, G. W. Koch, M. P. North, and G. R. Smith. 2013. Aligning ecology and markets in the forest carbon cycle. *Frontiers in Ecology and the Environment* 11:37–42.
- Johnson, E. A., and K. Miyanishi. 2008. Testing the assumptions of chronosequences in succession. *Ecology Letters* 11:419–431.
- Kautz, M., A. J. H. Meddens, R. J. Hall, and A. Arneth. 2017. Biotic disturbances in northern hemisphere forests—a

- synthesis of recent data, uncertainties and implications for forest monitoring and modelling. *Global Ecology and Biogeography* 26:533–552.
- Keenan, T. F., D. Y. Hollinger, G. Bohrer, D. Dragoni, J. W. Munger, H. P. Schmid, and A. D. Richardson. 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature* 499:324–327.
- Keith, H., D. Lindenmayer, B. Mackey, D. Blair, L. Carter, L. McBurney, S. Okada, and T. Konishi-Nagano. 2014. Managing temperate forests for carbon storage: Impacts of logging versus forest protection on carbon stocks. *Ecosphere* 5:75.
- Kosiba, A. M., G. W. Meigs, J. A. Duncan, J. A. Pontius, W. S. Keeton, and E. R. Tait. 2018. Spatiotemporal patterns of forest damage and disturbance in the Northeastern United States: 2000–2016. *Forest Ecology and Management* 430:94–104.
- Kweon, D., and P. G. Comeau. 2019. Factors influencing overyielding in young boreal mixedwood stands in western Canada. *Forest Ecology and Management* 432:546–557.
- Landhauser, S. M., and V. J. Lieffers. 2002. Leaf area renewal, root retention and carbohydrate reserves in a clonal tree species following above-ground disturbance. *Journal of Ecology* 90:658–665.
- Lasslop, G., M. Reichstein, D. Papale, A. D. Richardson, A. Arneeth, A. Barr, P. Stoy, and G. Wohlfahrt. 2010. Separation of net ecosystem exchange into assimilation and respiration using a light response curve approach: Critical issues and global evaluation. *Global Change Biology* 16:187–208.
- Lovett, G. M., C. D. Canham, M. A. Arthur, K. C. Weathers, and R. D. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. *BioScience* 56:395–405.
- Lu, H. C., G. M. J. Mohren, J. den Ouden, V. Goudiaby, and F. J. Sterck. 2016. Overyielding of temperate mixed forests occurs in evergreen-deciduous but not in deciduous-deciduous species mixtures over time in the Netherlands. *Forest Ecology and Management* 376:321–332.
- Luyssaert, S., E. D. Schulze, A. Borner, A. Knohl, D. Hessenmoller, B. E. Law, P. Ciais, and J. Grace. 2008. Old-growth forests as global carbon sinks. *Nature* 455:213–215.
- Matheny, A. M., et al. 2014. Species-specific transpiration responses to intermediate disturbance in a northern hardwood forest. *Journal of Geophysical Research: Biogeosciences* 119:2292–2311.
- Matheny, A. M., R. P. Fiorella, G. Bohrer, C. J. Poulsen, T. H. Morin, A. Wunderlich, C. S. Vogel, and P. S. Curtis. 2017. Contrasting strategies of hydraulic control in two codominant temperate tree species. *Ecohydrology* 10:e1815.
- Matsushita, K., M. Tomotsune, Y. Sakamaki, and H. Koizumi. 2015. Effects of management treatments on the carbon cycle of a cool-temperate broad-leaved deciduous forest and its potential as a bioenergy source. *Ecological Research* 30:293–302.
- Morin, T. H., G. Bohrer, R. P. M. Frasson, L. Naor-Azrieli, S. Mesi, K. Stefanik, and K. V. R. Schäfer. 2014a. Environmental drivers of methane fluxes from an urban temperate wetland park. *Journal of Geophysical Research: Biogeosciences* 119:2188–2208.
- Morin, T. H., G. Bohrer, L. Naor-Azrieli, S. Mesi, W. T. Kenny, W. J. Mitsch, and K. V. R. Schäfer. 2014b. The seasonal and diurnal dynamics of methane flux at a created urban wetland. *Ecological Engineering* 72:74–83.
- Mosier, S. L., E. S. Kane, D. L. Richter, E. A. Lilleskov, M. F. Jurgensen, A. J. Burton, and S. C. Resh. 2017. Interactive effects of climate change and fungal communities on wood-derived carbon in forest soils. *Soil Biology and Biochemistry* 115:297–309.
- Nave, L. E., et al. 2011a. Disturbance and the resilience of coupled carbon and nitrogen cycling in a north temperate forest. *Journal of Geophysical Research-Biogeosciences* 116:G04016.
- Nave, L. E., C. M. Gough, C. H. Perry, K. L. Hofmeister, J. M. Le Moine, G. M. Domke, C. W. Swanston, and K. J. Nadelhoffer. 2017. Physiographic factors underlie rates of biomass production during succession in great lakes forest landscapes. *Forest Ecology and Management* 397:157–173.
- Nave, L. E., J. P. Sparks, J. Le Moine, B. S. Hardiman, K. J. Nadelhoffer, J. M. Tallant, C. S. Vogel, B. D. Strahm, and P. S. Curtis. 2014. Changes in soil nitrogen cycling in a northern temperate forest ecosystem during succession. *Biogeochemistry* 121:471–488.
- Nilsen, E. B., D. E. Bowler, and J. D. C. Linnell. 2020. Exploratory and confirmatory research in the open science era. *Journal of Applied Ecology* 57:842–847.
- Odum, E. P. 1969. Strategy of ecosystem development. *Science* 164:262–270.
- Pan, Y., et al. 2011a. A large and persistent carbon sink in the world's forests. *Science* 333:988–993.
- Pan, Y., J. M. Chen, R. Birdsey, K. McCullough, L. He, and F. Deng. 2011b. Age structure and disturbance legacy of North American forests. *Biogeosciences* 8:715–732.
- Parker, G. G., D. J. Harding, and M. L. Berger. 2004. A portable lidar system for rapid determination of forest canopy structure. *Journal of Applied Ecology* 41:755–767.
- Pastorello, G., et al. 2020. The fluxnet2015 dataset and the one-flux processing pipeline for eddy covariance data. *Scientific Data* 7:225.
- Rastetter, E. B., G. W. Kling, G. R. Shaver, B. C. Crump, L. Gough, and K. L. Griffin. 2021. Ecosystem recovery from disturbance is constrained by N cycle openness, vegetation-soil N distribution, form of N losses, and the balance between vegetation and soil-microbial processes. *Ecosystems* 24:667–685.
- Rebmann, C., O. Kolle, B. Heinesch, R. Queck, A. Ibrom, and M. Aubinet. 2012. Data acquisition and flux calculation. Pages 59–83 in M. Aubinet, T. Vesala, and D. Papale, editors. *Eddy covariance, a practical guide to measurement and data analysis*. Springer Netherlands, New York, New York, USA.
- Reichstein, M., et al. 2005. On the separation of net ecosystem exchange into assimilation and ecosystem respiration: Review and improved algorithm. *Global Change Biology* 11:1424–1439.
- Richardson, A. D., et al. 2006. A multi-site analysis of random error in tower-based measurements of carbon and energy fluxes. *Agricultural and Forest Meteorology* 136:1–18.
- Sagara, B. T., R. T. Fahey, C. S. Vogel, A. T. Fotis, P. S. Curtis, and C. M. Gough. 2018. Moderate disturbance has similar effects on production regardless of site quality and composition. *Forests* 9:70.
- Scheuermann, C. M., L. E. Nave, R. T. Fahey, K. J. Nadelhoffer, and C. M. Gough. 2018. Effects of canopy structure and species diversity on primary production in Upper Great Lakes forests. *Oecologia* 188:405–415.
- Schmid, A. V., C. S. Vogel, E. Liebman, P. S. Curtis, and C. M. Gough. 2016. Coarse woody debris and the carbon balance of a moderately disturbed forest. *Forest Ecology and Management* 361:38–45.
- Schmid, H. P., H.-B. Su, C. S. Vogel, and P. S. Curtis. 2003. Ecosystem-atmosphere exchange of carbon dioxide over a mixed hardwood forest in northern lower Michigan. *Journal of Geophysical Research* 108:4417.
- Seidl, R., W. Rammer, and T. A. Spies. 2014. Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. *Ecological Applications* 24:2063–2077.

- Seidl, R., T. A. Spies, D. L. Peterson, S. L. Stephens, and J. A. Hicke. 2016. Searching for resilience: Addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology* 53:120–129.
- Stuart-Haentjens, E. J., P. S. Curtis, R. T. Fahey, C. S. Vogel, and C. M. Gough. 2015. Net primary production of a temperate deciduous forest exhibits a threshold response to increasing disturbance severity. *Ecology* 96:2478–2487.
- Stueve, K. M., C. H. Perry, M. D. Nelson, S. P. Healey, A. D. Hill, G. G. Moisen, W. B. Cohen, D. D. Gormanson, and C. Q. Huang. 2011. Ecological importance of intermediate windstorms rivals large, infrequent disturbances in the northern great lakes. *Ecosphere* 2:art2.
- Tamrakar, R., M. B. Rayment, F. Moyano, M. Mund, and A. Knohl. 2018. Implications of structural diversity for seasonal and annual carbon dioxide fluxes in two temperate deciduous forests. *Agricultural and Forest Meteorology* 263:465–476.
- Tang, X. G., H. P. Li, M. G. Ma, L. Yao, M. Peichl, A. Arain, X. B. Xu, and M. Goulden. 2017. How do disturbances and climate effects on carbon and water fluxes differ between multi-aged and even-aged coniferous forests? *Science of the Total Environment* 599:1583–1597.
- Townsend, P. A., A. Singh, J. R. Foster, N. J. Rehberg, C. C. Kingdon, K. N. Eshleman, and S. W. Seagle. 2012. A general landsat model to predict canopy defoliation in broadleaf deciduous forests. *Remote Sensing of Environment* 119:255–265.
- Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91:2833–2849.
- Urbanski, S., C. Barford, S. Wofsy, C. Kucharik, E. Pyle, J. Budney, K. McKain, D. Fitzjarrald, M. Czikowsky, and J. W. Munger. 2007. Factors controlling CO₂ exchange on time-scales from hourly to decadal at harvard forest. *Journal of Geophysical Research: Biogeosciences* 112:G02020.
- Van Pelt, R., S. C. Sillett, W. A. Kruse, J. A. Freund, and R. D. Kramer. 2016. Emergent crowns and light-use complementarity lead to global maximum biomass and leaf area in *Sequoia sempervirens* forests. *Forest Ecology and Management* 375:279–308.
- Vogel, C. S., and P. S. Curtis. 1995. Leaf gas-exchange and nitrogen dynamics of n-2-fixing field-grown *Alnus glutinosa* under elevated atmospheric CO₂. *Global Change Biology* 1:55–61.
- Wales, S. B., M. R. Kreider, J. Atkins, C. M. Hulshof, R. T. Fahey, L. E. Nave, K. J. Nadelhoffer, and C. M. Gough. 2020. Stand age, disturbance history and the temporal stability of forest production. *Forest Ecology and Management* 460:117865.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26:1–69.
- Williams, C. A., G. J. Collatz, J. Masek, C. Q. Huang, and S. N. Goward. 2014. Impacts of disturbance history on forest carbon stocks and fluxes: Merging satellite disturbance mapping with forest inventory data in a carbon cycle model framework. *Remote Sensing of Environment* 151:57–71.
- Williams, C. A., H. Gu, R. MacLean, J. G. Masek, and G. J. Collatz. 2016. Disturbance and the carbon balance of us forests: A quantitative review of impacts from harvests, fires, insects, and droughts. *Global and Planetary Change* 143:66–80.
- Wolter, P. T., and M. A. White. 2002. Recent forest cover type transitions and landscape structural changes in northeast Minnesota, USA. *Landscape Ecology* 17:133–155.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2417/full>

OPEN RESEARCH

Site instrumentation, meteorological data, soil moisture, fluxes and plot-level leaf area are available through AmeriFlux for sites US-UMB (Gough et al. 2021a, <https://doi.org/10.17190/AMF/1246107>) and US-UMd (Gough et al. 2021b, <https://doi.org/10.17190/AMF/1246134>). Additional data presented in figures, along with code for statistical analysis, are available via Figshare (Gough 2021, <https://doi.org/10.6084/m9.figshare.13286666.v1>).