



How do forest landscapes respond to elevated CO₂ and ozone? Scaling Aspen-FACE plot-scale experimental results

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Abstract. The Aspen-FACE (Free-Air Carbon Enrichment) experiment was an 11-yr study of the effect of elevated CO₂ and ozone (alone and in combination) on the growth productivity of model aspen communities (pure aspen, aspen-birch, and aspen-maple) in the field in northern Wisconsin, USA. Uncertainty remains about how these short-term plot-level responses might play out at landscape scales where climate change, competition, succession, and disturbances interact with tree-level responses. In this study, we used a recent physiology-based approach (PnET-Succession v3.1) within the forest landscape model LANDIS-II to scale the site-scale FACE results to landscape extents by mechanistically accounting for the globally changing drivers of CO₂, ozone, temperature, and precipitation. We conducted a factorial simulation experiment to test five hypotheses about the effects of three treatments (CO₂ concentration, cumulative ozone exposure, and disturbance). CO₂ was clearly the dominant driver of landscape response, with disturbance also having a large effect. Ozone was not a dominant driver of landscape dynamics or total landscape biomass, but its negative effect on mean landscape biomass was nevertheless significant. We found that CO₂ mitigation of water stress may not have a major effect on species composition or biomass accumulation. We found that species diversity was somewhat decreased by elevated CO₂ as expected, but somewhat increased by O₃, contrary to expectations. The spatial pattern of the landscape was minimally affected by the treatments. While rising CO₂ concentrations have some mitigating effect on the negative O₃ effect on the species studied, additional research is needed to confirm whether researchers and managers can be justified in disregarding O₃ as a primary driver of forest dynamics in other ecosystems. Our results also add more support to the growing consensus that projections of climate change effects must include robust, direct links between CO₂ and tree growth and competition; temperature effects (as demonstrated elsewhere) appear to be less by comparison.

Key words: Aspen-FACE; elevated CO₂; forest composition; forest landscape modeling; global change; LANDIS-II; ozone pollution; PnET-Succession; scaling; Wisconsin.

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INTRODUCTION

The atmosphere contains varying levels of CO₂ and pollutants, and these gases can directly impact forest productivity and health. Because

species differ in their response to the fertilizing effect of elevated CO₂ and their sensitivity to pollutants, competitive interactions can be modified, and successional trajectories and resilience can be impacted by these interactions (Bond and

Midgley 2000, Kgope et al. 2010). Tropospheric ozone, considered the most significant air pollutant negatively affecting forest productivity worldwide (Matyssek et al. 2013), is produced when combustion of fossil fuel releases nitrogen oxides (NO_x) that react with O_2 and volatile organic compounds (primarily methane), in the presence of sunlight to produce ozone (O_3). Ozone is a potent oxidizer that disrupts cell function, resulting in decreased plant productivity and increased mortality (Karnosky et al. 2005). On the other hand, elevated CO_2 is known to increase plant productivity and has stimulated the growth of forests (e.g., Cole et al. 2010, Gustafson et al. 2018a).

Free-Air Carbon Enrichment (FACE) experiments are an effective way to quantify the effects of elevated CO_2 on trees in a field setting (Karnosky et al. 2001, Paoletti et al. 2017). The Aspen-FACE experiment was conducted in northern Wisconsin, USA, and was unique in that it experimentally modified both CO_2 and O_3 concentrations on model forest ecosystems in a replicated, factorial experiment (Kubiske et al. 2007). The experiment used various tree community assemblages composed of several native aspen clones (*Populus tremuloides*), paper birch (*Betula papyrifera*), and sugar maple (*Acer saccharum*). These are among the most economically and ecologically important species in northern hardwood and sub-boreal forests of eastern North America (Dickson et al. 2000). However, it is not straightforward to extrapolate the results of the plot-scale (30 m) Aspen-FACE experiment to answer questions about the management of landscapes that face increased pollution from fossil fuel combustion (Smith 2012).

There have been attempts to scale Aspen-FACE results to broader spatial and temporal scales (Karnosky et al. 2005, Gustafson et al. 2013, 2018b), but these studies together suggest that simple extrapolations of the short-term plot-level responses to landscape scales may not be warranted when climate change, elevated CO_2 and O_3 , competition, succession, and disturbances interact with tree-level responses. Our study is the latest in a series of studies seeking to scale the Aspen-FACE experiment to landscape scale. Karnosky et al. (2005) made the first attempt, finding that in complex forest ecosystems, effects at one scale can be very different

than those at another scale. They concluded that to accurately scale the effects of atmospheric pollution, a model that links canopy-level processes with ecosystem processes is essential. In an attempt to do that, Gustafson et al. (2013) used the Biomass Succession extension of the forest landscape model LANDIS-II (Scheller et al. 2007) to project the Aspen-FACE experiment into the future at both site and landscape scales, although they did not attempt to simulate future climate. Their results showed that long-term trends generally resemble short-term trends, although shade tolerance increasingly becomes an important determinant of long-term outcomes. However, Biomass Succession simulates growth processes using a relatively phenomenological approach, where maximum aboveground net primary productivity (ANPP) of a species is estimated as an average under specific climate and atmospheric conditions. Although the Maximum-ANPP parameter can be varied through time as a function of variation in specific drivers (e.g., precipitation, temperature, CO_2 , O_3), this is typically implemented by coupling to an outside model, resulting in indirect links to individual drivers, making it potentially insensitive to the extreme events that can have a major effect on forest dynamics (Clark et al. 2016) and to dynamic driver interactions such as CO_2 acclimation and lengthened growing seasons. Furthermore, because Biomass Succession has weak links between abiotic drivers and growth response, using it for novel conditions without empirical analogs results in considerable uncertainty. This uncertainty can be greatly reduced with more mechanistic models having very direct links between abiotic drivers and growth response (Gustafson 2013). Gustafson et al. (2018b) took advantage of the creation of the more mechanistic PnET-Succession extension (De Bruijn et al. 2014) of LANDIS-II that is based on physiology first principles, to extrapolate the Aspen-FACE experiment 80 yr into the future. In contrast to their experiment using Biomass Succession, they found (as Karnosky et al. [2005] predicted) that short-term (11-year) empirical trajectories did not always persist for 80 yr. Dominant species sometimes switched dramatically over time. They calibrated PnET-Succession against observed growth under the single-factor treatments of the Aspen-FACE experiment

(control, elevated CO₂ only, and elevated O₃ only), and successfully validated it against the independent combined-factor treatment (elevated CO₂ and O₃ together). They were also able to parameterize other species that were not studied in the Aspen-FACE experiment based on life history traits found in the literature. However, that study was conducted aspatially (simulating a single cell, representing a FACE ring) to avoid the confounding effects of spatial processes, and that model has not been applied to landscapes to evaluate how elevated CO₂ and O₃ might interact with warming and the spatial processes of dispersal and disturbance to impact the dynamics of diverse forests. This study features individual cells that differ from our prior study in that they contain a much wider diversity of species, and they are influenced by the spatial context of varying abundances of species (providing propagules) and spatially explicit disturbances. These cells are embedded in a real landscape where the abundance of various species in a neighborhood generates successional inertia that can be disrupted by disturbance.

In this study, we used PnET-Succession to scale the Aspen-FACE results to landscape scales by mechanistically accounting for the interacting effects of elevated CO₂, O₃, and temperature on photosynthesis and competition while also simulating the spatial processes of seed dispersal, establishment, and disturbance. Our purpose was to greatly reduce the uncertainty associated with prior results obtained using a much less mechanistic modeling approach. We used existing process-based disturbance extensions (modules) within LANDIS to simulate the major disturbances that structure forests in northern Wisconsin (where the Aspen-FACE experiment was conducted), thus accounting for interactions between the main abiotic drivers and the disturbances that alter competitive environments within individual sites. Our specific objective was to test five hypotheses about how CO₂ enrichment (following specific Representative Concentration Pathways [RCP]; Meinshausen et al. 2011; as described below) and O₃ pollution might affect forest productivity and composition on real landscapes. (1) CO₂ enrichment will disproportionately increase the landscape biomass of inherently fast-growing species (high photosynthetic capacity under the light conditions for

which they are adapted) at the expense of slower-growing species, as shown in simulations at the site scale by Gustafson et al. (2018a). (2) Elevated O₃ pollution will shift the landscape biomass of species in inverse proportion to their ozone tolerance, as shown at the site scale by Gustafson et al. (2018b). (3) The combination of elevated CO₂ (RCP 6.0) and elevated O₃ will produce compensatory landscape-level responses to produce conditions similar to ambient (control; RCP 2.6-ambient O₃) as was observed in the Aspen-FACE experiment (Kubiske et al. 2007). (4) The mitigating effect of high CO₂ concentrations on water stress as shown by Gustafson et al. (2018a) in simulations of those interactions at the site scale will result in less difference in biomass growth between droughty soils (SAND) and mesic soil (LOAM) under elevated CO₂ (RCP 6.0) compared to lower CO₂ levels (RCP 2.6). (5) Species diversity will be reduced by elevated CO₂ (and concurrent climate change) and O₃ by selecting against slow-growing and ozone-intolerant species, but diversity will be increased by an intermediate level of disturbance as predicted by the intermediate disturbance hypothesis (Connell 1978). The major difference with our prior study is that we are addressing these questions within an appropriate and realistic spatial context.

METHODS

Experiment design

Using the validated PnET-Succession extension (v3.1; Gustafson et al. 2018b), we extrapolated the Aspen-FACE experiment to the landscapes of northern Wisconsin by conducting factorial landscape simulation experiments with main treatment effects of emissions scenario (combination of CO₂ concentration, temperature, and precipitation), O₃ concentration, and disturbances (all or none). The experiments were conducted using a raster representation (resolution = 30 m) of a 104,471-ha sub-boreal mixed forest landscape in Oconto County, Wisconsin, USA. Topographic relief is minimal, so climate was assumed to be homogeneous across the study area. LANDIS land types were delineated based on soil type by assigning SSURGO (Soil Survey Staff 2013) soil map polygons to one of the three soil types used in prior studies

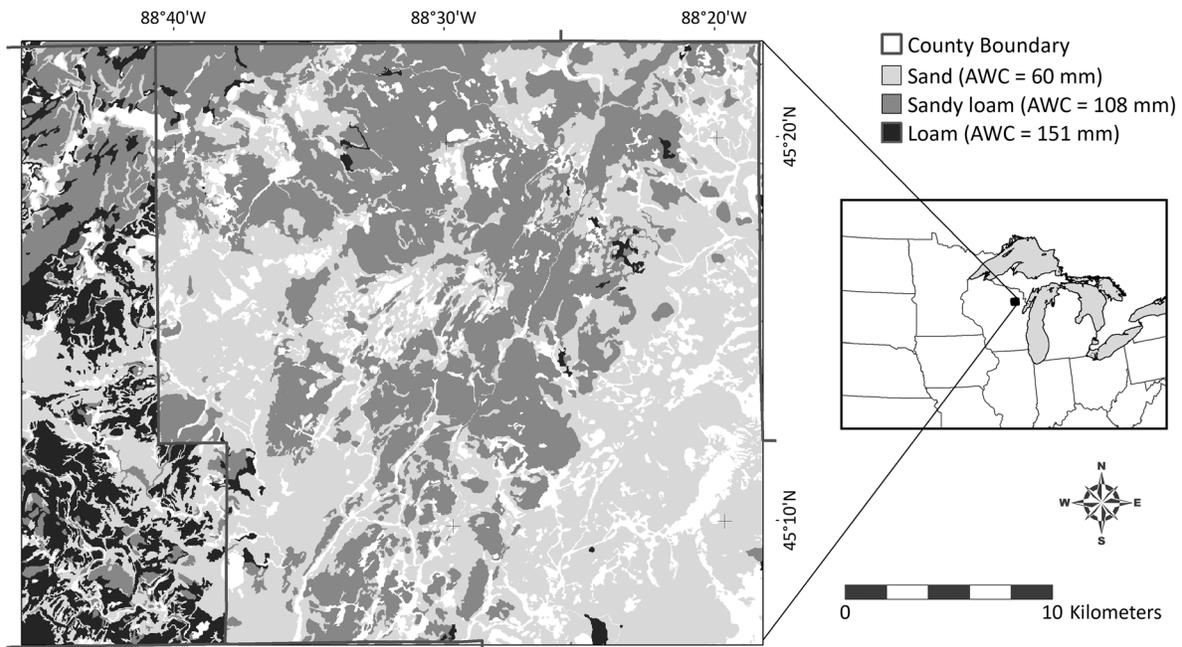


Fig. 1. Soil types (and available water capacity) used in the study area in Oconto County (Wisconsin, USA). Non-forested areas are unshaded and were not included in the simulation.

(Fig. 1). The initial forest conditions (species and age classes) were those of Janowiak et al. (2014), created from Forest Service Forest Inventory and Analysis data using the imputation methods of Wilson et al. (2012). We randomly assigned quaking aspen (*Populus tremuloides*) cohorts to either clone 8 (ozone-tolerant) or clone 216 (ozone-intolerant), representative of taxa that were studied in the Aspen-FACE experiment.

The experiments were conducted as a 3×2 factorial (Table 1) using fixed treatment effects through time, simulating six replicates of forest dynamics for 200 yr based on starting conditions as of 2006. The emissions scenario factor used two RCP scenarios that combined both CO_2 concentration and climate (temperature and precipitation), but CO_2 and climate were dynamic through time. The RCP 2.6 emissions scenario represents minor climate change, assuming that CO_2 atmospheric concentrations peak at 442 ppm around the year 2050 and decline thereafter. The RCP 6.0 emissions scenario represents a significant change in climate, assuming that CO_2 concentration will level off at 752 ppm around the year 2150 (as extended beyond 2100

Table 1. Levels of the three landscape-scale experimental treatment factors, resulting in six combinations of levels.

Treatment factor	Low	High
Emissions scenario	RCP 2.6†	RCP 6.0‡
Avg. growing season cumulative ozone dose (nmol/mol/hr >40)	30,157	93,929
Disturbances	None	All

† Average May–October monthly temperature (13.9° – 18.6°C) and average annual precipitation (600.6 mm) were projected by the GFDL GCM model from the RCP 2.6 emissions scenario ($\text{CO}_2 = 380$ – 442 ppm), each varying monthly.

‡ Average May–October monthly temperature (13.9° – 20.4°C) and average annual precipitation (572.2 mm) were projected by the GFDL GCM model from the RCP 6.0 emissions scenario ($\text{CO}_2 = 381$ – 752 ppm), each varying monthly.

by Meinshausen et al. [2011]; Fig. 2). We used monthly climate projections for each RCP scenario generated by the General Fluid Dynamics Laboratory earth system model (GFDL-ESM2G, r1i1p1; Dunne et al. 2012). Because the climate projections ended at the year 2100, we duplicated the last 30 yr of the precipitation and temperature series (negligible temporal trend) for an additional century to produce a time series

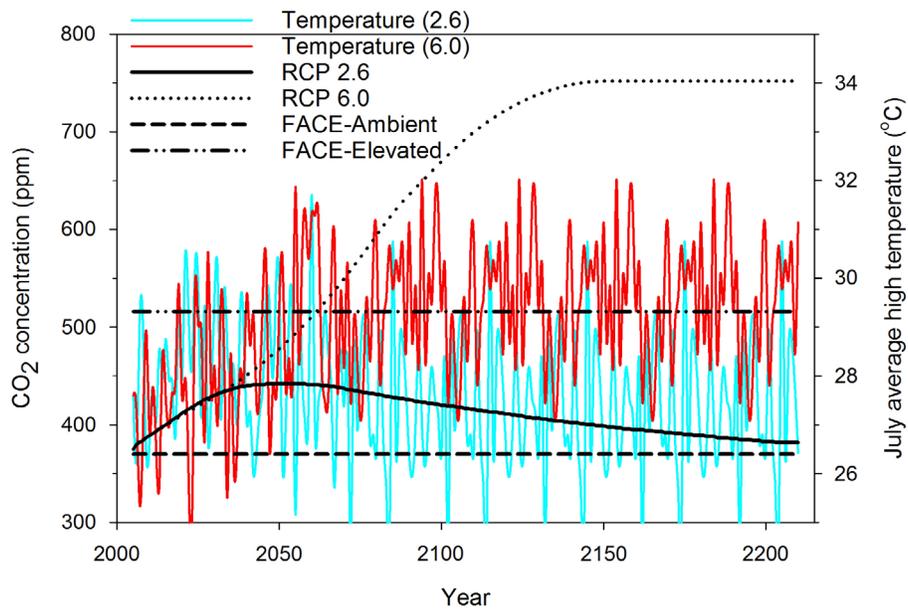


Fig. 2. Projected atmospheric CO₂ concentrations under each RCP scenario (Meinshausen (2011) and the scenarios that reflect the Aspen-FACE experiment (Dickson et al. 2000). Average July maximum temperatures for the RCP scenarios are included for reference.

through the year 2205 that maintained periods of drought and wet through time to avoid confounding the experiment. To directly compare landscape results to the plot-scale Aspen-FACE experiment (Hypothesis 3), we also conducted dedicated simulations using the mean CO₂ and O₃ concentrations of the Aspen-FACE experiment (Fig. 2).

The ozone factor had a current ozone level and an elevated ozone level, following those derived by Gustafson et al. (2018b) from the Aspen-FACE experiment. Cumulative ozone dose varied monthly (Table 1), given as the current month's cumulative O₃ dose above a threshold concentration of 40 nmol/mol since the beginning of the (annually dynamic) growing season, and was compiled from hourly values (08:00–19:00 h; Ollinger et al. 1997). The disturbance factor had two levels: all of the disturbances typical of this landscape (insect outbreaks, fire, windthrow, and timber harvest), representing an intermediate level of disturbance; or no disturbances. The disturbance treatment was designed to create a realistic, generic disturbance regime rather than create an arbitrary disturbance regime or replicate an actual

regime. Jack pine budworm outbreaks were simulated using the Biological Disturbance Agent extension (Sturtevant et al. 2004). Fires were simulated using the Base Fire extension (Scheller and Domingo 2017), parameterized from Sturtevant et al. (2009). Microburst wind events were simulated using the Base Wind extension (Scheller and Domingo 2011), parameterized based on data in Rich et al. (2007). Tornadoes and derechos were simulated using the Linear Wind extension (Gustafson et al. 2016a), parameterized using data in Hjelmfelt (2007) and online sources (<http://www.wunderground.com/resources/education/tornadoFAQ.asp?MR=1>). Timber harvest was simulated using the Biomass Harvest extension (Gustafson et al. 2000), using generic harvest prescriptions based loosely on those of another study in the region (Sturtevant et al. 2009). Harvest prescriptions included a mix of clear-cut, shelterwood, and selection cutting methods, collectively cutting about 3% of the landscape each decade, with half of the cuts being clear-cuts. Clear-cuts removed all biomass and tended to favor pioneer species; shelterwood cuts favored oaks, pines, and hemlock; and selection cuts removed 10% of the biomass of all

cohorts >80 yr of age and tended to favor shade-tolerant species. The cumulative area disturbed by all disturbances (of all intensities) was typically about 9% of the active cells in the study area per decade. All LANDIS extension input files are included in Data S1.

Model description

LANDIS is a forest landscape model that uses a process approach to simulate forest development (dispersal, establishment, growth, and competition) and degeneration (senescence and disturbance) at broad spatial (>10⁵ ha) and temporal (centuries) scales. Landscapes are represented as a grid of spatially interacting cells on which species composition and canopy layering are assumed to be homogeneous, and these cells are spatially aggregated into land types with homogeneous climate and soils. Forest composition on each cell is represented as age cohorts of one or more tree species that interact via a suite of vital attributes (e.g., fire tolerance, shade tolerance, longevity, seed dispersal, ability to sprout vegetatively) to generate nondeterministic successional pathways that are driven by competition, disturbance type, and severity (Mladenoff, 2004). We used LANDIS-II v6.2 (Scheller et al. 2007), which consists of a collection of libraries and extensions that simulate specific ecological processes of interest.

To simulate cohort growth and competition processes, we used PnET-Succession (v3.1), an extension that embeds functions from the PnET-II ecophysiology model (Aber et al. 1995) to simulate cohort growth as a competition for light and water. PnET-Succession scales leaf-level (i.e., per gram foliage) biochemical processes such as photosynthesis, respiration, and transpiration to the grid cell by integrating light extinction and water consumption through stacked canopy layers and tracking a dynamic soil water balance. This is done by estimating A_{max} (species-cohort photosynthetic capacity under optimal conditions) as a function of foliar nitrogen concentration. Actual photosynthesis (A) in each month and stratum of the canopy is calculated by applying multiple reduction multipliers (0.0–1.0) that reflect departure from optimal conditions (stress). The key limiting factors are light and available soil water, but age (senescence), temperature, and ozone dose are also included. Soil

water on each grid cell is tracked using a bulk-hydrology model based on precipitation, runoff, loss to evaporation and percolation out of the rooting zone, and transpiration by the cohorts. Access to light and soil water is proportional to cohort biomass, with smaller cohorts having stochastic access to these resources when they are limited. When water is not limiting, cohort photosynthesis is determined by light availability, which is dependent on canopy position and leaf area, and decreases with departure from optimal temperature and age. Photosynthesis decreases as soil water availability decreases, according to the water stress reduction factor (f_{Water}), such that $f_{Water} = 0.0$ whenever water potential falls below the species' drought tolerance. PnET-Succession accounts for growth and maintenance respiration using a Q10 relationship (Atkins 1978), such that maintenance respiration depends on temperature and biomass, while foliar respiration rate depends on temperature and moisture. Acclimation of respiration to elevated temperature is simulated as in Wythers et al. (2013). Net photosynthesis output is allocated to biomass pools of wood, root, foliage, and reserves (non-structural carbon) according to allocation parameters. New cohorts are stochastically established with species-specific establishment probabilities calculated monthly based on soil water and sub-canopy light. Independent disturbance extensions simulate the other processes that kill cohorts or remove some of their biomass. Thus, the LANDIS framework robustly scales site-level physiological mechanisms to the landscape scale through the interaction of grid cells via dispersal and multiple spatial disturbance processes.

Our study relied heavily on the capabilities of PnET-Succession to simulate the species-specific effects of CO₂ and O₃ on photosynthetic output. In the PnET-II model, elevated CO₂ concentration is assumed to reduce stomatal conductance and increase internal leaf CO₂ concentration (Ollinger et al. 2002), thereby reducing transpiration losses and increasing water use efficiency, and photosynthetic capacity (e.g., De Kauwe et al. 2013). This is implemented by computing a CO₂ enhancement factor ($DelA_{max}$) that also accounts for CO₂ acclimation based on the equation developed by Franks et al. (2013) as modified by Gustafson et al. (2018b). Ozone induces

stomatal sluggishness (Paoletti 2005) that increases water loss and allows ozone to enter the leaf and impair leaf-level physiological functions (Hoshika et al. 2012). Gustafson et al. (2018b) developed algorithms to model O₃ effects to more explicitly account for these mechanisms than does the PnET-II model (Ollinger et al. 1997). PnET-Succession v3.1 was calibrated and validated against the Aspen-FACE experimental results by Gustafson et al. (2018b).

Analysis procedures

To understand the outcome of the simulation experiment and quantitatively test the hypotheses, we used a combination of visual evaluation of simulated trends (with uncertainty estimates) and statistical tests of hypotheses. The primary response variable was mean landscape above-ground woody biomass of species groups, classified by life history traits relevant to individual hypotheses (Table 2), with ecological complexity (computed as the mean species diversity on cells across the landscape) used to evaluate Hypothesis 5. We also computed measures of landscape spatial pattern (composition and patchiness) as a function of treatments to assess the spatial effects of the treatments. To best evaluate the general trend of response to the treatments, we focused primarily on average values of each response variable from the years 150 to 200, when CO₂ levels in RCP 6.0 stabilize (Fig. 2). Because simulation models can arbitrarily produce high statistical power through replication (White et al. 2014), we generated only six replicates and evaluated the magnitude of treatment effects visually and by looking for overlap between 95% confidence intervals. Interested readers can find statistical hypothesis tests computed using Generalized Linear Mixed Models in Appendix S1.

RESULTS

Total landscape biomass

All treatments had a significant effect (non-overlapping 95% confidence intervals) on total landscape biomass (Table 3). The emissions treatment produced the greatest effect on total landscape biomass (compare colors in Fig. 3), and it is very likely that this response was driven more by CO₂ concentration (compare shape of curves

in Fig. 3 to the shape of CO₂ curves in Fig. 2) than climate (Gustafson et al. 2018a). The next greatest effect was disturbance, with less biomass seen when disturbances were simulated (open symbols) compared to no disturbance (closed symbols) in Fig. 3. Disturbances also resulted in more variability in biomass trajectory. Finally, ozone had a negative effect on landscape biomass, being particularly clear under the no disturbance scenarios (Fig. 3).

Hypotheses tests

Hypothesis 1 stated that CO₂ enrichment would disproportionately increase the landscape biomass of inherently fast-growing species at the expense of slower-growing species. While biomass of all growth classes increased under CO₂ enrichment (RCP 6.0), the strength of the positive response was strongly related to growth capacity as evidenced by the magnitude of the percent difference values in Table 4, providing good support for Hypothesis 1. However, it appears that the advantage to fast-growing species did not come at the expense of slower-growing species. Red and sugar maple dominated this landscape (Appendix S1: Figs. S1, S2) because they were initially dominant, and the disturbance regimes mostly favored shade-tolerant species through partial cohort removal (single-tree selection, variable-intensity wind), and these are the conditions under which these species are relatively fast-growing.

Hypothesis 2 stated that elevated O₃ pollution would reduce the landscape biomass of species in inverse proportion to their ozone tolerance. Elevated ozone reduced the biomass of all ozone tolerance groups, but the magnitude of the reduction was indeed inversely related to ozone tolerance (Table 5). We assessed CO₂ by O₃ interactions, but they were not significant. The divergence of curves by symbol shape (ozone treatment levels) in Fig. 4 is greatest for ozone-intolerant species, while the curves for the ozone-tolerant species group are almost perfectly superimposed through time, indicating that ozone had almost no effect on ozone-tolerant species. These results clearly support Hypothesis 2.

Hypothesis 3 posited that the combination of the specific elevated concentrations (CO₂ and O₃) used in the Aspen-FACE experiment would

Table 2. Assignment of species to life history classes for analysis purposes.

Species	O ₃ tolerance	Shade tolerance	Drought tolerance	Growth capacity†	Optimal temperature
<i>Abies balsamea</i>	Tolerant	Tolerant	Intolerant	Intermediate	Low
<i>Acer rubrum</i>	Sensitive	Tolerant	Intermediate	Fast	High
<i>Acer saccharum</i> ‡	Tolerant	Tolerant	Intolerant	Fast	Intermediate
<i>Betula alleghaniensis</i>	Sensitive	Tolerant	Intolerant	Intermediate	Low
<i>Betula papyrifera</i> ‡	Intermediate	Intolerant	Intolerant	Fast	Low
<i>Carya cordiformis</i>	Intermediate	Intolerant	Intolerant	Intermediate	High
<i>Fagus grandifolia</i>	Intermediate	Tolerant	Intermediate	Fast	Intermediate
<i>Fraxinus americana</i>	Sensitive	Intermediate	Intermediate	Intermediate	High
<i>Fraxinus nigra</i>	Sensitive	Intolerant	Intolerant	Fast	Intermediate
<i>Fraxinus pennsylvanica</i>	Sensitive	Intermediate	Intermediate	Intermediate	High
<i>Picea glauca</i>	Tolerant	Intermediate	Intermediate	Fast	Low
<i>Picea mariana</i>	Intermediate	Intermediate	Intermediate	Slow	Low
<i>Pinus banksiana</i>	Intermediate	Intolerant	Tolerant	Fast	Low
<i>Pinus resinosa</i>	Tolerant	Intolerant	Tolerant	Fast	Low
<i>Pinus strobus</i>	Sensitive	Intermediate	Intermediate	Fast	Low
<i>Populus balsamea</i>	Sensitive	Intolerant	Intolerant	Fast	Low
<i>Populus grandidentata</i>	Sensitive	Intolerant	Intolerant	Fast	Intermediate
<i>P. tremuloides</i> –clone 8‡	Tolerant	Intolerant	Intolerant	Fast	Low
<i>P. tremuloides</i> –clone 216‡	Sensitive	Intolerant	Intolerant	Fast	Low
<i>Prunus serotina</i>	Sensitive	Intolerant	Intermediate	Fast	High
<i>Quercus alba</i>	Tolerant	Intolerant	Tolerant	Intermediate	High
<i>Quercus ellipsoidalis</i>	Intermediate	Intolerant	Tolerant	Intermediate	Low
<i>Quercus macrocarpa</i>	Intermediate	Intermediate	Tolerant	Fast	Intermediate
<i>Quercus rubra</i>	Tolerant	Intermediate	Intermediate	Intermediate	Intermediate
<i>Quercus velutina</i>	Intermediate	Intermediate	Intermediate	Intermediate	Intermediate
<i>Thuja occidentalis</i>	Tolerant	Intermediate	Intolerant	Slow	Low
<i>Tilia americana</i>	Tolerant	Tolerant	Intermediate	Fast	Intermediate
<i>Tsuga canadensis</i>	Tolerant	Tolerant	Intolerant	Fast	Intermediate

† Species photosynthetic capacity under the light conditions for which they are adapted.

‡ Species included in the Aspen-FACE empirical experiment.

Table 3. Assessment of relative effect of the treatment factors on total landscape biomass (all species) using least squares means to estimate 95% confidence intervals.

Treatment	Total landscape biomass (g/m ²)		Difference (%)
	Low level	High level	
Emissions/CO ₂	18,364–18,636	27,293–27,697	+48.6
Ozone	22,865–23,203	21,920–22,245	–4.1
Disturbance	23,061–23,403	21,733–22,055	–5.8

produce landscape-level responses similar to ambient (control) conditions, as seen in Aspen-FACE results. We used Aspen-FACE-specific atmospheric inputs to evaluate this hypothesis. Although the two treatments produced similar

response (Fig. 5), least squares 95% confidence intervals of total landscape biomass from the years 150 to 200 for the ambient conditions and the elevated CO₂ and O₃ conditions were 17,904–18,136 and 19,547–19,779 g/m², respectively. Because these ranges did not quite overlap, Hypothesis 3 was not clearly supported.

Hypothesis 4 stated that a mitigating effect of elevated CO₂ on water stress will result in less difference in biomass growth between cohorts grown on droughty soil (SAND) and mesic soil (LOAM) under elevated CO₂ (RCP 6.0) compared to lower CO₂ levels (RCP 2.6). Normalized growth (percentage of starting biomass) was higher on SAND (35.0–42.1%) than on LOAM (28.0–35.2%) under the low level of CO₂ (RCP 2.6), but growth was much higher on LOAM (108.2–112.0%) than SAND (93.1–96.9) under the high level of CO₂ (RCP 6.0). Thus, elevated CO₂

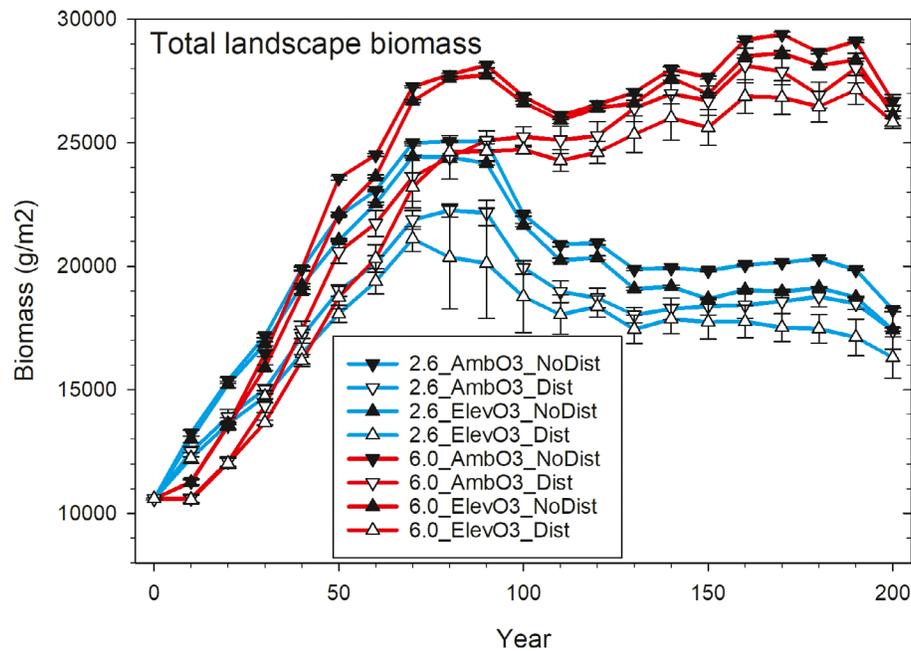


Fig. 3. Effect of the treatments on total landscape biomass (all species). Colors indicate CO₂ (emissions) treatment, shape indicates ozone treatment, and symbol fill indicates disturbance treatment. Error bars show the 95% confidence interval around the means of six replicates.

Table 4. Effect of emissions scenario (CO₂) on landscape biomass by species growth capacity class computed as 95% confidence intervals using least squares means (one for each growth class), accounting for all three treatment factors.

Growth class	Biomass RCP 2.6 (g/m ²)	Biomass RCP 6.0 (g/m ²)	Difference (%)
Slow-growing	166.5–176.9	212.9–226.1	+27.8
Intermediate	2,836.1–2938.6	3,801.9–3,904.4	+33.4
Fast-growing	15,313–15,552	23,264–23,503	+51.5

did not enhance growth to a greater extent on the droughty SAND soils compared to the mesic LOAM soils. Elevated CO₂ (RCP 6.0) appeared to make less of a difference in the growth of drought-tolerant species than the less-drought-tolerant species (Fig. 6), although drought tolerance tends to be negatively correlated with shade tolerance, making such comparisons somewhat confounded.

Hypothesis 5 stated that site-level species diversity would be reduced by elevated O₃ and

Table 5. Effect of ozone (O₃) on landscape biomass by species ozone tolerance class computed as 95% confidence intervals using least squares means (one for each O₃ tolerance class), accounting for all three treatment factors.

O ₃ tolerance	Biomass Ambient O ₃ (g/m ²)	Biomass Elevated O ₃ (g/m ²)	Difference (%)
O ₃ -sensitive	9,795–10,139	9,088–9,433	-7.1
Intermediate	817.5–848.5	772.9–802.2	-5.5
O ₃ -tolerant	12,467–12,834	12,313–12,680	-1.8

CO₂ (with concurrent climate change) by selecting against slow-growing and ozone-intolerant species, but that diversity would be increased by disturbance. The hypothesis was supported by our results, with the greatest effect produced by disturbance (Fig. 7, Table 6).

Landscape composition was affected mostly by disturbance, with disturbance increasing aspen and mixed hardwoods at the expense of the other types, while ozone and emissions scenario had negligible effects at the forest type level (not shown). Landscape spatial pattern was

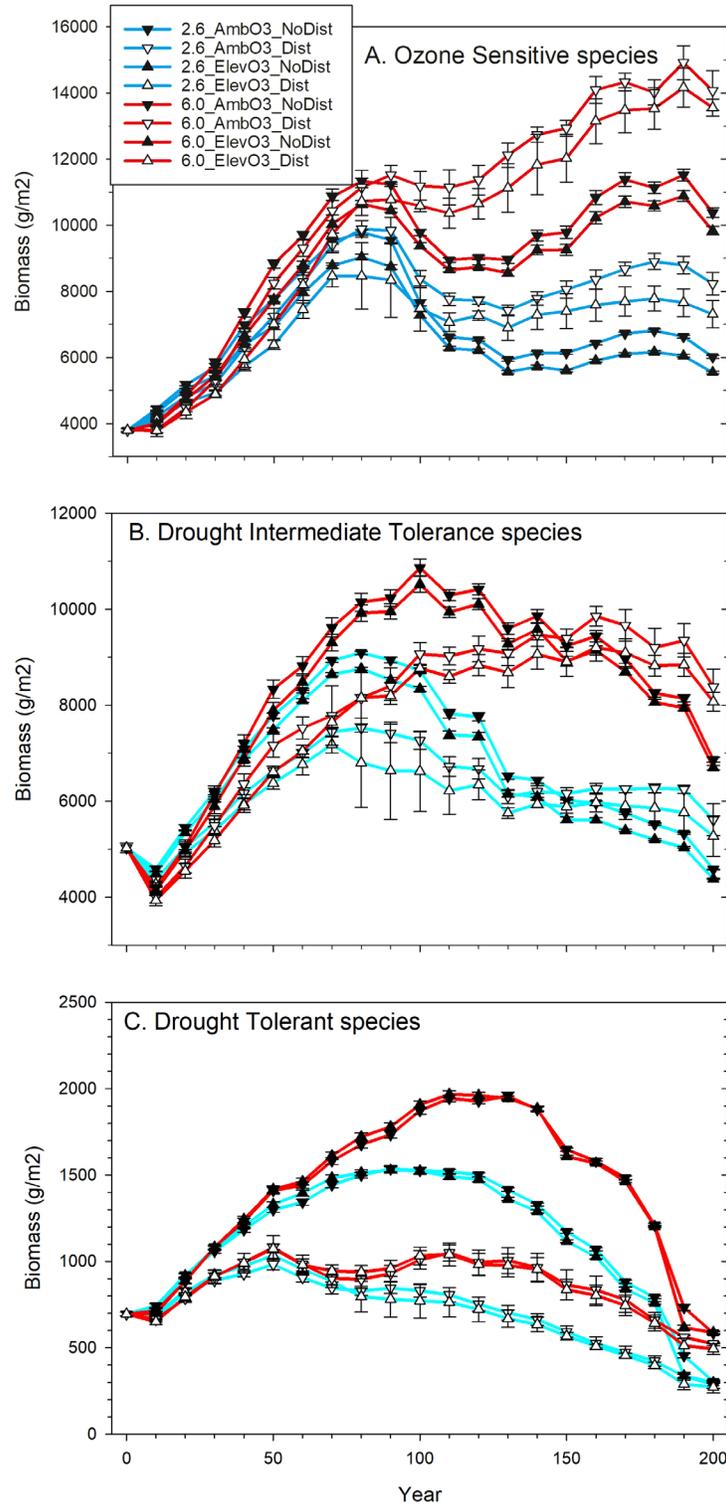


Fig. 4. Effect of the treatments on landscape biomass of species by ozone tolerance class. Colors indicate CO₂ (emissions) treatment, shape indicates ozone treatment, and symbol fill indicates disturbance treatment. Error bars show the 95% confidence interval around the means of six replicates.

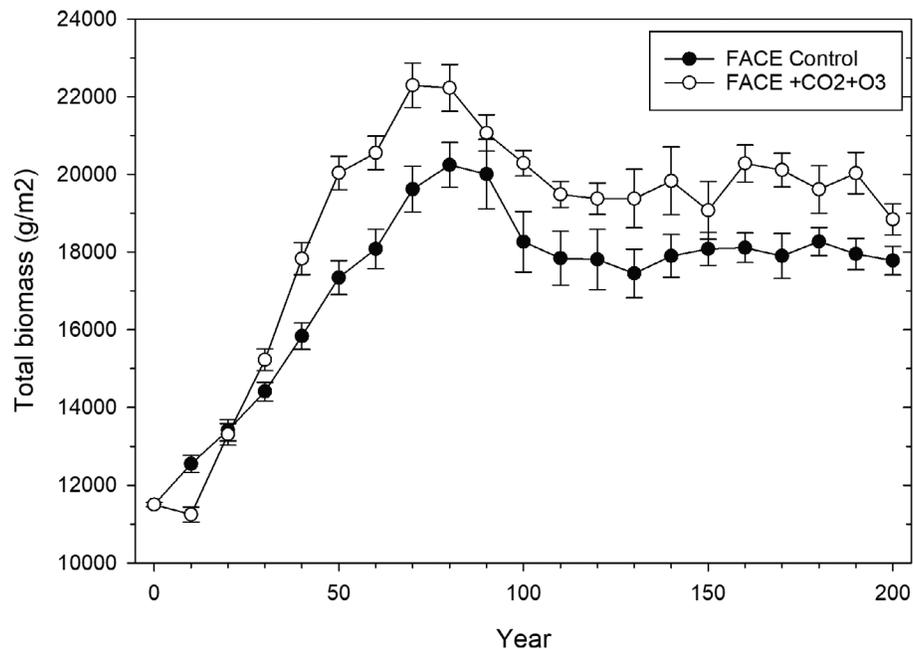


Fig. 5. Comparison of the effects on total landscape biomass of the specific concentrations of the Aspen-FACE control and elevated CO₂ and O₃ treatments, including the effect of disturbances. Error bars show the 95% confidence interval around the means of six replicates.

also most impacted by disturbance, with patch size (Fig. 8) being smaller and distance between patches (not shown, but with similar response as in Fig. 8) being greater when disturbance was present. In early years, elevated ozone seemed to marginally increase patch size, but by year 100, none of the treatments had a significant effect (Fig. 8).

DISCUSSION

Of the three treatment factors studied, emissions scenario was clearly the dominant driver. Each emissions scenario had three components: CO₂ concentration, temperature, and precipitation. Our experiment did not partition the effects of these components, but a controlled simulation experiment (not involving ozone) conducted by Gustafson et al. (2018a) did partition the effects of these components and showed that CO₂ had by far the most dominant effect. This dominance derives from a number of specific effects that cumulatively produce a major impact. (1) Elevated CO₂ concentrations in leaf interiors increase the efficiency of photosynthesis by

providing more of the raw material for photosynthesis (Farquhar and Sharkey 1982) and reducing photorespiration by increasing the ratio of CO₂ to O₂ (Long 1991). (2) When CO₂ concentrations inside the leaf are high, stomata need to open less often to let in CO₂, reducing water loss and increasing water use efficiency (Drake et al. 1997), thus increasing productivity given the water available in the soil. (3) When stomata are open less, ozone is less able to enter leaf interiors, reducing ozone damage to chloroplasts (Karnosky et al. 2005). (4) Elevated CO₂ can mitigate the negative effect of elevated temperatures on photosynthesis and respiration (Gustafson et al. 2018a).

Ozone was not a dominant driver of landscape dynamics nor total landscape biomass, but its negative effect on mean landscape biomass was nevertheless significant. This overall effect comes in spite of the fact that biomass growth of individual species was clearly inversely related to their ozone susceptibility (Table 5). In graphs of the biomass of individual species (Appendix S1: Figs. S1, S2), the only subjectively discernible effect of ozone was that the ozone-tolerant clone

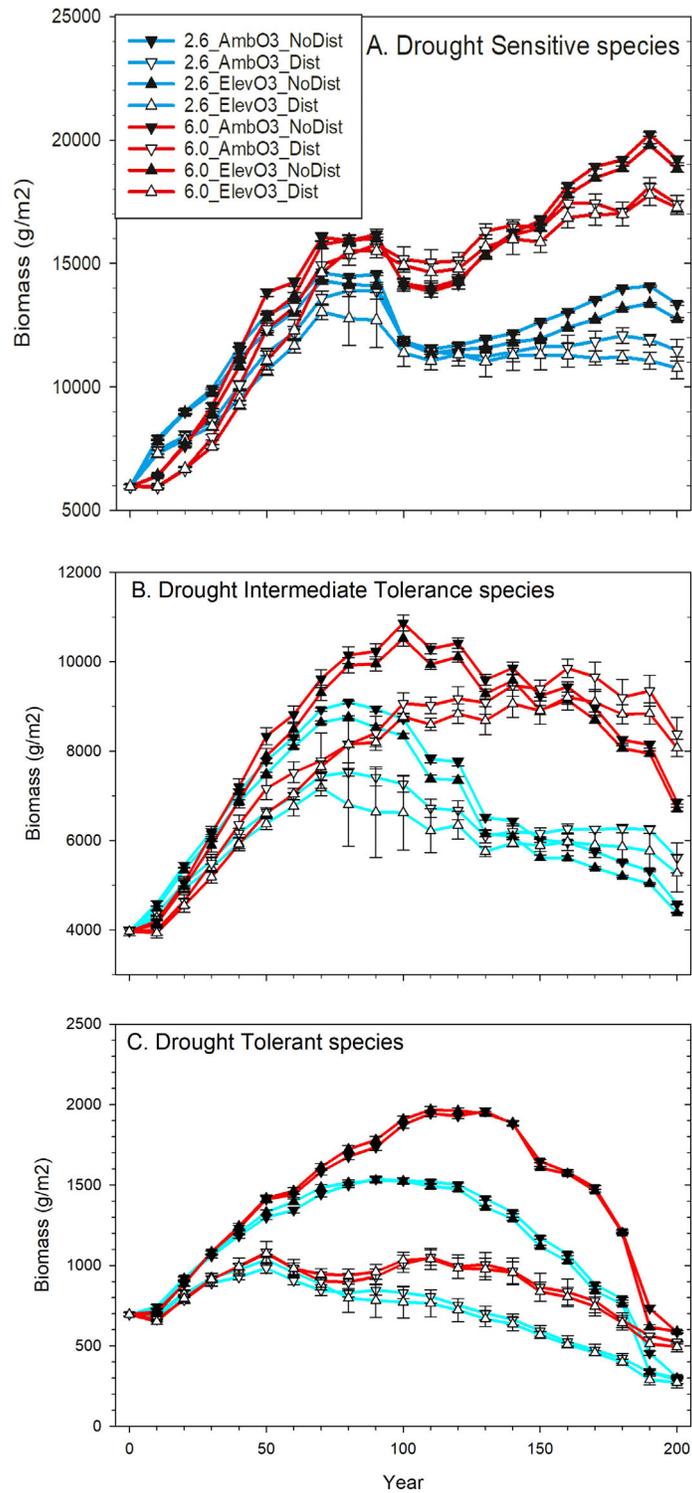


Fig. 6. Effect of the treatments on landscape biomass of species by drought tolerance class. Colors indicate CO₂ (emissions) treatment, shape indicates ozone treatment, and symbol fill indicates disturbance treatment. Error bars show the 95% confidence interval around the means of six replicates.

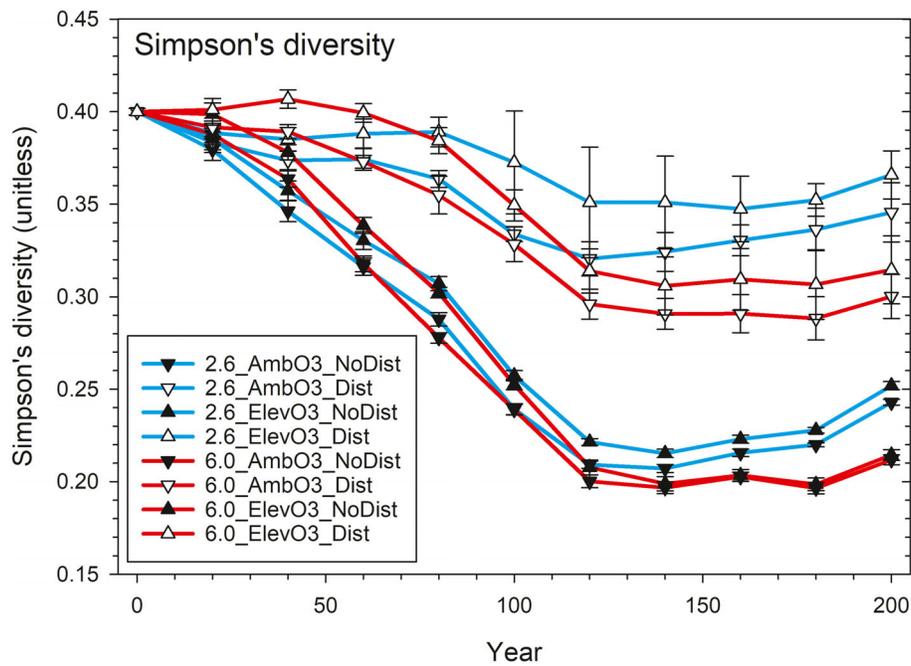


Fig. 7. Effect of the treatments on species diversity. Colors indicate CO₂ (emissions) treatment, shape indicates ozone treatment, and symbol fill indicates disturbance treatment. Error bars show the standard error around the means of six replicates.

Table 6. Effect of treatments on species diversity inverse Simpson's D (Simpson 1949) computed as 95% confidence intervals using least squares means accounting for all three treatment factors.

Treatment	Low level	High level	Difference (%)
Emissions/CO ₂	0.284–0.292	0.249–0.257	–12.2
Ozone	0.261–0.269	0.272–0.280	+4.2
Disturbance	0.213–0.222	0.320–0.328	+49.0

of aspen (clone 8) increased in biomass under elevated ozone, while the ozone-sensitive clone (clone 216) was minimally affected. In terms of individual species' biomass, it appears that the primary effect of ozone at landscape scale was compensatory, such that the biomass of ozone winners and losers offset each other across simulation replicates.

A key motivation of our study was to assess how the short-term, site-scale Aspen-FACE experimental results might be generalized to landscape scales and long time periods using a process-based landscape model. In the Aspen-FACE experiment, the positive effect of elevated CO₂ on biomass growth was approximately

equally offset by the negative effect of O₃. Hypothesis 3 was designed to assess the generality of this result on the Oconto County landscape. Although this hypothesis was not supported by the absence of response range overlap, visualization of the test (Fig. 5) revealed that elevated O₃ was mostly mitigated by elevated CO₂ and that the landscapes may be ecologically or functionally unchanged when both CO₂ and O₃ are elevated. Toward the end of the empirical Aspen-FACE experiment under the combined treatment, the plots began to be dominated by O₃-tolerant individuals as O₃-sensitive individuals died, and growth began to exceed that on control plots, and our results also show this trend. Differences between Aspen-FACE results and our landscape results may be partly caused by differences in species mixtures (see Appendix S1: Figs. S1, S2 for the behavior of individual species in the landscape experiment), by disturbance, and by the fact that initial 10-year trajectories do not always hold over longer time frames (Gustafson et al. 2018b). Our landscape simulations suggest that the Aspen-FACE

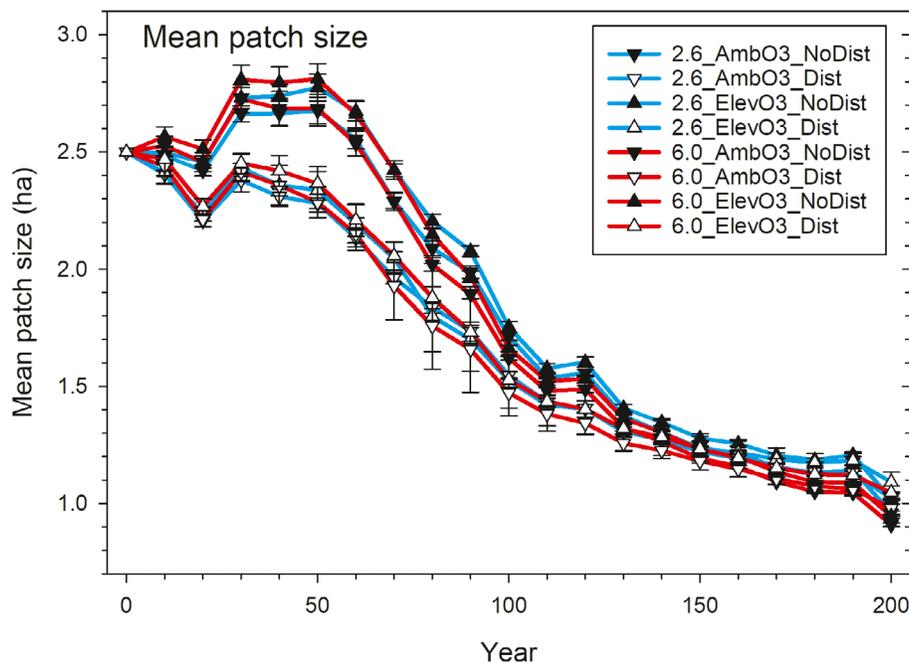


Fig. 8. Effect of the treatments on patch size. Colors indicate CO₂ (emissions) treatment, shape indicates ozone treatment, and symbol fill indicates disturbance treatment. Error bars show the standard error around the means of six replicates.

results provide a general indication of how elevated CO₂ and O₃ affect forests, but that spatially explicit, mechanistic simulations are needed to understand the likely outcome of elevated CO₂ and O₃ on specific forested ecosystems having specific disturbance regimes.

The atmospheric composition treatment factors can be considered to act as a press disturbance, meaning that they are chronic and aspatial because they were applied constantly and evenly across the entire landscape. The other disturbances (fire, wind, insects, harvest) were applied as pulse disturbances, also applied consistently across the treatments, but occurring in temporal and spatial pulses, interacting with the composition and spatial pattern of the landscape. These disturbance regimes have reciprocal interactions with the landscape in that the regimes and their impacts are somewhat driven by the landscape characteristics and the disturbances also change landscape characteristics. The interactions between the press and pulse disturbances were expected to be subtle, with considerable lag time. The atmospheric composition treatments

were not expected to directly modify disturbance regimes, although the associated temperature regime was expected to somewhat modify fire and wind regimes. A potential indirect interaction might be that a change in forest composition caused by the treatments might change all the disturbance regimes by changing average susceptibility to each disturbance. Our experimental design did not include variation in pulse disturbances as a treatment factor, so we were not able to quantify their explicit interactions with the press disturbances, but that is potentially a topic for future investigations. None of the treatments had a particularly strong impact on landscape pattern, but disturbance had the greatest effect. Given that the treatments affected individual species differently, but did not differentially affect species assemblages (forest types), we infer that species-level effects wash out when considering the landscape-level distribution of forest types.

We also attempted to further evaluate whether elevated CO₂ mitigates water stress (Hypothesis 4). It has been shown to do so at the cohort level

(Gustafson et al. 2018a), but our results at landscape scales indicate that CO₂ effects on water stress may not have a major effect on species composition or biomass accumulation. Elevated CO₂ did not promote growth on droughty soil to a greater extent than it did on mesic soil, and in fact, it promoted growth more on the mesic soil. However, our experiment does not constitute a definitive test of this hypothesis (e.g., in the presence of drought, controlling for shade tolerance), so this question should be addressed further.

Finally, we examined the effect of the treatments on species diversity, as a potential indicator of ecological resilience (Peterson et al. 1998). We found that disturbance had a much greater effect on diversity than climate (CO₂) or ozone (Fig. 7). After 200 yr, elevated CO₂ modestly decreased diversity, while elevated ozone increased it to an even lesser extent. Our results are consistent with those of Gustafson et al. (2018c), obtained using the same model, who found that elevated CO₂ (RCP 8.5) on Maryland landscapes reduced mean number of species growing on sites by favoring fast-growing species at the expense of slower-growing species.

Assumptions and caveats

It is important to consider the generality of our study. It should not be assumed that the Oconto County landscape is representative of all landscapes with these soils and species, but is rather a case study containing three general soil types typically found in the region where the Aspen-FACE experiment was conducted. We did not replicate across landscapes, nor did we conduct a formal landscape selection process to find a representative landscape. Thus, our results represent a heuristic scaling of the Aspen-FACE results to landscape spatial and temporal scales using a mechanistic landscape model. As such, our results provide considerable insight into scaling questions, but the generality of our results to other landscapes remains to be demonstrated.

The sensitivity of individual tree species to ozone is somewhat uncertain. The Aspen-FACE experiment reduced uncertainty about the sensitivity to ozone of aspen, maple, and birch. For most other species, we used the estimates of Coulston et al. (2003), and the uncertainty of these estimates varies by species. We were unable to find any estimates of ozone sensitivity

in the literature for *Carya cordiformes*, *Fagus grandifolia*, *Picea mariana*, *Pinus banksiana*, and *Quercus macrocarpa*. We arbitrarily assigned an intermediate ozone sensitivity to these species, which are not abundant in the study area. There is therefore some uncertainty about our findings that ozone is not a strong driver of forest dynamics at the landscape scale, but given the fact that most of our sensitivity estimates have empirical support suggest that the general result is fairly robust.

Our model does not include recent suggestions that enhanced growth rates may induce premature mortality related to size limitations (e.g., Büntgen et al. 2019). There is considerable uncertainty about how general this phenomenon may be across genera and ecosystems. However, such a limitation would reduce the magnitude of the CO₂ fertilization effect that was observed in our study.

The current model does not consider the effects of either CO₂ or O₃ concentrations on trophic interactions that could potentially influence tree growth and stress. For example, a recent analysis of the Aspen-FACE experiment demonstrates that insect herbivory reduced ANPP in both enriched CO₂ and CO₂ × O₃ treatments, but effects of insect herbivory under enriched O₃ alone was less than that observed under the control (Couture et al. 2015).

Implications for research and management

The effect of emissions (elevated CO₂) on biomass growth at the landscape scale is dramatically positive. On the other hand, O₃ has a modest, but significant, negative effect. Although we found that rising CO₂ concentrations have a mitigating effect on the negative O₃ effect on the species studied, additional research is needed to confirm whether researchers and managers can be justified in disregarding O₃ as a primary driver of forest dynamics in this and other ecosystems. Our results also add more support to the growing consensus that projections of the effects of climate change on forests must include robust links between CO₂ and tree growth and competition (Korzukhin et al. 1996, Cuddington et al. 2013, Gustafson 2013). Temperature effects appear to be modest by comparison as can be seen by comparing the divergence of biomass trends (e.g., Fig. 3) to the divergence between levels in the CO₂ vs. temperature trends in Fig. 2, similar to the results in the controlled site-scale

experiments of Gustafson et al. (2018a). We find it extremely difficult to have confidence in a scaling of the interacting effects of the abiotic drivers of CO₂, ozone, and disturbance that does not include direct, mechanistic links between the drivers and the system responses of growth and competition, or one that does not fundamentally scale canopy-level processes to landscape scale (Karnosky et al. 2005). Our study did not evaluate the relative effect of precipitation (and soil water-holding capacity) and droughts, but those factors have been shown to be very important in other studies (Gustafson et al. 2016b, 2017, 2018a). There is a compelling need for reliable projections of future forest dynamics that use mechanistic functions based on first principles rather than predicting the future based on the past, and include most of the drivers that determine forest dynamics (e.g., climate, atmospheric composition, disturbances, competition, seed dispersal). Our study represents the most robust attempt to date to scale the site-level AspenFACE experiment to landscape spatial and temporal scales.

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