Alteration of forest succession and carbon cycling under elevated CO$_2$

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Abstract

Regenerating forests influence the global carbon (C) cycle, and understanding how climate change will affect patterns of regeneration and C storage is necessary to predict the rate of atmospheric carbon dioxide (CO$_2$) increase in future decades. While experimental elevation of CO$_2$ has revealed that young forests respond with increased productivity, there remains considerable uncertainty as to how the long-term dynamics of forest regrowth are shaped by elevated CO$_2$ (eCO$_2$). Here, we use the mechanistic size- and age- structured Ecosystem Demography model to investigate the effects of CO$_2$ enrichment on forest regeneration, using data from the Duke Forest Free-Air Carbon dioxide Enrichment (FACE) experiment, a forest chronosequence, and an eddy-covariance tower for model parameterization and evaluation. We find that the dynamics of forest regeneration are accelerated, and stands consistently hit a variety of developmental benchmarks earlier under eCO$_2$. Because responses to eCO$_2$ varied by plant functional type, successional pathways, and mature forest composition differed under eCO$_2$, with mid- and late-successional hardwood functional types experiencing greater increases in biomass compared to early-successional functional types and the pine canopy. Over the simulation period, eCO$_2$ led to an increase in total ecosystem C storage of 9.7 Mg C ha^{-1}. Model predictions of mature forest biomass and ecosystem–atmosphere exchange of CO$_2$ and H$_2$O were sensitive to assumptions about nitrogen limitation; both the magnitude and persistence of the ecosystem response to eCO$_2$ were reduced under N limitation. In summary, our simulations demonstrate that eCO$_2$ can result in a general acceleration of forest regeneration while altering the course of successional change and having a lasting impact on forest ecosystems.

Keywords: climate change, duke FACE, ecosystem demography model, forest regeneration, succession, simulation

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Introduction

The world's forests are being impacted by multifaceted global change pressures, resulting in changes in structure, function, and feedbacks to the climate system (e.g., Anderson-Teixeira *et al.*, 2013). Globally, the majority of these forests are secondary; 64% of forests on Earth are either naturally regenerating following past disturbance or planted (Food and Agriculture Organization of the United Nations, 2010). Secondary forests play an important role in climate regulation because they are strong carbon (C) sinks, with net ecosystem productivity (NEP) sometimes exceeding 10 Mg C ha^{-1} yr^{-1} (Anderson-Teixeira *et al.*, 2013). On a global scale, forest regrowth sequestered > 1.6 Pg C

yr^{-1} from 1990 to 2007, contributing substantially to the estimated net forest sink of 2.4 Pg C yr^{-1} (Pan *et al.*, 2011). Moreover, forests are important reservoirs of biodiversity and provide valuable ecosystem services (Barlow *et al.*, 2007; Anderson-Teixeira & DeLucia, 2011; Chazdon, 2014).

Given the importance of secondary forests, it is critical to understand how global change pressures affect forest regeneration, and accurately representing these processes in models is important for reducing the uncertainty of future climate projections. The terrestrial C cycle—in which secondary forests play a key role—currently accounts for the single largest source of uncertainty in earth system models, leading to projections that differ in atmospheric CO$_2$ concentrations by 350 ppm by 2100 (Friedlingstein *et al.*, 2006, 2014). Global change is likely to affect forest regeneration in complex ways, because forest regrowth following

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disturbance involves wholesale reorganization of ecosystem and community properties, and forest responses to global change pressures vary with stand age (Anderson-Teixeira *et al.*, 2013).

One of the most important global change pressures is the increasing concentration of atmospheric CO_2, which affects forests directly through its effect on leaf-level gas exchange, and indirectly through its effect on climate. Anthropogenic activities have driven an increase in atmospheric CO_2 of nearly 100 ppm since 1950, and the concentration is currently increasing at 2 ppm yr^{-1} (Tans & Keeling, 2014). The impact of elevated CO_2 (eCO_2) on forests is, most immediately, increased productivity driven by CO_2 fertilization (DeLucia *et al.*, 1999; Ainsworth & Long, 2005). Through Free Air CO_2 Enrichment (FACE) experiments, it is well established that exposure to eCO_2 initially increases the net primary productivity (NPP) and above ground biomass (AGB) of young temperate forests (DeLucia *et al.*, 1999; Norby *et al.*, 2010). However, it remains unknown whether this stimulus is sustained over time as forests age and whether eCO_2 increases the productivity and biomass of mature forests (Körner *et al.*, 2005; Norby *et al.*, 2010; Anderson-Teixeira *et al.*, 2013). In large part, the persistence of augmented biomass under elevated CO_2 depends upon nitrogen (N) limitation to NPP (Hungate *et al.*, 2003; Norby *et al.*, 2010) and will depend not only on the degree to which eCO_2 enhances NPP but also its effect on C residence time (Dybzinski *et al.*, 2015).

Furthermore, it is well established that responses to eCO_2 are heterogeneous within a forest community. Species- or plant functional type (PFT)-specific responses to eCO_2 have frequently been documented (Anderson-Teixeira *et al.*, 2013), and growth stimulus is also affected by light and nutrient availability (Bazzaz *et al.*, 1990; Bazzaz & Miao, 1993). While there have been some *in situ* observations of species-specific responses to eCO_2 (e.g. Mohan *et al.*, 2007), the time-scale of forest regeneration prohibits experimental tests of how these different reactions will interact with population dynamics in the long term, and how altered community composition will in turn affect ecosystem function. Thus, our understanding of the long-term responses of forests to eCO_2 remains limited.

Elevated CO_2 may impact the long-term dynamics of forest regrowth in a variety of ways (Anderson-Teixeira *et al.*, 2013). Here, we explore three broad hypotheses regarding these impacts. Our first hypothesis is that the rate at which the forest moves along a successional trajectory toward 'maturity' will be altered. This hypothesis does not make any claims about the states toward which the ecosystem eventually converges and is restricted to the rate of changes in forest composition and function. Specifically, increased NPP under eCO_2

may accelerate the rates of tree growth, biomass accumulation, C sequestration, and successional change such that the forest reaches a variety of benchmarks earlier, such as the age at which the largest trees reach a certain diameter at breast height (DBH) or the ecosystem reaches a threshold in above ground biomass (AGB). Accelerated rates of change may imply not only faster biomass accumulation in relatively young forests, but also earlier onset of significant N limitation (e.g., Norby *et al.*, 2010) or declines in NPP and NEP associated with forest aging (e.g., Baldocchi, 2008; Luyssaert *et al.*, 2008; Drake *et al.*, 2011; Goulden *et al.*, 2011). Our second hypothesis is that successional pathways will be altered; for instance, different PFTs may respond differently in terms of biomass, and these effects could result in lasting changes to forest composition at a mature state. Such changes to forest community composition would inevitably result in at least modest changes to forest function (e.g. Beck *et al.*, 2011) and may impact C accumulation via changes to NPP and NEP. Our third hypothesis is that there will be persistent changes to forest function and ecosystem–atmosphere interactions. For instance, CO_2 fertilization may result in long-term stimulation of gross primary productivity (GPP) and potentially persistent increases in NPP and NEP—a phenomenon predicted by some ecosystem models, although data and nutrient models suggest that NPP stimulus should abate (Rastetter *et al.*, 1997; Norby *et al.*, 2010).

To investigate how eCO_2 may impact the long-term dynamics of forest regrowth, we use the Ecosystem Demography model (ED), which tracks the size and age structure of forest stands, resource competition between distinct functional types, and allows for spatial and temporal heterogeneity in resources — features that are necessary for modeling forest succession. Using Duke Forest (NC, USA) as a model system, we first evaluate the ED model against the FACE experiment, a forest chronosequence, and eddy-covariance data. We then use the model to test the three main possibilities outlined above: that eCO_2 alters rates of C cycling and successional change, successional pathways and forest composition at maturity, and long-term ecosystem–atmosphere gas exchange. Our intent is to understand the long-term effects of eCO_2 in isolation; model runs are not intended to represent real-world scenarios, which would involve gradual increases in CO_2 and changes in climate.

Materials and methods

Site description

We modeled the long-term effects of CO_2 enrichment on productivity and succession at Duke Forest (Durham, NC, USA;

35 ° 97′ N 79 ° 09′ W), which is an ideal study system for this purpose given that it contains a Free Air CO$_2$ Enrichment (FACE) experiment, a nearby forest chronosequence of stand measurements, and an eddy-covariance tower. Climate is warm temperate, with mean annual temperature of 15.5 °C and mean annual precipitation of 1140 mm yr^{-1} distributed relatively evenly throughout the year. Duke Forest contains >50 tree species, with dominants including early-successional loblolly pine (*Pinus taeda* L.) and variety of broadleaf deciduous hardwoods such as sweetgum (*Liquidambar styraciflua* L.) and tulip poplar (*Liriodendron tulipifera* L.; early-successional), oaks (Quercus spp.; mid successional), and red maple (*Acer rubrum* L.; late successional) (Dietze & Clark, 2008).

The Duke Forest FACE experiment was situated in a loblolly pine plantation, planted in 1983. At the initiation of the FACE experiment in 1996, loblolly pines formed a dominant and highly uniform overstory, with a median height of 13 m, and 15 cm diameter breast height (DBH). Hardwoods were present in the understory, with key species including sweetgum and tulip poplar (Myers *et al.*, 1999). Six 30-m diameter paired rings were constructed, with three receiving ambient CO$_2$, and three receiving a target enrichment of +200 ppm (total 550–581 ppm) CO$_2$. Carbon cycling and other elements of ecosystem function were monitored intensively (McCarthy *et al.*, 2010). Data from the Duke-FACE experiment were used to define initial forest structure and composition and evaluate model results for young (13–21 years old) forests under ambient and elevated CO$_2$ (detailed in Model inputs and evaluation below).

In 2007, a chronosequence study was established in Duke Forest representing forests ranging in age from 10 to 115 years (Drake *et al.*, 2010). Soil type was similar across stands in the chronosequence and to that at the FACE sites, which are about 5 km away from the chronosequence. Additionally, sites were selected to have similar management history and initial stocking densities, and statistical tests have confirmed that most differences between sites are age related (Drake *et al.*, 2010). Typical forests within the Piedmont region are dominated by pines in early succession, then later hardwood PFT recruit to

the canopy and occupy about 33% of basal area after about 100 years of regeneration (Christensen & Peet, 1984). DBH, NPP, and GPP data from this chronosequence (Drake *et al.*, 2010) were used to evaluate model performance for forests up to age 103 years under ambient CO$_2$.

Finally, Duke Forest has an eddy-covariance tower in the same loblolly pine forest as the Duke-FACE experiment (US-Dk3) (e.g., Stoy *et al.*, 2006a,b, 2008). Data from this site were used for meteorological drivers for the model and to evaluate model estimates of GPP and NEP (Table 1).

Model description

We used the Ecosystem Demography model [version 2.1.r82] (Moorcroft *et al.*, 2001; Medvigy *et al.*, 2009) to project the long-term effects of CO$_2$ enrichment on productivity and succession at Duke Forest. ED explicitly models photosynthesis, plant carbon allocation, respiration, and turnover, CENTURY-based soil biogeochemistry (Parton *et al.*, 1992), and dynamic land surface biophysics and hydrology. A critical distinction of ED for our purposes is that it is one of the few models able to predict patterns of forest growth, while explicitly modeling tree physiology in heterogeneous environments, retaining size and age structure, and allowing for multiple PFTs with different successional status to compete (e.g., light requirements, water use, etc.). ED has been used successfully for short-term simulations of the Duke-FACE experiment (De Kauwe *et al.*, 2013; Walker *et al.*, 2014; Zaehle *et al.*, 2014; Medlyn *et al.*, 2015) and has been extensively compared to forest inventory and eddy-covariance data across eastern forests (Medvigy *et al.*, 2010; Dietze *et al.*, 2011; Medvigy & Moorcroft, 2012; Stoy *et al.*, 2013). ED contains about 50 PFT-specific parameters that govern plant morphology and physiology (see Medvigy *et al.*, 2009, for full details).

Model inputs and evaluation

Unless otherwise noted, model inputs and parameters were the same as those used in a previous model comparison

Table 1 Comparison of long-term model projections with and without N limitation with empirical observations of C stocks and fluxes at Duke Forest

Variable	Stand age	Modeled: with N limitation Mean (range)	Modeled: no N limitation Mean (range)	Observed	Observation source
GPP (Mg C ha^{-1} yr^{-1})	18–22 yrs	25.7 (23.3–28.1)	26.3 (23.7–29.1)	20.6 (18.5–22.4)	US-Dk3 2001–2005
	19 yrs	27.1	27.4	27.0	Baldocchi (2008)
	97 yrs	11.4	16.4	12.0	Stoy *et al.* (2006b) Chronosequence; Drake *et al.* (2010) Chronosequence; Drake *et al.* (2010)
NEP* (Mg C ha^{-1} yr^{-1})	18–22 yrs	+10.5 (8.4–12)	+10.8 (8.6–12.4)	+3.7 (−0.2 to +7.7)	US-Dk3 2001–2005 Baldocchi (2008)
	24–28 yrs	+4.8 (1.5–7.3)	+9.4 (7.5–11.1)	N/A	Stoy *et al.* (2006b)

*Sign convention for NEP: + indicates C sink.

project focused on FACE experiments (Walker *et al.*, 2014). Specifically, pine PFT parameters and all model configuration settings were taken from Walker *et al.* (2014), while Dietze *et al.* (2014) was the source of hardwood PFT parameters (Table S1). Initial forest structure and composition for the FACE experiment (i.e., 1996, prior to initiation of CO_2 fertilization) was defined based on the 1996 census of all trees >1 cm DBH (Norby *et al.*, 2005), and each tree was used to initialize a cohort in the simulation. Soil C and N were initialized with site level means, and no 'spin-up' was performed. No large-scale disturbance or harvest was simulated after simulation began, although simulated tree fall was allowed to occur. Results presented here are based on a configuration of ED that models the Duke-FACE ring 2 with separate resource environments (e.g., light, water, soil conditions) in 40 distinct patches, with each patch allowed up to 40 cohorts. Cohorts are usually considered to be groups of trees with very similar size and age structure, but in our case the 1600 patch × cohort combinations allow the model to create a cohort to represent each individual tree. The 1996 census of Duke ring 2 had 324 trees >1 cm DBH, and many more seedlings that were not counted. This configuration was selected as the most appropriate for this study because modeling a greater number of patches and cohorts allows for less binning of tree growth processes by cohort and patch. ED2 treats soil and light conditions as homogenous within patches, and patches have vertical structure in terms of heights of cohorts. Thus, allowing simulation of many distinct patches and cohorts allows the model predict factors such as soil moisture and understory light with greater resolution compared to low numbers of patches and cohorts. At low patch and cohort numbers, hardwood species were suppressed (Fig. S2).

Meteorological drivers for ED (including radiation, precipitation, atmospheric CO_2) were obtained from an AmeriFlux tower located within one of the ambient rings (US-Dk3, 1996–2005, Barr *et al.*, 2013) for the period over which the model was evaluated against FACE data (1996–2005). For long-term runs, yearly meteorological data were randomly drawn from this period. Our decision to draw randomly from this 10-year period represents a compromise between including enough years of data to avoid undue influence of anomalous years and avoiding the confounding influence of any directional change in climate. Sensitivity analysis indicated that results were not significantly affected by the sequence of meteorological data. For atmospheric CO_2, we used ambient CO_2 recorded during the FACE experiment for the control (averaging roughly 360 ppm) and a fixed value of 560 ppm (target enrichment for the FACE experiment) for the elevated CO_2 scenario.

There is an N limitation option in ED (Medvigy *et al.*, 2009), and this routine has been used to successfully model the Duke- FACE experiment (De Kauwe *et al.*, 2013; Walker *et al.*, 2014; Zaehle *et al.*, 2014). Our analysis focused primarily on runs with growth limited by N availability, but we also ran the model without N limitation.

Because long-term simulations using the pine density of the Duke-FACE plantation were inconsistent with observations in that hardwoods remained suppressed (see 'Model Performance', Results section), we 'thinned' the pine canopy by 50%

relative to the Duke-FACE plantation before starting the simulation, at stand age 13 years. This thinning allowed for better recruitment of hardwood PFT to the canopy, and better alignment with chronosequence data (Christensen & Peet, 1984; Drake *et al.*, 2010). Our model thinning is consistent with historical records of thinning at Duke Forest (provided by the Office of the Duke Forest), which indicate a mean age at first thinning of 16.3 years for Loblolly stands in the region of the Drake *et al.* (2010) chronosequence.

Sensitivity analysis

As with any ecosystem model, ED2 is subject to inherent uncertainty associated with model parameterization and representation of mechanisms. We examined how changes to model configuration or parameters affected model output. Specifically, we tested the effects of (i) N limitation, (ii) initial pine density (at original and thinned densities), (iii) smaller numbers of patches/cohorts, and (iv) disabling tree fall disturbance (Table S2). Moreover, to quantify the effects of successional changes to PFT composition on C cycling, we initialized a pine-only run with all hardwood PFTs replaced by Loblolly pine. These model runs show how the model predictions depend on configurations and initial conditions, and also give insight into ecological effects of different treatments and initial conditions (Figs S1–S5). While we present some results that do not include the effects of N limitation, all results presented below refer to N-limited runs unless otherwise stated.

Results

Model performance

The model predictions for above ground biomass were consistent with observations over the entire period of the FACE experiment for both ambient and elevated CO_2 (Fig. 1a), and the modeled average NPP stimulation of 26% due to eCO_2 was in close agreement with the empirical estimate of 27–28%, (Hamilton *et al.*, 2002; McCarthy *et al.*, 2010). However, long-term simulations with the pine density of the Duke-FACE experiment predicted suppression of hardwood species (Fig. S1) that was inconsistent with observations from the region (Christensen & Peet, 1984; Drake *et al.*, 2010).

Long-term runs with lower pine density were fairly consistent with chronosequence data and other observations from Duke Forest and the region (Fig. 1; Table 1). Modeled NPP was consistent with chronosequence data, although the model slightly under predicted NPP for stands over 100 years of age (Fig. 1b; Drake *et al.*, 2010; He *et al.*, 2012). For relatively young loblolly pine plantations, modeled GPP was in broad agreement with eddy-covariance estimates. Modeled NEP was notably higher than measured at US-Dk3 up
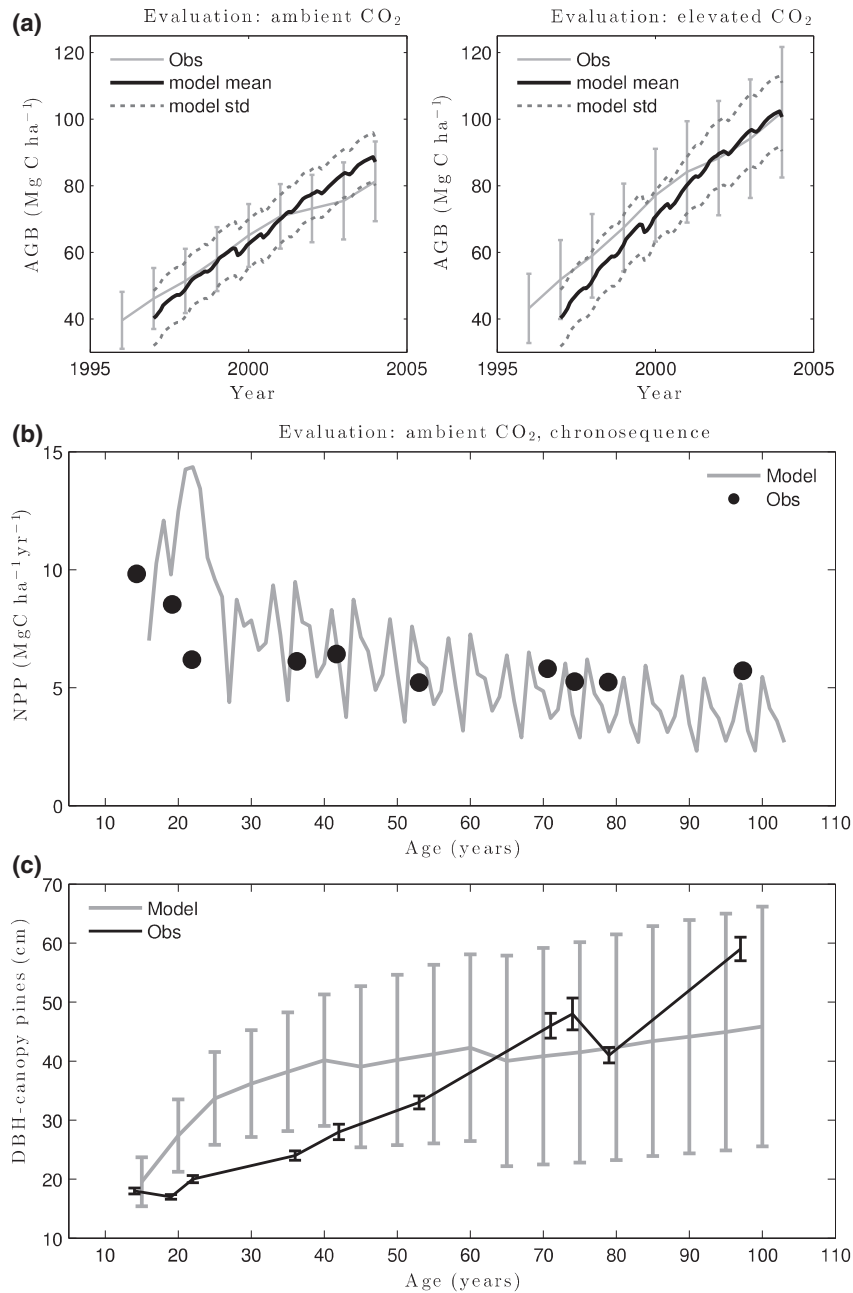
Fig. 1. Evaluation of model runs against Duke Forest data. (a) Comparison of modeled biomass under ambient and elevated CO$_2$ with biomass measurements from the Duke-FACE experiment (McCarthy *et al.*, 2010). Model and empirical standard deviation is computed for variation among Duke-FACE rings 1–6. (b) Comparison of modeled total NPP over 100 years of forest succession with observations from the Drake chronosequence (Drake *et al.*, 2010). (c) Comparison of modeled DBH of canopy pines under ambient conditions over 120 years of forest succession with observations from the Drake chronosequence. Bars show standard deviation of modeled canopy pine cohorts DBH (*n* = 6). All plots show data for whole simulated years, and partial data for 1996 are not plotted. Age is age of oldest cohort.

to age stand age 22 (7.7 Mg C ha^{-1} estimated from tower, 12.4 Mg C ha^{-1} modeled at age 22), but quickly declined to a value similar to the empirical estimates (8.2 Mg C ha^{-1} modeled at age 25; Table 1). Although modeled DBH of canopy pines was highly variable between cohorts, DBH of the model's largest cohorts was within the variation in observed DBH of canopy pines for most of the simulation period (Fig. 1c). Finally, the model predicted a decline in stand-level transpiration, qualitatively consistent with empirical

findings that stomatal conductance and concentration of CO_2 within needle air spaces of Loblolly pines declines with stand age (Drake *et al.*, 2010).

Model runs without N limitation were less consistent with empirical observations than those with N limitation, particularly for older stands. For older stands, our model runs with and without N limitation bracketed observations, whereas model runs with N limitation slightly underestimated GPP and NPP in older stands (Table 1, Fig. 1b), runs without N limitation greatly overestimated these variables (Table 1). Specifically, runs without N limitation dramatically over-predicted GPP, NEP, and NPP of older stands and missed the expected decline in NPP with increasing forest age (Table 1, Figs 1b and 2b; Drake *et al.*, 2010; He *et al.*, 2012). In terms of AGB, N unlimited runs predicted biomass of 186 Mg C ha^{-1} for 100-year-old stands (Fig. 2a), which exceeded AGB values for the region (Kellndorfer *et al.*, 2012). Furthermore, modeled maintenance of high transpiration (Fig. 2) was inconsistent with observations of decreases in transpiration (via stomatal conductance and CO_2 concentrations within needle air space) with stand age in the Duke chronosequence (Drake *et al.*, 2010). Thus, although the model with N limitation has a slight tendency to underestimate productivity for old stands, model predictions with N limitation were more consistent with observations than those without.

Rates of C cycling and successional change

Rates of C accumulation and successional change were accelerated under elevated CO_2. Although absolute rates of C accumulation and successional change differed between N-limited and unlimited model runs (Fig. 2), acceleration of succession was observed under both model configurations (Table 2, Fig. S3).

In young stands, rates of C sequestration and biomass accumulation increased under eCO$_2$. Specifically, in N-limited runs, ecosystem-level biomass accumulation rate from ages 13 to 21 increased from 5.17 to 6.77 Mg C ha^{-1} yr^{-1} (31%) under eCO$_2$ (Fig. 2a). Similarly, GPP (+32%), NPP (+33%), and NEP (+36%) increased under eCO$_2$ (Fig. 2). As a result of an accelerated C cycling, forest development under elevated CO_2 reached certain benchmarks earlier (Table 2, Fig. 2). For instance, under eCO$_2$, total biomass C surpassed 70 Mg C ha^{-1} 8 years earlier. GPP and NPP increased more rapidly under eCO$_2$, reaching near-maximum values 3 years earlier than under ambient CO_2.

As the stands aged, however, declines in C cycling (mostly associated with N limitation) also occurred earlier under eCO$_2$. NEP peaked 4 years earlier under eCO$_2$ and subsequently declined, falling below 4 Mg C
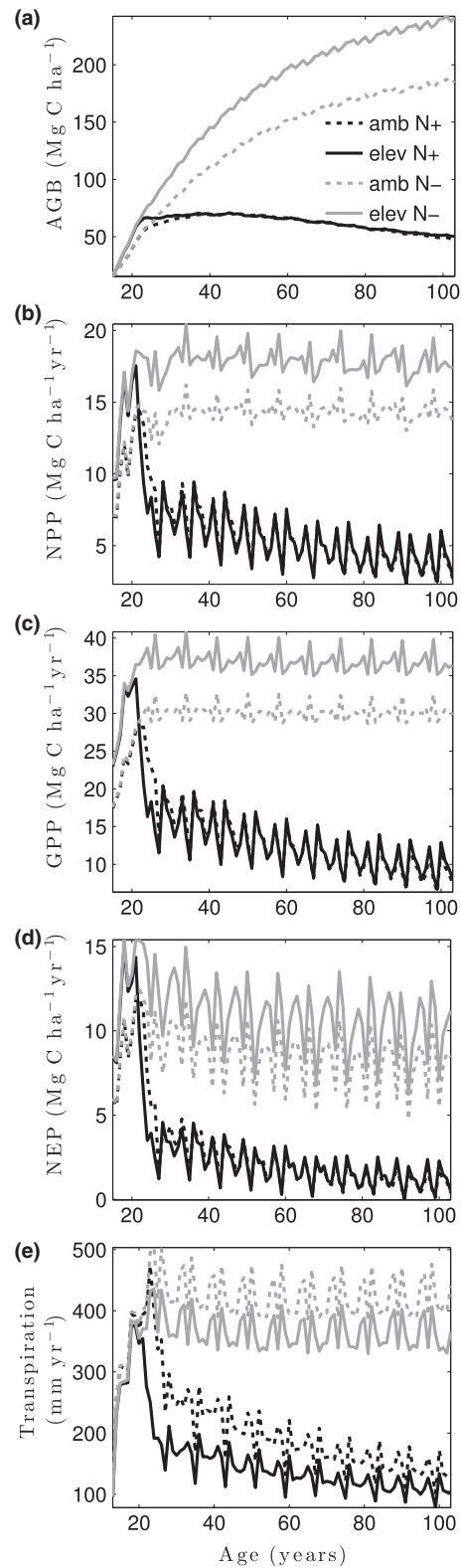

Fig. 2. Model projections of changes in C cycling and transpiration under ambient and elevated CO_2: (a) AGB, (b) total NPP, (c) GPP, (d) NEP, (e) transpiration. Shown are runs with and without N limitation (N+, N−, respectively).

Table 2 Age at which a variety of successional benchmarks are reached under ambient and eCO₂ for runs with and without N limitation

| Successional benchmark | Age at which benchmark is reached (yrs) | | | | | |
| | With N limitation | | | No N limitation | | |
	Ambient CO₂	Elevated CO₂	Change	Ambient CO₂	Elevated CO₂	Change
C cycle						
Total biomass C exceeds 50 Mg C ha⁻¹	23	21	−2	23	21	−2
Total biomass C exceeds 70 Mg C ha⁻¹	45	37	−8	28	24	−4
Total biomass C exceeds 100 Mg C ha⁻¹	NA	NA	NA	37	31	−6
Total ecosystem C exceeds 200 Mg C ha⁻¹	27	24	−3	26	23	−3
LAI peaks	24	21	−3	27	24	−3
GPP exceeds 20 Mg C ha⁻¹yr⁻¹	17	14	−3	17	14	−3
NPP exceeds 10 Mg C ha⁻¹yr⁻¹	17	14	−3	17	14	−3
NEP exceeds 8 Mg C ha⁻¹yr⁻¹r	18	14	−4	14	14	0
NEP peaks	22	18	−4	22	18	−4
NEP falls below 4 Mg C ha⁻¹yr⁻¹	27	24	−3	NA	NA	NA
Community composition						
DBH of largest pines exceeds 50 cm	31	28	−3	28	24	−4
DBH of largest hardwoods exceeds 19 cm	34	20	−14	30	20	−10
Pine biomass C exceeds 50 Mg C ha⁻¹	29	23	−6	26	22	−4
Hardwood biomass C exceeds 15 Mg C ha⁻¹	21	20	−1	21	20	−1
Mid hardwood biomass surpasses early hardwood biomass	98	71	−26	NA	NA	NA

ha⁻¹ yr⁻¹ 3 years earlier under eCO₂. Without N limitation, NEP did not decline as steeply with forest age, and 5-year average NEP fell below a threshold of 11 Mg C ha⁻¹ yr⁻¹ 18 years earlier under eCO₂ (Fig. 2d).

Successional change also occurred more rapidly under eCO₂. Within each PFT, the largest individuals passed certain size thresholds earlier under elevated CO₂ ; for example, the largest pine cohort reached 50 cm DBH 3 years sooner under eCO₂. As a result, individual PFTs hit various biomass thresholds at earlier ages (Table 2). In addition, compositional thresholds were passed earlier. Notably, mid-successional hardwood biomass surpassed early-successional hardwood biomass 26 years earlier under elevated CO₂.

Community composition

Responses to elevated CO₂ varied by PFT, resulting in changes in successional pathways and final community composition. This held true in both with and without N limitation (Figs 3 and S3). In addition to accelerating the rate of community change, eCO₂ also altered the relative dominance of PFTs. Early in succession (stand age <30 years), pines exhibited the greatest biomass growth stimulus to elevated CO₂, both in absolute and relative terms (Fig. 3). However, this stimulus declined starting at age 20. By age 40, late-successional hard-woods exhibited the greatest percentage stimulation, although by age 60 mid hardwood PFT exhibited the greatest percentage AGB stimulation. Mid-successional PFTs had the greatest absolute biomass difference among hardwood PFTs under eCO₂ for all stands over 30 years of age. Although the growth stimulus of hardwood PFTs remained modest (never exceeding 1.3 Mg C ha⁻¹), it persisted past age 100, at which point biomass of mid- and late-successional hardwoods was 58% and 41% greater, respectively, under eCO₂. The early hardwood PFT exhibited modest growth stimulus early in succession, but also declined faster, resulting in 8% less early hardwood biomass by age 100. Thus, dominance in terms of biomass was altered, with a greater percentage of AGB residing in mid- and late-hardwood species under CO₂ enrichment (Fig. 3). Stimulus to tree height (Fig. 3) and basal area (Fig. S5) showed similar trends. Hardwoods played a substantive role in ecosystem-level C cycling, and their importance was slightly higher under eCO₂ . Under ambient CO₂, disallowing PFT succession (by replacing all hardwood PFT with pine) reduced total ecosystem C by 45.6 Mg C ha⁻¹ over the 91-year simulation period, a reduction of 18% compared to the successional model. Under eCO₂ , lack of succession reduced ecosystem C by 55.4 Mg C ha⁻¹ (21%). Thus, the changes in community composition due to eCO₂ also resulted in changes to ecosystem function.
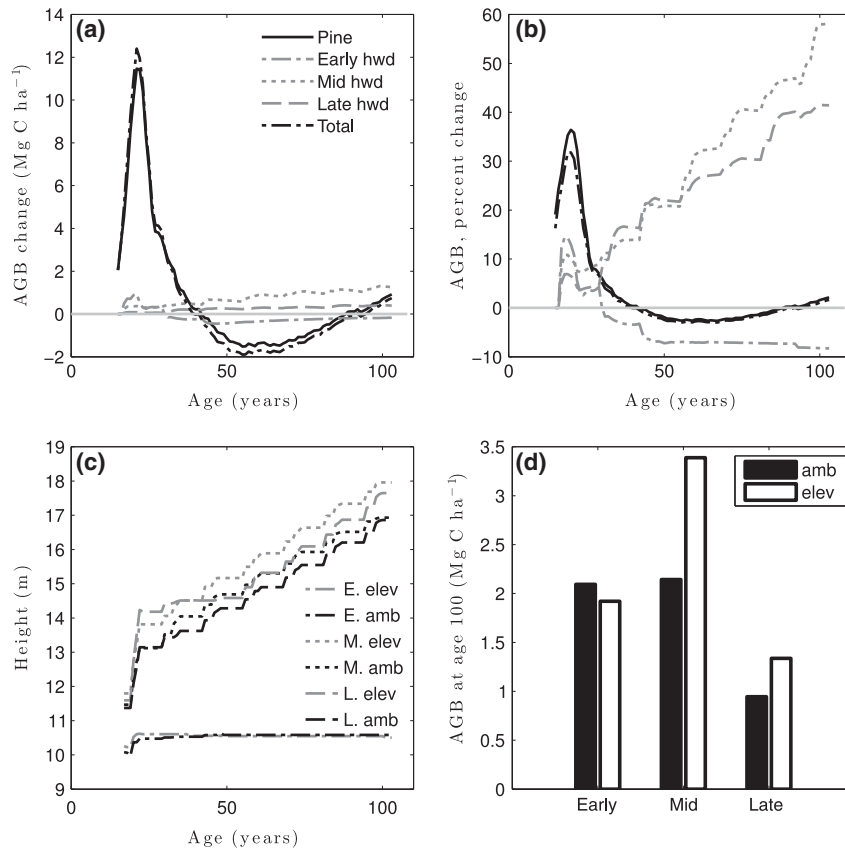
Fig. 3. Model predictions of change in aboveground biomass and height under eCO$_2$ by PFT: (a) absolute differences: change = elevated AGB - ambient AGB for each year and PFT; (b) percent change by PFT, change = [(elevated AGB-ambient AGB) /ambient AGB]; (c) height of tallest hardwood cohort by PFT; (d) hardwood AGB after 100 years of regrowth.

Trajectories of community composition were sensitive to model configuration. Model projections without N limitation differed in that augmentation of pine biomass persisted at >30% through the end of the simulation, while mid and late hardwoods exhibited less growth stimulus (Fig. S3). What remained robust to presence of N limitation was the general finding that successional trajectories and final community composition were altered by eCO$_2$.

Ecosystem–atmosphere gas exchange

Ecosystem–atmosphere exchange of CO$_2$ (GPP, NEP) and H$_2$O (transpiration, ET) was at least moderately altered long term under elevated CO$_2$ (Figs 2 and 4). However, the extent to which effects on the C cycle persisted beyond early succession depended on N limitation. Elevated CO$_2$ increased C sequestration early in succession both with and without N limitation (Fig. 2), but this effect only persisted in the absence of N limitation. As described above, both GPP and NEP were stimulated during the first 20 years of succession, with peak stimulation occurring at age 19 in both models.

The degree of stimulation was initially similar with and without N limitation; for instance, GPP at age 17 was increased by 34% under elevated CO$_2$ under both treatments (Fig. 2c). However, with N limitation, differences between elevated and ambient CO$_2$ treatments quickly diminished as the forest aged such that by age 30, there was little difference between ambient and elevated CO$_2$ (Figs 2 and 4). In contrast, without N limitation, both GPP and NEP continued to be augmented by elevated CO$_2$ through the end of the runs (Fig. 2). Average stimulation from ages 90 to 100 was 22% (range: 20–24%) for GPP and 28% (range: 23–36%) for NEP, with little change as the forests aged. These model differences in C flux projections led to substantive differences in predictions of eCO$_2$'s effect on biomass and total ecosystem C by age 100: 2.4 Mg C ha^{-1} with N limitation and 54 Mg C ha^{-1} without.

In contrast to the C cycle, whose stimulation rapidly declined under N limitation, changes to transpiration and ET were sustained under both N limitation treatments (Figs 2 and 4). With N limitation, transpiration was reduced by 19% in young stands (<25 yrs), and the difference between ambient and elevated stands
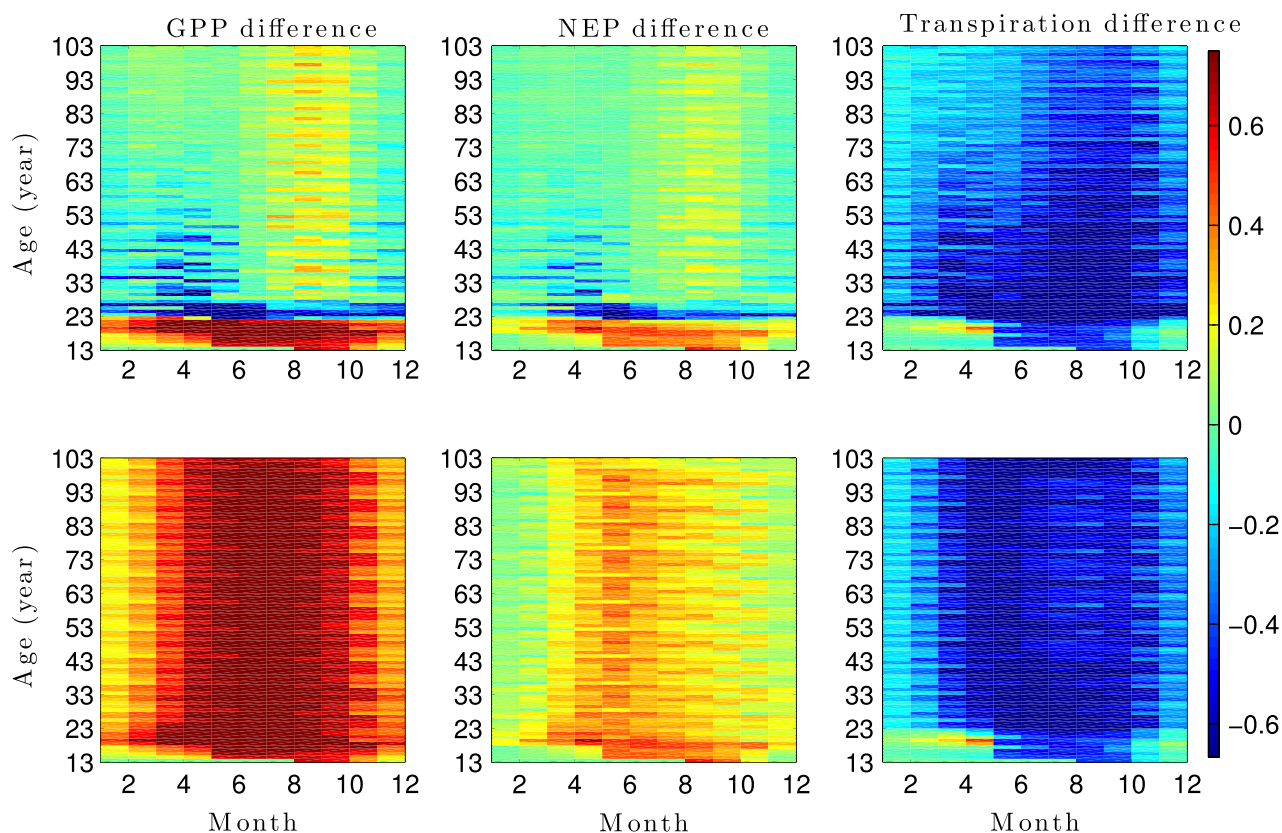
Fig. 4. Changes in ecosystem–atmosphere gas exchange by season and year due to eCO$_2$ (variable under eCO$_2$ - variable with ambient CO$_2$), in model runs with and without N limitation. Top row includes N limitation, bottom row is without N limitation. Units are Mg C ha^{-1} mo^{-1} for GPP and NEP, and cm mo^{-1} for transpiration.

increased slightly as the forest aged, such that exposure to elevated CO$_2$ reduced transpiration of 90- to 100-year-old stands by 23%. When N limitation was removed, transpiration was reduced by 9% in young (<25 yrs) stands, and the difference between ambient and elevated stands increased as the forest aged, such that exposure to elevated CO$_2$ reduced transpiration of 90- to 100-year-old stands by 15%. Both N limitation treatments converge to a reduction in transpiration by 20 ($\pm$2)% due to eCO$_2$ by age 100.

The responses of ecosystem–atmosphere exchange of CO$_2$ and H$_2$O to eCO$_2$ varied seasonally (Fig. 4). Under N limitation, peak stimulation of GPP and NEP and maximum reduction of transpiration generally occurred in the late summer and early fall. In contrast, without N limitation, peak differences in ecosystem–atmosphere exchange occurred during early to mid summer (Fig. 4).

Discussion

The ED2 model, as configured and parameterized here, reproduced observations of young forest responses to

eCO$_2$, long-term trends in forest productivity, and ecosystem–atmosphere gas exchange (Fig. 1; Table 1), justifying its use for characterizing long-term impacts of eCO$_2$ on the dynamics of secondary forests. Over the 91 years of our model simulation (forest ages 13–103), elevated CO$_2$ altered the rate of forest change, successional pathway, and long-term functioning of forests. Rates of C accumulation and successional change increased under eCO$_2$ such that forest reached developmental benchmarks faster under eCO$_2$ (Table 2, Figs 2 and 3). Successional pathways were altered under eCO$_2$, as PFTs responded differentially (Fig. 3). Ecosystem–atmosphere exchange of CO$_2$ (GPP, NEP) and H$_2$O (transpiration, ET) were altered under eCO$_2$, although after the age of 22, the magnitude and persistence of these alterations depended on N limitation (Figs 2 and 4). Over the simulation period, total ecosystem C storage was increased by 9.7 Mg C ha^{-1} due to eCO$_2$.

Rates of C cycling and successional change

Our model simulations demonstrate that changes to forest function are generally accelerated under elevated

CO_2, supporting our first hypothesis. Consistent with a large body of evidence that C sequestration by young forests is enhanced under eCO_2 (e.g., DeLucia *et al.*, 1999; Norby *et al.*, 2005; Anderson-Teixeira *et al.*, 2013) our model projected that eCO_2 stimulated forest productivity in young stands (Fig. 2).

A question that is fundamental to understanding long-term forest responses to eCO_2 is whether productivity increases in young stands reflect fundamental ecophysiological or biogeochemical changes that lead to higher biomass in mature stands or whether increased productivity simply causes the forest to move faster along a developmental trajectory, hitting light or nutrient limitations earlier (Anderson-Teixeira *et al.*, 2013; Dybzinski *et al.*, 2015). Our model simulations provide evidence that the latter dynamic is important; regardless of whether or not N limitation is implemented, eCO_2 increased the rate of forest development such that a variety of benchmarks were reached earlier (Table 2). Not only did eCO_2 decrease the time required for the forest to reach certain benchmarks associated with the aggrading phase of ecosystem development (*sensu* Bormann *et al.*, 1979), it also decreased the time to benchmarks associated with commonly observed declines in C sequestration associated with forest aging (e.g., reduced NPP, NEP; Table 2). N limitation caused a sharp decline in forest productivity earlier under eCO_2 (age 21 for eCO_2, age 22 for ambient CO_2; Table 2), such that NPP was higher under ambient CO_2 for 39 years during stand ages 22–67 years (Figs 2 and 4). While the question as to whether mature forest C stocks and ecosystem–atmosphere exchange will exhibit persistent changes under eCO_2 is strongly dependent upon N limitation (discussed below), our model suggests that forests may hit negative feedbacks to C accumulation associated with forest aging (e.g., N limitation) faster under eCO_2.

Our model also predicts a general acceleration of successional change. Under eCO_2, trees grow faster, individual PFTs surpass certain biomass thresholds earlier, and mid- and late-hardwood PFTs surpass early hardwoods sooner in terms of biomass (Table 2). Thus, both in terms of composition and function, our model predicts accelerated change under eCO_2, supporting our first hypothesis that eCO_2 can cause forests to reach compositional and functional benchmarks earlier than under ambient conditions.

Community composition

Our model simulations predict substantial alteration of successional pathways under elevated CO_2 (Table 2) and also alter mature forest composition (Fig. 3). This prediction is consistent with previous empirical results showing that PFTs respond differentially to CO_2 enrichment in growth chambers (Bazzaz *et al.*, 1990; Bazzaz & Miao, 1993), FACE experiments (Mohan *et al.*, 2007; Anderson-Teixeira *et al.*, 2013), and in a trait-based model study tested against another FACE experiment (Ali *et al.*, 2013). Our results (Fig. 3, Table 2) show how the short-term effects of differential growth play out on longer time scales, altering the pathway of successional community change and having a lasting impact on community composition, and supporting our second hypothesis.

Our simulations predicted greatest relative increases for mid- and late-successional hardwood PFTs. While these increases are consistent with growth chamber (Bazzaz *et al.*, 1990) and field experiments on seedlings (Mohan *et al.*, 2007), our long-term projections show how these short-term effects interact with community processes to change C cycling on the century time scale. Our results for pine-only simulations indicate that PFT diversity accounts for more change in total ecosystem C storage than eCO_2 treatment and that the effects of eCO_2 are slightly greater when PFT diversity is included. As Duke-FACE rings were planted Loblolly stands, hardwoods have limited ability to alter stand-level dynamics, but we hypothesize based on our results here that changes in PFT composition would allow for stronger interactive effects of altered succession and eCO_2 in higher diversity forests. Beyond Duke Forest, many forest types have the potential to experience changes in successional trajectory and C cycling due to elevated CO_2, because growth stimulus seems to be related both PFT regeneration niches (*sensu* Grubb, 1977) and individuals' resource environments. In this manner, we expect differential responses to CO_2 enrichment to interact with population processes to cause long-lasting change in community composition and function, compared to forests regenerating under historical CO_2 levels.

Because forest tree species composition affects everything from biodiversity of other taxa to ecosystem functioning and ecosystem–climate interactions, changes in community composition can, in turn, have widespread implications. By altering competitive interactions among tree PFTs, eCO_2 is likely to have cascading effects on other plant and animal species. A recent meta-analysis concluded that indirect and biotic mechanisms (e.g., altered species performance and interactions) had generally greater effects on populations than direct, abiotic mechanisms such as temperature (Ockendon *et al.*, 2014). Furthermore, differences in community composition can affect ecosystem–climate interactions. Species composition can affect not only C sequestration (Tilman *et al.*, 2012), but also transpiration and albedo (Beck *et al.*, 2011; Zhao & Jackson,

2014). In North America, broadleaf and evergreen forests have very different effects on land surface energy balance (Zhao & Jackson, 2014), so an accelerated transition to broadleaf-dominated forest could influence land surface temperatures due to increased albedo of broadleaf forests relative to coniferous. This acceleration to a higher albedo forest could conceivably result in a negative feedback to warming.

Ecosystem–atmosphere gas exchange

Ecosystem–atmosphere exchange of CO$_2$ (GPP, NEP) and H$_2$O (transpiration) was altered under eCO$_2$, but the magnitude and persistence of these alterations depended on N limitation (Figs 2 and 4). Stimulation of CO$_2$ sequestration under eCO$_2$ persisted without—but not with—N limitation (Fig. 2). This result aligns with previous model results that long-term stimulation of C sequestration under eCO$_2$ is strongly influenced by N limitation (Walker *et al*, 2014). Characterizing the dynamics of N limitation as forests age remains an important area of uncertainty in ecosystem models (Zaehle *et al.*, 2014). Our N-limited model version appears to be better suited for modeling this system in that it successfully reproduces known age-related declines in NPP and NEP (Figs 1 and 2; Baldocchi, 2008; Luyssaert *et al.*, 2008; Drake *et al.*, 2011; He *et al.*, 2012), more closely matches observed NPP, GPP, and NEP of mature forests in the region (Fig. 1, Table 1), and represents biogeochemical processes known to affect forest C dynamics (e.g., Luo *et al.*, 2004). This model version predicts that stimulation of GPP, NPP, and NEP under eCO$_2$ is transient (Figs 2–4), suggesting that the observed eCO$_2$ response of young forests may not hold true for mature forests (Körner *et al.*, 2005)—presumably because the young forests are not strongly N limited (Würth *et al.*, 2005; Asshoff *et al.*, 2006).

Regardless of N limitation, eCO$_2$ resulted in a persistent decrease in transpiration (Figs 2 and 4). This decrease can be explained as the result of reduced stomatal conductance and reduced CO$_2$ concentrations in stomata (Drake *et al.*, 2010). Implications of reduced transpiration are reduced latent cooling and consequent warming of the land surface, reduced evapotranspiration and consequent reductions in cloud formation, and increased soil water storage and/or runoff (Gedney *et al.*, 2006; Meir *et al.*, 2006). Thus, regardless of whether N limitation prevents long-term stimulation of CO$_2$ sequestration as forests age, impacts on transpiration may result in persistent alteration of ecosystem–atmosphere exchange under eCO$_2$, due to changes in community composition and increase in relative abundance of broadleaf PFTs. Thus, we conclude partial

support for our hypothesis of sustained changes to function—while stimulus to transpiration is persistent in all model configurations, stimulus to NEP, NPP, and GPP decays under N limitation, and by the end of the simulation period ambient and elevated CO$_2$ treatments resulted in similar values for these variables.

Our model results provide insights into the effect of eCO$_2$ on forest regrowth dynamics; however, important uncertainties remain. First, while the qualitative trends observed here are robust under a variety of model scenarios (Figs 2, 3 and S3–S4; Table 2), model projections should not be regarded as quantitatively precise. Our model projections are not in perfect agreement with empirical observations (Fig. 1, Table 1)—and never can be, given that no model captures all the mechanisms and processes in a real forest system. Improvement of model representation of the mechanisms that influence successional dynamics—for example, N limitation and tree mortality—will be of value for improving the model's ability to more closely reproduce empirical observations and provide more quantitatively reliable projections of forest dynamics under future conditions. Second, the present study focuses on the effects of eCO$_2$ in isolation and does not incorporate the effects of changes in climate, nor does it represent the increasing trend in CO$_2$. Real-world projections that examine forest regeneration under future climate scenarios will be of great value to understand how climate change may interact with eCO$_2$ to shape forest regeneration dynamics in the future. The present study advances understanding of how forest regeneration is likely to respond to one element of global change; future efforts will be valuable for advancing our understanding of the broader impacts of global change on forest regeneration.

As atmospheric CO$_2$ increases, climate change progresses, and other global change drivers intensify, an increasing number of forests will be regenerating under conditions that differ substantially from those under which existing forests developed. This will be exacerbated if global change leads to an increased frequency of stand-clearing disturbances (e.g., fires; Westerling *et al.*, 2006). Young secondary forests are relatively high-turnover communities and may be more strongly affected by global change pressures than mature forests (Anderson, 2007; Anderson-Teixeira *et al.*, 2013; Kröel-Dulay *et al.*, 2015). Our findings suggest that successional processes play a key part in determining ecosystem productivity under future climates. Indeed, in this system, effects of succession had a larger effect on total ecosystem C storage than the effect caused by eCO$_2$. While the interactions between diversity, disturbance, and productivity are well studied (e.g., Kondoh, 2001; Miller *et al.*, 2011; Tilman *et al.*, 2012; Kröel-Dulay

et al., 2015), the potential for impacts of climate change to be mediated by successional processes will be an important area for future research. Understanding how elevated CO_2, climate change, and other global change pressures interact with changing disturbance regimes to affect the structure and function of secondary forests will be a fruitful area for future research—particularly in situations where one or more PFT responds dramatically to global change drivers.

Acknowledgements

References

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2. *New Phytologist*, **165**, 351–372.

Ali AA, Medlyn BE, Crous KY, Reich PB (2013) A trait-based ecosystem model suggests that long-term responsiveness to rising atmospheric co2 concentration is greater in slow-growing than fast-growing plants. *Functional Ecology*, **27**, 1011–1022.

Anderson KJ (2007) Temporal patterns in rates of community change during succession. *The American Naturalist*, **169**, 780–793.

Anderson-Teixeira KJ, DeLucia E (2011) The greenhouse gas value of ecosystems. *Global Change Biology*, **17**, 425–438.

Anderson-Teixeira KJ, Miller AD, Mohan JE, Hudiburg TW, Duval BD, DeLucia EH (2013) Altered dynamics of forest recovery under a changing climate. *Global Change Biology*, **19**, 2001–2021.

Asshoff R, Zotz G, Koerner C (2006) Growth and phenology of mature temperate forest trees in elevated CO2. *Global Change Biology*, **12**, 848–861.

Baldocchi D (2008) Turner review no. 15. 'breathing' of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Australian Journal of Botany*, **56**, 1–26.

Barlow J, Gardner TA, Araujo IS et al. (2007) Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 18555–18560.

Barr A, Ricciuto D, Schaefer K et al. (2013) Nacp Site: Tower Meteorology, Flux Observations with Uncertainty, and Ancillary Data. Data set. Available on-line [http://daac.ornl.gov] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN, USA. http://dx.doi.org/10.3334/ORNLDAAC/1178.

Bazzaz F, Miao S (1993) Successional status, seed size, and responses of tree seedlings to CO2, light, and nutrients. *Ecology*, **74**, 104–112.

Bazzaz F, Coleman J, Morse S (1990) Growth responses of seven major co-occurring tree species of the northeastern united states to elevated CO2. *Canadian Journal of Forest Research*, **20**, 1479–1484.

Beck PS, Goetz SJ, Mack MC, Alexander HD, Jin Y, Randerson JT, Loranty M (2011) The impacts and implications of an intensifying fire regime on alaskan boreal forest composition and albedo. *Global Change Biology*, **17**, 2853–2866.

Bormann FH, Likens GE et al. (1979) *Pattern and Process in a Forested Ecosystem*. Springer-Verlag, New York.

Chazdon RL (2014) *Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation*. University of Chicago Press, Chicago, IL.

Christensen NL, Peet RK (1984) Convergence during secondary forest succession. *The Journal of Ecology*, **72**, 25–36.

De Kauwe MG, Medlyn BE, Zaehle S et al. (2013) Forest water use and water use efficiency at elevated CO2: a model-data intercomparison at two contrasting temperate forest face sites. *Global Change Biology*, **19**, 1759–1779.

DeLucia EH, Hamilton JG, Naidu SL et al. (1999) Net primary production of a forest ecosystem with experimental CO2 enrichment. *Science*, **284**, 1177–1179.

Dietze MC, Clark JS (2008) Changing the gap dynamics paradigm: vegetative regeneration control on forest response to disturbance. *Ecological Monographs*, **78**, 331–347.

Dietze MC, Vargas R, Richardson AD et al. (2011) Characterizing the performance of ecosystem models across time scales: a spectral analysis of the north american carbon program site-level synthesis. *Journal of Geophysical Research: Biogeosciences*, **116**, G04029.

Dietze MC, Serbin SP, Davidson C et al. (2014) A quantitative assessment of a terrestrial biosphere model's data needs across north american biomes. *Journal of Geophysical Research: Biogeosciences*, **119**, 286–300.

Drake J, Raetz L, Davis S, DeLucia E (2010) Hydraulic limitation not declining nitrogen availability causes the age-related photosynthetic decline in loblolly pine (*Pinus taeda* l.). *Plant, Cell & Environment*, **33**, 1756–1766.

Drake J, Davis S, Raetz L, DeLucia E (2011) Mechanisms of age-related changes in forest production: the influence of physiological and successional changes. *Global Change Biology*, **17**, 1522–1535.

Dybzinski R, Farrior CE, Pacala SW (2015) Increased forest carbon storage with increased atmospheric CO2 despite nitrogen limitation: a game-theoretic allocation model for trees in competition for nitrogen and light. *Global Change Biology*, **21**, 1182–1196.

Food and Agriculture Organization of the United Nations (2010) *Global Forest Resources Assessment 2010: Main Report*. Food and Agriculture Organization of the United Nations, Rome, Italy. ISBN 978-92-106654-6.

Friedlingstein P, Cox P, Betts R et al. (2006) Climate-carbon cycle feedback analysis: Results from the c4mip model intercomparison. *Journal of Climate*, **19**, 3337–3353.

Friedlingstein P, Meinshausen M, Arora VK, Jones CD, Anav A, Liddicoat SK, Knutti R (2014) Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *Journal of Climate*, **27**, 511–526.

Gedney N, Cox P, Betts R, Boucher O, Huntingford C, Stott P (2006) Detection of a direct carbon dioxide effect in continental river runoff records. *Nature*, **439**, 835–838.

Goulden ML, McMillan A, Winston GC, Rocha AV, Manies KL, Harden JW, Bond-Lamberty B (2011) Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biology*, **17**, 855–871.

Grubb P (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biology Review*, **52**, 107–145.

Hamilton JG, DeLucia EH, George K, Naidu SL, Finzi AC, Schlesinger WH (2002) Forest carbon balance under elevated CO2. *Oecologia*, **131**, 250–260.

He L, Chen JM, Pan Y, Birdsey R, Kattge J (2012) Relationships between net primary productivity and forest stand age in us forests. *Global Biogeochemical Cycles*, **26**, GB3009.

Hungate BA, Dukes JS, Shaw MR, Luo Y, Field CB (2003) Nitrogen and climate change. *Science*, **302**, 1512–1513.

Kellndorfer J, Walker W, LaPoint E, Bishop J, Cormier T, Fiske G (2012) Nacp aboveground biomass and carbon baseline data (nbcd 2000), USA.

Kondoh M (2001) Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **268**, 269–271.

Körner C, Asshoff R, Bignucolo O et al. (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO2. *Science*, **309**, 1360–1362.

Kröel-Dulay G, Ransijn J, Schmidt IK et al. (2015) Increased sensitivity to climate change in disturbed ecosystems. *Nature Communications*, **6**, 6682.

Luo Y, Su B, Currie WS et al. (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience*, **54**, 731–739.

Luyssaert S, Schulze ED, Börner A et al. (2008) Old-growth forests as global carbon sinks. *Nature*, **455**, 213–215.

McCarthy HR, Oren R, Johnsen KH et al. (2010) Re-assessment of plant carbon dynamics at the duke free-air CO2 enrichment site: interactions of atmospheric [CO2] with nitrogen and water availability over stand development. *New Phytologist*, **185**, 514–528.

Medlyn B, Zaehle S, De Kauwe M et al. (2015) Using ecosystem experiments to improve vegetation models. *Nature Climate Change*, **5**, 528–534.

Medvigy D, Moorcroft PR (2012) Predicting ecosystem dynamics at regional scales: an evaluation of a terrestrial biosphere model for the forests of northeastern north america. *Philosophical Transactions of the Royal Society: B Biological Sciences*, **367**, 222–235.

Medvigy D, Wofsy S, Munger J, Hollinger D, Moorcroft P (2009) Mechanistic scaling of ecosystem function and dynamics in space and time: ecosystem demography model version. *Journal of Geophysical Research: Biogeosciences*, **114**, G01002.

Medvigy D, Wofsy SC, Munger JW, Moorcroft PR (2010) Responses of terrestrial ecosystems and carbon budgets to current and future environmental variability.

Proceedings of the National Academy of Sciences of the United States of America, **107**, 8275–8280.

Meir P, Cox P, Grace J (2006) The influence of terrestrial ecosystems on climate. *Trends in Ecology & Evolution*, **21**, 254–260.

Miller A, Roxburgh S, Shea K (2011) How frequency and intensity shape diversity–disturbance relationships. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 5643–5648.

Mohan JE, Clark JS, Schlesinger WH (2007) Long-term CO2 enrichment of a forest ecosystem: implications for forest regeneration and succession. *Ecological Applications*, **17**, 1198–1212.

Moorcroft P, Hurtt G, Pacala SW (2001) A method for scaling vegetation dynamics: the ecosystem demography model (ed). *Ecological Monographs*, **71**, 557–586.

Myers D, Thomas R, DeLucia E (1999) Photosynthetic capacity of loblolly pine (*Pinus taeda* l.) trees during the first year of carbon dioxide enrichment in a forest ecosystem. *Plant, Cell & Environment*, **22**, 473–481.

Norby RJ, DeLucia EH, Gielen B *et al.* (2005) Forest response to elevated CO2 is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 18052–18056.

Norby RJ, Warren JM, Iversen CM, Medlyn BE, McMurtrie RE (2010) CO2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 19368–19373.

Ockendon N, Baker DJ, Carr JA *et al.* (2014) Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Global Change Biology*, **20**, 2221–2229.

Pan Y, Birdsey RA, Fang J *et al.* (2011) A large and persistent carbon sink in the world's forests. *Science*, **333**, 988–993.

Parton WJ, Ojima DS, Schimel DS, Kittel TG (1992) Development of simplified ecosystem models for applications in earth system studies: the century experience.

Rastetter EB, Ågren , GI Shaver, GR (1997) Responses of n-limited ecosystems to increased CO2: a balanced-nutrition, coupled-element-cycles model. *Ecological Applications*, **7**, 444–460.

Stoy PC, Katul GG, Siqueira M *et al.* (2006a) Separating the effects of climate and vegetation on evapotranspiration along a successional chronosequence in the southeastern us. *Global Change Biology*, **12**, 2115–2135.

Stoy PC, Katul GG, Siqueira MB, Juang JY, Novick KA, Uebelherr JM, Oren R (2006b) An evaluation of models for partitioning eddy covariance-measured net ecosystem exchange into photosynthesis and respiration. *Agricultural and Forest Meteorology*, **141**, 2–18.

Stoy PC, Katul GG, Siqueira M *et al.* (2008) Role of vegetation in determining carbon sequestration along ecological succession in the southeastern united states. *Global Change Biology*, **14**, 1409–1427.

Stoy P, Dietze M, Richardson A *et al.* (2013) Evaluating the agreement between measurements and models of net ecosystem exchange at different times and timescales using wavelet coherence: an example using data from the north american carbon program site-level interim synthesis. *Biogeosciences*, **10**, 6893–6909.

Tans P, Keeling R (2014) Trends in atmospheric carbon dioxide, national oceanic & atmospheric administration, earth system research laboratory (NOAA/ESRL) & scripps institution of oceanography.

Tilman D, Reich PB, Isbell F (2012) Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 10394–10397.

Walker AP, Hanson PJ, De Kauwe MG *et al.* (2014) Comprehensive ecosystem model-data synthesis using multiple data sets at two temperate forest free-air CO2 enrichment experiments model: performance at ambient CO2concentration. *Journal of Geophysical Research: Biogeosciences*, **119**, 937–964.

Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western us forest wildfire activity. *Science*, **313**, 940–943.

Würth MK, Pelaez-Riedl S, Wright SJ, Körner C (2005) Non-structural carbohydrate pools in a tropical forest. *Oecologia*, **143**, 11–24.

Zaehle S, Medlyn BE, De Kauwe MG *et al.* (2014) Evaluation of 11 terrestrial carbon–nitrogen cycle models against observations from two temperate free-air CO2 enrichment studies. *New Phytologist*, **202**, 803–822.

Zhao K, Jackson RB (2014) Biophysical forcings of land-use changes from potential forestry activities in north america. *Ecological Monographs*, **84**, 329–353.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 PFT parameter sets for main model run.

Table S2 Summary of simulation congurations used in main text and supplementary information.

Figure S1 Model predictions of AGB by PFT using full initial pine density and no thinning.

Figure S2 (a) A run using max patches/cohorts = 4/4, (b) max patches/cohorts = 20/20, (c) max patches/cohorts = 40/4, (d) max patches/cohorts = 4/40.

Figure S3 Model predictions of change in community composition due to eCO$_2$, plotted by PFT.

Figure S4 Model predictions of change in community composition due to eCO$_2$, plotted by PFT.

Figure S5 Model predictions of change in community composition due to eCO$_2$, plotting basal area by PFT.