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Effects of rising atmospheric CO_2, climate change, and nitrogen deposition on aboveground net primary production in a temperate forest

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Abstract

Temperate forests regrowing from historical land use and land cover change in the eastern US serve as carbon (C) sinks. Environmental drivers have been significantly altered (e.g. rising atmospheric CO_2 concentration, warmer temperature, and elevated nitrogen (N) deposition) and will have a wide range of impacts on future forest C sinks. However, the interactions among these environmental drivers are unclear and their effects are subject to uncertainty. We assessed the combined and interactive effects of rising CO_2 concentration, climate change (temperature, precipitation), and N deposition on forest aboveground net primary production (ANPP) and their relative contribution to ANPP changes of a temperate forest in the eastern US. We used a process-based ecosystem model PnET-day to simulate coupled cycles of C, water, and N of forest ecosystems. We found that (1) climate change exerted negative effects on ANPP (-0.250 kg C m^{-2} yr^{-1}) whereas rising CO_2 and N deposition enhanced ANPP ($+0.253$, $+0.014$ kg C m^{-2} yr^{-1}); (2) climate change interacted with rising CO_2 and N deposition to decrease ANPP (-0.032, -0.018 kg C m^{-2} yr^{-1}); rising CO_2 and N deposition acted in synergy to increase ANPP ($+0.014$ kg C m^{-2} yr^{-1}); (3) changes in ANPP were mainly attributed to rising CO_2 and climate change whereas N deposition effects and any two- or three-factor interactive effects were relatively small. Our results suggest that the total negative effect sizes will not be offset by the total positive effect sizes, thus resulting in reductions in forest ANPP over the 21st century.

1. Introduction

Temperate forests, making up 25% of all forest area, sequestrate approximately 30% global carbon (C) emissions and store about 15% of global C (Martin *et al* 2001). The C sinks taken up by temperate forests have increased in the past decades primarily because of increasing density of biomass and great increases in forest area (Pan *et al* 2011). Recent studies generally agree that contemporary C sinks of temperate forests in eastern US have been largely attributed to forest regrowth from historical land use and land cover change such as forest clearing, cropland expansion, and followed agricultural abandonment (Caspersen *et al* 2000, Pacala *et al* 2007). However, the future persistence and magnitude of C sinks of the temperate forests in the eastern US remain uncertain.

Environmental conditions have been significantly altered by human-induced activities over the past century and will continue to change in the future such as rising atmospheric CO_2 concentration, warmer temperature, altered precipitation regimes, and elevated nitrogen (N) deposition (IPCC 2014). Both individually and interactively, these changes of environmental drivers have a wide range of impacts on future forest C sinks (Fekete *et al* 2017, Houtven *et al* 2019). Rising CO_2 concentration and warmer temperature will favor net primary productivity (NPP) and water use efficiency of trees and thus promote C sequestration (Fang *et al* 2014, Fernández-Martínez *et al* 2019), though the extent of CO_2 fertilization effects will depend upon other factors such as nutrients (de Vries *et al* 2017). Altered precipitation regimes such as increased drought stress will decrease tree growth and even trigger tree mortality under severe water limited conditions (Ibáñez *et al* 2018). Elevated N deposition is almost likely to increase tree growth, thus leading to higher C accumulation given that N is often the limiting nutrient in many forest ecosystems (Feng *et al* 2015, Maes *et al* 2019). However, the fertilization effects of elevated N deposition on tree growth are expected to saturate or even likely to decline with continuous N enrichment because of nonlinear responses of tree growth to accumulated N deposition (Tian *et al* 2016). These environmental drivers are also believed to act in synergy resulting significant interactive effects (Norby *et al* 2010, Dusenge *et al* 2019). For example, concurrent rise in CO_2 concentration and N deposition could bring out strong synergistic fertilization effects especially in the forest ecosystems with N limitation (O'Sullivan *et al* 2019). Understanding the combined effects of these environmental drivers is, therefore, needed to generate reliable projections of future forest C dynamics, which are essential for land managers and policy makers to design effective plans for natural resource conservation and adaptation strategies for climate change.

In our study, we assessed the combined effects of rising atmospheric CO_2 concentration, climate change (temperature, precipitation), and N deposition on aboveground net primary production (ANPP) of a temperate forest in the eastern US We used a process-based ecosystem model PnET-day to simulate physiological responses of forest ecosystems to rising atmospheric CO_2, climate change, and elevating N deposition. We used PnET-day model because it simulates the coupled cycles of C, water, and N of forest ecosystems driven by daily environmental data (Aber *et al* 1996). It has been validated against inventory data and eddy-flux tower measurements and applied to various forests (Aber and Federer 1992, Aber *et al* 1996, Ryu *et al* 2008, Jin *et al* 2016). We addressed the following questions: (1) how forest ANPP will change under rising CO_2, climate change, and N deposition over the 21st century? and (2) what is the relative contribution of rising CO_2, climate change, N deposition, and the interaction of any two- and three-combination of these three environmental drivers on forest ANPP changes?

2. Data and methods

2.1. Study area

Our study area included the Current River Hills ecological subsection (223 Af) within the Ozark Highland ecological section (223A) (McNab *et al* 2007) and was located in the US state of Missouri (figure 1). The study area covered approximately 810 000 hectares. It is a mature dissected plateau with dolomite and sandstone bedrock, and soils primarily developed from cherty limestones (McNab *et al* 2007). The climate is continental temperate with warm and humid summers and relatively dry and cold winters. The average annual temperature is 13.4 °C and average annual precipitation is 1100 mm.

We chose the Current River Hills ecological subsection as the study area because it contained one of the largest blocks of forest in the eastern US (figure 1). This area was primarily composed of secondary upland oak-hickory and oak-pine forests. The dominant tree species included white oak (*Quercus alba* L.), black oak (*Q. velutina* Lamb.), scarlet oak (*Q. coccinea* Muenchh.), bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch], and pignut hickory (C. *glabra* Miller) (Shifley and Brookshire 2000). Oaks and hickories have been the dominant tree species for the past thousands of years and are the keystone species of major importance in maintaining biodiversity, ecosystem functions and services. Similar to many forests in the eastern US, current forests in the study area are regrowing from previous disturbances (mainly tree harvesting and agricultural abandonment) and the average stand age is approximately 70 years.

2.2. Modeling approach and experimental design

We designed a three-factor factorial experimental design with two levels of CO_2 concentration (current CO_2 concentration and future rising CO_2 concentration), four levels of climate (current climate and three climate change scenarios), and two levels of N deposition (current N and future elevated N deposition), resulting in total of 16 simulation scenarios. We treated the current CO_2 concentration, climate (temperature and precipitation), and N deposition scenario as the baseline scenario. We used PnET-day model to simulate the C, N and water dynamics of forest ecosystems for the 16 simulation scenarios.

2.2.1. Climate data and climate change scenarios

We included current climate and three climate change scenarios based on CanESM2, GFDL-ESM2M, and MIROC5 global climate models (GCMs) under the representative concentration pathway (RCP) 8.5 (Riahi *et al* 2007). Since the three GCMs projected different future climate change patterns, we were able

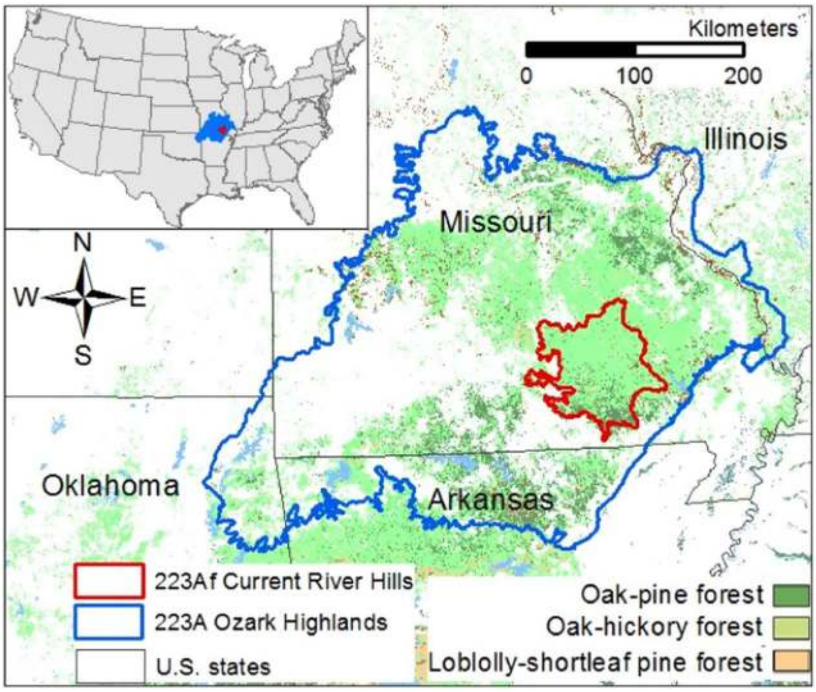

Figure 1. The study area included the Current River Hills ecological subsection (223 Af) within the Ozark Highland ecological section (223A) and was located in the US state of Missouri and dominated by oak-hickory forests.

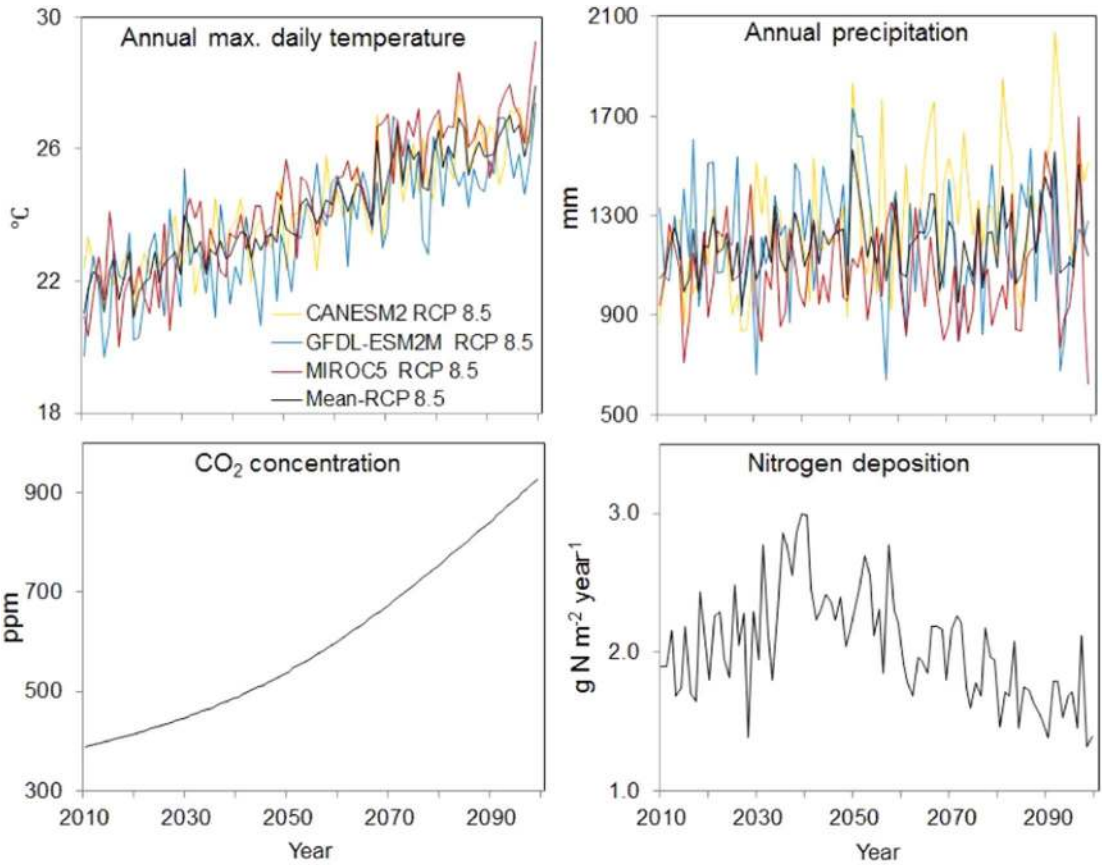

Figure 2. Annual maximum daily temperature and annual precipitation projected by three global climate models (CanESM2, GFDL-ESM2M, and MIROC5) and their mean values under RCP8.5, future rising CO_2 concentration, and elevated nitrogen deposition under RCP 8.5 from 2010 to 2099 for the Current River Hills ecological subsection.

to generate a range of projections to incorporate uncertainties in future climate projections (figure 2, Rupp *et al* 2013).

We used daily maximum and minimum temperature, precipitation, and solar radiation for each climate scenario. We obtained the current climate data (1980–2009) for our study area at 1 km resolution from DAYMET (Thornton *et al* 2016). We downloaded the future climate data (2010–2099) for three climate change scenarios from the Coupled Model Intercomparison Project phase 5 (CMIP5, https://cmip.llnl.gov/cmip5/data_portal.html). Compared to the current climate scenario, three climate change scenarios projected the annual maximum daily temperature to increase by 4 °C–6 °C in 2070–2099 (figure 2), in which the CanESM2 and MIROC5 RCP 8.5 scenarios showed more dramatic increases than the GFDL-ESM2M RCP 8.5 scenario. Annual precipitation on average had relatively small anomalies from current climates with increased annual variations after 2050 (figure 2).

2.2.2. CO_2 concentration scenarios

We obtained the annual CO_2 concentration for the current CO_2 scenario (1980–2009) from Mauna Loa Observatory (http://esrl.noaa.gov/gmd/obop/mlo/). We used the atmospheric CO_2 concentration projection (2010–2099) under RCP 8.5 as the future rising CO_2 scenario (https://cmip.llnl.gov/cmip5/data_portal.html). CO_2 concentration under RCP 8.5 was projected to continue rising over 900 ppm and averaged 600 ppm over the 21st century (figure 2).

2.2.3. N deposition scenarios

We downloaded the N deposition data (1980–2009) for the current N deposition scenario from the National Atmospheric Deposition Program (http://nadp.sws.uiuc.edu/committees/tdep/tdepmaps/). Since RCP 8.5 did not have N deposition projections to the end of this century, we used the projections of atmosphere mass content of nitrate dry aerosol from 2006 to 2100 to derive the future N deposition based on the proportional relationship between N deposition and the atmosphere mass content of nitrate dry aerosol (Elliott *et al* 2009). Projected N deposition increased to 2040 followed by a decreasing trend and averaged 2.02 $g\,m^{-2}\,yr^{-1}$ over the 21st century (figure 2).

2.3. PnET-day parameterization and validation

We used PnET-day model, an improved version of PnET-CN, to simulate the effects of rising CO_2 concentration, climate change, and N deposition on forest ANPP (http://pnet.sr.unh.edu/, Aber *et al* 1996, Ollinger *et al* 2002). PnET family models are process-based ecosystem models that simulate the C, water, and N dynamics of forest ecosystems (Aber and Federer 1992, Ollinger *et al* 2002). The core of PnET-day was a daily time-step canopy submodel that simulated physiological processes of a multi-layered canopy using generalized leaf-trait relationships and vertical gradients in physical environmental conditions (Aber *et al* 1996). PnET-day model represented the vegetation using three major components: leaves, wood, and roots. It simulated the maximum potential net photosynthetic rate under light-saturated condition as a function of foliar N concentration and simulated water use efficiency (mg C fixed per g H_2O transpired) as a function of vapor pressure deficit. Based on these two principles, a link between C dynamics and water transpiration was established and the computation load for water transpiration was greatly reduced because it only depended on vapor pressure deficit. A complete N cycle in PnET-day model included N mineralization, nitrification, plant N uptake and leaching losses. Since PnET-day model simulated the interactions between C and N cycles, forest C sequestration was affected by both plant and soil N pools. The annual net primary productivity was summarized based on the net photosynthetic rate and the annual aboveground net primary productivity was allocated from the annual net primary productivity (Aber *et al* 1996).

We obtained the average water holding capacity for the entire subsection from Soil Survey Geographic Database (SSURGO, Soil Survey Staff 2014). We initialized the forests using average C mass of leaves, wood, and roots from forest inventory and analysis (FIA) data (O'Connell *et al* 2015). We used the generalized parameters for the broad-leaved deciduous forests (e.g. light attenuation constant, Q_{10} for leaf respiration, minimum and optimum daytime temperature) from previous studies (Reich *et al* 1995, Aber *et al* 1996, Ollinger *et al* 2002). We derived the site-specific parameters (e.g. foliar N content, specific leaf weight, growing degree days to start or complete foliar production, max. or min. winter foliar biomass) based on previous studies (Aber and Federer 1992, Tjoelker *et al* 2001, Scheller and Mladenoff 2005, Ryu *et al* 2008, Xu *et al* 2009) and the eddy-flux tower measures in the Missouri Ozarks AmeriFlux (MOFLUX) site (doi.org/10.17190/AMF/1246081).

We used historical FIA data to validate mode simulation results. We firstly initialized the forest ecosystems in PnET-day model using 136 FIA plots from the 2000 survey cycle and then run the model from 2000 to 2010 under the baseline scenario (with current climate, CO_2 and N deposition). We compared the average aboveground ANPP predicted by PnET-day model with the average ANPP estimated from FIA data over a 10 year period (2000–2010). Since FIA data did not contain ANPP information, we calculated three components: net C density increment from 2000 to 2010, aboveground mortality, and aboveground C removed due to disturbances; we then divided the sum of these three components by a time interval of 10 years to obtain the average ANPP. Predicted average ANPP from PnET-day from 2000 to 2010 was 0.551 kg C m^{-2} yr^{-1}, which was comparable to the observed average ANPP (0.576 kg C m^{-2} yr^{-1}) from FIA data for the same period. Thus, PnET-day model simulated consistent ANPP with observed field inventories in our study area. Finally, we reinitialized the PnET-day model using 142 FIA plots in the 2010 survey cycle and then simulated forest ecosystems from 2010 to 2099 for the 16 simulation scenarios.

2.4. Analysis of simulation results

We calculated the ΔANPPs for the simulation scenario i as the difference in ANPP between the simulation scenario i and the baseline scenario ($ANPP_i - ANPP_{\_baseline}$). We also calculated the average ΔANPPs for the period 2010–2100 for each simulation scenario. We averaged the ΔANPPs for the three climate change scenarios to focus on an average response, which was referred to as mean RCP 8.5 results.

We estimated the single-factor effect size of rising CO_2 concentration, climate change, or N deposition as the difference in ΔANPPs from 2010 to 2009 between the baseline scenario and the simulation scenario in which the single factor was only included; We calculated any two- and three-factor combined effect as the difference in ΔANPPs between the baseline scenario and the simulation scenario in which the given two or three factors were included simultaneously; We calculated any two-factor interactive effect by subtracting both two single-factor effects from the given two-factor combined effect; we finally calculated the three-factor interactive effect by subtracting both the three single-factor effects and three two-factor interactive effects from the three-factor combined effect (Temperli *et al* 2013). We averaged the single-factor effects, two-and three-factor interactive effects for the period 2010–2100 to represent the average effect sizes. Note that our analyses focused on average responses among three climate change scenarios and effect sizes rather than statistical significance.

3. Results

3.1. Temporal changes in ANPP under future scenarios

ΔANPPs varied greatly annually (figure 3) and averaged −0.041 kg C m^{-2} yr^{-1} under the RCP 8.5 climates, future rising CO_2 and N deposition scenario over the 21st century (figure 4). ΔANPPs on average were overall less with climate change and greater with rising CO_2 and N deposition (figure 3). With climate change, the average ΔANPP was reduced by 0.250 kg C m^{-2} yr^{-1} under the mean RCP8.5 with greatest decreases under CanESM2 RCP 8.5 climate scenario followed by GFDL-ESM2M and MIROC5 RCP 8.5 climate scenarios, in comparison with the baseline scenario (figures 3 and 4). Future rising CO_2 and N deposition increased the ΔANPP by 0.253 and 0.014 kg C m^{-2} yr^{-1}, respectively, compared with the baseline (figures 3 and 4). Climate change interacted with rising CO_2 and N deposition to reduce the average ΔANPP by 0.029 and 0.255 kg C m^{-2} yr^{-1}, respectively, while rising CO_2 interacted with N deposition to increase the average ΔANPP by 0.28 kg C m^{-2} yr^{-1} (figure 4). The interaction of climate change, rising CO_2 and N deposition resulted in reductions in average ΔANPP by 0.041 kg C m^{-2} yr^{-1} (figure 4).

3.2. Interactive effects of rising CO_2, climate change, and N deposition

The effect sizes of climate change on ΔANPP overall increased with great annual variation and averaged −0.250 kg C m^{-2} yr^{-1} whereas the effect sizes of rising CO_2 continued increasing and averaged 0.253 kg C m^{-2} yr^{-1} (figures 5 and 6). The effect sizes of N deposition on ΔANPP increased by mid-century followed a decreasing trend and averaged 0.014 kg C m^{-2} yr^{-1} (figures 5 and 6). The average effect sizes for the interaction of rising CO_2 and climate change and the interaction of climate change and N deposition on ΔANPP were −0.032 and −0.018 kg C m^{-2} yr^{-1}, respectively (figure 6). The effect sizes for the interaction of rising CO_2 and N deposition on ΔANPP averaged 0.014 kg C m^{-2} yr^{-1} (figure 6). The average effect sizes for the interaction of climate change, rising CO_2, and N deposition on ΔANPP were −0.020 kg C m^{-2} yr^{-1} (figure 6). Thus, on average, the changes in ANPP were mainly attributed to rising CO_2 and climate change while the interactive effects of any two- and three-combination of rising CO_2, climate change, and N deposition were relatively small. The total positive effect sizes (e.g. rising CO_2, N deposition, the interaction of rising CO_2 and N deposition) were not enough to offset the total negative effect sizes (e.g. climate change, interaction of rising CO_2 and climate change), thus resulting in reductions in ANPP over the 21st century.

4. Discussion

It is important to note that our simulations are not to be interpreted as forecasts of future. Rather, we assessed the combined effects of three environmental drivers (rising CO_2 concentration, climate change, and N deposition) on forest ANPP and their relative contribution to ANPP changes. We found rising CO_2 and N deposition enhanced ANPP whereas climate change exerted negative effects on ANPP; rising CO_2 and N deposition acted in synergy to increase ANPP; climate change interacted with rising CO_2 or/and N deposition to decrease ANPP; future changes in ANPP were mainly attributed to rising CO_2 and climate

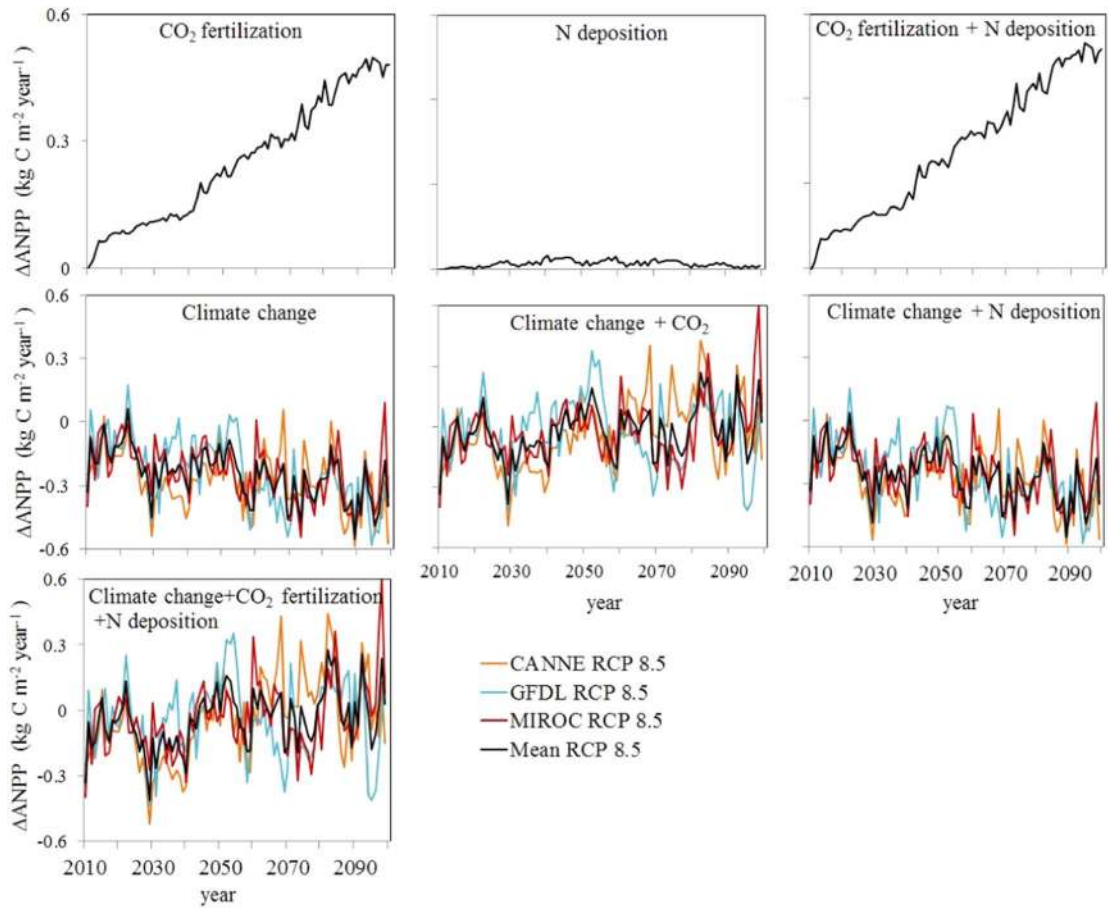

Figure 3. ΔANPP (kg C m^{-2} yr^{-1}) predicted by PnET-day model under alternative simulation scenarios: rising CO_2 concentration alone, N deposition alone, both rising CO_2 and N deposition, climate change alone, both climate change and rising CO_2, both climate change and N deposition, and all climate change, rising CO_2 and N deposition from 2010 to 2099 for the Current River Hills ecological subsection, compared to the baseline scenario.

change whereas N deposition effects and any two- or three-factor interactive effects were relatively small.

The largest positive effects on ANPP was found for rising CO_2 concentration among three environmental drivers, which agree with many studies (Fernández-Martínez *et al* 2019, Tharammal *et al* 2019). Our results showed that, under current climates and N deposition level, ANPP with elevated CO_2 concentrations of 600 ppm increased by 0.253 kg C m^{-2} yr^{-1} (21%). These estimates were similar to those of free-air CO_2 enrichment (FACE) experiments. For example, the FACE experiments conducted in four temperate forest sites in the Northern Hemisphere showed an average increase of 18% in NPP under the elevated CO_2 concentration (approx. 550 ppm) (Norby *et al* 2010). However, it is difficult to compare our results under higher CO_2 concentrations (>550 ppm) in a long timeframe with field-based forest ecosystem studies. We also found although CO_2 concentration kept increasing after 2080, most of CO_2 fertilization effects were found in the period of 2040–2080 with much smaller changes in ΔANPP after 2080, suggesting CO_2 saturation effects. Enhanced photosynthesis under elevated CO_2 concentration may be reduced via physiological adjustments or limited by N availability (Voelker *et al* 2016). It should be noted that the PnET model, similar to many other process-based models, scales up the leaf level responses to CO_2 fertilization directly to the ecosystem level, and thus our results should be considered to be at the upper bound of possible responses of forest ecosystems to rising CO_2 (Ollinger *et al* 2008).

Climatic warming had a secondary effects on forest ANPP changes. ANPPs under the RCP 8.5 climates declined compared to those under current climates. Our results were consistent with predictions by Peters *et al* (2013) using PnET-CN model in Great Lakes forests in the northern US under the GFDL A1FI climate change scenario over the 21st century. However, Peters *et al* (2013) showed that ANPP was projected to slightly increase under the moderate climate change scenario PCM B1, which might indicate the saturation effects of warming climates. Moderate warming climates could enhance forest productivity by accelerating photosynthesis (Fang *et al* 2014, Bowling *et al* 2018) and lengthening growing season (Babst *et al* 2019). However, under more severe climate scenarios (e.g. RCP 8.5, GFDL A1FI), the negative effects of climate change could be because the elevated temperature was beyond the optimal temperature of photosynthesis

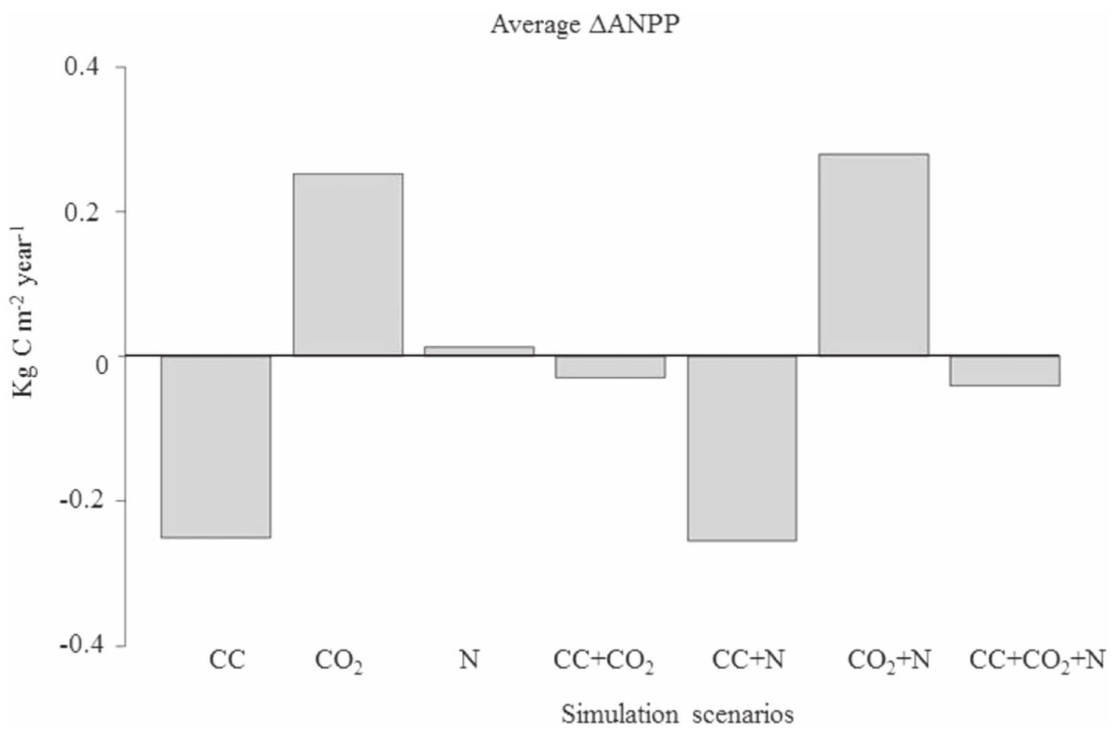

Figure 4. The average ΔANPP (kg C m^{-2} yr^{-1}) predicted by PnET-day model under alternative simulation scenarios (climate change alone (CC), rising CO_2 concentration alone (CO_2), and N deposition alone (N), both climate change and rising CO_2 (CC + CO_2), both climate change and N deposition (CC + N), both rising CO_2 and N deposition (CO_2 + N), and climate change, rising CO_2 and N deposition (CC + CO_2 + N)) from 2010 to 2099 for the Current River Hills ecological subsection, compared to the baseline scenario.

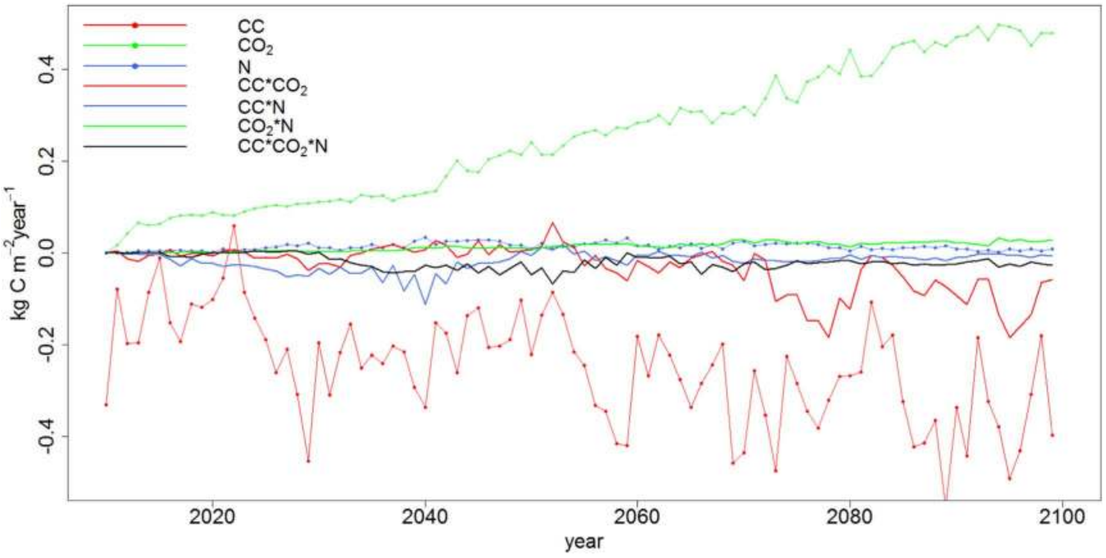

Figure 5. The effect size (kg C m^{-2} yr^{-1}) of individual environmental driver (climate change (CC), rising CO_2 concentration (CO_2), and N deposition (N)), two-factor interaction (CC*CO_2, CC*N, CO_2*N), and three-factor interaction (CC*CO_2*N) on forest ANPP from 2010 to 2099.

and thus caused photosynthetic rate to decline (Bagley *et al* 2015), and/or that the respiration increased with temperature (Ballantyne *et al* 2017), and/or that water was limited under extreme climate change scenario (Helman *et al* 2017), among other factors.

Among rising CO_2 concentration, climate change, and N deposition, our study suggested that N deposition had the smallest effect on ANPP (+0.043 kg C m^{-2} yr^{-1}). The interactive effects of N deposition with climate change and/or CO_2 fertilization were also relatively small compared to effects of CO_2 fertilization, climate change, and interaction of climate change and CO_2 fertilization. Our results generally agreed with some previous studies showing that

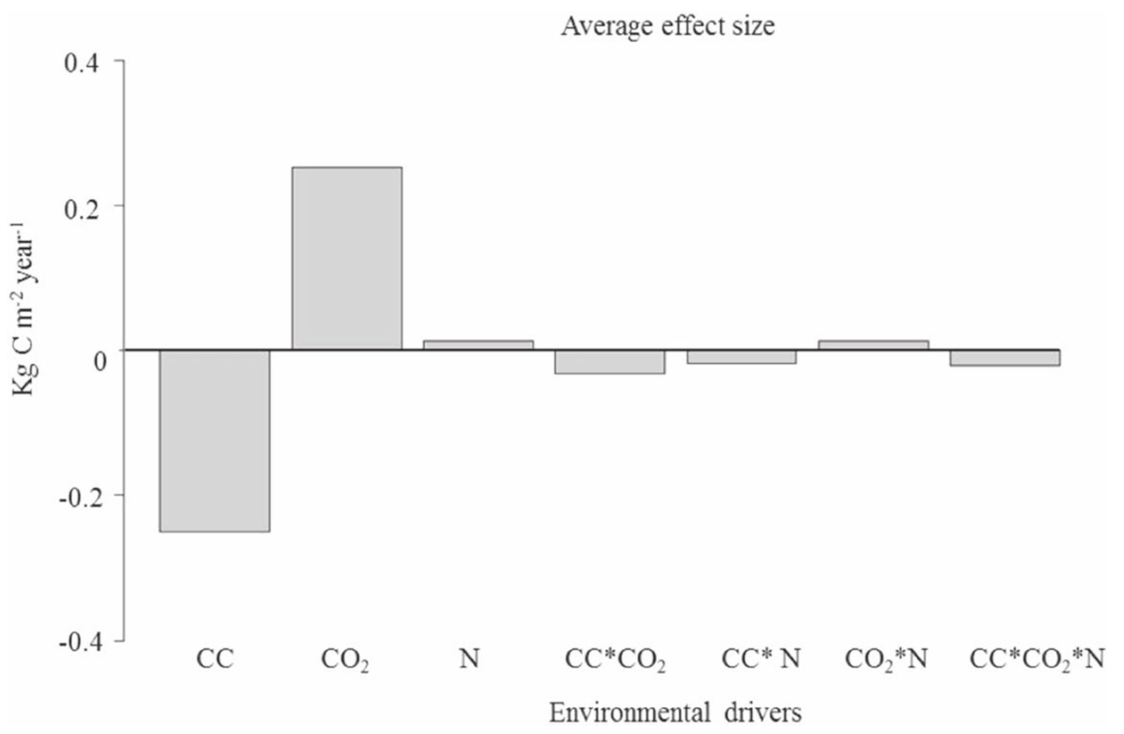

Figure 6. The average effect size (kg C m^{-2} yr^{-1}) of individual environmental driver (climate change (CC), rising CO_2 concentration (CO_2), and N deposition (N)), two-factor interaction (CC^*CO_2, CC^*N, $CO_2{}^*N$), and three-factor interaction ($CC^*CO_2{}^*N$) on forest ANPP from 2010 to 2099.

N deposition made only minor contributions to C sequestration in temperate forests (e.g. Fernández-Martínez *et al* 2017). However, our results differed with some field experimental studies of N fertilization (e.g. Lovett *et al* 2013, Etzold *et al* 2014) because most experiments had higher N deposition rates than those used in our study. For example, Lovett *et al* (2013) conducted 6 year increased N deposition experiments in southeastern New York State with an increased N deposition rate of 5 g N m^{-2} yr^{-1}, which did not significantly enhance ANPP for any tree species but significantly increased C stock in forest soils. This may be because only a small fraction of added N entered the trees, while most of added N remained in soil organic matter (Goodale 2017). This finding was supported by Etzold *et al* (2014) which showed that N deposition enhanced forest productivity with an increased N deposition rate of 2–3 g N m^{-2} yr^{-1} and no further growth increased beyond that threshold. N can be absorbed directly into trees through canopies in temperate forests (Guerrieri *et al* 2015, Wang *et al* 2017a), however, in most forest models (including PnET) and field experiments, N enters the forest ecosystem in the forest soil surface, the effect of which may be different from that of equivalent N addition from atmospheric deposition.

Our study suggest the negative interactive effects of rising CO_2 and climate change on forest ANPP, which were consistent for observational and modeling studies that indicated the CO_2 fertilization effects on forest production were constrained by climate warming (e.g. Fernández-Martínez *et al* 2019). The negative interactive effects may arise because of higher respiratory rates and drought stress under future warmer and drier climates. Rising CO_2 were expected to interact with elevated N deposition to increase forest production because N addition moderated N limitation (Norby *et al* 2010). Many forest ecosystem models are considered to have a tendency to overestimate the CO_2 fertilization effects because N limitation is not included in model formulations (He *et al* 2017, Fatichi *et al* 2019). However, PnET-day model was able to capture the effects of N on photosynthetic rate through simulating N cycles and its interaction with C cycles (Ollinger *et al* 2002).

It should be noted that there are several limitations in this study. First, PnET treats forest ecosystem as a lumped system consisting of different plant organs (e.g. roots, leaves), neither individual plant species nor functional types were represented; thus forest demographic processes and composition changes cannot be simulated. Most of temperate forests are relatively young and are typically 'regrown' from historical land management activities (e.g. harvest, agricultural abandonment) and are expected to continue taking up large amounts of C in the future (Reich and Frelich 2002). Recent studies suggest that age-driven forest demographic processes alone might play a larger role than growth enhancement from environmental changes (e.g. rising CO_2) (Liang *et al* 2015, Jin *et al* 2017, Wang *et al* 2017b, 2018, 2019, Pugh *et al* 2019). Secondly, PnET does not simulate effect of nutrients other than N, e.g. phosphorus (P), on ANPP. It has been suggested the models neglecting P limitations may overestimate terrestrial C uptake (Fernández-Martínez *et al* 2017) and there could be interactions between N and P cycles (Schulte-Uebbing and de Vries 2017). Nevertheless, our modeling approach is well suited-for assessing the effects of rising atmospheric CO_2 concentration, climate change, and N deposition on forest production. PnET-day model can be directly parameterized from forest inventory data and has been well validated against inventory data and eddy-flux tower measurements (e.g. Ryu *et al* 2008). With our modeling approach, we were able to incorporate the physiological responses of forest ecosystems to environmental changes through simulating coupled cycles of C, water, and N that would not be possible with some other models.

Acknowledgments

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