

Dear Dr. Liu.

Thank you for your comments. We have made additions to address your comments.

***Reply to editor's comments:***

1. *The impacts of clear- and partial-cutting on carbon/biomass have been studied extensively, and the authors have read some major ones. In addition, I would like to encourage the authors to read two recent and very relevant papers on this topic (e.g., Zhou, D, S Liu, J Oeding, S Zhao, 2013. Forest Cutting and Impacts on Carbon in the Eastern United States. NATURE Scientific Report 3: 3547, DOI: 10.1038/srep03547; Zhou, Decheng, Shuqing Zhao, Shuguang Liu, Jennifer Oeding, 2013. A Meta-Analysis on the Impacts of Partial Cutting on Forest Structure and Carbon Storage. Biogeosciences 10: 3691–3703). Some words discussing variability and uncertainty in responses/recovery-pathways to cutting in light of these two papers would strengthen the paper and help answer comment #2 raised by reviewer #1.*

**Our reply:** We read the two recent papers about the effects of partial cutting on forest growth and carbon stocks. SR (Scientific Report) paper was cited in the introduction (P2 Line 23) for a “big picture”. We added two sentences in the discussion to compare our findings (sensitivity analysis) with those reported in the BG paper (P16 Lines 28-31).

***Reply to reviewer 2's comments (updated):***

*# 9: Moreover, for a MS to be submitted to a Special Issue “Impacts of extreme climate events and disturbances on carbon dynamics”, maybe authors should be focused more on extreme ones not only regularly anthropogenic disturbances (such as clearing, etc.), they should discuss about extreme climate or other events' effect on carbon dynamics and their trajectory. You should add more references about extreme disturbance to make your MS fallen well in the scope of this special issue.*

**Our reply:** We have decided to remove the previous additions in response to this comment, since the impacts of fire and extreme climate events are really beyond our scope.

***Reply to reviewer 3's comments (updated):***

*# 16: The discussion on the difference between DBF and NEF is more attractive. It seems to meet the objective on testing the role of forest composition on successional question on trajectories of forest C dynamics. However, I do not think “forest compostion” is the right word in this case, it is better to use plant functional types consistently.*

**Our reply:** We corrected “plant function type” to “plant **functional** type” in the revision. We prefer to use plant functional type in this study.

1 **Quantifying Legacies the effects of clearcut clear-cut**  
2 **harvesting on carbon fluxes and biomass carbon stock**  
3 **stocks in northern temperate forests**

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15  
16 **Abstract**

17 Harvest disturbance has substantial impacts on forest carbon (C) fluxes and stocks. The  
18 quantification of these effects is essential for better understanding of forest C dynamics and  
19 informing forest management in the context of global change. We ~~evaluated~~ used a process-  
20 based forest ecosystem model, PnET-CN, to evaluate ~~for~~ how, and by what mechanisms, clear-  
21 cuts alter ecosystem C fluxes, aboveground C stocks (AGC), and leaf area index (LAI) in  
22 northern temperate forests. ~~–We compared C fluxes and stocks predicted by the model and~~  
23 estimated the effects of stand-replacing harvesting on C fluxes and stocks using at two  
24 chronosequences of eddy covariance flux sites for deciduous broadleaf forests (DBF) and  
25 evergreen needleleaf forests (ENF) in the Upper Midwest region of northern Wisconsin and  
26 Michigan, U.S.A. The average normalized root mean square error (NRMSE) and the Willmott  
27 index of agreement ( $d$ ) for carbon fluxes, LAI, and AGC in the two chronosequences were 20%  
28 and 0.90, respectively. Simulated gross primary productivity (GPP) increased with stand age,

1 reaching a maximum ( $\sim 1200\text{--}1500 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) at 11–30 years of age, and leveled off thereafter  
2 ( $\sim 900\text{--}1000 \text{ g C m}^{-2} \text{ yr}^{-1}$ ). Simulated ecosystem respiration (ER) for both plant functional types  
3 (PFTs) was initially as high as  $\sim 700\text{--}1000 \text{ g C m}^{-2} \text{ yr}^{-1}$  in the first or second year after harvesting,  
4 decreased with age ( $\sim 400\text{--}800 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) before canopy closure at 10–25 years of age, and  
5 increased to  $\sim 800\text{--}900 \text{ g C m}^{-2} \text{ yr}^{-1}$  with stand development after canopy recovery. Simulated net  
6 ecosystem productivity (NEP) for both PFTs was initially negative, with net C losses of  $\sim 400\text{--}$   
7  $700 \text{ g C m}^{-2} \text{ yr}^{-1}$  for 6–17 years after ~~clearcuts~~ clear-cuts, ~~reached~~ reaching the peak values of  
8  $\sim 400\text{--}600 \text{ g C m}^{-2} \text{ yr}^{-1}$  at 14–29 years of age, and eventually became stable stabilizing in mature  
9 forests (>60 years old) with ~~and~~ a weak C sink ( $\sim 100\text{--}200 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) ~~in mature forests (>60~~  
10 ~~years old)~~. The decline of NEP with age was caused by the relative flattening of GPP and gradual  
11 increase of ER. ENF recovered more slowly ~~lower~~ from a net C source to a net sink, and lost  
12 more C than DBF-. This suggests ~~ing~~ that in general ENF ~~is in general~~ may be likely slower to  
13 recover to full C assimilation capacity after stand-replacing harvests, arising from slower  
14 development of photosynthesis with stand age. Model results indicated that increased harvesting  
15 intensity would delay the recovery of NEP after ~~clear-cuts~~, but ~~this~~ had little effect on C  
16 dynamics during late succession. Future modeling studies of disturbance effects will benefit from  
17 the incorporation of forest population dynamics (e.g., regeneration and mortality) and,  
18 relationships between age-related model parameters and state variables (e.g., LAI), and  
19 silvicultural practices into the model.

20

## 21 **1 Introduction**

22 Disturbance has been widely recognized as a key factor influencing ecosystem structure  
23 and function at decadal to century scales (Magnani et al., 2007; Williams et al., 2012; Kasischke  
24 et al., 2013). Harvesting is an important anthropogenic disturbance shaping North American  
25 forest landscapes. Approximately  $61,000 \text{ km}^2$  of forests were affected by harvests every year  
26 during the 2000s (Masek et al., 2011). Harvests affect alter forest age structure and alter the  
27 forest carbon (C) cycle balance (Magnani et al., 2007; Pan et al., 2011; Williams et al., 2012;  
28 Zhou et al., 2013a). Quantifying the legacies of harvest disturbances under the context of climate  
29 change is essential for predicting forest C dynamics, informing climate policy-making, and  
30 improving forest management. Here, we focus on assessment of an ecosystem model's ability to  
31 assess the C cycle response ~~from one type of harvest, the to~~ clear-cut forest harvesting.

1 Harvests transfer living biomass C to harvested wood C and litter C, resulting in  
2 successional changes in C fluxes and stocks. Leaf biomass increases rapidly in secondary  
3 succession and then typically stabilizes at a certain level that is determined by light, water,  
4 nutrient availability, and forest type (Sprugel, 1985). Gross primary productivity (GPP) thus  
5 increases gradually over time, reaches its maximum in middle age, ~~and declining slightly~~  
6 ~~thereafter~~ in response to nutrient limitations and aging ~~responses slightly declines thereafter~~  
7 (Odum, 1969; Chapin et al., 2002; Tang et al., 2014). The successional change in plant  
8 respiration (i.e., autotrophic respiration) after stand-replacing harvesting is similar to that of  
9 GPP, although the C use efficiency, ~~(the ratio of net primary productivity, (NPP), to GPP (or,~~  
10 ~~NPP/GPP), could generally decline with forest age (DeLucia et al., 2007). As a result of these~~  
11 ~~patterns, along with increases in C loss through woody litterfall,~~ living tree biomass C gradually  
12 increases following a typical logistic growth curve (Odum, 1969; Sprugel, 1985).

13 Heterotrophic respiration following stand-replacing harvesting ~~could~~ can be stimulated at  
14 the beginning of stand development because the removal of trees alters the environmental  
15 conditions (e.g., soil temperature, moisture, and nutrients) and possibly leads to increasechanges  
16 in litter quantity depending on harvest types (e.g., stem-only harvesting) ~~(Chapin et al., 2002).~~  
17 Heterotrophic respiration is expected to gradually decrease thereafter because the regrowing  
18 forest reduces net radiation, water, and nutrient availability to the soil (Chapin et al., 2002) and  
19 the amount of decomposable soil organic matter from the prior forest and harvest residue (e.g.,  
20 litter, coarse woody debris, and soil organic C) also gradually decreases. Over time, however,  
21 heterotrophic respiration could ~~again~~ be enhanced because of accumulation of woody debris and  
22 litter with stand development. This theorized successional trajectory in ecosystem respiration  
23 (ER; the sum of autotrophic and heterotrophic respiration) may can also be ~~strongly~~ influenced  
24 by harvest types and forest composition. Unlike GPP or NPP, quantifying the trajectory of  
25 heterotrophic respiration (and consequently total ecosystem respiration) with age is not as  
26 straightforward well-understood (Amiro et al., 2010). Observational studies ~~to date~~ have shown  
27 that forest ecosystems generally become C sources (i.e., negative net ecosystem productivity,  
28 NEP) immediately following stand-replacing harvests, approach the maximum NEP as they  
29 mature, and then experience a gradual decline in NEP thereafter (e.g., Law et al., 2003; Gough et  
30 al., 2007; Goulden et al., 2011), following the trajectories hypothesized by ~~Odum (1969) and~~  
31 Chapin et al. (2002).

1           The changes ~~of~~in C fluxes and stocks after harvesting have been examined in many  
2 forest ecosystems using ecological measurements (e.g., eddy covariance or EC observations)  
3 from chronosequences using a space-for-time substitution approach (e.g., Gough et al., 2007;  
4 Goulden et al., 2011). The trajectoryies and amplitude of C fluxes and stocks vary with forest  
5 ecosystem types (Amiro et al., 2010). For example, Noormets et al. (2007) reported that a young  
6 red pine (*Pinus resinosa*) stand at 8 years of age was a net C sink ( $313 \pm 14 \text{ g C m}^{-2} \text{ yr}^{-1}$ ), but a  
7 young hardwood site at age of 3 was a net C source ( $-128 \pm 17 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) over the growing  
8 season in northern Wisconsin, U.S.A. Young stands in northern Wisconsin may become net C  
9 sinks within 10-15 years after harvesting (Noormets et al., 2007). More rapid recovery after  
10 stand-replacing harvesting (< 6 years) was found for temperate forests in northern Michigan  
11 (Gough et al., 2007). These studies have produced a wealth of information on ecosystem C  
12 dynamics after stand-replacing disturbances, and this information can be translated to more  
13 process-based and quantitative understanding of disturbance effects on the C cycle using  
14 ecosystem models (Goulden et al., 2011). Process models require evaluation on how source/sink  
15 transition and long-term carbon flux dynamics respond to differences in vegetation type, harvest  
16 intensity, and age since clearing.

17           Although using the chronosequence approach to evaluate the changes of ecological  
18 processes with age after disturbances is attractive, this approach is often limited by the lack of  
19 biological and climatic data (Yanai et al., 2003; Bond-Lamberty et al., 2006) and full  
20 representation of stand development stages. Process-based ecosystem models provide a means of  
21 quantifying the effects of disturbances on C dynamics under changing climate over various  
22 spatial and temporal scales. Ecosystem models have been used to assess the effects of ~~clearcuts~~  
23 clear-cuts and climate change on forest C dynamics at the stand/ecosystem (e.g., Bond-Lamberty  
24 et al., 2006; Grant et al., 2009; Wang et al., 2012b) or regional scales (Desai et al., 2007; Dangal  
25 et al., 2014). Moreover, ecosystem models can also be used to assess forest C dynamics under  
26 various scenarios of climate change and harvesting regimes (e.g., Albani et al., 2006; Peckham et  
27 al., 2012), since these models have been developed based on physiological, biogeochemical, and  
28 ecological theories. However, few studies have used ecosystem models to examine the changes  
29 of C fluxes and stocks with stand regrowth after stand-replacing disturbances for forest  
30 chronosequences.

1           The objectives of this study were to evaluate the ability of an ecosystem model to capture  
2 the trajectories of forest C dynamics after stand-replacing harvests for two northern temperate  
3 plant functional types (PFTs: deciduous broadleaf forests, DBF; evergreen needleleaf forests,  
4 ENF), to examine which processes influence successional trajectories in these ecosystems, and to  
5 test the role of plant function type PFT on successional trajectory of C fluxes. We applied a  
6 process-based forest ecosystem model, PnET-CN (Aber et al., 1997; Ollinger et al., 2002), to  
7 simulate the effects of clearcut clear-cut on forest C dynamics, and evaluated the simulated C  
8 fluxes and stocks for both PFTs using in-situ measurements (e.g., eddy covariance EC  
9 observations and aboveground biomass C, AGC). We hypothesized that (1) both DBF and ENF  
10 will have similar successional patterns in C fluxes (GPP, ER, and NEP) and aboveground  
11 biomass C stocks after stand-replacing harvests, but (2) DBF will recover faster than ENF from a  
12 net C source to a net C sink and lose a smaller amount of C (negative NEP) following a stand-  
13 replacing harvest.

## 14   **2    Methods**

### 15   **2.1   Study sites and field data**

16           Our study sites consist of 8 eddy covariance EC sites in the Upper Midwest region of  
17 northern Wisconsin and Michigan (Chen et al., 2008; Table 1). The study area is characterized  
18 by a humid-continental climate with hot summers and cold winters. The mean annual  
19 temperature is 4.4 °C and the mean annual precipitation is 768.9 mm (as measured between 1981  
20 and 2010 at Rest Lake weather station, 46.12° N 89.87° W, <http://www.ncdc.noaa.gov>). The  
21 dominant soil type is glacial sandy loam and loamy tills (Noormets et al., 2008). The region has  
22 been strongly influenced by forest industry. Most forest stands are less than 100 years old in this  
23 region, having regenerated following past harvesting operations (Amiro et al., 2010).

24           Our sites consist of four DBF sites (YHW, IHW, WIC, and UMBS) and four ENF sites  
25 (YRP, YJP, IRP, and MRP). The four DBF sites range from 3 to 86 years in age and constitute a  
26 chronosequence. Dominant tree species are bigtooth aspen (*Populus grandidentata*), trembling  
27 aspen (*Populus tremuloides* Michx.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer*  
28 *rubrum*), red oak (*Quercus rubra* L.), basswood (*Tilia americana*), and green ash (*Fraxinus*  
29 *pennsylvanica*). The four ENF sites also represent a chronosequence with stand age ranging from  
30 8 to 66 years. Red pine and jack pine (*Pinus banksiana*) are the dominant tree species in the four

1 | ENF sites. ~~At t~~The two chronosequences, most sites were initiated by stand-replacing harvests.  
2 | We obtained monthly C fluxes (observed NEP and its inferred data products GPP and ER) from  
3 | AmeriFlux (<http://public.ornl.gov/ameriflux/>) for the eight ~~eddy covariance~~EC flux tower sites  
4 | (Table 1). Harmonized level 4 data were used in this study. These flux data have been described  
5 | and used in our previous studies (e.g., Noormets et al., 2007; Chen et al., 2008; Desai et al.,  
6 | 2008; Xiao et al., 2011; Xiao et al., 2014). We also obtained [leaf area index \(LAI\)](#) and AGC data  
7 | from the literature for each site (Table 1).

## 8 | 2.2 Model description

9 | The PnET-CN model is a process-based forest ecosystem model ~~that eand~~designed to  
10 | simulate C, nitrogen (N), and water dynamics at [daily to](#) monthly time steps. PnET-CN is driven  
11 | by [climate variables](#) (temperature, precipitation, photosynthetically active radiation (PAR)), [site](#)  
12 | [variables and atmospheric properties \(soil moisture, disturbance history,](#) wet and dry ~~nitrogen~~N  
13 | deposition, and atmospheric CO<sub>2</sub> concentration), [and vegetation input parameters describing](#)  
14 | [physiological and structural plant traits](#) (Aber and Driscoll, 1997; Aber et al., 1997; Ollinger et  
15 | al., 2002). The model has been applied and tested in the USA and Europe for simulating the  
16 | effects of climate variability, rising atmospheric CO<sub>2</sub>, ozone pollution, and disturbance on  
17 | ecosystem processes and functions (e.g., Aber et al., 2002; Pan et al., 2009; Peters et al., 2013).

18 | ~~One of the unique features~~A characteristic feature of PnET-CN is [its use of generalized](#)  
19 | [leaf trait relationships](#) to simulate potential photosynthesis ~~using foliar nitrogen concentration~~  
20 | ~~and light use efficiency~~ in a multilayered canopy (Aber and Federer, 1992). [Actual](#)  
21 | ~~p~~Photosynthesis is then constrained by air temperature, vapor pressure deficit, and soil water  
22 | availability for simulating actual GPP. The effects of elevated CO<sub>2</sub> concentration on leaf  
23 | photosynthetic rates are calculated using constant ratios of leaf internal to ambient CO<sub>2</sub>  
24 | concentration (C<sub>i</sub>/C<sub>a</sub>) (Ollinger et al., 2002). PnET-CN incorporates a total of seven C pools, five  
25 | of which are structural C pools (foliage, woods, fine roots, woody debris, and soil organic  
26 | matter) and two of which are non-structural C pools stored in woods and fine roots.  
27 | Photosynthetic production is allocated to each living plant component (i.e., foliage, woods, and  
28 | fine roots) and to growth and maintenance respiration. Living biomass is transferred to dead  
29 | woody biomass and/or to soil organic C through leaf, ~~and~~-root [and wood](#) turnover, tree mortality,  
30 | and disturbance. The decomposition of coarse woody debris is a constant fraction of its C

1 content. The decomposition of soil organic C is calculated as a function of maximum  
2 decomposition rate and effects of temperature and soil moisture.

3 PnET-CN includes a complete **nitrogenN** cycle, and simulates **nitrogenN** mineralization  
4 and nitrification, plant **nitrogenN** uptake, allocation, and leaching losses. **NitrogenN** depositions  
5 ~~areis added to imposed into~~ corresponding soil **nitrogenN** pools (NH<sub>4</sub> and NO<sub>3</sub>). As with C  
6 pools, **nitrogenN** is divided into five structural pools (foliage, woods, fine roots, woody debris,  
7 and soil organic matter) and one non-structural **nitrogenN** pool stored in the trees. C and  
8 **nitrogenN** cycles interact closely in the model. High leaf **nitrogenN** concentration increases net  
9 photosynthesis rate in the absence of water stress, thereby resulting in the high demand for non-  
10 structural **nitrogenN** in plant tissues (Aber et al., 1997). When plant non-structural **nitrogenN** is  
11 low, plant **nitrogenN** uptake efficiency from available soil mineral **nitrogenN** is increased in the  
12 model (Aber et al., 1997). In addition, high C:N ratios in biomass, litter, and soil organic matter  
13 reduce net mineralization rates. ~~In general, the nitrogen cycle in the model is governed by a~~  
14 ~~negative feedback loop.~~

15 The model also simulates key hydrological processes including rainfall interception,  
16 evaporation, transpiration, surface runoff, and drainage at each time step. Rainfall interception is  
17 treated as a constant fraction of precipitation. Transpiration is estimated based on water use  
18 efficiency ~~and plant demand via photosynthesis~~. Surface runoff is calculated as a constant  
19 fraction of the difference between precipitation and evaporation. Drainage is estimated when  
20 potential soil water exceeds soil water holding capacity.

21 Prescribed disturbance events can be simulated in the model through four parameters:  
22 disturbance year, disturbance intensity, biomass removal fraction (~~live and dead~~), and the loss  
23 rate of soil organic matter. In this study, when stand-replacing disturbance events occur, a  
24 uniform ~~PFTplant function type~~ was assumed to be regenerated on-site. For the first year after  
25 ~~clearcuts clear-cuts~~, minimum LAI of 0.1 was assumed to regulate maximum potential foliage  
26 mass that controls leaf production. The photosynthetic production is transported to plant non-  
27 structural C pool where C could be allocated to leaves, stems, and roots. There is, therefore, no  
28 need for initialization (e.g., stand density) after disturbances in the model. More details about the  
29 model structure and processes have been described elsewhere (Aber et al., 1997; Ollinger et al.,  
30 2002).



## 1 2.3 Model inputs

2 The model inputs include temperature, precipitation, PAR, wet and dry **nitrogenN**  
3 deposition, atmospheric CO<sub>2</sub> concentrations, and disturbance history. The climate data used in all  
4 simulations were derived from the Daymet database (Thornton et al., 2012). For each site,  
5 monthly maximum temperature, minimum air temperature, and precipitation were calculated  
6 from the daily Daymet data for the period 1981-2010. PAR (mol m<sup>-2</sup> s<sup>-1</sup>) was estimated from  
7 solar radiation (RAD, MJ m<sup>-2</sup> day<sup>-1</sup>) using the empirical relationship (PAR = 2.05 RAD) (Aber et  
8 al., 1996). The data from 1981 ~~to~~ through 2010 were repeated as needed to create the time series  
9 from 1850 to 1980.

10 Annual rates of wet and dry **nitrogenN** deposition were obtained from the United States  
11 Environmental Protection Agency (EPA; <http://java.epa.gov/castnet/clearsession.do>). The  
12 **nitrogenN** deposition rates were measured at the Wellston station (44.22° N; 85.82° W) for the  
13 period 1994-2011. We also obtained the **nitrogenN** deposition rates in 1860 estimated by  
14 Galloway et al. (2004). For each year prior to 1994, we used an exponential ramp function to  
15 estimate the annual deposition rates by interpolating the historical (1860) and current **nitrogenN**  
16 deposition rates. Monthly wet deposition rates, needed for the model, were generated from  
17 annual wet **nitrogenN** deposition through the weighted coefficients (the ratio of monthly  
18 precipitation to total precipitation from March to November). We assumed that there is no wet  
19 **nitrogenN** deposition in the winter. The soil water holding capacity in the rooting zone (100 cm)  
20 for each site was derived from the gridded multi-layer soil characteristics dataset (STATSGO,  
21 Miller and White, 1998). For the period 1959-2010, we used the CO<sub>2</sub> concentrations data from  
22 Mauna Loa. For the time period 1901–1958, we derived the time series of the historical  
23 atmospheric CO<sub>2</sub> mixing ratio using a spline fit to the ice-core record (Etheridge et al., 1996), as  
24 described by McGuire et al. (2001) and used by Xiao et al. (2009). We used the CO<sub>2</sub>  
25 concentration in 1901 for the simulation period prior to 1901 and spin up.

26 For each site, we prescribed the disturbance events using the site disturbance history  
27 (Table 1). For each stand-replacing harvest, stand mortality was assumed to be 100%. The  
28 merchantable wood removal (biomass removal out of the ecosystem) fraction was assumed to be  
29 0.8 in this study. The soil removal fraction was assumed to be zero, given that the content of soil  
30 organic C might not be considerably affected by harvesting (Johnson and Curtis, 2001; Yanai et

1 al., 2003). We also conducted a sensitivity analysis to these assumptions as described below in  
2 section 2.4.

### 3 **2.4 Parameterization, initialization, validation, and sensitivity analysis**

4 PnET-CN has been parameterized and tested for temperate DBF (Aber et al., 1997;  
5 Ollinger et al., 2002; Peters et al., 2013), temperate ENF\_ (Aber et al., 1997; Peters et al., 2013),  
6 and mixed forests (Aber et al., 1997) for forest productivity, net **nitrogenN** mineralization, and  
7 foliar **nitrogenN** concentrations. The parameter values used in this study are given in supplement  
8 Table S1. To apply the model to the transient simulation period (1860-2010), a 200-year spin up  
9 run was conducted to ensure that the equilibrium ( $\Delta\text{-NEP} < 10 \text{ g m}^{-2} \text{ month}^{-1}$  and  $\Delta$  soil organic C  
10  $< 1\%$ ) was reached for each chronosequence site. [The Thirty year](#) climate normals (1981-2010),  
11 pre-industry **nitrogenN** deposition rates, and historical CO<sub>2</sub> concentrations were used for the spin  
12 up runs.

13 To examine ~~the~~ stand-replacing harvest legacies, we conducted all simulations using the  
14 site disturbance history (Table 1), vegetation parameters (Supplement Table S1), climate,  
15 **nitrogenN** deposition, and atmospheric CO<sub>2</sub> for each of the chronosequence sites. The model  
16 simulations were evaluated against C fluxes (GPP, ER, and NEP), AGC, and LAI data collected  
17 at the [eddy covarianceEC](#) flux sites. We used two statistical measures to evaluate the overall  
18 model performance: the normalized root mean square error (NRMSE) and the Willmott index of  
19 agreement. The NRMSE (Eq. (1)) was used to assess the difference between predicted ( $P$ ) and  
20 observed ( $O$ ) variables, and can be expressed as:

$$21 \text{ NRMSE} = (O_{\max} - O_{\min})^{-1} \left[ \frac{\sum_{i=1}^n (P_i - O_i)^2}{n} \right]^{0.5} \times 100\% \quad (1)$$

22 where  $O_{\max}$  and  $O_{\min}$  are the maximum and minimum observed values, respectively;  $i$  is the  $i^{\text{th}}$   
23 observation; and  $n$  is the total number of observations. A value close to 0 indicates perfect  
24 agreement and a value of 100% suggests poor agreement. The Willmott index of agreement ( $d$ ) is  
25 an indicator of modeling efficiency and is expressed as:

$$26 d = 1 - \left[ \frac{\sum_{i=1}^n (P_i - O_i)^2}{\sum_{i=1}^n (|P_i| + |O_i|)^2} \right] \quad (2)$$

1 A value of 1 indicates perfect agreement and a value near 0 indicates weak agreement (Willmott,  
2 1982).

3 The sensitivity of ecosystem C dynamics to changes in harvesting practices during the  
4 secondary succession was assessed using sensitivity analysis. The model was run at WIC and  
5 MRP for 100 years after scenario harvests in 1910 using the same climate data sequence.  
6 Sensitivity scenarios involved applying the stand mortality (80% and 60%, compare to 100% in  
7 the model test), soil organic matter loss (20% and 40%, compare to zero in the model test) to  
8 ~~reveal-assess the~~ effects of different harvest intensity and soil organic matter loss ~~scenarios~~ on C  
9 dynamics. We also tested the model sensitivity to CO<sub>2</sub> fertilization for evaluating potential  
10 climate change effects.

### 11 **3 Results**

#### 12 **3.1 Evaluation of modeled carbon fluxes and stocks**

13 ~~The S~~imulated C fluxes were generally consistent with ~~eddy covariance~~EC derived C  
14 fluxes for both DBF and ENF sites (Figs. 1 and 2). The NRMSE between simulated and tower  
15 fluxes (GPP, ER, and NEP) were between 10% ~~and~~ -21% (Table 2). The Willmott index of  
16 agreement between simulated and tower C fluxes for both ~~PFTs plant function types~~ ranged from  
17 0.91 to 0.94 with the exception of NEP ( $d= 0.73$ ,  $n= 235$ ). The model underestimated GPP for  
18 the DBF sites and predicted ER fairly well for all DBF sites, except for the intermediate-aged  
19 hardwood site, IHW. As a result, the model underestimated NEP for most DBF sites. For IHW,  
20 the model substantially underestimated both GPP and ER but predicted NEP fairly well. For the  
21 ENF sites, the model underestimated GPP. The model predicted ER fairly well for YRP (8 years  
22 old), YJP (15-16 years old) and IRP (23 years old), but overestimated ER for the older MRP  
23 sites. Thus, the model underestimated NEP for the ENF sites.

24 The simulated and observed stand characteristics (LAI and AGC) showed good  
25 agreement (Table 2 and Fig. 3). The model slightly underestimated LAI for the young forest sites,  
26 and overestimated LAI for the mature forest sites. Generally, the model overestimated AGC for  
27 the mature forest sites. The NRMSE was 28% for AGC and 31% for LAI. The Willmott index of  
28 agreement was 0.95 and 0.96 for AGC and LAI, respectively. Overall, the model evaluation  
29 metrics indicated that the model performed better in the DBF sites than in the ENF sites.

### 3.2 Legacy Effects of ~~clearcut-clear-cutsting~~ on carbon fluxes and stocks

PnET-CN generally captured the changes of C fluxes following the ~~clearcuts-clear-cuts~~ for each chronosequence site (Fig. 4). The predicted annual GPP generally increased with time since disturbance and approached the peak values ( $\sim 1200\text{--}1500\text{ g C m}^{-2}\text{ yr}^{-1}$ ) between 11 and 26 years of age and between 29 and 30 years of age for the DBF (IHW, WIC, and UMBS) and the ENF (IRP and MRP) sites, respectively; thereafter, the forest stands reached maturity and GPP became relatively stable with mean values of  $940\text{--}1000\text{ g C m}^{-2}\text{ yr}^{-1}$ .

Predicted annual ER was initially as high as  $860\text{--}1030$  and  $710\text{--}860\text{ g C m}^{-2}\text{ yr}^{-1}$  within the first two years for the DBF and the ENF sites, respectively. During canopy recovery, predicted ER generally decreased to  $620\text{--}780\text{ g C m}^{-2}\text{ yr}^{-1}$  between 10 and 25 years of age for the DBF sites and to  $360\text{--}380\text{ g C m}^{-2}\text{ yr}^{-1}$  between 14 and 17 years of age for the ENF sites (Fig. 4). For forest age older than 60 years, the predicted annual ER for both PFTs showed a relatively flat pattern, contrary to theoretical expectations, arising from the little change of both autotrophic and heterotrophic respiration with age (Supplement Fig. S1). Average annual ER for mature forests was  $810\text{--}880$  and  $780\text{ g C m}^{-2}\text{ yr}^{-1}$  for the DBF sites (WIC and UMBS) and the ENF (MRP) site, respectively.

As expected, the ratio of annual GPP to annual ER (GPP:ER) simulated by PnET-CN was low during the early years after ~~clearcutting-clear-cutting~~ for both DBF and ENF (Fig. 5). Within  $\sim 6$  years for the DBF sites and  $\sim 17$  years for the ENF sites, the GPP:ER ratio gradually increased and its average value became larger than 1 (NEP $>0$ ). The simulated peak GPP:ER ratio for DBF (1.6) occurred at 18 years after stand-replacing harvests, and the simulated peak ratio for ENF was 1.8 at 26 years. After those peaks, the ratio became relatively stable, with the mean values of 1.1 and 1.2 for mature DBF and mature ENF, respectively.

The model predicted negative NEP (C source) for the first 6 and 17 years after stand-replacing harvests for the DBF and the ENF, respectively (Fig. 4). The simulated peak annual net C loss occurred in the first or second year after ~~clearcuttingclear-cutting~~. The average C loss was  $530\text{--}710\text{ g C m}^{-2}\text{ yr}^{-1}$  for the DBF sites and  $380\text{--}400\text{ g C m}^{-2}\text{ yr}^{-1}$  for the ENF sites. The total C loss was  $3.2\text{--}4.3$  and  $6.4\text{--}6.9\text{ kg C m}^{-2}$  for the DBF and the ENF sites, respectively. The maximum net C gain was  $387\text{--}433\text{ g C m}^{-2}\text{ yr}^{-1}$  at 14–26 years of age for the DBF sites (WIC and UMBS) and was  $567\text{--}602\text{ g C m}^{-2}\text{ yr}^{-1}$  at 29 years of age for the ENF sites (IRP and MRP).

1 Simulated annual NEP decreased thereafter and became as low as 120–180 g C m<sup>-2</sup> yr<sup>-1</sup> after 17–  
2 31 years for the DBF sites and 170 g C m<sup>-2</sup> yr<sup>-1</sup> after 44 years for the ENF sites.

3 ~~Forest canopy as measured by LAI gradually recovered over time following clearcuts~~  
4 ~~clear cuts (Fig. 6).~~ LAI fully recovered within 10–15 years after disturbance for the DBF sites  
5 and within 40 years of age for the ENF sites (Fig. 6). The ~~gradual~~ recovery of LAI led to the  
6 gradual increase in GPP and the subsequent increase in AGC (Fig. 7). In general, AGC recovered  
7 much more slowly than C fluxes and LAI. The changes of simulated AGC followed the logistic  
8 growth curve with slow accumulation in the early years, fast accumulation in the middle age, and  
9 slow accumulation afterwards. The predicted LAI and AGC generally fell within the range of  
10 observed values across two chronosequences (Figs. 3, 6, 7). For mature forests (>60 years of  
11 age) in 2010, the DBF sites generally stored more C in aboveground biomass than the ENF sites  
12 (10–12 vs. 8.5 kg C m<sup>-2</sup>; Fig. 7).

### 13 3.3 Sensitivity analysis

14 Harvest intensity had little effect on ~~the~~ long-term C dynamics for both PFTs, but it had  
15 sizeable effects during early succession (Fig. 8). ~~Greater~~Increasing harvest intensity ~~led to earlier~~  
16 ~~delayed rising~~ GPP (Fig. 8 a and f) and LAI (Fig. 8 d and i) ~~rises and led to lower reduction in~~  
17 ~~ER but delayed reduction in ER~~ (Fig. 8 b and g), resulting in later rising NEP (Fig. 8 c and g).  
18 High harvest intensity (e.g., 100% removal of living trees) also directly reduced living tree AGC  
19 (Fig. 8 e and i). By reducing harvest intensity parameter to 80% and 60% from 100% used in the  
20 original model, average annual NEP over 100 years for DBF decreased by 104 and 88 g C m<sup>-2</sup> yr<sup>-1</sup>,  
21 respectively. The increased remaining tree biomass resulted in an increase in AGC about 12%  
22 and 16%, respectively, after a 100-yr harvest cycle. For ENF average annual NEP decreased  
23 about 1% and AGC decreased nearly 6% for both reduced harvest intensity scenarios. Increasing  
24 ~~the~~ soil removal fraction parameter resulted in lower GPP and ER along succession and lower  
25 NEP in middle succession for both DBF and ENF (Fig. S2 a-c and f-h). Greater soil removal  
26 fraction ~~promoted-enhanced~~ the leaf ~~biomass production~~ of DBF in middle and late succession  
27 (Fig. S2 d), but restricted the leaf ~~biomass production~~ of ENF in late succession (Fig. S2 i).  
28 Increasing ~~the~~ soil removal fraction parameter (20% and 40% removal of soil organic matter)  
29 strongly reduced living AGC (16% and 39%, respectively) for DBF (Fig. S2 e) but slightly

1 | decrease living AGC (up to 5%) for ENF (Fig. S2 j). There were ~~little~~-insignificant effects of  
2 | CO<sub>2</sub> fertilization on carbon dynamics for both DBF and ENF in our sensitivity analysis (Fig. S3).

## 3 | **4 Discussion**

### 4 | **4.1 Carbon fluxes and stocks following ~~clearcuts~~ clear-cutting**

5 | PnET-CN generally simulated the expected post-harvest trajectories in C fluxes (GPP,  
6 | ER, and NEP) and stock (LAI and AGC). The model was unable to simulate high GPP rates  
7 | estimated by ~~eddy covariance~~the EC technique in mature forests regardless of vegetation type,  
8 | suggesting that there is room for improvement in model simulation of secondary succession.

9 | Our simulations showed that LAI increased rapidly first and then stabilized during the  
10 | following development stages, ~~given that~~because the model estimates foliage growth through the  
11 | parameter of maximum relative growth rate (Table S1) with the ~~restriction~~limitation of current  
12 | foliage biomass and resource availability. This modeled response is consistent with the previous  
13 | finding that foliage biomass increased rapidly after disturbance and then stabilized (Sprugel  
14 | 1985). Our chronosequence-based results are generally consistent with previous results. For  
15 | example, Goulden et al. (2011) observed that LAI along a chronosequence of boreal forest stands  
16 | increased rapidly from 0.3 m<sup>2</sup> m<sup>-2</sup> ~~one~~+ year after fire, and then generally leveled off at 5.3–7.2  
17 | m<sup>2</sup> m<sup>-2</sup> from 23 to 154 years after stand-replacing crown fire. A modeling study based on a  
18 | modified version of Biome-BGC (Bond-Lamberty et al., 2005) also showed a similar  
19 | successional change in LAI for boreal DBF and ENF.

20 | The simulated successional change in annual GPP for both PFTs generally followed the  
21 | trajectory hypothesized by Odum (1969). However, despite a slight decrease in GPP  
22 | hypothesized in Odum's trajectories, our simulations show a relatively flat GPP in mature forests  
23 | (Figs. 4 and 10). In the model, GPP tracks LAI in the absence of significant changes in light,  
24 | water or nutrient stress. As LAI stabilizes in mature forests, GPP also stabilizes. Our results are  
25 | consistent with previous studies showing relatively flat pattern in GPP after 20 years following  
26 | harvests in temperate pine forests in Florida (Clark et al., 2004), northern temperate DBF in  
27 | Wisconsin (Desai et al., 2008), and boreal jack pine forests in Saskatchewan (Zha et al., 2009).  
28 | Furthermore, Humphreys et al. (2006) reported continuous increases of GPP with increasing  
29 | forest age for temperate rainforests using three different stands at different stages of development  
30 | (2, 14, and 53 years of age) following ~~clearcuts~~-clear-cuts in British Columbia, Canada.

1 However, northern temperate ENF showed a small difference in GPP between young and mature  
2 sites (Noormets et al., 2007; Desai et al., 2008). Desai et al. (2005) found that a nearby old-  
3 growth mixed forest had slightly lower GPP and significantly higher ER than nearby DBF sites.  
4 Site-to-site variations in species and soil fertility could result in variations in the successional  
5 trajectory of GPP after ~~clearcuts-clear-cuts so such~~ that the observed trajectories may deviate  
6 from hypothesized or modeled trajectories. In addition, our chronosequences lack old-growth  
7 sites and do not encompass the full range of forest development stages, which limits the  
8 representativeness of the C flux and stock trajectories derived from chronosequence studies  
9 based on ~~eddy covariance~~EC or other ecological observations (e.g., Clark et al., 2004;  
10 Humphreys et al., 2006; Noormets et al., 2007).

11 ~~We found~~Our simulations show that annual ER for secondary temperate forests ~~slightly~~  
12 declined ~~slightly~~ in the first ten years because of low autotrophic respiration at first after the  
13 removal of trees. Amiro et al. (2010) reported that ER ~~was~~ reduced in the very first year  
14 following harvests for a number of ~~eddy covariance~~EC flux sites over North America. Previous  
15 field studies showed that ER following ~~clearcuts-clear-cuts~~ increased with forest age (e.g.,  
16 Humphreys et al., 2006; Zha et al., 2009), partly supporting our results that ER slightly increased  
17 after the short decline period (10-25 years of age) in northern temperate forests until the stands  
18 reached maturity. Martin and Bolstad (2005) showed that chamber-based soil respiration in DBF  
19 of northern Wisconsin ranged from 857–1143 g C m<sup>-2</sup> yr<sup>-1</sup> in 1998 and 1013–1357 g C m<sup>-2</sup> yr<sup>-1</sup> in  
20 1999, which is higher than tower ER (825±133 g C m<sup>-2</sup> yr<sup>-1</sup>, WIC) from 1999-2006 in the same  
21 region. ~~But~~ Tang et al. (2009) reported that growing-season soil respiration in 2005 was 690 g C  
22 m<sup>-2</sup> in a mature DBF near WIC tower site, which is in the range of our simulations (Supplement  
23 Fig. S1). Soil respiration of 690 g C m<sup>-2</sup> over the growing season of 2005 in a mature DBF near  
24 WIC tower site was reported (Tang et al., 2009). Our simulated respiration components (e.g., soil  
25 respiration) for DBF were lower than those reported values (Supplement Fig. S1). The model  
26 underestimated GPP, but estimated ER well for mature DBF sites, indicating that the model  
27 likely overestimated ~~root~~ autotrophic respiration. ~~Eddy covariance~~EC derived ER were usually  
28 lower than chamber-based estimate at the WIC site due to uncertainties induced by measurement  
29 methods, decoupling of surface and canopy fluxes at night, and spatial scaling (Bolstad et al.,  
30 2004; Cook et al., 2004). For ENF, the model overestimated ER for the mature site because of  
31 overestimated soil decomposition rate. Our simulations also show that DBF had slightly higher

1 soil respiration rate than ENF (Supplement Fig. S1), which is consistent with the finding that  
2 chamber-based soil respiration was slightly higher for DBF than for ENF (~~no significant~~  
3 ~~difference~~) in Wisconsin (Euskirchen et al., 2003). The changes of ER in secondary forests after  
4 ~~clearcutting-clear-cutting~~ differ among sites because of different site conditions (e.g., quantity  
5 and quality of soil organic C and litter C) and harvesting types (e.g., Tang et al., 2009).

6 The trajectory of our simulated GPP:ER ratio is similar to the curve derived by Amiro et  
7 al. (2010) using EC observations and forest age from fire and harvest chronosequences across  
8 North America ( $GPP:ER = 1.23 * [1 - \exp(-0.224 * AGE)]$ ). Our simulated ratios are within the  
9 observed range of 0.9–1.6 for the DBF sites (Fig. 5a), although the model underestimated the  
10 ~~observed~~ ratios for mature sites. ~~The~~ Growing season GPP:ER ratios are typically higher than  
11 the annual ratios because winter soil organic C decomposition is important to annual C balance  
12 (Aanderud et al., 2013). However, the simulated ratios for the ENF sites are much lower than  
13 tower-derived growth season ratios (1.9–4.7, Fig. 5b), and close to the annual range of 1.6–2.2  
14 estimated by Desai et al. (2008). The standard gap-filling methods ~~of for~~ the ~~eddy covariance~~ EC  
15 flux data may lead to the overestimation of net ecosystem exchange due to the lack of winter C  
16 flux observations for the ENF sites and two of the DBF sites (YHW and IHW).

17 Our simulated successional dynamics of NEP following ~~clearcuts-clear-cuts~~ generally  
18 supported the ~~trajectory-trajectories hypothesized by Odum (1969) and of~~ Chapin et al. (2002).  
19 ~~The similar trajectories, however, were caused by but for~~ different reasons. ~~Odum's~~ ~~The~~  
20 ~~hypothesized~~ trajectories show declining GPP and relatively flat ~~community respiration~~ ER with  
21 time. Our simulated decline in NEP resulted from relatively flat GPP and growing ER with stand  
22 development (Figs. 4 and 8). This has been observed for northern temperate hardwood  
23 chronosequence sites (Desai et al., 2008), northern temperate pine forests (Peichl et al. 2010),  
24 and boreal DBF forests (e.g., Goulden et al., 2011). A recent North American Carbon Program  
25 (NACP) synthesis study showed similar changes in NEP after either stand-replacing fire or  
26 harvest based on ~~eddy covariance~~ EC chronosequence measurements across North America  
27 (Amiro et al., 2010).

28 Chapin et al. (2002) hypothesized that heterotrophic respiration is initially high ~~following~~  
29 ~~disturbance~~, declines in ~~early middle~~ succession, ~~and~~ rises ~~in middle succession, and declines~~  
30 thereafter, while NPP reaches a peak in middle age and declines in old stands. The simulated



1 | successional trajectories in heterotrophic respiration ~~were supported by the pattern~~ hypothesized  
2 | ~~pattern change, whereas although~~ our simulated NPP did not decline in mature stands  
3 | (Supplement Fig. S1). Previous studies also support our simulated trajectory in heterotrophic  
4 | respiration. For example, Pregitzer and Euskirchen (2004) reported that heterotrophic respiration  
5 | was high (mean value of  $970 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) in young temperate forests, declined with age in  
6 | middle succession, and increased with time for mature forests, ~~although for old temperate forests~~  
7 | ~~(>120 years) the decline in NPP reduced heterotrophic respiration. The~~ decline of NPP with  
8 | age was not predicted in this study. ~~Recent studies found that a decline of NPP with age is not~~  
9 | ~~“universal”~~ (Ollinger and Smith, 2005; He et al., 2012). Validation of the simulated NPP was not  
10 | possible in this study due to the lack of NPP measurements across all sites. Our simulated  
11 | heterotrophic respiration for mature DBF is close to the observation of  $502 \pm 86 \text{ g C m}^{-2} \text{ yr}^{-1}$  in a  
12 | mature DBF near UMBS tower site between 1999 and 2003 (Gough et al., 2008). However, ENF  
13 | chronosequence sites in this study show that NEP continually increased with age because of  
14 | relatively flat and low ER ( $340 \pm 96 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) and increasing GPP. ~~Successional changes in C~~  
15 | ~~fluxes after fire and harvest are similar over chronosequence sites of North America (Amiro et~~  
16 | ~~al., 2010), although a specific chronosequence study in Saskatchewan, Canada, observed that C~~  
17 | ~~fluxes are greater at the burned site than the harvested sites (Mkhabela et al., 2009).~~

18 |         Although our model underestimated NEP and GPP for both the DBF and ENF sites in the  
19 | Upper Midwest region (Figs.1 and 2), our predicted NEP was comparable to estimates from  
20 | other studies in similar regions. For example, our predicted maximum NEP for the ENF sites  
21 | ( $567\text{--}602 \text{ g C m}^{-2} \text{ yr}^{-1}$ , 29 years of age) was slightly lower than the estimates ( $690 \text{ g C m}^{-2} \text{ yr}^{-1}$ ,  
22 | 15–20 years of age) for afforested white pine (*Pinus strobus*) forests in Ontario (Coursolle et al.,  
23 | 2012). For a northern temperate forest chronosequence study in northern Michigan, NEP higher  
24 | than  $200 \text{ g C m}^{-2} \text{ yr}^{-1}$  in young DBF forests could be derived from the reference forest ( $153 \pm 115$   
25 |  $\text{g C m}^{-2} \text{ yr}^{-1}$ , 85 years of age) (Gough et al., 2007), suggesting that our predictions ( $390\text{--}430 \text{ g C}$   
26 |  $\text{m}^{-2} \text{ yr}^{-1}$ , 14–26 years of age) for the DBF sites could be in the reasonable range. Furthermore, our  
27 | predicted mean annual NEP ( $123\text{--}177 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) for mature DBF sites (>60 years) was close  
28 | to estimates for other northern DBF, including a northern hardwood forest of central  
29 | Massachusetts ( $200 \pm 40 \text{ g C m}^{-2} \text{ yr}^{-1}$ , Barford et al., 2001) and four eastern North American DBF  
30 | ( $167\text{--}236 \text{ g C m}^{-2} \text{ yr}^{-1}$ ; Curtis et al., 2002).

1 We found that the simulated AGC during forest regrowth gradually increased following  
2 the typical logistic growth curve (Sprugel, 1985). In the model, low NPP in the early stages  
3 results in slow AGC accumulation. Once the amount of NPP approximately equals annual dead  
4 biomass C that is largely controlled by the wood turnover rate, the trajectory of AGC reaches a  
5 plateau. Previous chronosequence studies showed that AGC increased with increasing age (e.g.,  
6 Peichl and Arain, 2006; Goulden et al., 2011; Powers et al., 2012). Powers et al. (2012) reported  
7 that AGC increased rapidly with age in young red pine stands across a chronosequence in  
8 northern Minnesota, USA. The representativeness and generalization of these findings were  
9 limited by the small number of young stands (Powers et al., 2012).

10 Sensitivity analysis shows that more intensive harvests could have larger and longer  
11 impacts on successional trajectories of C dynamics in early succession for both DBF and ENF.  
12 Fewer flux tower based studies have investigated the effects of harvest intensity on forest C  
13 fluxes (e.g., GPP, ER, and NEP) because of the high establishment cost of ~~eddy covariance~~  
14 ~~systems~~[EC systems](#). Nevertheless, some modeling studies have provided insights into how forest C  
15 fluxes and stocks are affected by harvest intensity. Our findings are supported by previous  
16 modeling studies. For example, a recent modeling study of temperate forests reported that more  
17 intensive harvests increased the recovery time of NPP for ENF and DBF in Minnesota and  
18 Wisconsin, USA (Peters et al. 2013). In the boreal forest of central Canada, less intensive harvest  
19 and longer rotation length might increase total C sink (~~sum of biomass C and soil organic C~~) up  
20 to 40% (Peng et al. 2002), although recent studies indicate that longer rotation length could not  
21 necessarily increase C sequestration under changing climate conditions (Wang et al., 2012b;  
22 Wang et al., 2013). [A recent synthesis study on the effects of partial cutting on forest carbon  
23 stocks found that partial cutting has no significant effects on litter C and soil organic C, although  
24 more intensive cutting can reduce more AGC \(Zhou et al., 2013b\). This synthesis study is not  
25 able to determine the recovery duration due to the lack of long-term observations](#) ~~data~~. If  
26 harvesting operations largely reduce soil organic matter, C fluxes (e.g., GPP, NPP, ER, and  
27 NEP) and living AGC are reduced for both PFTs. Consistent with this, Peters et al. (2013)  
28 showed that simulated NPP could not recover to pre-harvesting levels due to greater removal of  
29 soil organic matter. Therefore, our model results suggest management practices should aim to  
30 decrease soil disturbance caused by harvest operations.

## 4.2 Differences between ~~DBF and ENF~~ deciduous broadleaf and evergreen needleleaf forests

~~Our results showed~~ We found that DBF may reach a peak in LAI and GPP faster than ENF after ~~clearcutting~~ clear-cutting, showing clear differences in pattern of ecosystem development between the DBF and ENF sites. More rapid recovery of LAI and GPP for DBF sites lead to sooner recovery of NEP and AGC regardless of harvest intensity, supporting our second hypothesis. The foliage related parameters such as FolRelGroMax and AmaxB mainly govern the differences in successional trajectories between the two PFTs (Supplement Table S1). DBF is assumed to have more productive foliage than ENF, and more photosynthetic production then can lead to more foliage production. With this positive feedback in the model, GPP, NEP, and AGC of the DBF sites recover more rapidly than those of the ENF sites. Our findings are consistent with the chronosequence studies showing that the temperate DBF in northern Michigan rapidly became a net C sink after six years following disturbances (Gough et al., 2007) and that ENF stands in northern Wisconsin became net C sinks within 10-15 years after harvesting (Noormets et al., 2007). Through the analysis of the Forest Inventory and Analysis (FIA) data, Williams et al. (2012) suggested that faster growth in AGC at high productivity sites caused higher C fluxes and stocks. Our findings are also consistent with a recent modeling study suggesting that temperate DBF switches to positive NEP faster than temperate ENF after ~~clearcuts~~ clear-cuts, and DBF has a higher peak in NEP compared to ENF (Peckham et al., 2012). A modeling study conducted in boreal forests also reported that low productive boreal ENF needed 1-3 more years to attain a positive NEP than boreal DBF after ~~clearcuts~~ clear-cuts in Saskatchewan, Canada (Wang et al., 2012b). These observed and modeled successional changes further indicate that DBF tend to have higher photosynthetic capacity than ENF in the early stage of stand development following stand-replacing harvests.

The sensitivity analysis suggests that more productive forests could be more strongly affected by greater soil removal fraction, as soil removal reduces soil organic matter thereby resulting in relatively low nitrogen mineralization in the model. Peters et al (2013) showed that NPP was more strongly reduced for Aspen than for jack pine in their simulations. However, productive lodgepole pine (*Pinus contorta* Dougl. ex Loud.) could maintain high productivity at 12 years after harvest disturbance regardless of soil organic carbon removal and soil compaction treatments because beneficial ectomycorrhizal fungi associated with lodgepole pine could help

1 | access **nitrogen**N from organic matter; while hybrid white spruce (*Picea glauca* × *engelmannii*  
2 | [Moench] Voss) was more sensitive to the treatments (Kranabetter et al., 2006). The discrepancy  
3 | might be caused by the lack of representation of relationship between fungi and plants in the  
4 | model.

### 5 | **4.3 Limitations and challenges**

6 | PnET-CN can explicitly simulate the effects of disturbance, pollution, and climate change  
7 | on forest C dynamics (e.g., Ollinger et al., 2002; Pan et al., 2009; Peters et al., 2013). Despite the  
8 | capability of the model, ~~we do recognize that~~ the model has some limitations in simulating  
9 | harvesting effects, and ~~that the~~ accurate representation of the trajectories of C fluxes and stocks  
10 | following harvests still remains a challenge.

11 | ~~First, T~~he performance of the model to simulate forest regrowth after harvests is limited  
12 | by the absence of population and community dynamics ~~associate~~associated with regeneration  
13 | regeneration and understory in the model. Most process-based models such as PnET-CN and  
14 | TEM (Raich et al., 1991) have been ~~mainly~~ developed primarily to simulate C balance for  
15 | mature forests over the past decades (Landsberg, 2003), resulting in no provision for simulating  
16 | regeneration such as shrub component and species-specific successional dynamics in these  
17 | models. Changes in forest composition (e.g., evergreen and deciduous tree species and  
18 | understory shrubs) along the course of succession are not fully considered by most ecosystem  
19 | models. PnET-CN does not simulate shrubs and herbs that likely dominate stands in the early  
20 | successional stage after stand-replacing harvests. ~~Therefore, T~~he model thus is not able to  
21 | simulate the particularly high GPP and ER in the young forests where forest canopy has not yet  
22 | fully recovered.

23 | Understory layer is also an important component for mature forest ecosystems in terms of  
24 | C fluxes and stocks. Misson et al. (2007) reported that understory can contribute 11% (range, 0–  
25 | 39%) of GPP at 10 sites across a wide range of forest type and climate. PnET-CN slightly  
26 | overestimated overstory LAI for the mature DBF sites and reasonably predicted foliar **nitrogen**N  
27 | concentration compared to satellite-based estimates ~~(data not shown)~~. The lack of understory  
28 | layer in the model is possibly responsible for the underestimation of GPP for mature DBF sites.  
29 | Species competition and cohort methods that have been employed in other models such as ED

1 (Medvigy et al., 2009) and LPG-Guess (Smith et al., 2001) could be used to improve the  
2 regeneration and understory components of PnET-CN in the future.

3 ~~Second, P~~parameter values used in the model were generally derived from specific  
4 measurements for a given stand development stage particularly mature forests, although the  
5 parameter values likely differ with stand development. For example, the canopy light attenuation  
6 constant coefficient is typically measured in mature forests (e.g., Ryu et al., 2008), although the  
7 coefficient is known to change with canopy cover (Brantley and Young, 2007). The use of the  
8 canopy light attenuation coefficient measured in mature forest for whole forest life simulations  
9 could slow down stand development due to the underestimation of photosynthesis in young  
10 forests. Understanding the relationship between such parameters and state variables (e.g., LAI) is  
11 thus one of the challenges to simulate the effects of stand-replacing harvests on forest C  
12 dynamics.

13 ~~Third, c~~Changing climate conditions can also affect the values of some parameters. For  
14 example, wood turnover rate (%), tree mortality in terms of biomass losses), to which wood living  
15 biomass C and soil organic C are sensitive, could be altered by extreme weather conditions  
16 including droughts (Allen et al., 2010; Wang et al., 2012a). Most process-based models are not  
17 able to simulate the mechanistic processes associated with tree mortality under changing climate  
18 conditions (McDowell, 2011; Wang et al., 2012a), although there is growing interest in the  
19 mechanistic modeling of forest mortality (e.g., McDowell et al., 2013; Powell et al., 2013).  
20 Recent studies have revealed that climate and disturbance legacies govern forest C dynamics  
21 (Magnani et al., 2007; Bond-Lamberty et al., 2013). Future modeling efforts can benefit from  
22 improved understanding of the effects of climate change on parameter values that are assumed to  
23 be constant in the model.

24 ~~Finally, the whole silvicultural system (e.g., harvests) is not fully considered in the~~  
25 ~~model.~~ Harvest methods depend on forest types, management needs, and species to be  
26 regenerated. For example, selective harvesting or shelterwood system is typically used for  
27 hardwoods in Wisconsin (Wisconsin Department of Natural Resources, 2011). Stand-replacing  
28 harvesting was assumed for both DBF and ENF chronosequence sites due to the lack of  
29 harvesting information and the types of clearing applied to the sites studied. The sensitivity  
30 analysis conducted in this study suggests that harvest intensity affects C dynamics in early

1 succession after harvesting. Observations in residuals and post stands after each operation type  
2 (e.g., pre-commercial thinning and selective harvesting) are needed to parameterize process-  
3 based models for better mechanistic understanding of the harvest effects on forest C dynamics.

4 ~~Besides disturbances, climate is also a key driver of ecosystem structure and function.~~  
5 ~~Climate extremes such as drought induce forest die-off and reduction of carbon uptake globally~~  
6 ~~(Ciais et al., 2005; Kurz et al., 2008; van Mantgem et al., 2009; Zhao and Running, 2010; Peng~~  
7 ~~et al., 2011; Ma et al., 2012; Schwalm et al., 2012). In North America, droughts and disturbance~~  
8 ~~are two main sources of interannual variability in carbon fluxes (Xiao et al. 2011, 2014). Future~~  
9 ~~modeling studies should explicitly the effects of both disturbance and climate extremes.~~

## 10 **5 Conclusions**

11 The PnET-CN model ~~is~~was generally able to simulate the effects of stand-replacing  
12 harvests on forest C dynamics (C fluxes and AGC) for two northern temperate forest  
13 chronosequences. The predicted dynamics in NEP and AGC following ~~clearcuts~~clear-cuts  
14 generally follow the hypothesized trajectories (~~Odum, 1969; Chapin et al., 2002~~), although our  
15 simulations show that the decline in NEP was due to relatively flattening-stable GPP and  
16 gradually increasing ER. Our study also shows that DBF recovered faster (11 years) from net C  
17 sources to net sinks and accumulated more C in AGC than ENF. Northern temperate ENF is  
18 more vulnerable to stand-replacing harvests than northern temperate DBF. Future research is  
19 needed to better understand how respiration components (e.g., ecosystem and soil respiration)  
20 and production components (e.g., overstory and understory) change with forest age and their  
21 determinants. Modeling the combined effects of climate change and forest management will  
22 benefit from the incorporation of forest population dynamics (e.g., regeneration and mortality),  
23 relationships between age-related model parameters and state variables (e.g., LAI), and  
24 silvicultural system into the model. With these improvements, process-based ecosystem models  
25 can better simulate regional C balance associated with disturbance regime under changing  
26 climate.

## 27 **Acknowledgements**

28 This study was supported by the National Science Foundation (NSF) through  
29 MacroSystems Biology (award number 1065777; ~~PI: J. Xiao~~) and by the National Aeronautics  
30 and Space Administration (NASA) through Terrestrial Ecology Program (award number

1 | [NNX11AB88G](#) and Carbon Cycle Science Program (award number [NNX14AJ18G](#)). We thank  
2 Lucie Lepine, Zaixing Zhou, Andrew Ouimette, and Alexandra Thorn for helpful discussion. We  
3 also thank the anonymous reviewers and Peter Curtis for their constructive comments on the  
4 manuscript.  
5

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8

1 **Tables**

2 Table 1 Site characteristics for two chronosequences of deciduous broadleaf forests (DBF) and evergreen needleleaf forests (ENF) in  
 3 Upper Midwest region of Wisconsin and Michigan, United States.

Site	ID	Location	Plant function type	Dominant species	Year of recent disturbance	AGC (Mg ha <sup>-1</sup> , 2005)	LAI (m <sup>2</sup> m <sup>-2</sup> , 2002)	Data period	Reference
Clearcut young hardwood	YHW	46.72°N 91.25°W	DBF	Aspen, red maple	1999	3.3 (1.3)	0.79 (0.6)	2002	Noormets et al. 2007
Intermediate hardwood	IHW	46.73°N 91.23°W	DBF	Aspen	1984	47.6 (15.6)	3.0	2003	Noormets et al. 2008
Willow creek	WIC	45.80°N 90.08°W	DBF	Sugar maple, basswood, green ash	1875 <sup>a</sup> , 1933	74.9 <sup>b</sup>	5.36 (0.47) <sup>c</sup>	2000-2006	Cook et al., 2008, Curtis et al. 2002
University of Michigan Biological Station	UMBS	45.56°N 84.71°W	DBF	Aspen, white pine, red oak, sugar maple	1920	73.2 (3.1) <sup>d</sup>	3.54 (0.31) <sup>e</sup>	2000-2003	Gough et al. 2008
Young red pine	YRP	46.72°N 91.18°W	ENF	Red pine, jack pine	1993	7.7 (8.3)	0.52 (0.3)	2002	Noormets et al. 2007
Young jack pine	YJP	46.62°N 91.08°W	ENF	Jack pine	1987	4.9 (5.0)	0.93	2004-2005	Noormets et al. 2008
Intermediate red pine	IRP	46.69°N 91.15°W	ENF	Red pine	1980	47.7 (37.3)	3.0	2003	Desai et al. 2008
Mature red pine	MRP	46.74°N 91.17°W	ENF	Red pine, aspen	1939	56.9 (33.1)	2.7 (0.8)	2002-2005	Noormets et al. 2007

4 <sup>a</sup> estimated year of disturbance based on Ameriflux site description in AmeriFlux.  
 5 <sup>b</sup> sum of wood and foliage biomass carbon from Curtis et al., 2002.  
 6 <sup>c</sup> estimated values based on measurements in 1998 to 2000 and 2002 from Cook et al., 2008.,  
 7 <sup>d</sup> value in 2003 from Gough et al. 2008.  
 8 <sup>e</sup> calculated based on multi-year (1999-2003) estimations with litter traps from Gough et al. 2008.

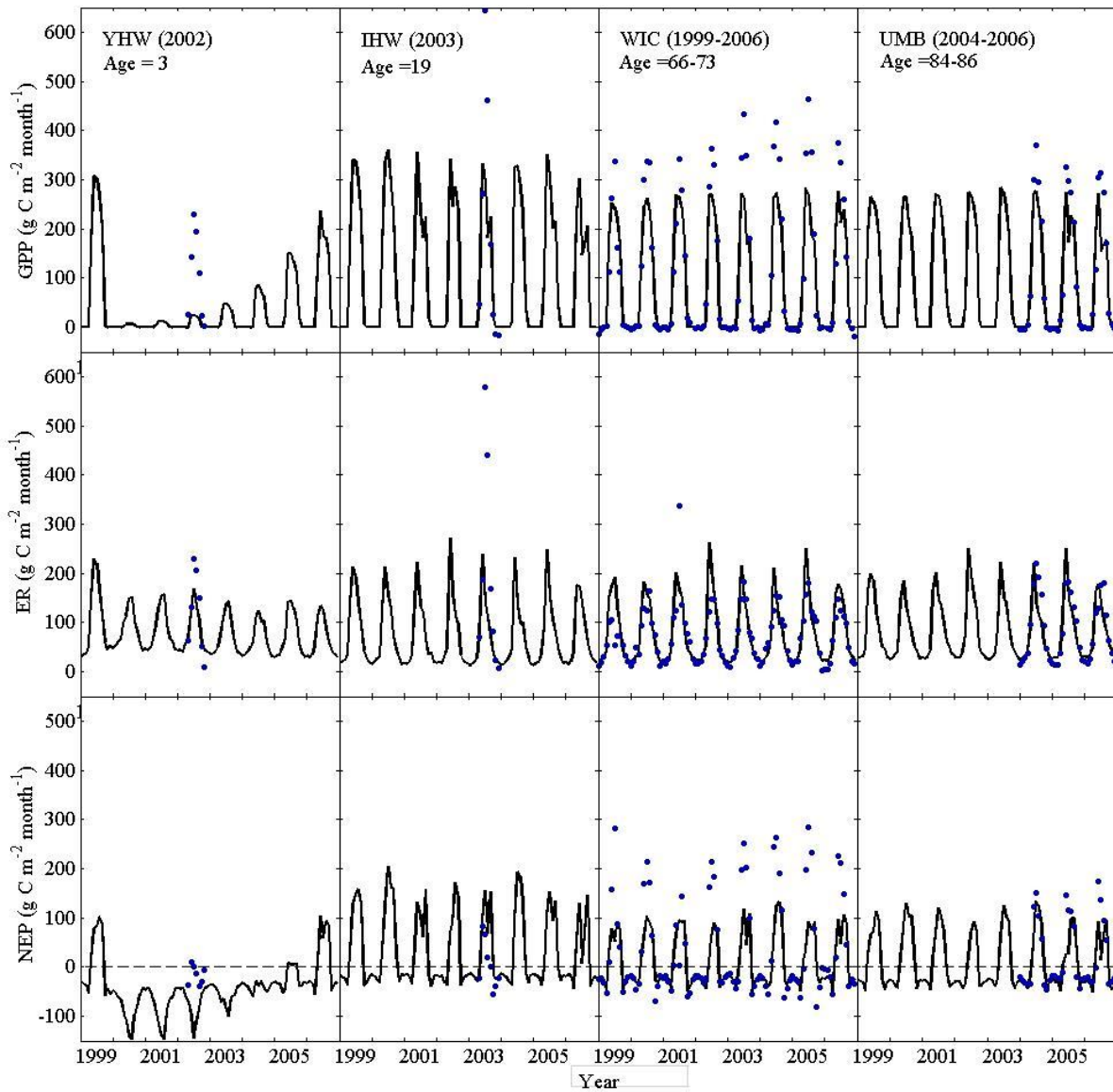
1 | Table 2 ~~PnET-PnET-CN~~ model performance in monthly carbon fluxes (GPP: gross primary  
 2 | productivity; ER: ecosystem respiration; NEP: net ecosystem productivity), leaf area index  
 3 | (LAI), and aboveground carbon stock (AGC) for the two chronosequences.

	<b>NRMSE%<sup>a</sup></b>	<b><i>d</i><sup>b</sup></b>	<b>n</b>
<b><i>DBF</i></b>			
GPP	10	0.95	147
ER	10	0.92	147
NEP	17	0.81	147
LAI	33	0.97	4
AGC	42	0.95	4
<b><i>ENF</i></b>			
GPP	28	0.91	64
ER	37	0.88	64
NEP	46	0.58	64
LAI	29	0.96	4
AGC	37	0.94	4
<b><i>Overall</i></b>			
GPP	11	0.94	211
ER	10	0.91	211
NEP	21	0.73	211
LAI	31	0.96	8
AGC	28	0.95	8
Total performance <sup>c</sup>	20	0.90	

4 <sup>a</sup> Normalized root mean square error.

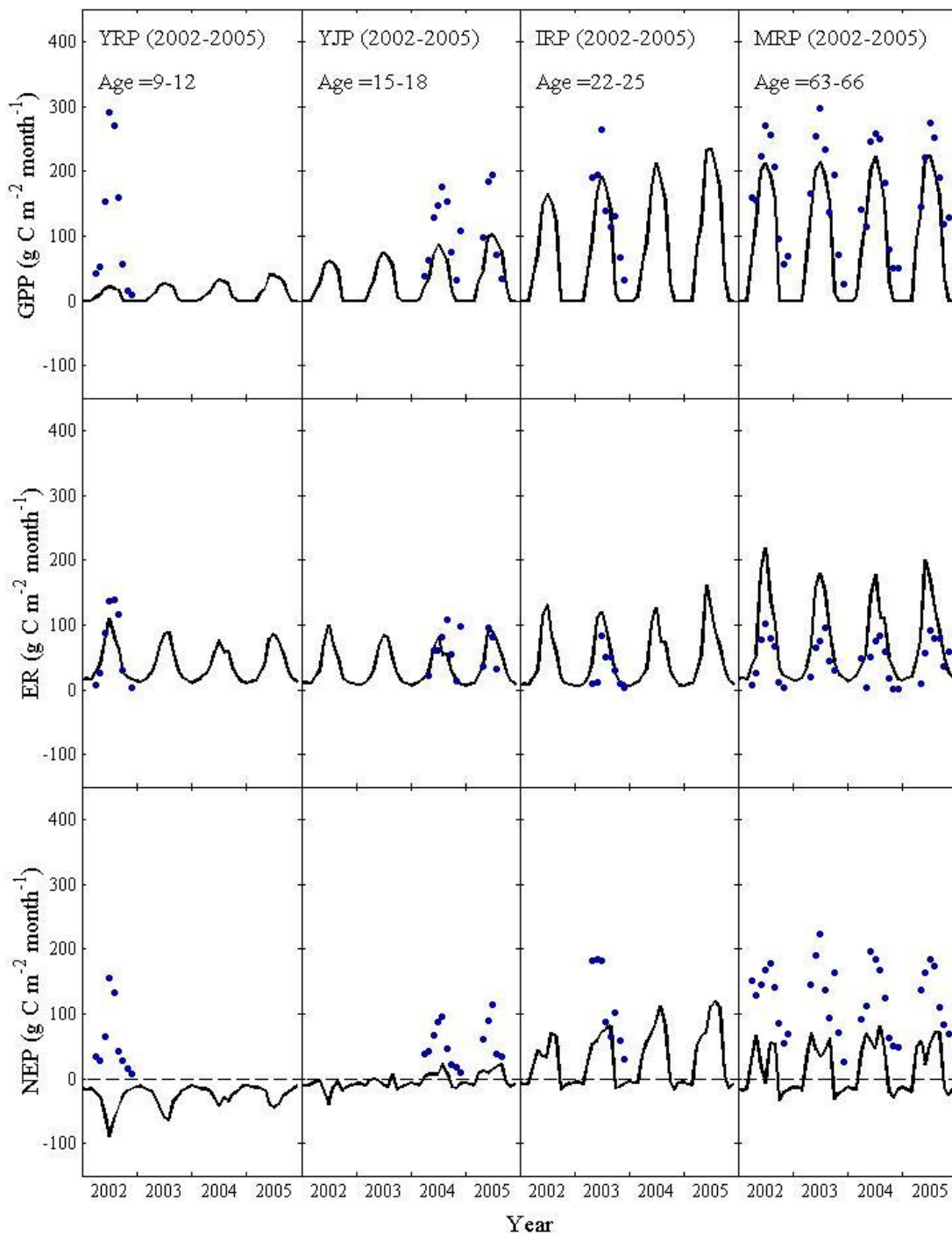
5 <sup>b</sup> Willmott index.

6 <sup>c</sup> Mean value of evaluating statistics for all tested variables.



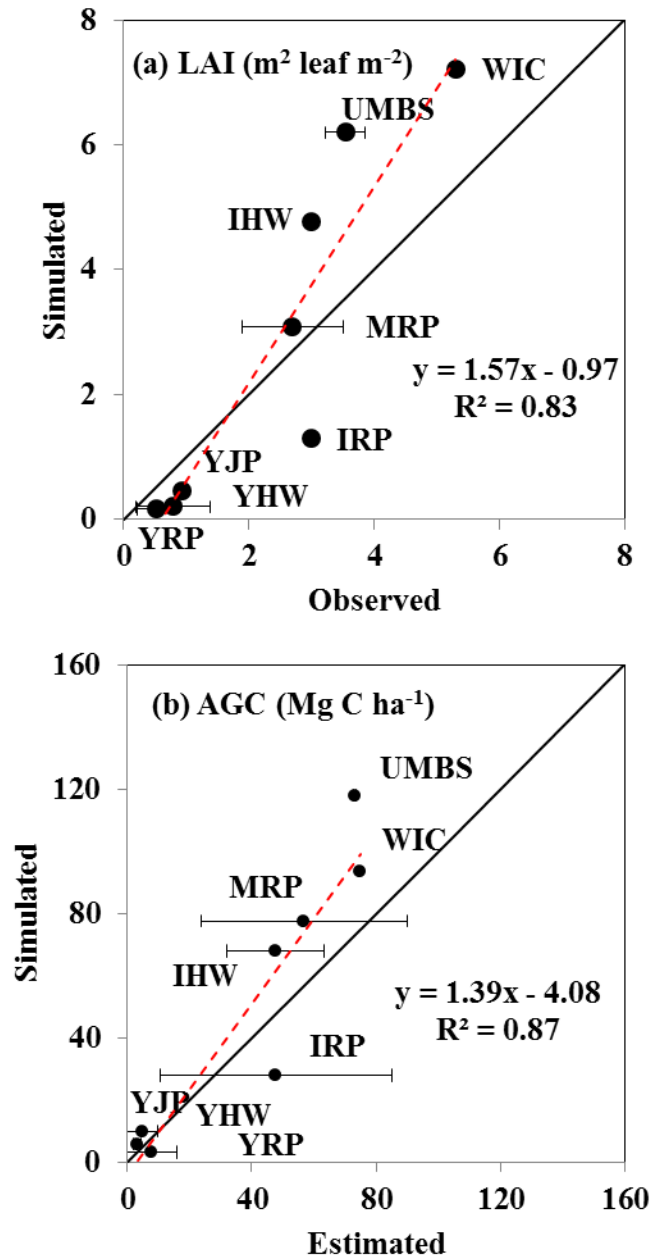
1  
 2 Figure 1. Simulated (lines) and observed (symbols) monthly carbon fluxes: GPP, ER, and NEP  
 3 for the deciduous broadleaf chronosequence sites from 1999-2007.  
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 2 Figure 2. Simulated (lines) and observed (symbols) monthly carbon fluxes: GPP, ER, and NEP  
 3 for the evergreen coniferous chronosequence study sites from 2002-2005.

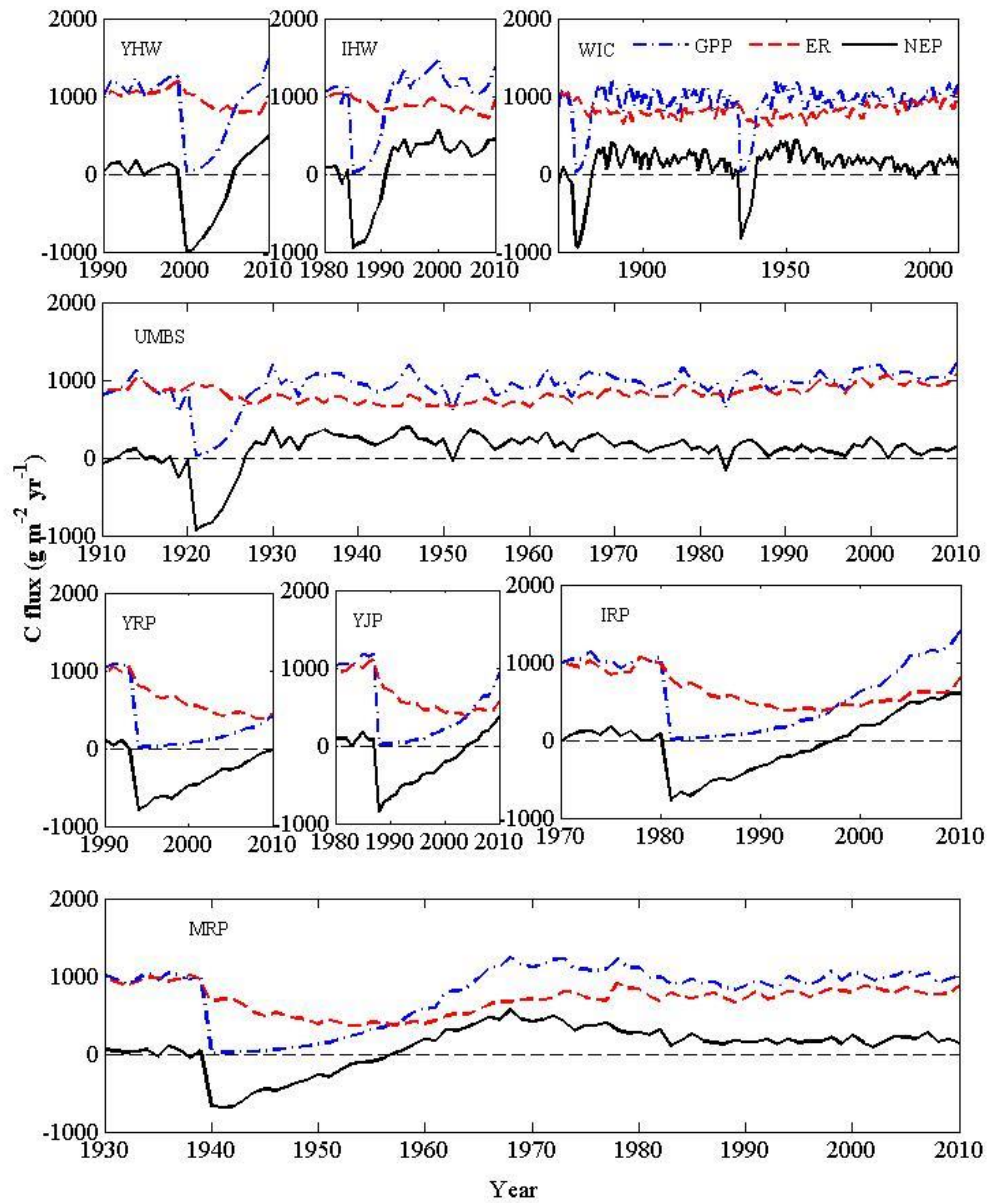
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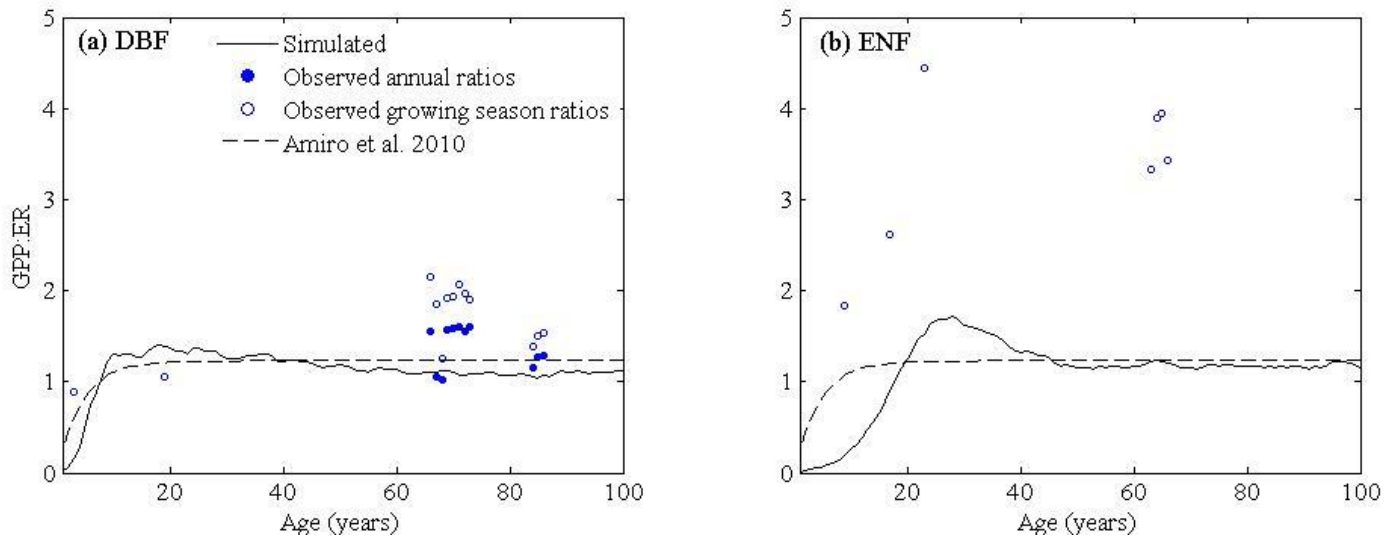
2 Figure 3. Comparisons of simulated and observed (a) leaf area index (LAI) and  
 3 aboveground carbon stock (AGC) for all eight sites.

4



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 2 Figure 4. Simulated trajectories of GPP, ER, and NEP for each site based on the site disturbance  
 3 history (Table 1). The time series started from the earliest major disturbance for each site.  
 4

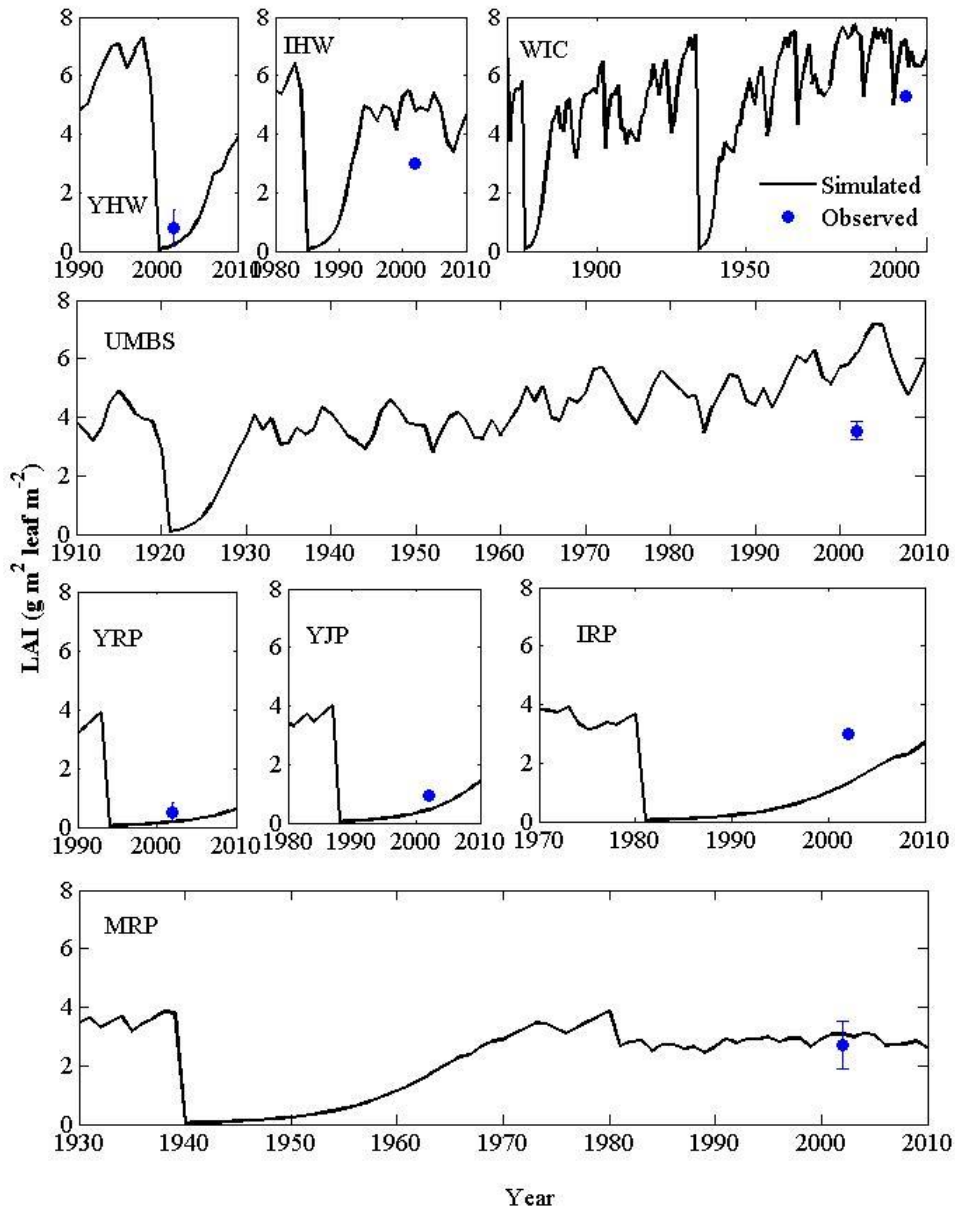
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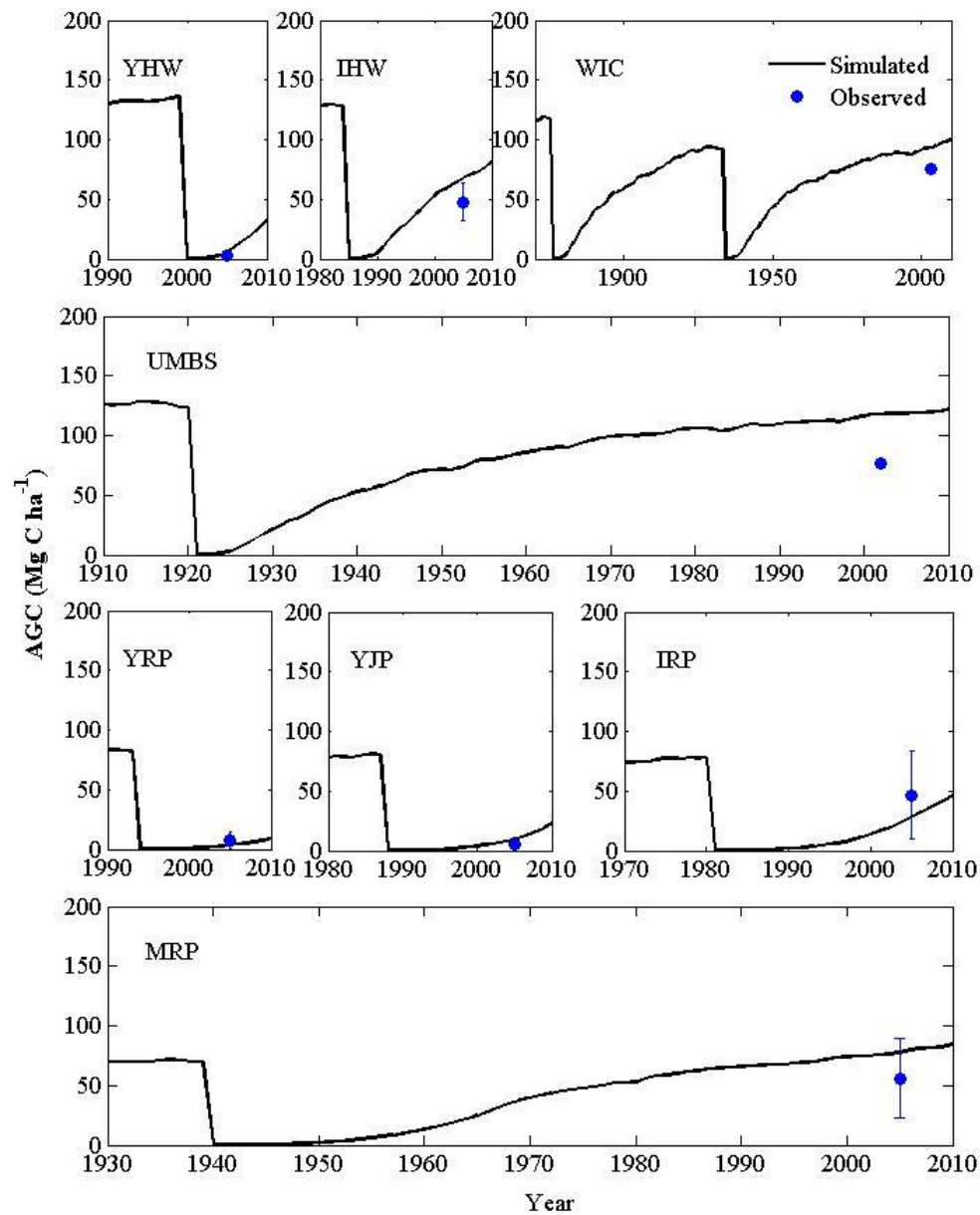
3 Figure 5. Simulated trajectories of the annual GPP/ER ratio with stand age for (a) deciduous  
4 broadleaf forests (DBF) and (b) evergreen ~~coniferous-needleleaf~~ forests (ENF). The dashed line  
5 is a fitted curve derived by Amiro et al. (2010) using eddy covariance observations from forest  
6 chronosequences ~~forests~~ in North America. Solid and hollow circles represent measured annual  
7 and growing season (May to October) ratios, respectively. The simulated curves were smoothed  
8 using a moving average filter with a span of 5.

9



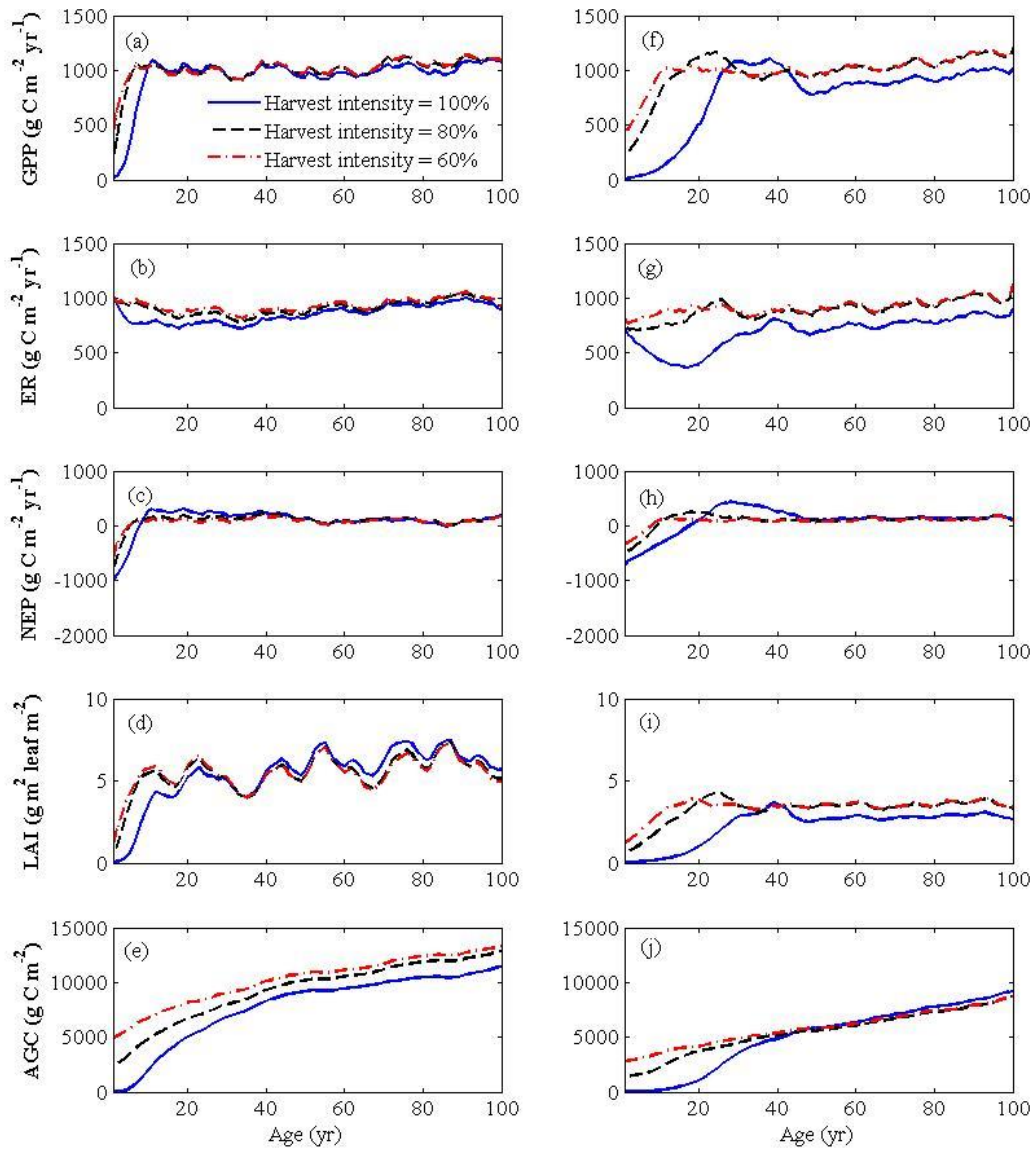
1  
 2 Figure 6. Simulated trajectories of LAI for each site based on the site disturbance history (Table  
 3 1). The time series started from the earliest major disturbance for each site. Symbols represent  
 4 measured LAI.

5



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2 Figure 7. Simulated trajectories of aboveground biomass carbon (AGC) for each site based on  
 3 the site disturbance history (Table 1). The time series started from the earliest major disturbance  
 4 for each site. Symbols represent estimated AGC.



1  
 2 Figure 8. Sensitivity of carbon fluxes (GPP, gross primary production; ER, ecosystem  
 3 respiration; NEP, net ecosystem production) and stand characteristics (LAI: leaf area index;  
 4 AGC: aboveground carbon stock) to changes in harvest intensity (reduced by 0.2 and 0.4  
 5 compared to 1 for assumed clearcuts-clear-cuts used in the model tests) for (a-e) deciduous  
 6 broadleaf forests (DBF) at Willow creek and (f-j) evergreen coniferous forests (ENF) at Mature  
 7 red pine site over a 100-yr harvest cycle. The simulated curves were smoothed using a moving  
 8 average filter with a span of 5.

9

We also made some edits to improve the language. Please see the marked manuscript as below.

Thank you and the three reviewers for your great help on this manuscript.

Yours sincerely,

Weifeng Wang