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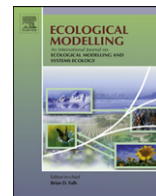
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# The effects of forest harvest intensity in combination with wind disturbance on carbon dynamics in Lake States Mesic Forests

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## ABSTRACT

Total forest carbon (C) storage is determined by succession, disturbances, climate, and the edaphic properties of a site or region. Forest harvesting substantially affects C dynamics; these effects may be amplified if forest harvesting is intensified to provide biofuel feedstock. We tested the effects of harvest intensity on landscape C using a simulation modeling approach that included C dynamics, multiple disturbances, and successional changes in composition. We developed a new extension for the LANDIS-II forest landscape disturbance and succession model that incorporates belowground soil C dynamics derived from the CENTURY soil model. The extension was parameterized and calibrated using data from an experimental forest in northeastern Wisconsin, USA. We simulated a 9800 ha forested landscape over 400 years with wind disturbance combined with no harvesting, harvesting with residual slash left on site ('standard harvest'), and whole-tree harvesting. We also simulated landscapes without wind disturbance and without eastern hemlock (*Tsuga canadensis*) to examine the effects of detrital quantity and quality on C dynamics. We estimated changes in live C, detrital C, soil organic C, total C, and forest composition. Overall, the simulations without harvesting had substantially greater total C and continued to sequester C. Standard harvest simulations had more C than the whole tree harvest simulations. Under both harvest regimes, C accrual was not evident after 150 years. Without hemlock, SOC was reduced due to a decline in detritus and a shift in detrital chemistry. In conclusion, if the intensity of harvesting increases we can expect a corresponding reduction in potential C storage. Compositional changes due to historic circumstances (loss of hemlock) may also affect forest C although to a lesser degree than harvesting. The modeling approach presented enabled us to consider multiple, interacting drivers of landscape change and the subsequent changes in forest C.

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## 1. Introduction

Forests are an essential component of the carbon cycle (Dixon, 1994; Houghton and Hackler, 2000; Goodale et al., 2002; Birdsey et al., 2006). In the U.S., soils contain ~60% of total forest carbon on average (Birdsey and Heath, 1995). Forests are subject to a wide range of disturbances overlapping in space and time that alter biomass, species composition and successional trends (Pregitzer and Euskirchen, 2004). Disturbances also have cumulative and diverse effects on soil C and N (Schimel, 1997; Overby et al., 2003; Hurteau et al., 2008). Forest management has a significant, although widely varying, effect on detrital, forest floor, and soil C

(Johnson and Curtis, 2001; Currie et al., 2003; Yanai et al., 2003; Heath et al., 2003). Soil N (and to a lesser extent, C) will feed back to the overstory through species replacement over time (Pastor and Post, 1986; Reich et al., 1997; Ollinger et al., 2002a,b). This complex suite of interactions creates obstacles to understanding and predicting ecosystem responses. Because of these interactions, disturbances cannot be studied in isolation from other factors. The scale of inquiry must accommodate the expected range of disturbance sizes, frequencies, and intensities.

There have been numerous empirical studies of the total carbon balance (commonly referred to as Net Biome Production [NBP] or Net Ecosystem Exchange [NEE]), including disturbance effects, at landscape (Gough et al., 2007), regional (Law et al., 2004), and sub-continental spatial scales (Kurz and Apps, 1999). Such empirical studies are essential to understanding forest dynamics. However, they do not provide a framework for understanding longer-term disturbance, succession, and soil interactions and provide limited predictive capacity. The effects of spatially and temporally over-

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lapping disturbance regimes are less well understood due to the requisite long durations and large extents over which they occur (Paine et al., 1998; Platt et al., 2002).

Models are often applied to improve understanding forest carbon dynamics especially when multiple factors need be considered. Some models of canopy–soil interactions simulate a constant forest composition while allowing the simulated forest plot to age (Peltoniemi et al., 2004). Plant functional types (Smith and Huston, 1989) are often used to represent forest change (e.g., Bachelet et al., 2001; Running and Hunt, 1993; Moorcroft et al., 2001) to represent the interactions among forest biomes and biogeochemistry at continental scales (VEMAP Members, 1995; Pan et al., 1998; Burke et al., 2003). However, there is large variation among and within genera in response to different disturbance regimes (Loehle, 2000). For example, within *Pinus*, species response to fire is diverse—including epicormic resprouting (e.g., *P. rigida*), serotiny (e.g., *P. banksiana*), or substantial fire tolerance due to thick bark (e.g., *P. ponderosa*). Consideration of species response to multiple disturbances is critical to understanding forest change at regional or landscape scales ( $<10^7$  ha).

As species composition shifts, litter (including leaf or needle, wood, and root litter) chemistry will likewise change. Litter chemistry is a dominant control on rates of decomposition (Cornwell et al., 2008) and nitrogen mineralization (Ollinger et al., 2002b) and will therefore exert control over gross primary productivity (Finzi et al., 1998; Lovett et al., 2004; Cornwell et al., 2008).

Our objective was to assess the effects of forest harvesting, harvest intensity, and wind disturbances on total forest carbon, taking into account shift in species composition due to disturbance, succession, and historical loss of former canopy dominants. To do so, we expanded an existing model of succession and disturbance interactions, LANDIS-II (Scheller et al., 2007), by creating a new model extension derived from a widely used soil dynamics model, CENTURY (Parton et al., 1983, 1993, 1994; Schimel et al., 1994; Schimel, 1997; Pan et al., 1998). Next, we applied the new model extension to a landscape calibrated and parameterized with data from an experimental forest in northeastern Wisconsin, USA. A series of comparative scenarios were used to explore the effects of harvesting, wind, and species composition on forest C.

## 2. Methods

### 2.1. Study area

The Willow Creek experimental forest, located in the Chequamegon-Nicolet National Forest in north Central Wisconsin, USA (45.806°N, 90.080°W) was used to parameterize and calibrate our simulations (Cook et al., 2004; Martin and Bolstad, 2005; Desai et al., 2005). The topography of Willow Creek is dominated by glacial drumlins, moraines, and depressions and the soil is sandy loam derived from glacial till (see Cook et al., 2004 for further details). Willow Creek contains 12 long-term measurement plots and an AmeriFlux tower for monitoring forest–atmosphere exchange of CO<sub>2</sub> (Cook et al., 2004; Desai et al., 2005; Martin and Bolstad, 2005). The climate is cold continental (January mean temperature =  $-12^{\circ}\text{C}$ , July =  $19.3^{\circ}\text{C}$ ) with most precipitation occurring during the summer. The sites are diverse with overstory dominance by sugar maple (*Acer saccharum*), red maple (*A. rubrum*), green ash (*Fraxinus pensylvanica*), and basswood (*Tilia americana*) (Cook et al., 2004). Other species historically or currently common in the area include balsam fir (*Abies balsamifera*), yellow birch (*Betula alleghaniensis*), paper birch (*Betula papyrifera*), white pine (*Pinus strobus*), trembling aspen (*Populus tremuloides*), red oak (*Quercus rubrum*), white cedar (*Thuja occidentalis*), and eastern hemlock (*Tsuga canadensis*).

### 2.2. LANDIS-II description

LANDIS-II simulates disturbance, dispersal, and succession and is substantially derived from earlier LANDIS models (Mladenoff et al., 1996; Mladenoff, 2004; Scheller et al., 2007, 2010). LANDIS models represent a landscape as square cells which are assigned to an ecoregion (or ‘landtype’) with homogeneous soil properties and climate. Individual species with unique life history attributes, including tolerance to various disturbances, are represented as cohorts that are defined by species and age. Within LANDIS models, trees are represented as species and age cohorts rather than as individuals or density of individuals. There may be multiple species and multiple cohorts per species in each cell. In LANDIS-II, the ages represented by each cohort are determined by the successional time step. LANDIS models have been used to address the effects of climate change (Scheller and Mladenoff, 2005, 2008; Xu et al., 2007, 2009), wildfire (Scheller et al., 2005, 2008; Sturtevant et al., 2009), harvesting (Ward et al., 2005), insect defoliations (Sturtevant et al., 2004), and other disturbance or management scenarios.

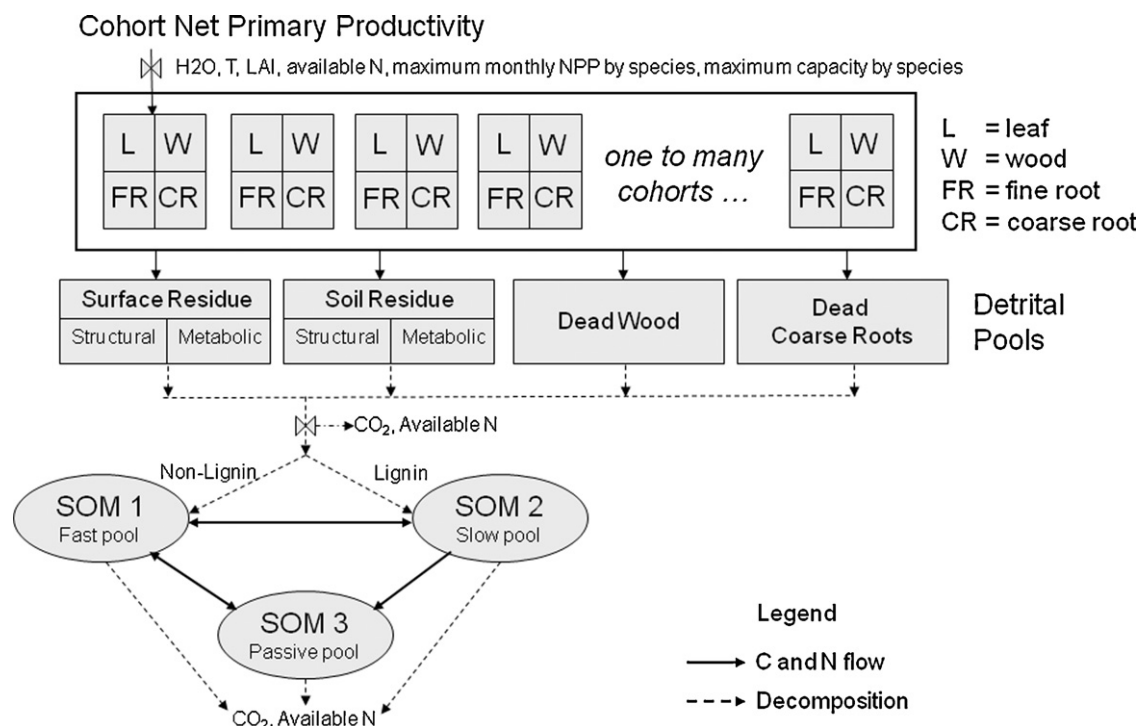
### 2.3. CENTURY description

CENTURY is a plot-scale model that projects soil carbon, nitrogen, and other limiting nutrients with a fixed aboveground biome type and a non-spatial disturbance module. CENTURY was originally developed for grassland ecosystems and was expanded to simulate many biomes, including savannah, tundra, and forest (Kirschbaum and Paul, 2002; Parton et al., 1983, 1993, 1994; Schimel et al., 1994; Pan et al., 1998). CENTURY divides soil organic matter (SOM) into three principal compartments: fast, slow, and passive. Soil organic matter includes carbon and nitrogen at a minimum and can also include sulphur and phosphorous. There are also surface and soil litter layers (each divided into structural and metabolic components). Aboveground dynamics are represented as a single forest or biome type with five carbon pools: leaf, fine branch, large wood, fine root, and coarse root. Snags are not explicitly represented. There are no successional dynamics *per se*: forest composition does not change over time. CENTURY and its derivatives have been widely applied to forests worldwide (e.g., Schimel et al., 1994; Schimel, 1997; Kirschbaum and Paul, 2002).

### 2.4. Development of the CENTURY succession extension

We developed a new succession extension for LANDIS-II that links aboveground processes of stand dynamics to below ground processes of soil carbon and nitrogen dynamics (Fig. 1). The new extension combines elements of the existing Biomass Succession extension v2.1 (Scheller and Mladenoff, 2004) and CENTURY v4.5 (<http://www.nrel.colostate.edu/projects/century/>). The new extension offers advantages over either model alone: (1) use of existing models of interactions between forest canopy and forest disturbance regimes in a spatial context; (2) changes in species composition over time are explicitly coupled with soil dynamics.

Within the CENTURY extension, each species–age cohort has an associated leaf biomass, aboveground wood biomass, coarse root biomass, and fine root biomass ( $\text{g m}^{-2}$ ) (Fig. 1). The size of each cohort component is a function of net primary productivity, C allocation (detailed below), and mortality. Annual fraction leaf and fine root mortality is the inverse of leaf longevity and occurs at a user-designated month. Monthly fraction aboveground wood and coarse root mortality is user determined and includes all forms of wood mortality including thinning and loss of branches. In addition, age-related mortality will begin substantially reducing AGB after a cohort reaches 80% of maximum longevity (Scheller and Mladenoff, 2004). Seed dispersal operates identically to previous LANDIS-II succession extensions (Ward et al., 2005). We incorpo-



**Fig. 1.** Schematic diagram of the CENTURY succession extension for LANDIS-II. In the top panel, species and age cohorts with leaf, wood, fine root, and coarse root components are represented. Following mortality, this biomass is transferred to one of the detrital pools. Foliage is transferred to the surface residue pool; fine roots to the soil residue pool. As decay progresses, carbon and nitrogen are transferred to and among the fast, slow, and passive soil organic matter (SOM) pools, with some loss to the atmosphere and through leaching.

rated the probability of establishment (Scheller et al., 2005) into the extension to take advantage of the dynamic weather and site specific available N (see below).

A number of simplifications in the representation of soil processes from CENTURY were required for model integration. Additional simplifications became possible because the extension is intended for forests alone whereas CENTURY was designed for all biomes. First, we limited our simulations to a single soil layer containing the three CENTURY soil pools, which is more congruent with the coarse data typically available for large forested landscapes. The original CENTURY allows up to 10 soil layers. Second, only nitrogen was simulated as a limiting nutrient. Broad-scale data for which to parameterize and calibrate additional nutrients, such as phosphorus or calcium, is currently not widely available for forest ecosystems. Third, because only forests were simulated, a number of parameters were given fixed values (Appendix A). Parameters not relevant to forest dynamics were eliminated, e.g., irrigation. Fourth, we did not include fine branches.

Although LANDIS-II operates at annual or multi-year time steps, within the CENTURY extension both growth and decomposition are calculated on a monthly time step. As growth and decomposition occur at monthly time steps, monthly climate is a required input. Required monthly climate inputs include minimum temperature (°C), maximum temperature, standard deviation of mean temperature, precipitation (cm), and standard deviation of precipitation. Climate inputs can be used to stochastically generate annual weather from the monthly means and standard deviations. The climate data can be updated at any annual time step. Because LANDIS-II limits disturbances and reproduction to annual events, the monthly cycle within the CENTURY extension proceeds from July to June, reflecting the fact that most disturbances occur in the summer months.

Individual cohort NPP was estimated from the CENTURY growth function whereby NPP is governed by a maximum monthly NPP and

further limited by soil moisture, available N, soil temperature, and leaf area index (LAI) (Parton et al., 1993). A maximum aboveground biomass (AGB) also limits the capacity of each cohort (Scheller and Mladenoff, 2004). Competition emerges from N limitations (larger cohorts access a larger portion of mineral N, scaled to the square root of AGB) and LAI limitations (older cohorts typically have larger LAI). Aboveground NPP allocation to leaves and wood is determined by an input value. Fine root and coarse root biomass are calculated as a fixed fraction of the leaf (0.7) and wood components (0.25), respectively.

The new extension requires three general input types. Species-specific inputs include C, N, lignin (estimated from published CENTURY forest type data) and other physiological attributes (Table 1). Species are also assigned to functional types allowing for simplification of parameters that do not vary significantly among specific groups or are poorly known (Table 2). Ecoregion inputs include soil properties and initial conditions (Table 3). Sensitivity tests of the CENTURY model to soil and climate have been conducted previously (e.g., Parton et al., 1994; Peng and Apps, 1999; Bricklemeyer et al., 2007).

The extension was written in the C# programming language (Archer and Whitechapel, 2002) using an object oriented design (Sequeira et al., 1997; Lorek and Sonnenschein, 1999). Each SOM pool at each site is a separate object with an associated C (g m<sup>-2</sup>), N (g m<sup>-2</sup>), type (soil or surface), lignin fraction, and net N mineralization.

## 2.5. Extension calibration

We calibrated the CENTURY succession extension by comparing simulated Net Ecosystem Exchange (NEE, carbon flux into and out of the entire landscape including NPP and heterotrophic respiration; not including exported biomass) against measured NEE at the Willow Creek flux tower (Cook et al., 2004). We initial-



**Table 1**  
Physiological parameters for 13 common tree species in northern Wisconsin, USA.

Species name	Functional type	Nitrogen tolerance	Leaf longevity (years)	Leaf lignin (%)	Fine root lignin (%)	Wood lignin (%)	Coarse root lignin (%)	Leaf CN ratio	Fine root CN ratio	Wood CN ratio	Coarse root CN ratio	Litter CN ratio
<i>Abies balsamifera</i>	2	2	3	0.2	0.2	0.35	0.35	100	50	380	170	100
<i>Acer rubrum</i>	1	2	1	0.223	0.255	0.255	0.255	25	45	90	90	45
<i>Acer saccharum</i>	1	2	1	0.223	0.255	0.255	0.255	25	45	90	90	45
<i>Betula alleghaniensis</i>	1	2	1	0.223	0.255	0.255	0.255	25	45	90	90	45
<i>Betula papyrifera</i>	1	2	1	0.223	0.255	0.255	0.255	30	45	90	90	45
<i>Fraxinus pennsylvanica</i>	1	1	1	0.223	0.255	0.255	0.255	25	45	90	90	45
<i>Pinus strobus</i>	2	2	3	0.2	0.2	0.35	0.35	100	50	380	170	100
<i>Populus tremuloides</i>	1	3	1	0.223	0.255	0.255	0.255	30	45	90	90	45
<i>Quercus rubrum</i>	3	2	1	0.175	0.23	0.23	0.23	52	48	500	333	50
<i>Thuja occidentalis</i>	2	3	4	0.2	0.2	0.35	0.35	100	50	380	170	100
<i>Tilia americana</i>	1	1	1	0.223	0.255	0.255	0.255	25	45	90	90	45
<i>Tsuga canadensis</i>	2	2	3	0.2	0.2	0.35	0.35	100	50	380	170	100

**Table 2**  
Functional type parameters for the species listed in Table 1.

Name	Functional type index	PPDF1 mean	PPDF2 max	PPDF3 shape 1	PPDF4 shape 2	NPP leaf (%)
NHardwoods	1	20	32	0.2	8	0.5
Conifer	2	15	32	1	3.5	0.37
Oaks	3	25	45	1	3	0.5

Name	BTOLAI	KLAI	MAXLAI	PPRPTS2	PPRPTS3	Wood mortality (%/mo)
NHardwoods	0.00823	3000	20	1	0.8	0.003
Conifer	0.00823	3000	10	1	0.8	0.003
Oaks	0.00823	2000	20	1	0.8	0.003

ized a single cell with a hardwood forest having a similar age and species composition as found near Willow Creek (Cook et al., 2004). We averaged edaphic characteristics across 12 measurement sites (Table 4; Martin and Bolstad, 2005). Species parameters were estimated from the CENTURY web site or from the literature, where available (Table 1).

## 2.6. Landscape simulation

Our scenarios were designed to assess whether and to what degree different harvest practices, wind disturbance, and species composition affect long-term changes in SOC and total C. We were not attempting to predict long-term change within the Willow Creek experimental forest or to mimic any specific management regime. Rather we sought to broadly assess harvest and disturbance effects. Therefore, we chose a neutral landscape modeling approach (Gardner et al., 1987), whereby a fractal pattern was imposed on the landscape, to demonstrate general model behavior. We simulated a 9800 ha square (99 × 99 cells) landscape at a resolution of 1 ha containing only a single ecoregion. We simulated 400 years of change and each scenario was replicated five times. Five replicates were a compromise between inherent stochastic variation and requisite computing time. The initial soil conditions from our model calibration were used across the entire landscape. We created seven initial communities comprised of 12 species (Appendix B). These seven

communities represent a broad mixture of successional types and functional groups, allowing our landscape to evolve over time in response to succession and disturbance. Our initial communities were randomly arranged in a fractal pattern (Gardner et al., 1987).

In order to assess the effects of harvesting on forest C, we compared the effects of different harvest regimes against a scenario with no harvesting. We simulated three harvest scenarios: no harvesting vs. standard harvesting vs. whole-tree harvesting (5 year time steps). Standard harvesting (or 'saw log' harvesting) removed 60% of the aboveground wood from each cohort, leaving the remaining wood and leaves on site (Jenkins et al., 2003). Whole tree harvesting removed 100% of aboveground cohort wood and leaves. Both harvest types ranked stands by age (stand age is the average of the age of the oldest cohort within each cell in the stand) with the oldest stands harvested first. Harvests were implemented as 5 ha patch cuts that harvested all cohorts. We simulated a conservative harvest regime whereby 5% of stands were patch cut (25% of the stand clearcut in 5 ha patches); harvest rotation period was ~95 years. Wind was simulated using the Base Wind extension (Scheller and Domingo) with a 50-year rotation period (50 years is required for an area equivalent to the total landscape to be disturbed by wind, sensu Frelich, 2002) and an average disturbance size of 100 ha. Wind disturbance includes all levels of wind disturbance from very light (low mortality) to complete mortality and is age-dependent with the oldest cohorts being most vulnerable;

**Table 3**  
Ecoregion fixed parameters derived from data from the Willow Creek experimental forest, Wisconsin, USA.

Name	Soil depth (cm)	Sand (%)	Clay (%)	Field capacity (%)	Wilting Point (%)	Storm flow fraction	Base flow fraction	Drain (%)	Atmos N slope	Atmos N intercept	Latitude
eco1	50	0.591	0.069	0.3	0.2	0.4	0.4	0.75	0.06	0.05	44

**Table 4**  
Initial ecoregion parameters. All parameter units g m<sup>-2</sup>.

Name	SOM1 C surface	SOM1 N surface	SOM1 C soil	SOM1 N soil	SOM2 C	SOM2 N	SOM3 C	SOM3 N	Mineral N
eco1	45.6	2.93	132	13.92	2765	45.95	1294	41.47	3

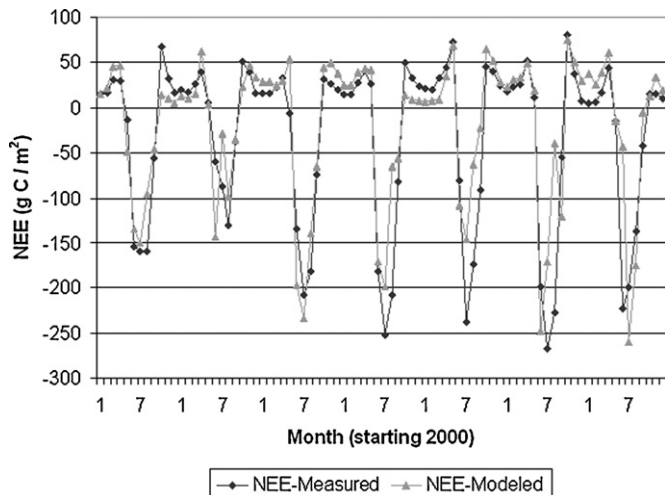


Fig. 2. Calibration results comparing Net Ecosystem Exchange (NEE,  $\text{g C m}^{-2}$ ) measured at Willow Creek, WI and modeled NEE.

there is no species differentiation in mortality risk (Mladenoff and He, 1999). We also tested the effects of excluding wind from the no harvesting scenario.

Finally, we tested the effects of removing eastern hemlock from our no harvest scenario. Hemlock was a common late-successional component of northern hardwood forests (Schulte et al., 2002) that was largely logged out of the landscape and is currently regenerating poorly due to deer browsing and lack of available seed source (Mladenoff and Stearns, 1993). Although the physiological parameters of hemlock are generally similar to other conifers, it is distinguished due to its longevity and high shade tolerance (see Scheller and Mladenoff, 2005). In the 'no hemlock' scenarios, hemlock was eliminated by setting its maximum biomass to zero.

### 3. Results

#### 3.1. Calibration

The agreement between observed and modeled NEE was generally good ( $R^2 = 0.73$ ) although the model under-predicted NEE overall (model =  $0.77 \text{ observed} + 6.8$ ) (Figs. 2 and 3). In particular, during the summers of 2004 and 2005, modeled NEE was higher than observed (lower NPP) due to water limitations (Fig. 2). Calibration required altering the relationship between N deposition

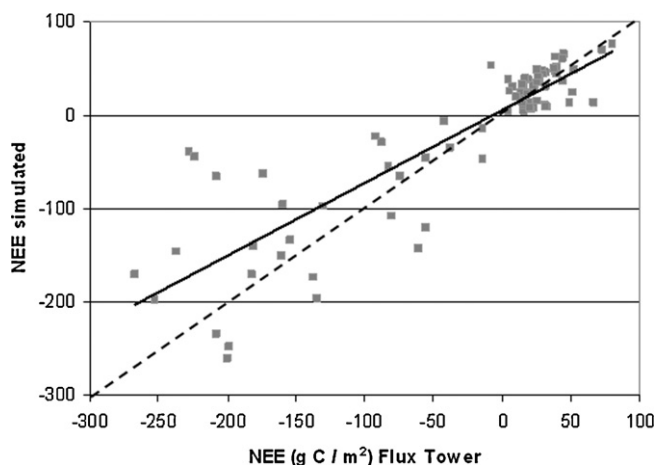


Fig. 3. Calibration NEE plotted against observed NEE. The solid line is a linear regression ( $R^2 = 0.73$ , model =  $0.77 \text{ observed} + 6.8$ ); the dashed line is 1:1.

and precipitation by increasing the slope ( $\text{g dry/wet N deposition m}^{-2} = 0.05 + 0.06 \times \text{cm ppt}$ ). Estimates of NPP were otherwise too low due to N limitations. We also iteratively calibrated the functional group temperature parameters (photosynthetic temperature mean, temperature maximum, and two shape parameters) to capture the expected phenology of NPP for each functional type.

#### 3.2. Landscape simulations

Our simulations with both wind disturbances and eastern hemlock (Fig. 4) display temporal variation within each scenario due to wind disturbances, stochastic weather, and regeneration. We did not partition these sources of variation. Harvesting of any kind caused an immediate decline of  $\sim 18\%$  on live carbon (both above and belowground) (Fig. 4a). This initial decline is due to the absence of any harvesting during model initialization to starting conditions. After harvesting begins (at year zero), live C reflects the balance between biomass removal and re-growth. Whole tree harvesting causes a larger reduction in total C compared to standard harvesting (Fig. 4d).

Live C (including coarse and fine roots) initially declines steeply in the first 50 years of the two harvest scenarios (Fig. 4a). This is because the model initiation phase (prior to year zero, not shown) does not include any past harvesting and harvesting therefore begins operating on a landscape with relatively high biomass. In contrast, the scenario without harvesting remains at relative equilibrium throughout the simulation suggesting that the initial live C is balanced by wind disturbances over time (Fig. 4a). The oldest cohorts are most susceptible to simulated wind disturbances, however, such cohorts have lower biomass due to age-related decline. Individual wind events are not visually apparent as the average wind event is  $\sim 100 \text{ ha}$  and we averaged across the five replicates.

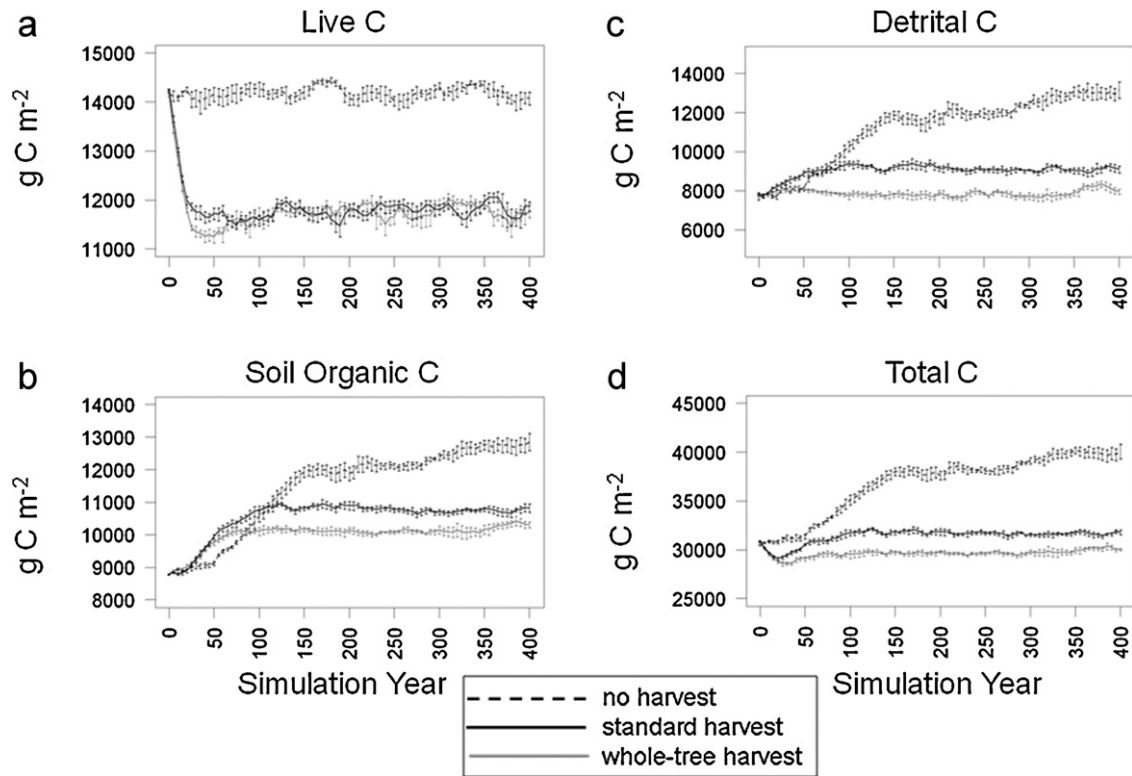
Detrital C increased only modestly for the two harvest scenarios and increased by  $\sim 50\%$  in the scenario without harvesting (Fig. 4b). SOC increased for the first 150 years for all scenarios, which generally reflects changes in detrital C. For the first 75 years, the standard harvesting scenarios had the most detrital C; subsequently the no harvest scenario had the most detrital C. Likewise, both harvest scenarios initially had more SOC but were exceeded by the no harvest scenario after 120 years (Fig. 4c).

The C of individual tree species (Fig. 5) demonstrates a shift towards late successional sugar maple and eastern hemlock with a significant yellow birch component when harvesting is excluded. With harvesting, sugar maple and yellow birch are dominant, with hemlock, basswood, and red oak as co-dominants. There was no difference between the two harvest types as the same area and same stand ranking algorithm was applied to both. Variance of any one species is relatively small due to averaging across the 9800 ha and across five replicates (Fig. 5).

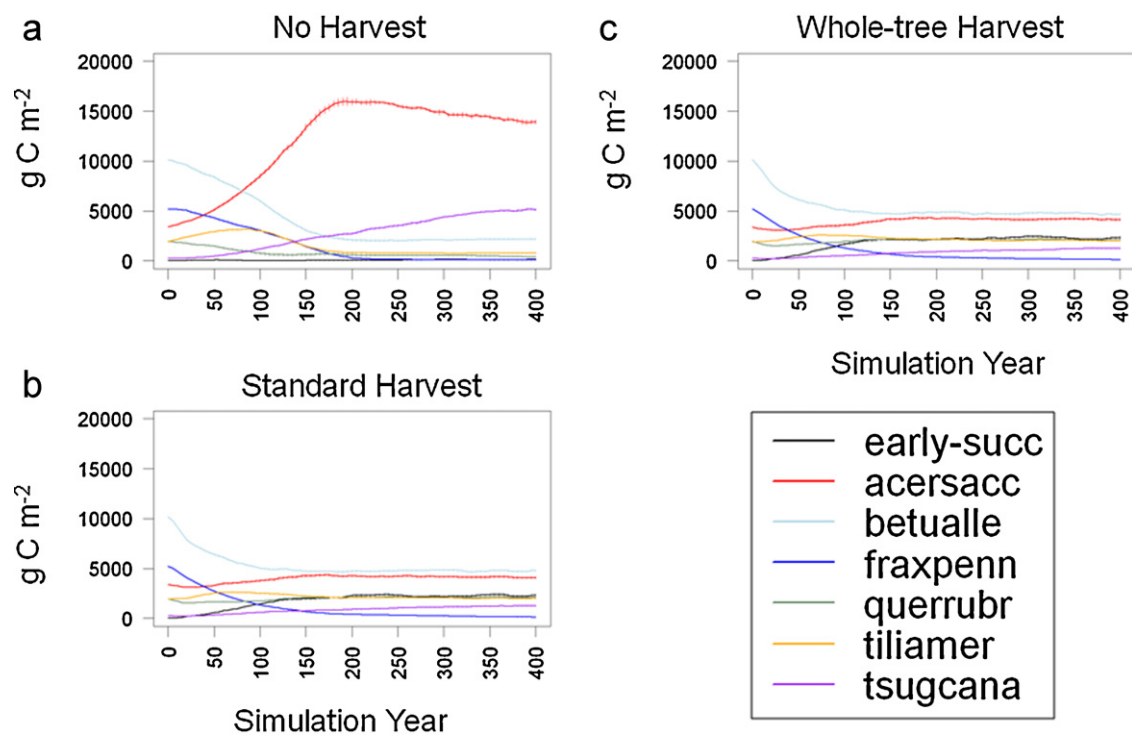
The exclusion of wind disturbance eventually resulted in more C for all pools as compared to simulations with wind (Fig. 6). The exclusion of hemlock resulted in reduced detrital C and total C (Fig. 7c and d).

### 4. Discussion

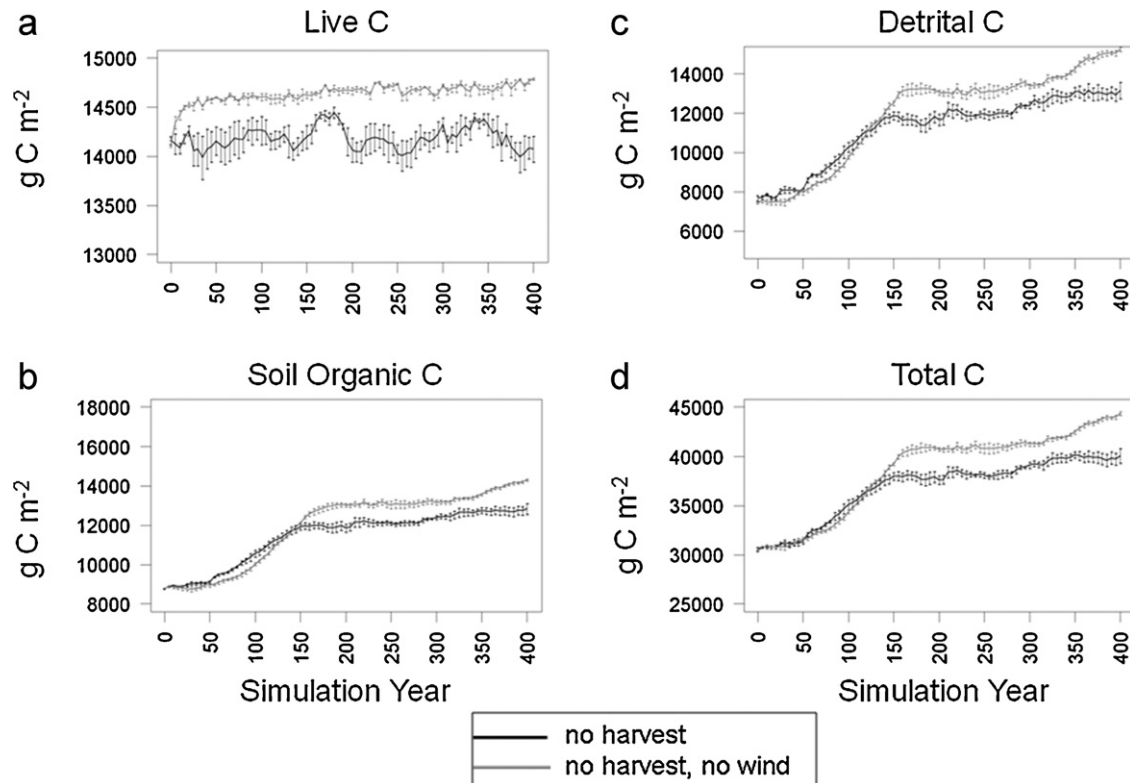
There are a multitude of factors that affect forest carbon dynamics, including forest type, disturbances, litter inputs, soil temperature, and soil texture (Schimel et al., 1994; Peng and Apps, 1999; Brickley et al., 2007). Because soil texture and climate were held constant across simulations, we could not assess whether the model was relatively more sensitive to the rate of soil inputs or decomposition. Rather, our simulations focused on the potential sensitivity of forest C to a select few drivers: canopy composition, harvesting intensity, and wind disturbance.



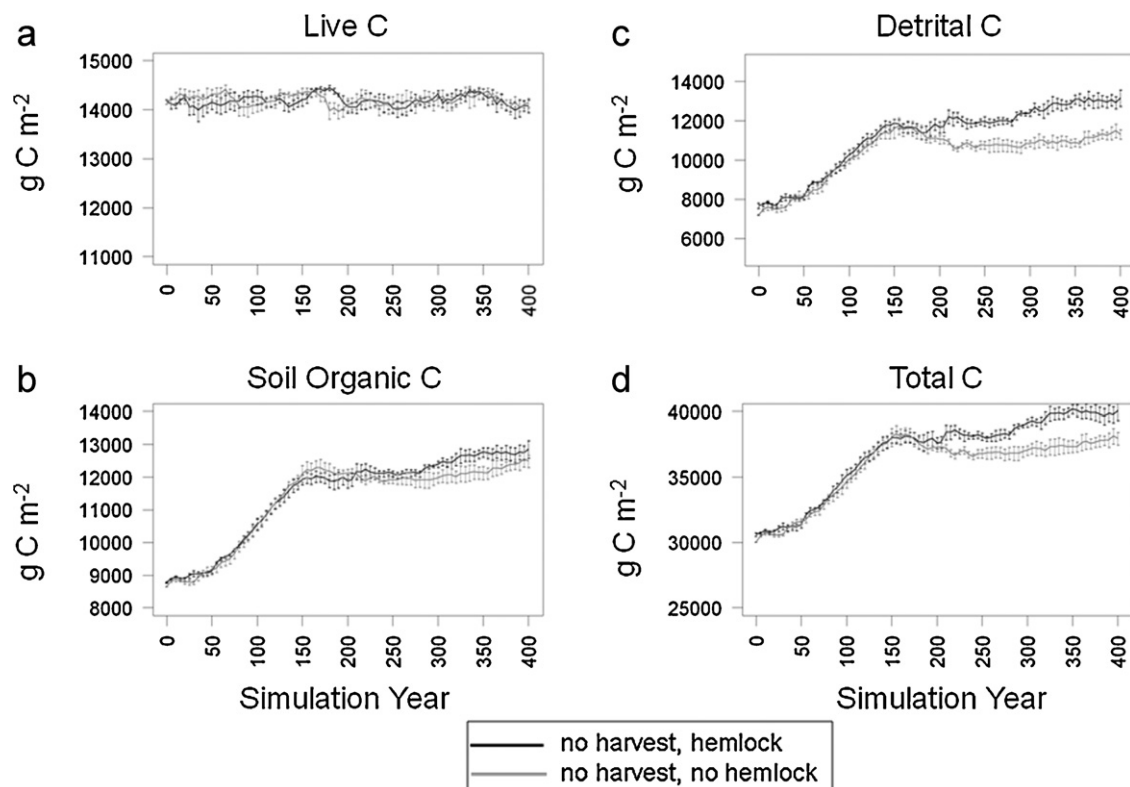
**Fig. 4.** Simulated C (g C m<sup>-2</sup>) from three scenarios: no harvest, standard harvest, and whole tree harvest. Standard harvest left all slash in place and 15% of wood. Whole tree harvest removed all detritus. All scenarios were replicated 5× and wind disturbance was simulated with a 50-year rotation period: (a) live carbon including above and below ground, (b) detrital carbon including dead coarse roots and fine roots, (c) soil organic carbon, and (d) total carbon. All estimates were averaged over 9800 cells representing 9800 ha.



**Fig. 5.** The response of the most common tree species C (g C m<sup>-2</sup>) from three scenarios: no harvest, standard harvest, and whole tree harvest. Standard harvest left all slash in place and 15% of wood. Whole tree harvest removed all detritus. Species codes are derived from the first four letters of genus and species combined (Table 1). 'early-succ' is the combined biomass of early successional species, *Populus tremuloides* and *Betula papyrifera*. All scenarios were replicated 5× and wind disturbance was simulated with a 50-year rotation period. All estimates were averaged over 9800 cells representing 9800 ha.



**Fig. 6.** Simulated C ( $\text{g C m}^{-2}$ ) from scenarios with no disturbance (no-harvest-no-wind) and with wind simulated at a 50-year rotation period. All scenarios were replicated 5 $\times$ : (a) live carbon including above and below ground, (b) detrital carbon including dead coarse roots and fine roots, (c) soil organic carbon, and (d) total carbon. All estimates were averaged over 9800 cells representing 9800 ha.



**Fig. 7.** Simulated C ( $\text{g C m}^{-2}$ ) from scenarios with no harvesting and with wind simulated at a 50-year rotation period, with and without eastern hemlock (*Tsuga canadensis*). All scenarios were replicated 5 $\times$ : (a) live carbon including above and below ground, (b) detrital carbon including dead coarse roots and fine roots, (c) soil organic carbon, and (d) total carbon. All estimates were averaged over 9800 cells representing 9800 ha.



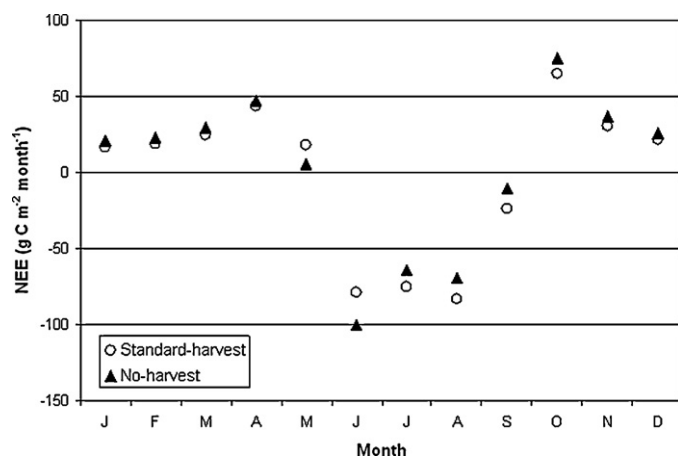


Fig. 8. Comparison of monthly mean NEE ( $\text{g C m}^{-2}$ ) ( $N=80$ ) between single simulations of no harvest and standard harvest landscapes.

Our calibration generally produced good fidelity to measured NEE (Cook et al., 2004). It should be noted that NEE measurements themselves contain some degree of uncertainty due to micrometeorological conditions that are not suitable for measuring NEE; these data are screened and corrected (Cook et al., 2004). Our underestimates during dry years indicate that we either underestimated the water holding capacity or trees were accessing water below the 1 m soil depth simulated. Schimel (1997) also found that CENTURY tended to underestimate NPP.

Our long-term SOC estimates compare favorably to a chronosequence from northern Wisconsin and the upper peninsula of Michigan (Tang et al., 2009). Tang et al. (2009) observed  $\sim 9000 \text{ g C m}^{-2}$  in the top 60 cm of soil for 'intermediate aspen' and 'mature hardwoods' which approximate our initial conditions. They measured  $\sim 10,500 \text{ g C m}^{-2}$  at an old-growth (estimated age 350 years) *A. saccharum* and *T. canadensis* dominated forest. Our simulations of SOC (100 cm depth) began at  $\sim 9000 \text{ g C m}^{-2}$  and are  $\sim 13,000 \text{ g C m}^{-2}$  after 400 years within the old-growth (no harvest) landscape. Our simulations suggest the potential for continued SOC accrual as found in a recent meta-analysis of old forest C dynamics and a study of old-growth forest soils (Luyssaert et al., 2008).

Over the 400-year simulation, mean NEE of the harvested landscape was not substantially different from the mean NEE of the non-harvested landscape (Fig. 8). Both simulations had a mean seasonal NEE similar to Sylvania Wilderness Area, an old-growth forest in Michigan (Desai et al., 2005, Fig. 5). This suggests that although our simulated harvesting reduced soil and detrital C pools, the simulated forests were on average absorbing C at a rate similar to that of an old-growth forest.

Similar to the meta analysis by Johnson and Curtis (2001) we found that whole-tree harvesting resulted in less soil C than saw log (our 'standard') harvesting. However, their meta analysis also indicated increases in soil C relative to the control over shorter time periods (compiled data were typically gathered from <20 year studies). Our simulations also indicate a short-term increase in detritus and SOC due to harvesting. However, this is followed by a long-term reduction in soil C relative to the no harvest scenario. Essentially, harvesting practices dictate long-term detrital inputs. If these are reduced, SOC will also be reduced in the long-term regardless of the smaller detrital pulses from the harvesting activity itself.

Gough et al. (2007) found that repeated disturbance (harvest and fire) reduced forest C storage by lowering net ecosystem production (NEP) for many decades. Similarly, our landscapes with repeated harvesting had reduced C storage. Our harvested landscapes also had reduced NEP, as indicated by summer NEE (Fig. 8).

The simulated decline is likely due to a reduced average stand age (Peltoniemi et al., 2004) as simulated available N did not decline (data not shown).

Yanai et al. (2003) suggest that mixing of the forest floor with mineral soil may account for a decline in organic matter in the surface layers due to harvesting. We did not simulate this process and yet found an  $\sim 15\%$  decline in total SOM when comparing non-harvested to harvested landscapes. The decline we simulated can be directly attributed to the approximately 30% decline in detritus when landscapes were harvested. The decline in detritus is not directly due to harvesting, which causes short-term increases detritus, but rather due to the long-term decline in late successional forests and their associated higher levels of detritus. Although our simulated harvesting was relatively infrequent (95 year rotation period), our harvests targeted the oldest stands, which contribute proportionately more detritus due to the larger total live C and the effect of simulated senescence (age-decline) on older cohorts. Our simulations of a landscape without harvesting and without wind confirm the importance of older cohorts to detritus production and SOC. Without wind, both live C and detrital C are larger (Fig. 6a and c), even though wind disturbance leaves all aboveground wood and leaves on the forest floor.

Our scenario without harvesting and without hemlock represents a potential trajectory for many areas in the Great Lakes forests due to heavy deer browsing (Mladenoff and Stearns, 1993). The scenario also demonstrates the importance of inter-specific variation in litter and wood quality. Hemlock has higher percent leaf and wood lignin than the other late-successional dominants, sugar maple and yellow birch (Table 2). As a result, hemlock litter is expected to decay slower (Cornwell et al., 2008) and is characterized by slower N cycling (Lovett et al., 2004). Simulated hemlock dominance resulted in increased detritus and SOC, as measured elsewhere (Finzi et al., 1998; Goodburn and Lorimer, 1998) despite similar live C (Fig. 7).

Numerous caveats apply to our model and model simulations. First and foremost, we did not validate the model – only calibrate – although relatively successful validation with independent NEE data has been achieved in the New Jersey pine barrens (unpublished data). However, NEE data will always only provide a limited validation. The purpose of the model is to estimate the long-term consequences of disturbance, management, and succession over a spatially extensive landscape. Empirical NEE data currently represent only a short period and a limited area. True validation of large spatial and long temporal scales is not strictly possible although the validation of shorter duration processes ultimately builds confidence in projections that exceed the scope of data available for empirical validation.

Finally, the ability to simulate growth, mortality, and heterotrophic respiration at a monthly scale increased model complexity and parameterization as compared to other LANDIS-II succession extensions. In addition, the addition of leaf biomass as a separately tracked pool and a monthly time step significantly increases the requisite computational resources. Future simulations will require careful consideration of the desired detail, spatial resolution and extent, and duration.

Although the new model extension enabled us to examine the interactions among disturbances, succession, and forest C, a number of improvements could be made. For example, the effects of soil mixing during harvesting (Yanai et al., 2003) on soil decay and tree regeneration are not currently represented. Phosphorus, sulfur, magnesium, and calcium may all limit species NPP and the long-term ability of soils to sustain growth under select circumstances (Likens et al., 1970; Shugart et al., 1976; Federer et al., 1989; Kolka et al., 1996; Grigal, 2000; Lovett et al., 2004). CENTURY has a simple water sub-module which does not consider dynamic transport of water across the landscape. Finally, both initial N pool

size and N deposition were poorly parameterized. Actual values could be added to the climate data where available. In addition, we did not simulate the presence of N fixing plants (e.g., alder) which may be locally important. Alternatively, trees may be able to directly access organic N (Schimel and Bennett, 2004), a process not currently represented in our model.

## 5. Conclusions

Our simulations demonstrate the effects of multiple, overlapping disturbances and changes in species composition on multiple forest C pools. In general, any decline in detritus will generate a concomitant decline in SOC over fairly long time scales. However, disturbance effects on detritus are not always intuitive. For example, although wind throw immediately generates detritus, the long-term effect is reduced detritus due to the loss of older, larger cohorts. Simulated whole-tree harvesting reduced total C, however, the actual implementation of such a policy will vary widely. Historic legacies (loss of hemlock) and forest management will also have a large effect on detritus and SOC as mediated by tree species composition. The historic loss of hemlock and its continued lack of regeneration may have significant detrimental effects on the ability of these forests to store carbon, even if they are managed for other old-growth characters.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2010.09.009.

## References

Archer, T., Whitechapel, A., 2002. Inside C#. Microsoft Press, Redmond, WA, USA.

Bachelet, D., Lenihan, J.M., Daly, C., Neilson, R.P., Ojima, D.S., Parton, W.J., 2001. MCI: A Dynamic Vegetation Model for Estimating the Distribution of Vegetation and Associated Ecosystem Fluxes of Carbon, Nutrients, and Water. PNW-GTR-508. USDA Forest Service Pacific Northwest Research Station, Portland, OR, USA.

Birdsey, R., Pregitzer, K., Lucier, A., 2006. Forest carbon management in the United States: 1600–2100. *Journal of Environmental Quality* 35, 1461–1469.

Birdsey, R.A., Heath, L.S., 1995. Productivity of America's Forests and Climate Change. RM-GTR-271. Rocky Mountain Forest and Experiment Station, USDA Forest Service, Ft. Collins, CO, USA.

Bricklemeyer, R.S., Miller, P.R., Turk, P.J., Paustian, K., Keck, T., Nielsen, G.A., 2007. Sensitivity of the Century model to scale-related soil texture variability. *Soil Science Society of America Journal* 71, 784–792.

Burke, I.C., Kaye, J.P., Bird, S.P., Hall, S.A., McCulley, R.L., Sommerville, G.L., 2003. Evaluating and testing models of terrestrial biogeochemistry: the role of temperature in controlling decomposition. In: Canham, C.D., Cole, J.J., Lauenroth, W.K. (Eds.), *The Role of Models in Ecosystem Science*. Princeton University Press, Princeton, NJ, USA, pp. 225–253.

Cook, B.D., Davis, K.J., Wang, W., Desai, A., Berger, B.W., Teclaw, R.M., Martin, J.G., Bolstad, P.V., Bakwin, P.S., Yi, C., Heilman, W., 2004. Carbon exchange and venting anomalies in an upland deciduous forest in northern Wisconsin, USA. *Agricultural and Forest Meteorology* 126, 271–295.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Perez-Harguindeguy, N., Quested, H.M.S.L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Diaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieritti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11, 1065–1071.

Currie, W.S., Yanai, R.D., Piatek, K.B., Prescott, C.E., Goodale, C.L., 2003. Processes affecting carbon storage in the forest floor and in downed woody debris. In: Kimble, J.M., Lal, R., Birdsey, R., Heath, L.S. (Eds.), *The Potential of U.S. Forests to Sequester Carbon and Mitigate the Greenhouse Effect*. CRC Press, Inc., Boca Raton, FL, USA, pp. 135–147.

Desai, A.R., Bolstad, P.V., Cook, B.D., Davis, K.J., Carey, E.V., 2005. Comparing net ecosystem exchange of carbon dioxide between an old-growth and mature forest in the upper Midwest, USA. *Agricultural and Forest Meteorology* 128, 33–55.

Dixon, R.K., 1994. Carbon pools and flux of global forest ecosystems. *Science* 265, 171.

Federer, C.A., Hornbeck, J.W., Tritton, L.M., Martin, C.W., Pierce, R.S., Smith, C.T., 1989. Long-term depletion of calcium and other nutrients in eastern US forests. *Environmental Management* 13, 593–601.

Finzi, A.C., Van Breemen, N., Canham, C.D., 1998. Canopy tree-soil interactions within temperate forests: species effects on soil carbon and nitrogen. *Ecological Applications* 8, 440–446.

Frelich, L.E., 2002. *Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests*. Cambridge University Press, Cambridge, UK.

Gardner, R.H., Milne, B.T., Turner, M.G., O'Neill, R.V., 1987. Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecology* 1, 19–28.

Goodale, C.L., Apps, M.J., Birdsey, R.A., Field, C.B., Heath, L.S., Houghton, R.A., Jenkins, J.C., Kohlmaier, G.H., Kurz, W., Liu, S.R., Nabuurs, G.J., Nilsson, S., Shvidenko, A.Z., 2002. Forest carbon sinks in the northern hemisphere. *Ecological Applications* 12, 891–899.

Goodburn, J.M., Lorimer, C.G., 1998. Cavity trees and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan. *Canadian Journal of Forest Research* 28, 427–438.

Gough, C.M., Vogel, C.S., Harrold, K.H., George, K., Curtis, P.S., 2007. The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. *Global Change Biology* 13, 1935–1949.

Grigal, D.F., 2000. Effects of extensive forest management on soil productivity. *Forest Ecology and Management* 138, 167–185.

Heath, L.S., Smith, J.E., Birdsey, R.A., 2003. Carbon trends in U.S. forestlands: a context for the role of soils in forest carbon sequestration. In: Kimble, J.M., Lal, R., Birdsey, R., Heath, L.S. (Eds.), *The Potential of U.S. Forests to Sequester Carbon and Mitigate the Greenhouse Effect*. CRC Press, Inc., Boca Raton, FL, USA, pp. 35–45.

Houghton, R.A., Hackler, J.L., 2000. Changes in terrestrial carbon storage in the United States. I. The roles of agriculture and forestry. *Global Ecology and Biogeography* 9, 125–144.

Hurteau, M.D., Koch, G.W., Hungate, B.A., 2008. Carbon protection and fire risk reduction: toward a full accounting of forest carbon offsets. *Frontiers in Ecology and the Environment* 6, 493–498.

Jenkins, J.C., Chojnacky, D.C., Heath, L.S., Birdsey, R.A., 2003. National-scale biomass estimators for United States tree species. *Forest Science* 49, 12–35.

Johnson, D.W., Curtis, P.S., 2001. Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology and Management* 140, 227–238.

Kirschbaum, M.U.F., Paul, K.I., 2002. Modelling C and N dynamics in forest soils with a modified version of the CENTURY model. *Soil Biology & Biogeochemistry* 34, 341–354.

Kolka, R.K., Grigal, D.F., Nater, E.A., 1996. Forest soil mineral weathering rates: use of multiple approaches. *Geoderma* 73, 1–21.

Kurz, W.A., Apps, M.J., 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecological Applications* 9, 526–547.

Law, B.E., Turner, D., Campbell, J., Sun, O.J., Van Tuyl, S., Ritts, W.D., Cohen, W.B., 2004. Disturbance and climate effects on carbon stocks and fluxes across western Oregon, USA. *Global Change Biology* 10, 1429–1444.

Likens, G.E., Bormann, F.H., Johnson, N.M., Fisher, D.W., Pierce, R.S., 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecological Monographs* 40, 23–47.

Loehle, C., 2000. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *The American Naturalist* 156, 15–33.

Lorek, H., Sonnenschein, M., 1999. Object-oriented support for modelling and simulation of individual-oriented ecological models. *Ecological Modelling* 108, 77–96.

Lovett, G.M., Weathers, K.C., Arthur, M.A., Schultz, J.C., 2004. Nitrogen cycling in a northern hardwood forest: do species matter? *Biogeochemistry* 67, 289–308.

Luyssaert, S., Detlef Schulze, E., Börner, A., Knohl, A., Hessenmoller, D., Law, B.E., Ciais, P., Grace, J., 2008. Old-growth forests as global carbon sinks. *Nature* 455, 213–215.

Martin, J.G., Bolstad, P.V., 2005. Annual soil respiration in broadleaf forests of northern Wisconsin: influence of moisture and site biological, chemical, and physical characteristics. *Biogeochemistry* 73, 149–182.

Mladenoff, D.J., 2004. LANDIS and forest landscape models. *Ecological Modelling* 180, 7–19.

Mladenoff, D.J., He, H.S., 1999. Design, behavior and application of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: Mladenoff, D.J., Baker, W.L. (Eds.), *Spatial Modeling of Forest Landscape Change*. Cambridge University Press, Cambridge, UK, pp. 125–162.

Mladenoff, D.J., Host, G.E., Boeder, J., Crow, T.R., 1996. LANDIS: a spatial model of forest landscape disturbance, succession, and management. In: Goodchild, M.F., Steyaert, L.T., Parks, B.O., Johnston, C.A., Maidment, D., Crane, M., Glendinning, S. (Eds.), *GIS and Environmental Modeling: Progress and Research Issues*. GIS World Books, Fort Collins, CO, USA, pp. 175–179.

Mladenoff, D.J., Stearns, F., 1993. Eastern hemlock regeneration and deer browsing in the northern Great Lakes region: a re-examination and model simulation. *Conservation Biology* 7, 889–900.

Moorecroft, P.R., Hurtt, G.C., Pacala, S.W., 2001. A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecological Monographs* 71, 557–586.

- Ollinger, S.V., Aber, J.D., Reich, P.B., Freuder, R.J., 2002a. Interactive effects of nitrogen deposition, tropospheric ozone, elevated CO<sub>2</sub> and land use history on the carbon dynamics of northern hardwood forests. *Global Change Biology* 8, 545–562.
- Ollinger, S.V., Smith, M.L., Martin, M.E., Hallett, R.A., Goodale, C.L., Aber, J.D., 2002b. Regional variation in foliar chemistry and N cycling among forests of diverse history and composition. *Ecology* 83, 339–355.
- Overby, S.T., Hart, S.C., Neary, D.G., 2003. Impacts of natural disturbance on soil carbon dynamics in forest ecosystems. In: Kimble, J.M., Lal, R., Birdsey, R.A., Heath, L.S. (Eds.), *The Potential of U.S. Forest Soils to Sequester Carbon and Mitigate the Greenhouse Effect*. CRC Press, Boca Raton, FL, USA.
- Paine, R.T., Tegner, M.J., Johnson, E.A., 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1, 535–545.
- Pan, Y., Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Pitelka, L.F., Hibbard, K., Pierce, L.L., Running, S.W., Ojima, D.S., Parton, W.J., Schimel, D.S., VEMAP Members, 1998. Modeled responses of terrestrial ecosystems to elevated atmospheric CO<sub>2</sub>: a comparison of simulations by the biogeochemistry models of the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP). *Oecologia* 114, 389–404.
- Parton, W.J., Anderson, D.W., Cole, C.V., Steward, J.W.B., 1983. Simulation of soil organic matter formation and mineralization in semiarid agroecosystems. In: Lowrance, R.R., Todd, R.L., Asmussen, L.E., Leonard, R.A. (Eds.), *Nutrient Cycling in Agricultural Ecosystems*. vol. Special Publication No. 23. The University of Georgia, College of Agriculture Experiment Stations, Athens, GA, USA.
- Parton, W.J., Ojima, D.S., Cole, C.V., Schimel, D.S., 1994. A general model for soil organic matters dynamics: sensitivity to litter chemistry, texture and management. In: Bryant, R.B., Arnold, R.W. (Eds.), *Quantitative Modeling of Soil Forming Processes: Proceedings of a Symposium Sponsored by Divisions S-5 and S-9 of the Soil Science Society of America*. Minneapolis, Minnesota, USA. Soil Science Society of America, Madison, WI, USA, pp. 147–167.
- Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Gilmanov, T.G., Scholes, R.J., Schimel, D.S., Kirchner, T., Menaut, J.C., Seastedt, T., Garcia Moya, E., Kamnalrut, A., Kinyamario, J.I., 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles* 7, 785–809.
- Pastor, J., Post, W.M., 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2, 3–27.
- Peltoniemi, M., Makipaa, R., Liski, J., Tamminen, P., 2004. Changes in soil carbon with stand age—an evaluation of a modelling method with empirical data. *Global Change Biology* 10, 2078–2091.
- Peng, C., Apps, M.J., 1999. Modelling the response of net primary productivity (NPP) of boreal forest ecosystems to changes in climate and fire disturbance regimes. *Ecological Modelling* 122, 175–193.
- Platt, W.J., Beckage, B., Doren, R.F., Slater, H.H., 2002. Interactions of large-scale disturbances: prior fire regimes and hurricane mortality of savanna pines. *Ecology* 83, 1566–1572.
- Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biology* 10, 2052–2077.
- Reich, P.B., Grigal, D.F., Aber, J.D., Gower, S.T., 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* 78, 335–347.
- Running, S.W., Hunt Jr., E.R., 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global scale models. In: Ehleringer, J.R., Field, C.B. (Eds.), *Scaling Physiological Processes: Leaf to Globe*. Academic Press, Inc., San Diego, CA, USA, pp. 141–158.
- Scheller, R.M., Domingo, J.B. LANDIS-II Base Wind Extension (v1.0) User Guide. <http://landis.forest.wisc.edu/documentation>.
- Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J., Mladenoff, D.J., 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible spatial and temporal resolution. *Ecological Modelling* 201, 409–419.
- Scheller, R.M., Mladenoff, D.J., 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. *Ecological Modelling* 180, 211–229.
- Scheller, R.M., Mladenoff, D.J., 2005. A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. *Global Change Biology* 11, 307–321.
- Scheller, R.M., Mladenoff, D.J., 2008. Simulated effects of climate change, tree species migrations, and forest fragmentation on aboveground carbon storage on a forested landscape. *Climate Research* 36, 191–202.
- Scheller, R.M., Mladenoff, D.J., Crow, T.R., Sickley, T.S., 2005. Simulating the effects of fire reintroduction versus continued suppression on forest composition and landscape structure in the Boundary Waters Canoe Area, northern Minnesota (USA). *Ecosystems* 8, 396–411.
- Scheller, R.M., Sturtevant, B.R., Gustafson, E.J., Mladenoff, D.J., Ward, B.C., 2010. Increasing the reliability of ecological models using modern software engineering techniques. *Frontiers in Ecology and the Environment* 8, 253–260.
- Scheller, R.M., Van Tuyl, S., Clark, K., Hayden, N.G., Hom, J., Mladenoff, D.J., 2008. Simulation of forest change in the New Jersey Pine Barrens under current and pre-colonial conditions. *Forest Ecology and Management* 255, 1489–1500.
- Schimel, D.S., Braswell, B.H., Holland, E.A., McKeown, R., Ojima, D.S., Painter, T.H., Parton, W.J., Townsend, A.R., 1994. Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. *Global Biogeochemical Cycles* 8, 279–293.
- Schimel, D.S., Braswell, B.H., VEMAP Participants, 1997. Continental scale variability in ecosystem processes: models, data, and the role of disturbance. *Ecological Monographs* 67, 251–271.
- Schimel, J.P., Bennett, J., 2004. Nitrogen mineralization: challenges of a changing paradigm. *Ecology* 85, 591–602.
- Schulte, L.A., Mladenoff, D.J., Nordheim, E.V., 2002. Quantitative classification of a historic northern Wisconsin (U.S.A.) landscape: mapping forests at regional scales. *Canadian Journal of Forest Research* 32, 1616–1638.
- Sequeira, R.A., Olson, R.L., Mckinion, J.M., 1997. Implementing generic, object-oriented models in biology. *Ecological Modelling* 94, 17–31.
- Shugart, H.H., Reichle, D.E., Edwards, N.T., Kercher, J.R., 1976. A model of calcium-cycling in a east Tennessee Lirodendron forest: model structure, parameters and frequency response analysis. *Ecology* 57, 99–109.
- Smith, T., Huston, M., 1989. A theory of the spatial and temporal dynamics of plant communities. *Vegetatio* 83, 49–69.
- Sturtevant, B.R., Gustafson, E.J., Li, W., He, H.S., 2004. Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. *Ecological Modelling* 180, 153–174.
- Sturtevant, B.R., Miranda, B.R., Yang, J., He, H.S., Gustafson, E.J., Scheller, R.M., 2009. Studying fire mitigation strategies in multi-ownership landscapes: balancing the management of fire-dependent ecosystems and fire risk. *Ecosystems* 12, 445–461.
- Tang, J., Bolstad, P.V., Martin, J.G., 2009. Soil carbon fluxes and stocks in a Great Lakes forest chronosequence. *Global Change Biology* 15, 145–155.
- VEMAP Members, 1995. Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO<sub>2</sub> doubling. *Global Biogeochemical Cycles* 9, 407–437.
- Ward, B.C., Mladenoff, D.J., Scheller, R.M., 2005. Landscape-level effects of the interaction between residential development and public forest management in northern Wisconsin, USA. *Forest Science* 51, 616–632.
- Xu, C., Gertner, G.Z., Scheller, R.M., 2007. Potential effects of interaction between CO<sub>2</sub> and temperature on Boundary Water Canoe Area's forest landscape response to global warming. *Global Change Biology* 13, 1469–1483.
- Xu, C., Gertner, G.Z., Scheller, R.M., 2009. Uncertainties in the response of a forest landscape to global climatic change. *Global Change Biology* 15, 116–131.
- Yanai, R.D., Currie, W.S., Goodale, C.L., 2003. Soil carbon dynamics after forest harvest: an ecosystem paradigm reconsidered. *Ecosystems* 6, 197–212.