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Hurricane impacts on dynamics, structure and carbon sequestration potential of forest ecosystems in Southern New England, USA

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ABSTRACT

The observed increase in hurricane intensity in the North Atlantic calls for an evaluation of the effects that these storms have on temperate forest ecosystems where much of the terrestrial carbon is sequestered. We use a data-based forest simulator to analyse the effects of both historical and potentially future hurricane disturbance regimes on the structure, dynamics and carbon sequestration potential of Southern New England forests. Baseline estimates of carbon sequestration in aboveground biomass from our simulations are in line with forest inventory data and range from 0.93 to 1.68 tons C ha^{-1} yr^{-1} with the greatest rates in areas subject to the most severe wind disturbance. To the degree that carbon in downed timber is incorporated into the soil, an increase in severe storms is likely to enhance carbon sequestration potential in forests in this region by generating conditions that foster tree growth. However, unsalvaged timber can also increase fire risk, thereby escalating the potential for carbon losses to the atmosphere. Effects of hurricane disturbance on community composition are complex and highlight the role that life history traits play in mediating species' idiosyncratic responses to wind disturbance. Incorporating disturbance in estimates of carbon sequestration in forests will improve congruence between models and data.

1. Introduction

Since 1995, the North Atlantic has had many active hurricane seasons, including the 2005 record-breaking season. This high-level of activity has been related to multi-decadal variability in the Atlantic Ocean (Goldenberg et al., 2001). Evidence of a trend in the intensity of Atlantic hurricanes in the past 30 yr has also been shown (Emanuel, 2005; Webster et al., 2005) in association with warmer sea surface temperatures (Mann and Emanuel, 2006). This global increase of sea surface temperature is primarily considered to be due to anthropogenic factors. There is still much controversy over this issue. Some studies attribute the trend in tropical cyclone activity to more accurately monitored measurements in the recent years (Landsea et al., 2006). An important influence on interannual Atlantic hurricane activity is El Niño-Southern Oscillation (ENSO) (Gray, 1984). Due to these many factors, the detection of a trend on hurricane activity is very difficult, but could be very important. The increasing frequency and intensity of hurricanes and the growing awareness of the importance of ecosystems to human well-being call for an evaluation of the effects that hurricanes have on ecosystems on which humans depend on and the development of appropriate mitigation strategies.

Hurricanes represent the dominant natural disturbance in mesic forests of Northeastern North America within 200–300 Km from the coast (e.g. Foster and Boose, 1992). Since forests may act either as sinks or sources of CO_2 emissions associated with global warming (IPCC, 2000), understanding the effects of a change in hurricane frequency and severity on forest ecosystems is crucial to predicting potential sinks and feedbacks to greenhouse gas emissions under a changing hurricane regime. Hurricanes can have dramatic, short-term effects on carbon stocks in forests. Assuming an average annual carbon sequestration in US forests of 200 Tg (Birdsey et al., 1993; Schimel et al., 2000), a strong, single hurricane can convert 10% of the total US forest carbon sequestration to dead biomass (McNulty, 2005). In the absence of post-hurricane salvage operations, a portion of the carbon in timber downed during a hurricane may return to the atmosphere through accelerated natural decomposition and soil carbon losses, or through heightened

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susceptibility to fire, potentially increasing greenhouse gas emissions (Miranda, 1996; Foster et al., 1997).

Understanding the long-term effects of a shift in hurricane disturbance on subsequent population responses, that is on forest recovery and productivity, and therefore on long-term forest carbon uptake after storms is far more complicated. Tree species differ in their susceptibility to disturbance by a wind of a given intensity, the nature of the damage they sustain from a given wind storm intensity, and their recovery from wind disturbance, at both the individual plant level through repair of damage, and at the population level through reproduction, seedling establishment and juvenile response to enhanced light availability (Glitzenstein and Harcombe, 1988; Peterson and Pickett, 1991; You and Petty, 1991; Walker, 1991; Boucher et al., 1994; Zimmerman et al., 1994; Peterson and Rebertus, 1997; Cooper-Ellis et al., 1999). Since hurricanes tend to damage larger, slower-growing trees, storm damage may increase short-term productivity (Sanford et al., 1991). However, losses of carbon in downed biomass and differences among species that benefit from wind damage in carbon uptake relative to those present before a storm may counteract these short-term gains over a longer time period (McNulty, 2005). Understanding the relative importance of these seemingly countervailing impacts on long-term changes in forest composition and carbon uptake can be furthered by the use of forest dynamics models. These models should be specifically designed to incorporate the effects of hurricanes on the basic demographic processes (i.e. recruitment, growth and mortality) that regulate forest community dynamics. To be predictive, the models must be solidly grounded in empirical research.

Historically, hurricanes have struck the Northeastern US on time scales of centuries to millennia, with well-defined regional gradients of intensity and frequency (Foster and Boose, 1995; Boose et al., 2001). However, if the return interval of severe storms increases so that it is shorter than the scale of population or community recovery, or if the severity of storms increases, we may observe shifts in the structure and dynamics of Northeastern US forests as well as changes in their carbon sequestration potential.

The purpose of this paper is to examine the effects of hurricanes on the structure, dynamics and carbon sequestration potential of forest ecosystems of Northeastern North America by using a data-based, spatially-explicit forest simulator, SORTIE (Pacala et al., 1996). Specifically, we explore two scenarios: First, we rely on historical data of hurricane frequency and severity to build an appropriate disturbance regime for Southern New England. Second, we assume an increasing trend in the long-term average frequency of severe hurricanes. We then use these scenarios to answer the following questions:

1. What is the impact of current and increased hurricane disturbance on regional forest structure and composition? We expect that the interaction between life history traits that determine susceptibility to wind disturbance and those that shape

their response to enhanced light availability after a storm will determine a species' long-term abundance across the regional gradient of disturbance.

2. What are the consequences of these hurricane-driven changes in forest composition and structure for carbon sequestration potential in these ecosystems? We expect that the length of storm-free periods will determine the ability of stands to add biomass, while the return interval and degree of storm severity will determine the proportion of added biomass felled.

2. Methods

2.1. The model

SORTIE is a spatially explicit, mixed-species forest dynamics model that makes population dynamic forecasts for juvenile and adult trees by predicting the fate of individuals (Pacala et al., 1996). SORTIE simulations use a mixture of mechanistically and empirically derived relationships found in five core submodels parametrized using field data that describe light availability, growth, mortality, recruitment and disturbance by windstorms. A brief description for each submodel follows.

Resources. The model focuses on light as the dominant limiting resource in forests and predicts light availability as a function of species-specific light transmission coefficients, crown geometry and the local sky brightness distribution at the sampled location (Canham et al., 1994, 1999). The model does not account for the effects of variation in soil nutrients and water on growth and mortality.

Growth. Species-specific equations predict radial growth of juvenile trees based on growing season light availability and tree size (Pacala et al., 1994). Growth of adult trees follows the constant area increment law (as in Phipps, 1967).

Mortality. For juveniles, species-specific equations predict the probability of survival for each juvenile tree as a function of recent (3–5 yr) radial growth rates (Kobe et al., 1995; Kobe and Coates, 1997). In the absence of disturbance, adult tree mortality is modelled as a random process with an annual rate of 1% (Runkle, 1981).

Recruitment. Mapped seedling traps or seed quadrats distributed at varying distances from the potential seed trees of each species provide the data to parametrize functions that describe both tree fecundity as a function of tree size and a the shape of the seed dispersal kernel (Ribbens et al., 1994).

Wind disturbance. The analysis for this submodel takes advantage of the fact that severe windstorms often contain dramatic spatial variation in intensity (e.g. Boose et al., 1994). The probability that an individual will experience any given level of damage is predicted as a logistic function of species taxonomic identity, individual tree size and local storm severity (as assessed using a relative, quantitative index) (Canham et al., 2001). The method uses maximum likelihood estimation to fit an ordinal

logistic model of the form:

$$\log(p_{iks}/(1 - p_{iks})) = a_{js} + c_s S_k DBH^{b_s}, \tag{1}$$

where p_{ijks} is the probability that individual i of species s in plot k is windthrown, and where a_{js}, b_s and c_s are species-specific parameters ($s = 1..m$ species), and S_k are the estimated storm severities (on a scale of $0 - 1$) for the $k = 1..n$ plots. For our analyses of wind disturbance in temperate forests, we only consider complete but not partial crown loss.

SORTIE has been parametrized for three regions where wind is a major natural disturbance agent: the transition oak-northern hardwood forests of the Northeastern U.S. (Pacala et al., 1996), the Interior Cedar–Hemlock forests of Northwestern British Columbia, Canada (Kobe and Coates, 1997; Wright et al., 1998; Canham et al., 1999; LePage et al., 2000), and the tropical forests of the Luquillo Mountains of Puerto Rico (Uriarte et al., 2004; 2005). In this paper, we use parameters obtained for nine species from transition oak-northern hardwoods forests in Northeastern North America for the first four submodels (Pacala et al. 1996). The species are (in roughly decreasing order of shade tolerance; Kobe et al., 1995): American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* L.), sugar maple (*Acer saccharum* Marsh), yellow birch (*Betula allegheniensis* Britton), black cherry (*Prunus serotina* Ehrh), red oak (*Quercus rubrum*), red maple (*A. rubrum* L.), white pine (*Pinus strobus*) and white ash (*Fraxinus americana*). These nine species are widespread in the northern hardwoods forests that stretch from the Appalachians in the south to New England in the northeast, account for approximately 50% of stems in the study region, and represent a good mix of early-mid to late successional species (Table 1). We obtained parameter estimates for the wind disturbance submodel for six of the nine species included in the analysis from Canham

Table 1. Average importance value for species x across counties in the four regions was calculated as IV (x) = 100* BA(x)/BA(all spp) + 100*No stems(x)/NoStems. We used data in the states of CT, MA, ME, NH, RI, and VT, Putnam, Rockland and Westschester County in New York. Data from Iverson & Prasad 1998. Data were not available for Long Island and urban areas surrounding New York City. A species in a monotypic stand would have an IV = 200

Species	Region 1	Region 2	Region 3	Region 4
Acer rubrum	44.23	65.50	41.00	31.23
Acer saccharum	6.38	8.00	7.56	11.68
Betula alleghaniensis	3.77	4.00	3.22	5.82
Fagus grandifolia	5.54	2.00	4.78	13.18
Fraxinus americana	5.08	7.50	14.11	6.27
Pinus strobus	11.31	16.50	17.00	22.36
Prunus serotina	8.00	7.50	5.78	4.14
Quercus rubrum	14.46	8.00	17.11	10.91
Tsuga canadensis	5.08	0.50	8.67	15.68
Total	103.85	119.50	119.22	121.27

et al. (2001). For the remaining three species (white ash, red oak and white pine), we assigned parameter values based on similarity in canopy allometry, wood density and canopy position with the other six species. We also tested patterns of mortality generated with these parameters with existing field damage data (Foster, 1988).

Forest characteristics at the sites where the model was parametrized are those of maturing, second-growth stands that have developed following a history of agriculture and logging, typical of land use history and forest development in Southern New England (Foster, 1988; Pacala et al., 1996). Changes in forest structure since the last severe hurricane to affect the region in 1938, namely, the greater number of larger, more susceptible trees, are likely to increase impacts of future wind storms on these forest ecosystems (Boose et al., 2001).

2.2. Disturbance regimes

New England is affected by Atlantic hurricanes that approach from the south, with greatest impact from hurricanes that pass over the warm waters of the Gulf Stream (Elsner et al., 2000). Simulation parameters for hurricane severity and frequency were derived from a reconstruction of regional variation in historical damage for 67 storms that affected six New England states plus adjacent New York City and Long Island since European settlement to the present (1620–1997) (Boose et al., 2001). The authors reconstructed regional maps of damage in the Fujita scale using both historical reports of wind damage and meteorological data (HURRDAT, Ludlum, 1963; Fernandez-Partagas and Diaz, 1995; Fig. 1). Given the difficulty in obtaining direct local measurements of wind speed at a given location, we used descriptions of tree damage in the Fujita scale to develop a synthetic index of storm severity ranging from 0 to 1 representing the approximate proportion of trees killed in a storm of a given intensity (Table 2) and converted this value to correspond with the storm severity index in Canham et al. (2001, *S* in eq. 1). We relied on maps from Boose et al. (2001, cf. Fig. 8) to partition regional variation in hurricane frequency and severity into four separate storm regimes (Table 3). These regions contained all of Rhode Island, Connecticut and Massachussetts, the southern counties of Vermont, New Hampshire and Maine, and Putnam, Rockland and Westschester counties in New York (Fig. 1).

To simulate the observed multi-decadal pattern in windstorm severity in the North Atlantic (Goldenberg et al., 2001), we calculated the probability of occurrence of a hurricane of a given intensity, *Pr(H)*, as a function of the average frequency (*B*) determined from Boose et al. (2001), (Table 3) and Y, a sine function that generates the periodicity observed in the historical record.

$$\Pr(H) = B * Y, \tag{2}$$

Y takes the form:

$$Y = \sin\frac{\pi x}{2} + 1, \tag{3a}$$

Table 2. Return intervals for windstorms in Southern New England (region 1 in Fig. 1) and description of likely forest damage

Fujita index	Mean Return Interval (yr)	Sustained wind speed (m s^{-1})	Damage	Estimated Mortality (proportion)
F0	5	18–25	Leaves & fruits broken	0
F1	10	26–35	Trees blown down	0.05–0.1
F2	85	36–47	Extensive blowdowns	0.2–0.5
F3	0	48–62	Most trees down	0.5–0.7
F4	0	NA	NA	NA

Table 3. Estimated hurricane return intervals (storm severity index) for four regional areas in Northeastern US. Data from Boose et al. (2001). These four storm regimes were used in simulations for four regions. Technically, it corresponds to the expected mean probability of mortality of a well-mixed stand with a full size distribution of trees. The actual mortality of an individual storm will depend on what species are present and what the size distribution is. In each 5-yr time step, we evaluate the occurrence of a hurricane by the probability of it occurring. A 10 yr severity storm has a 50% chance of happening. An 80 yr severity storm has a 6.25% chance of occurring. These storm regime is then used in the wind disturbance submodel to estimate probability of mortality for all trees in the stand

Return interval (yr)	Region 1	Region 2	Region 3	Region 4
10	0.10	0	0	0
20	0	0.13	0.11	0.08
80	0.47	0.47	0	0
160	0	0	0.53	0.
320	0	0	0	0.43

Fig. 1. Composite map of maximum wind damage from 1620 to 1997 in the Fujita scale in 0.5 increments. Regional gradient shows most severe impacts along the southern coastline and lesser damage to the north and west. Figure from Boose et al. (2001). Reprinted with permission from the Ecological Society of America. We limited our analyses to areas that have historically been subject to F1 damage.

where $x = 4t/A$, A is the duration of the multi-decadal cycle in years, and t is the number of years since the start of the cycle. We used $A = 40$ yr based on recent published data (Goldenberg et al., 2001).

We explored the implications of an increase in the return interval of severe hurricanes concurrent with the multi-decadal pattern by adding a trend to eq. 3a as follows:

$$Y = \sin \frac{\pi x}{2} + 1 + mx. \tag{3b}$$

Since two recent studies have reported a near doubling in destructive potential of hurricanes in the record (Emmanuel, 2005; Webster et al., 2005), we used a value of $m = 0.125$ which causes a doubling in hurricane regime severity over the length of two complete cycles (i.e. 80 yr). Technically, storm severity corresponds to the expected mean probability of mortality of a well-mixed stand with a full size distribution of trees (Table 3).

For each of these two scenarios (baseline & increased storm severity), we performed 10 simulations of 300 yr. Initial con-
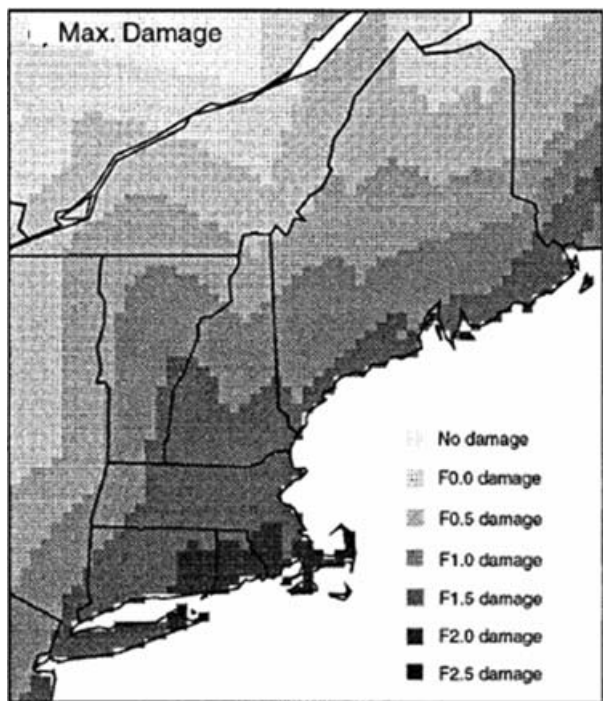
ditions for runs in each region had seedling numbers available for recruitment that were proportional to the average relative abundance of each species in the four storm disturbance regions (Table 1). These initial abundances were selected to create forest stands that were representative of 100-yr old conditions in each region. Abundance figures were calculated using US Forest Service inventory data (Iverson and Prasad, 1998) and were adjusted to produce an initial density of 225 seedlings ha^{-1}, which generate observed adult densities (Pacala et al., 1996). Seedlings were distributed randomly in a 300 × 300 m

simulated stand. The initial 100 yr of the simulations were used to generate forest stands representative of conditions (e.g. diameter distributions) observed in the region. Windstorm scenarios were applied starting at 100 yr through the end of the simulations (300 yr). At each time step, we calculated total number of trees for each species. Aboveground biomass was estimated using US Forest Service dimension analysis equations (Jenkins et al., 2003) and average percent carbon in tree biomass was assumed to be 50% (Koch, 1989). Carbon sequestration over the 300 yr of the simulations was calculated as net annual growth in biomass minus rate of biomass loss through mortality or wind damage (Brown and Schroeder, 1999). We also calculated total biomass in aboveground woody production downed in storms. Carbon in this pool may be incorporated into the soil through decomposition, although dead wood in these temperate forests may take many decades to decompose (Harmon et al., 1986). Alternatively, carbon in felled timber may be respired, salvaged for commercial uses or burned to the atmosphere due to increased susceptibility to fires (Foster et al., 1997; McNulty, 2005). Total aboveground productivity was calculated as net annual growth in biomass plus annual dead biomass (Brown and Schroeder, 1999).

To ensure that the range of carbon sequestration predicted by our model was within the range observed in other studies, we compared it with other independent estimates. However, the last severe storm to affect forests in the study region was the 1938 hurricane. Since independent data used to estimate biomass storage in aboveground biomass in the region (e.g. US Forest Service Inventory analyses in the NE) were collected in periods free of hurricanes (1970–1990), we used the model in a hurricane-free scenario to calibrate rates carbon sequestration in aboveground biomass. Estimates of carbon storage for 100, 150 and 200 yr periods in the absence of hurricanes were 1.69, 1.45 and 1.11 tons C ha^{-1} yr^{-1} well within the 1–4 tons C ha^{-1} yr^{-1} range measured from forest inventory data (Birdsey, 1992) and from eddy covariance methods (Goulden et al., 1996).

3. Results & discussion

3.1. Regional variation in carbon sequestration and loss to windstorms

3.1.1. Baseline conditions. Carbon sequestered in aboveground standing biomass over 300 yr decreased with increasing severity of storm disturbance across the regional gradient ranging from 0.70 tons ha^{-1} yr^{-1} in the less affected northern area (Regime 4) to 0.48 tons ha^{-1} yr^{-1} under the most severe regime in the southernmost region (Regime 1, Fig. 2a, df = 3, 77, p <0.0001). Estimates of carbon storage in aboveground production of woody biomass in this region obtained using USFS (United States Forestry Service) Forest Inventory Analyses data from the 1970′s and 1980′s range from 1 to 4 tons ha^{-1} yr^{-1} (Brown and Schroeder, 1999). However, these estimates

included biomass in dead trees. If we include aboveground biomass felled in storms in our calculations, carbon sequestration ranges from 0.93 to 1.68 tons C ha^{-1} yr^{-1}, with the largest rates of sequestration in aboveground woody biomass occurring in areas subject to the most severe storm regime (Fig. 2b & c). Therefore, our analyses produce estimates within the observed range from field data. Although some portion of carbon in felled timber could be lost to the atmosphere, a large proportion of carbon in felled timber is likely be incorporated into the soil and retained in the ecosystem over decadal scales.

Most large-scale estimates of carbon sequestration do not take into account the potentially large effects of disturbance (Schimel et al., 1997). A recent study along the Southern US coast estimated that a single storm event can convert the equivalent of 10% of the total annual carbon sequestered in US forests to dead and downed biomass (McNulty, 2005). Although the Northeastern US contains a lower portion of forested land that could be affected by storms, the impact of a severe hurricane on both short-term and long-term carbon sequestration could be equally dramatic. Incorporating spatially explicit information on disturbance and subsequent population responses in regional models of carbon sequestration will do much to improve congruence between models and data (Schimel et al., 1997).

The long-term impacts of storms on carbon sequestration will depend on the fate of downed timber. Overall, carbon sequestered in this pool outweighed biomass in standing aboveground biomass with the exception of the region with the mildest storm regime (Regime 4, Fig. 2). Therefore, incorporation of downed biomass into the soil pool where it may remain for decades, may be the largest sink of carbon (Harmon et al., 1990). Radiocarbon-based estimates of residence times in a New England forest in the region ranged from 2 to 5 yr for litter to 40–100 yr for low density humified materials and >100 yr for carbon associated with soil minerals (Gaudinski et al., 2000). To the degree that carbon in the felled timber pool is incorporated into the soil, storm events are likely to increase carbon sequestration potential in forests by generating resource conditions (e.g. light) and size–age distributions that foster tree growth. However, unsalvaged timber can generate stand conditions that enhance susceptibility to fire and insect outbreaks (McNulty, 2005), thereby decreasing carbon uptake or increasing potential for carbon losses to the atmosphere. Both natural and anthropogenic (e.g. harvesting cf Kitteridge et al., 2003) disturbance generates uncertainty in carbon sink estimates, emphasizing the need for monitoring.

3.1.2. Increasing storm severity scenario. In our second scenario in which we assumed increasing storm severity relative to the historical baseline, there was a net decrease in sequestered carbon in standing aboveground biomass and an increase in the amount of carbon in felled timber relative to the baseline scenario (df = 1, 79, p < 0.0001 for both values, Fig. 2a & b). The greater losses in aboveground biomass relative to baseline conditions were observed in areas with more severe windstorms, while
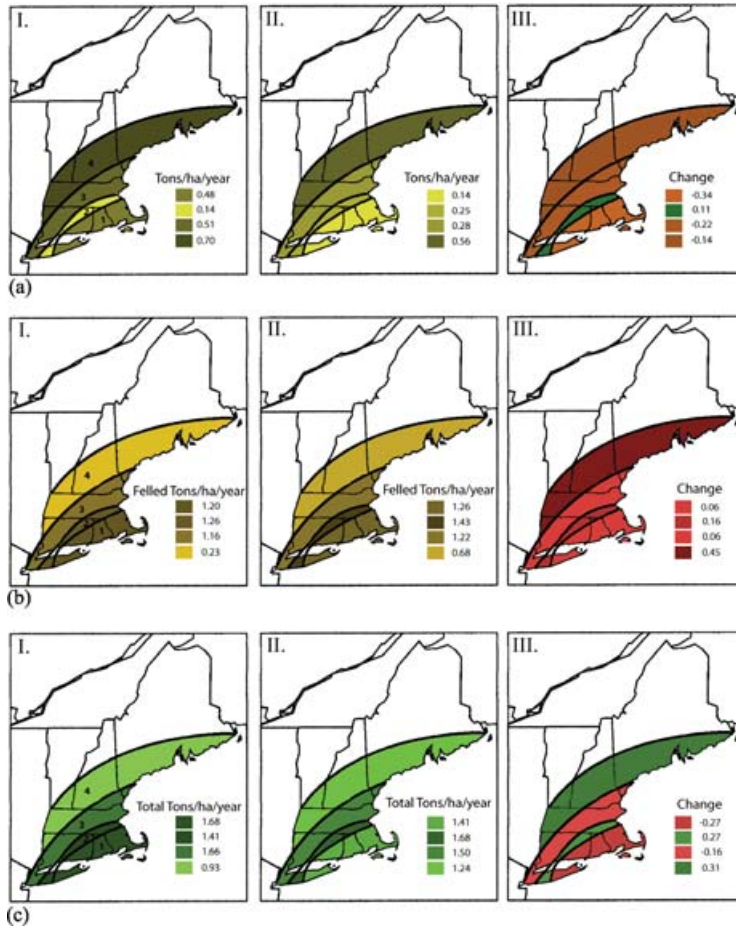
Fig. 2. Standing carbon production in: (a). Average biomass sequestered in standing aboveground biomass in tons per ha per year across a regional gradient in hurricane frequency and severity. (b) Average aboveground biomass in downed timber in tons per ha per year across a regional gradient in hurricane frequency and severity; (c) Average total carbon sequestered in tons per ha per year in standing and downed aboveground biomass. The numbers 1 – 4 in (a-c) correspond to the regions for the regimes that were determined using data from Boose et al. (2001). (I) Historical frequency and severity; (II) increasing severity; and (III) net gain or loss between the two regimes. Statistically significant differences ($p < 0.0001$) are indicated with*.

increases in felled biomass were most marked for regions that suffer less severe storms. Although average total carbon sequestration did not differ between baseline and increased hurricane conditions over the entire landscape (df = 1, 79, p = 0.41), the interaction of these two effects on standing and felled biomass resulted in opposite outcomes for overall carbon sequestration in aboveground biomass at each end of the regional disturbance gradient. Increased storm severity decreased overall carbon sequestration relative to baseline in the southernmost region because storm free periods were never long enough for the forest to reach peak basal area and biomass (Merrens and Peart, 1992). However, in the northernmost region, greater storm severity increased overall carbon sequestration by fostering carbon accumulation during interstorm periods and maintaining high carbon accumulation through periodic damage to accumulated biomass (Fig. 2).

3.2. Regional variation in community composition in response to storm regimes

Initial conditions in our simulations varied between hurricane disturbance regions. Therefore, we will compare community

composition within regions under baseline and increased storm severity scenarios. The effect of storm regimes on community composition highlighted complex interactions between species life history traits including shade-tolerance, wind resistance, and response to increases in light availability caused by wind damage to the canopy, with the successional age of the stand (Tables 4–5 Papaik and Canham, 2006, Loehle, 2000; Batista et al., 1998). The prevalence of the most shade-intolerant species shifted with generally increased hurricane disturbance. For instance, *Prunus serotina,* an early-succesional species, highly intolerant of shading, is also highly susceptible to windthrow in all size classes (Canham et al., 2001). After 300 yr of simulation, greater storm severity decreases the relative number of adults of this species and then slightly increases across the regional gradient of severity (Table 4). This pattern is likely generated by a balance between high susceptibility to windthrow of adult *P. serotina* trees in the most severe end of the regional disturbance gradient (region 1) and competitive exclusion as the canopy closes through succession over 300 yr at the least severe end of the gradient (Region 4) (Merrens and Peart 1992). *P. serotina* requires large openings for establishment (Marks, 1974). The relative increase in sapling numbers in 200-yr old stands across the disturbance gradient with

Table 4. Average sapling abundance/ha in 10 simulated 200-yr and 300-yr stands under four disturbance regimes under baseline and increasing storm severity (ISS) scenarios. Standard deviations are given in parentheses. Full species names are given in Table 1

		Regime 1 Baseline	Regime 1 ISS	Regime 2 Baseline	Regime 2 ISS	Regime 3 Baseline	Regime 3 ISS	Regime 4 Baseline	Regime 4 ISS
Acer r.	*200*	8.68 (4.2)	8.59 (3.6)	23.08 (14.9)	26.27 (12.9)	3.76 (4.8)	8.02 (5.8)	0.20 (0.2)	0.80 (2.3)
	300	0.86 (0.6)	1.30 (0.6)	7.16 (5.8)	10.36 (3.8)	0.70 (1.2)	1.22 (0.4)	0.19 (0.2)	0.24 (0.3)
Acer s.	*200*	0.41 (0.2)	0.34 (0.3)	0.70 (0.6)	1.54 (0.8)	0.46 (0.3)	0.59 (0.5)	0.13 (0.1)	0.40 (0.6)
	300	0.06 (0.1)	0.03 (0.1)	0.26 (0.2)	0.44 (0.3)	0.17 (0.3)	0.10 (0.1)	0.09 (0.1)	0.13 (0.1)
Betula	*200*	6.98 (1.8)	6.00 (1.8)	7.90 (2.3)	13.36 (2.8)	2.58 (1.4)	4.33 (1.8)	0.81 (0.4)	1.10 (1.5)
	300	5.14 (3.3)	6.92 (2.1)	14.56 (4.3)	27.36 (7.4)	1.32 (1.3)	6.04 (3.1)	0.53 (0.2)	0.51 (0.7)
Fagus	*200*	15.78 (8.1)	10.54 (4.4)	5.07 (3.8)	4.80 (2.0)	9.41 (6.1)	10.66 (4.7)	20.20 (2.3)	18.40 (8.6)
	300	11.99 (6.1)	3.89 (2.0)	8.51 (7.0)	5.00 (1.6)	10.40 (4.1)	12.26 (7.0)	22.20 (5.8)	19.16 (13.7)
Fraxinus	*200*	1.83 (1.1)	1.41 (0.6)	3.72 (2.6)	4.84 (2.6)	2.46 (4.0)	3.41 (2.7)	0.08 (0.1)	0.21 (0.4)
	300	0.19 (0.2)	0.13 (0.2)	1.49 (1.2)	1.89 (1.3)	0.31 (0.5)	0.59 (0.4)	0.01 (0.0)	0.11 (0.1)
Pinus	*200*	33.34 (12.7)	35.81 (14.6)	54.97 (33.9)	63.68 (25.2)	22.49 (25.8)	28.48 (19.1)	2.71 (1.2)	5.31 (7.0)
	300	10.18 (5.1)	12.62 (10.3)	37.53 (19.3)	68.06 (19.8)	8.18 (9.1)	16.36 (6.2)	2.31 (1.5)	2.30 (2.4)
Prunus	*200*	25.62 (8.8)	25.26 (8.1)	25.30 (18.5)	43.12 (13.5)	8.70 (6.6)	11.97 (7.2)	0.80 (0.4)	1.76 (2.7)
	300	8.30 (5.5)	13.90 (4.7)	20.69 (10.1)	45.64 (18.0)	3.07 (3.5)	6.33 (3.8)	0.79 (1.0)	0.39 (0.5)
Quercus	*200*	45.43 (14.9)	48.43 (15.3)	32.88 (14.4)	47.49 (16.4)	22.59 (22.1)	32.22 (18.9)	0.60 (0.4)	2.50 (3.5)
	300	15.81 (8.1)	26.38 (12.0)	30.23 (18.0)	61.97 (25.0)	6.74 (10.0)	16.87 (6.3)	0.61 (0.2)	0.89 (1.0)
Tsuga	*200*	96.58 (21.7)	76.47 (24.1)	7.80 (2.8)	10.01 (4.1)	105.84 (55.2)	97.41 (46.6)	50.14 (8.7)	69.83 (47.2)
	300	103.90 (35.9)	42.63 (22.3)	15.60 (6.8)	19.60 (3.3)	97.60 (45.0)	127.67 (20.5)	73.42 (25.5)	69.59 (51.7)

Table 5. Average adult stem density/ha in 10 simulated 200-yr and 300-yr stands under four disturbance regimes under baseline and increasing storm severity (ISS) scenarios. Standard deviations are given in parentheses. Full species names are given in Table 1

| | | Regime 1 | | | | Regime 2 | | | | Regime 3 | | | | Regime 4 | | | |
		Baseline		ISS		Baseline		ISS		Baseline		ISS		Baseline		ISS	
Acer r.	200	12.43	(5.2)	10.94	(3.5)	32.86	(15.3)	26.27	(12.9)	11.58	(3.6)	9.99	(3.2)	10.69	(1.1)	8.23	(3.1)
	300	10.94	(3.5)	1.89	(0.7)	14.77	(5.3)	10.36	(3.8)	2.74	(1.1)	1.92	(1.0)	3.53	(1.0)	1.92	(1.0)
Acer s.	200	1.02	(0.6)	0.53	(0.4)	2.09	(0.9)	1.54	(0.8)	1.83	(0.8)	1.19	(0.6)	2.87	(0.5)	3.00	(0.8)
	300	0.53	(0.4)	0.03	(0.1)	0.90	(0.5)	0.44	(0.3)	0.43	(0.3)	0.29	(0.1)	1.07	(0.3)	0.97	(0.4)
Betula	200	10.13	(3.8)	9.54	(2.2)	14.87	(3.6)	13.36	(2.8)	6.43	(1.9)	7.18	(3.0)	3.82	(0.5)	4.14	(2.0)
	300	9.54	(2.2)	12.72	(4.0)	30.29	(10.4)	27.36	(7.4)	5.46	(1.7)	11.01	(3.4)	2.60	(1.1)	2.82	(1.4)
Fagus	200	13.69	(3.4)	10.47	(6.1)	6.08	(2.3)	4.80	(2.0)	9.61	(1.6)	12.27	(3.6)	15.72	(1.5)	17.99	(9.4)
	300	10.47	(6.1)	7.10	(3.1)	11.56	(5.1)	5.00	(1.6)	14.68	(6.9)	14.91	(4.7)	26.48	(3.8)	26.30	(11.8)
Fraxinus	200	2.74	(1.4)	1.57	(0.8)	7.62	(3.1)	4.84	(2.6)	6.99	(2.9)	6.34	(0.7)	3.76	(0.5)	3.60	(1.5)
	300	1.57	(0.8)	0.33	(0.3)	3.88	(1.7)	1.89	(1.3)	2.44	(1.3)	1.24	(0.7)	1.43	(0.5)	1.38	(0.6)
Pinus	200	25.37	(11.0)	24.02	(10.9)	68.26	(28.8)	63.68	(25.2)	31.56	(14.2)	30.64	(11.5)	19.61	(1.6)	18.90	(12.9)
	300	24.02	(10.9)	22.33	(12.8)	63.56	(31.0)	68.06	(19.8)	18.41	(7.3)	21.60	(6.0)	10.28	(4.4)	12.62	(7.5)
Prunus	200	30.02	(12.2)	28.83	(14.0)	45.72	(18.3)	43.12	(13.5)	19.49	(7.7)	19.79	(6.0)	6.76	(0.9)	6.46	(3.6)
	300	28.83	(14.0)	18.97	(10.9)	54.89	(11.6)	45.64	(18.0)	15.83	(5.0)	15.30	(3.5)	4.44	(1.3)	4.68	(2.1)
Quercus	200	41.57	(22.7)	42.18	(13.2)	46.02	(18.8)	47.49	(16.4)	38.49	(13.8)	39.22	(11.3)	13.06	(1.5)	13.62	(5.5)
	300	42.18	(13.2)	37.52	(17.8)	54.09	(35.9)	61.97	(25.0)	22.11	(6.0)	29.50	(11.7)	6.77	(3.9)	9.32	(4.7)
Tsuga	200	65.30	(14.0)	51.94	(15.1)	8.94	(5.5)	10.01	(4.1)	88.96	(18.1)	95.72	(44.1)	50.27	(5.2)	70.90	(53.7)
	300	51.94	(15.1)	54.46	(22.1)	20.34	(6.3)	19.60	(3.3)	153.41	(65.7)	165.23	(42.2)	92.34	(15.2)	145.38	(77.6)

greater storm severity suggests that frequent, strong winds open up the canopy and increase understory light availability, enhancing sapling recruitment for this species (Table 4–5). However, increased storm severity does not affect sapling recruitment in 300-yr old stands in the low end of the disturbance gradient (Region 4), presumably because storm-free periods allow canopy closure and reduce recruitment of *P. serotina* saplings. Lower sapling numbers after 300 yr of stand development relative to 200 yr stands demonstrate the canopy closure over the course of succession had negative effects on the abundance of *P. serotina* ((Table 4–5. For this species, the direction of response to wind damage will be determined by the balance between susceptibility to windthrow, sapling response to enhanced light availability and the successional age of the stand. A second shade-intolerant species, *Pinus strobus*, also highly susceptible to windthrow had a very similar response to increased storm severity across the regional disturbance gradient.

More shade-tolerant species behave idiosyncratically in ways that appear to be determined by relative resistance to windthrow, dispersal ability and effects of disease (Tables 4–5). For instance, beech bark disease has made adults of *F. grandifolia* highly susceptible to windthrow by increasing the probability of stem break in moderately or highly infected beech trees (Papaik et al., 2005). In agreement with these findings, our simulations showed reduced abundance of *F. grandifolia* adults with greater storm severity in the severe end of the gradient (region 1), probably from a combination of high susceptibility to wind damage and

competitive displacement from *B. alleghaniensis* (Papaik and Canham, 2006). However, beech trees can persist through succession as an abundant understory species even in the most severe storm regime because of the wind resistance of small-sized trees (Batista et al., 1998; Canham et al., 2001) and its high shade tolerance (Kobe et al., 1995) (Table 5). Competitive displacement from *Tsuga canadensis*, which is highly resistant to wind damage, may have also contributed to the low numbers of *F. grandifolia* adults at the less severe end of the gradient.

Our results demonstrate that potential community responses to changes in hurricane disturbance regimes do not follow from any ranking of species by resistance to wind disturbance. Rather, variation in susceptibility in different size classes and other life history traits such as dispersal ability can influence the long-term response of species to increased storm severity. For instance, *T. canadensis* is the most susceptible species in low severity storms for all tree sizes but becomes relatively more windfirm (relative to other species in the same size range) as storm severity increases (see Canham et al., 2001). Therefore, milder storms act as a bottleneck limiting the long-term abundance of *T. canadensis*, particularly under the mildest northernmost storm regime (Papaik and Canham, 2006).

4. Conclusions

Our results suggest that if the trend towards increasingly severe hurricane regime continues, the effects on carbon sequestration

in aboveground forest biomass will depend on an interaction between baseline and future storm regimes, with potential increases and decreases at the landscape level. Areas that have historically had a low level of disturbance may experience an increase in aboveground production of biomass through death of old, slow-growing trees and growth of suppressed trees in the understory. However, greater carbon sequestration in aboveground biomass will only be effective to the degree that carbon in wood felled in storms is transferred to the soil pool and retained in the ecosystem. Incorporating disturbance in our estimates of carbon sequestration potential in forests will do much to improve congruence between models and data.

Life history traits, specifically, the interaction between wind disturbance, long life span, the ability to take advantage of enhanced light availability after storms and shade-tolerance will determine the response of forest communities to wind disturbance (Loehle, 1989). Our simulations demonstrated that resistance to disturbance dominated competitive ability (a combination of shade-tolerance and response to light) as a trait determining relative abundance under an increasing storm severity scenario. Lasting differences in succession among the regimes were a result of changes in the probability of relatively long disturbance-free periods. Periodic storms will allow interspecific differences in susceptibility to windthrow to play a strong role in successional dynamics, with forests becoming increasingly resistant to windstorms. Thus, susceptibility to winds will become the dominant life history trait under an increased severity scenario. Landscape variation in forest development will interact with these traits to determine successional trajectories and community composition at the regional level.

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