# Divergent carbon dynamics under climate change in forests with diverse soils, tree species, and land use histories

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**Abstract.** Accounting for both climate change and natural disturbances—which typically result in greenhouse gas emissions—is necessary to begin managing forest carbon sequestration. Gaining a complete understanding of forest carbon dynamics is, however, challenging in systems characterized by historic over-utilization, diverse soils and tree species, and frequent disturbance. In order to elucidate the cascading effects of potential climate change on such systems, we projected forest carbon dynamics, including soil carbon changes, and shifts in tree species composition as a consequence of wildfires and climate change in the New Jersey pine barrens (NJPB) over the next 100 years. To do so, we used the LANDIS-II succession and disturbance model combined with the CENTURY soil model. The model was calibrated and validated using data from three eddy flux towers and the available empirical or literature data. Our results suggest that climate change will not appreciably increase fire sizes and intensity. The recovery of C stocks following substantial disturbances at the turn of the 20th century will play a limited but important role in this system. In areas characterized by high soil water holding capacity, reduced soil moisture may lead to lower total C and these forests may switch from being carbon sinks to becoming carbon neutral towards the latter part of the 21st century. In contrast, other areas characterized by lower soil water holding capacity and drought tolerant species are projected to experience relatively little change over the next 100 years. Across all soil types, however, the regeneration of many key tree species may decline leading to longer-term (beyond 2100) risks to forest C. These divergent responses were largely a function of the dominant tree species, and their respective temperature and soil moisture tolerances, and soil water holding capacity. In summary, the system is initially C conservative but by the end of the 21st century, there is increasing risk of de-stabilization due to declining growth and regeneration.

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## INTRODUCTION

Anticipated climate change will have multi-faceted effects on forest ecosystems worldwide. Changing temperature and precipitation are expected to alter forest community composition and carbon dynamics, though it remains difficult to predict the magnitude and direction of the

changes. Determining how climate change will affect forests is complex, because rising temperatures and altered precipitation regimes affect tree physiological processes (e.g., photosynthesis, respiration, and seed production) and detrital and soil processes (e.g., decomposition), which are inextricably linked. Concerns over the ability of forests to maintain native diversity (Mote et al. 2003) and sequester carbon to offset rising $CO_2$ (Lal 2004, Canadell and Raupach 2008) fuel efforts to project how forests will adapt to climate change.

Gaining a complete understanding of forest carbon dynamics is, however, challenging in forested systems characterized by a history of extensive utilization, diverse soils, frequent disturbance, and risk of tree species compositional shifts due to climate change. The pine barrens and neighboring forests in New Jersey (NJPB), are broadly representative of such systems. The NJPB is characterized by sandy, nutrient-poor upland forests with inclusions of wet, lowland forests. Prior to European settlement, the more xeric, fire adapted and fire-prone areas had estimated rotation periods from 30-50 years (Forman and Boerner 1981, Scheller et al. 2008). Pines were dominant with a significant oak component. Due to its proximity to Philadelphia and New York City, the area was extensively disturbed up to the 20th century as fire wood, lumber, and bog iron were extracted (Wacker 1979), followed by a period of severe, widespread wildfires. The system appears to be in a period of continued carbon recovery from these disturbances and is projected to continue sequestering carbon in wood and soils over the next century, assuming the climate remains constant (Scheller et al. 2011b). Recent fragmentation and efficient fire suppression has reduced the size and frequency of wildfires on the landscape, causing a gradual shift towards oak domination (Scheller et al. 2008).

However, the continued sequestration of carbon (Scheller et al. 2011b) may cease as a consequence of climate change. Climate change is anticipated to increase temperatures from 2.9 to 5.3°C (Hayhoe et al. 2007). Warmer temperatures are expected to enhance growth where sufficient soil water is available (Scheller and Mladenoff 2005) but if soil water becomes limiting, growth may decline (Pastor and Post 1988). A longer growing season may also boost overall growth (White et al. 1999) but may potentially reduce carbon uptake overall (Piao et al. 2008). Likewise, soil and litter decomposition are sensitive to temperature and available soil moisture (Schmidt et al. 2011). In addition, overstory composition may shift towards tree species with a higher photosynthetic optimum temperature (Iverson and Prasad 2002). Sufficiently large changes in tree species composition will influence decomposition and N availability (Scheller et al. 2011a, Schmidt et al. 2011). This myriad of potential factors may generate a mosaic of responses to climate change across landscapes, dependent on local site conditions and the biological capacity (or lack thereof) to benefit from altered temperature and precipitation regimes.

A further concern is that climate change will alter disturbance regimes. These include modified wildfire regimes (Dale et al. 2001, Westerling et al. 2006, Smithwick et al. 2009), increased insect activity (Ward and Masters 2007, Kurz et al. 2008), more intense wind storms and more frequent hurricanes (Easterling et al. 2000). The effect of altered disturbance regimes may be larger than the physiological effects of altered temperatures and precipitation on growth and respiration. For example, a large fire in southwestern Oregon released 16 times as much carbon as the annual net ecosystem production of the landscape (Campbell et al. 2007). In British Columbia, mountain pine beetle outbreaks attributed to climate change have switched forests from modest carbon sinks to a significant source (Kurz et al. 2008). Projections of the effects of climate change on forested systems should therefore incorporate both physiological and disturbance mediated effects.

Our objectives were to further our understanding of the interactions of climate change and fire on carbon dynamics (including living, detrital, and soil) and species composition. The NJPB served as our exemplar system and we built upon our prior research consisting of empirical data analysis (Clark et al. 2010, Clark et al. 2011, Clark et al. 2012) and simulation modeling (Scheller et al. 2008, Scheller et al. 2011b) to achieve these objectives. Specifically, we used the down-scaled global circulation model projections in conjunction with the LANDIS-II forest change

model and a succession extension derived from the CENTURY soil model (Scheller et al. 2011a, b) to simulate landscape change up to the year 2100. We also simulated wildfire as an emergent property of changing fuels and climate.

## METHODS

### Study area

The New Jersey Pine Barrens (NJPB) is an extensive system of pine, oak and wetland forests, totaling 4451 km$^2$ that includes the Pinelands National Reserve. The NJPB is the last substantial contiguous forested area immediately adjacent to the eastern seaboard. Since 1900, logging and wildfire has declined while fragmentation by roads and housing developments has increased (Luque et al. 1994, Lathrop and Kaplan 2004, Scheller et al. 2008). Our study area was delimited to capture the major blocks of contiguous forests (Fig. 1).

The climate in the NJPB is cool temperate, with mean monthly temperatures of 0.3 and 23.8°C in January and June, respectively (1930–2009; NJ State Climatologist). Mean annual precipitation is 1123 ± 182 mm. The terrain consists of plains, low-angle slopes and wetlands, with a maximum elevation of 63 meters. Our analyses were segregated into three broad forest types, upland, wetland, and pine plains, described below.

Upland forests comprise 58% of forested lands in the NJPB and are dominated by pitch pine (*Pinus rigida*), and numerous oaks (*Quercus* spp.). Many tree and understory species in the uplands are highly adapted to fire and readily resprout following fire (Boerner 1981). Soils are coarse-textured, sandy, acidic, and have extremely low cation exchange capacity and nutrient status (Tedrow 1986) (see Supplement, Century inputs). Despite their nutrient-poor soils, upland forests are moderately productive (Pan et al. 2006, Clark et al. 2010).

Interlaced through the area are numerous rivers and streams; associated wetland forests (38% of forested land) are dominated by Atlantic white cedar (*Chamaecyparis thyoides*) red maple (*Acer rubrum*), swamp tupelo (*Nyssa sylvatica*), pitch pine, shortleaf pine (*P. echinata*), and mesic oaks, including white oak (*Q. alba*) and black oak (*Q. velutina*). Wetland forests have higher soil water holding capacity and are more prone to

saturation (see Supplement, Century inputs).

The pine plains (<5% forested area) are notably xeric with deep, sandy soils, low productivity, and a stunted overstory dominated by pitch pine.

### Experimental design

We simulated a baseline scenario (no climate change) and one emissions scenario from a single global circulation model. We selected the Hadley Community Model 3 (HadCM3) for predicting climate change for our study area. HadCM3 is a good predictor of the average temperature and precipitation changes due to climate change (Ruosteenoja et al. 2003). An initial analysis indicated that moderate B2 emissions would produce minimal changes in ANPP or the ability of tree species to establish, largely because the local climate is moderated by the Atlantic Ocean. Therefore we chose the A2 'high' emissions scenario (IPCC 2007) to highlight the maximum possible climate change effects. Each scenario was simulated out to the year 2100 and replicated five times; each replicate encapsulated a unique series of stochastic events predicated on the underlying probability distribution functions.

### Forest succession and disturbance model

We simulated forest landscape change using the LANDIS-II forest landscape model (Mladen-off 2004, Scheller et al. 2007). LANDIS-II simulates ecological processes (disturbances and succession) and management in a flexible framework that emphasizes spatial interactions across the landscape and among processes (e.g., climate change, wildfire, succession, and seed dispersal) over decades or centuries (Fig. 2). LANDIS-II simulates individual species and age cohorts of the dominant trees and shrubs; each species has unique life history attributes (e.g., longevity, seed dispersal distance, fire tolerance, and shade tolerance) (Roberts 1996) and responds uniquely to disturbance, available light, soils, and climate conditions. The successional dynamics of tree species are dependent upon their unique life history attributes, their growth rates, establishment (described below), and relative competitive abilities at a given location. LANDIS-II requires that the landscape be divided into 'ecoregions', areas with unique soil and climatic conditions; ecoregions need not be continuous.
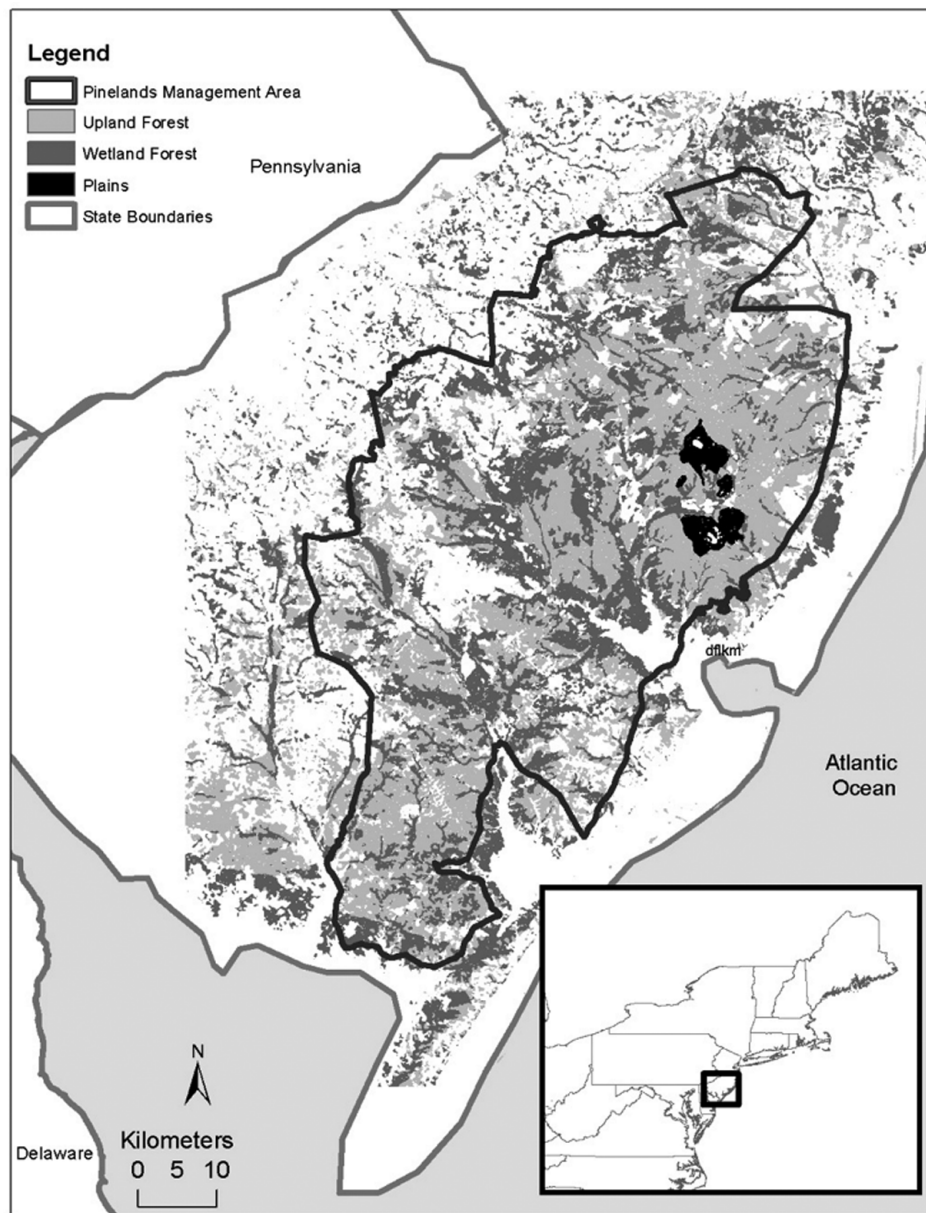
Fig. 1. Map of the study area.

We simulated landscape carbon dynamics using the Century Succession extension for LANDIS-II (Scheller et al. 2011*a*, *b*). The Century Succession extension enabled us to integrate the effects of climate change, wildfires, and species composition on landscape carbon dynamics. The Century Succession extension is derived from the CENTURY soil model (Parton et al. 1983, Parton et al. 1994) and simulates the regeneration and growth of trees and shrubs, wood and litter deposition and decomposition, soil accumulation and decomposition, and available soil water (Scheller et al. 2011*a*, *b*). The extension simulates all components of the carbon cycle—including the effects of disturbance—and therefore calculates net ecosystem exchange and net ecosystem production (Scheller et al. 2011*a*).

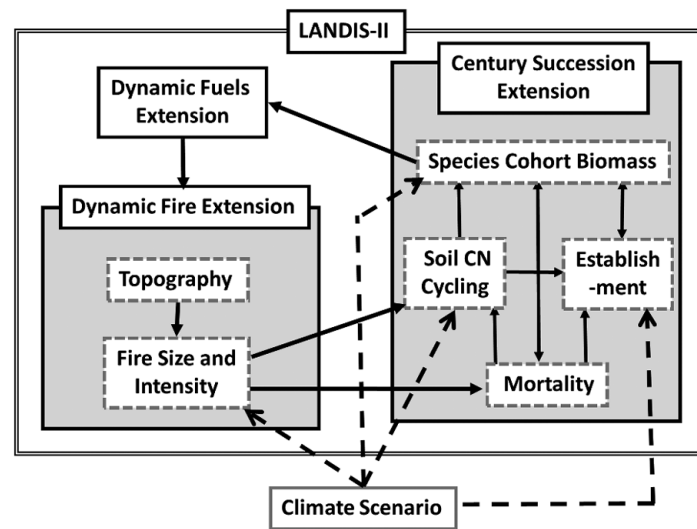The Century extension generates maps and

Fig. 2. Conceptual model of interactions between LANDIS-II extensions, components of the extensions and the climate scenarios.

time series data of aboveground net primary productivity (ANPP), net ecosystem exchange (NEE), soil organic carbon (SOC), detrital carbon, and aboveground biomass (AGB) by species. Successional and carbon dynamics for the NJPB have been previously published (Scheller et al. 2008, Scheller et al. 2011*b*). The landscape was divided into seven ecoregions (Scheller et al. 2011*b*), which were aggregated into three broad land types for interpretation: uplands, wetlands, and the pine plains. We did not simulate shrubs or other understory species. Although shrubs can contain a substantial fraction of overall site leaf area index (Clark et al. 2012), they are poorly parameterized at this time. The Century extension requires monthly climate data (temperature and precipitation) with 5-year species-age cohort bins. See Supplement, Century inputs for the complete list of model input parameters.

The probability of establishment—the probability that a new cohort will become established given sufficient light and the presence of propagules—was calculated as a function of the dynamic climate inputs (below). The probability of establishment is the minimum of three limiting factors: minimum January temperature (a binary limit), minimum and maximum number of growing degree days, and the fraction of drought days (with insufficient soil moisture for growth) in a growing season (Pastor and Post 1988,

Scheller et al. 2005). Species parameters are provided in Scheller et al. (2008) and in the Supplement, Century inputs.

### Changes to the Century Succession extension

We made several changes to the N cycle to the Century Succession extension (Scheller et al. 2011*a*). In this new version (version 3), the amount of N needed for growth (N demand) is calculated for each cohort at each monthly time-step. In the spring, cohorts first utilize resorbed N (i.e., retranslocated N) that was withdrawn from the leaves prior to autumn senescence and stored in woody tissue. In forest ecosystems, resorption is a significant source of N uptake in the spring (Ryan and Bormann 1982) and can be 10–80% of N uptake depending on species, site, and the time since disturbance (Killingbeck 1996, Covelo et al. 2008). Resorption is calculated in August each year as the difference between leaf and litter N and then used the following spring (April–June) to satisfy N demand ($N_{resorption}$). Once the pool of resorbed N is exhausted, the cohorts withdraw mineral N from the soil ($N_{uptake}$). If there is not enough N to satisfy the total demand for N across all cohorts, however, the amount of mineral N allocated to each cohort is determined by its coarse root biomass relative to other cohorts. Finally, the N limit to growth is computed for each cohort, using:

$$Limit = \frac{Resorption + Uptake}{Demand} \quad (1)$$

where Demand is calculated from maximum potential productivity given temperature, water, and LAI limits and the Limit is restricted to the range [0, 1]. This N limitation factor is then multiplied by the maximum potential productivity.

We also added N leaching to the Century Succession extension based in part on the calculations in the CENTURY model (Parton et al. 1983) using the following equations:

$$Leached = Slope + Intercept \times Fraction\ Sand$$
$$\times Mineral\ N \times FracNO_3^- \quad (2)$$

where Slope and Intercept (fleach(1) and fleach(2), respectively, in CENTURY) are the slope and intercept value to compute the fraction of mineral N which will leach when there is saturated water flow (slope $= 0.4$, intercept $= 0.6$); Fraction Sand is the fraction of sand; and FracNO$_3^-$ is the fraction of NO$_3^-$ in soil. Only nitrate is leached through the soil in significant quantities; ammonium is only about 5% of the mineral N present in NJPB soils (Dighton et al. 2004). The total amount of N leached is then calculated using:

$$Total\ Leached\ (g\ N) = Base\ flow \times Leached$$
$$+ Storm\ flow \times Leached$$
$$(3)$$

where storm and base flow are affected by precipitation and water movement through the soil (Parton et al. 1983).

Although this research did not address the effects of insects on the NJPB, C and N inputs from frass during insect defoliation events were added to the extension for future research.

Our changes to the Century Succession extension required modest re-calibration of decay constants (heterotrophic respiration), leaf area index (LAI) parameters, temperature parameters, and the addition of a functional group representing Atlantic white cedar (see Supplements, Century inputs). To more accurately reflect the growth response of tree species to changing temperature, parameters dictating the heat tolerance curve and optimal photosynthetic temperature for each tree functional group were updated. Empirical data on at least one species

from each functional group was used and more when available (Ledig et al. 1977, Dougherty et al. 1979, Epron 1997, Jull et al. 1999, Nedlo et al. 2009, Turnbull et al. 2001, Warren and Dreyer 2006, Weston and Bauerle 2007).

In addition, we conducted a more comprehensive calibration against empirical data. The model was calibrated such that: (1) estimates of ANPP were within range of literature values (Pan et al. 2006) for the appropriate ecoregion and within 25% of ANPP measurements at three flux tower sites; (2) NEE estimates fit flux tower estimates with an $R^2 > 0.6$; (3) contemporary SOC estimates were within 20% of SSURGO estimates; (4) SOC estimates increased at the landscape-scale given baseline climate and current disturbance regime over 25 years (ensuring that SOC is near equilibrium during model spin-up); and (5) estimates of mineral N were <25 g m$^{-2}$ at the landscape scale, consistent with literature values.

*Wildfire model*

Wildfire was simulated using the Dynamic Fire and Fuel System (DFS) extension (Sturtevant et al. 2009), which simulates mixed severity fires dependent upon fuels, weather conditions (from weather station data or climate projections), slope and topography. Following stochastic ignitions, wildfire will spread depending on fuel conditions and a stochastically generated Fire Weather Index (FWI). The Dynamic Fire extension utilizes the Scott and Burgan (2005) fuel models, based on dominant tree species, rather than detrital (fuel) quantities as estimated by the Century extension. Likewise, fuel moisture calculations are derived from the Canadian Fire Prediction System (Forestry Canada Fire Danger Group 1992, Sturtevant et al. 2009) and not from soil moisture as calculated within the Century extension, although both use the same climate inputs. Fuel classifications based on forest age and species have previously been developed for NJ (Scheller et al. 2011b). FWI calculations are described below. FWI and fuels determine wildfire intensity, which in combination with species fire tolerances, dictates cohort mortality and the amount of litter and wood consumed (see Supplement, DFS inputs). After model calibration for current conditions, the fire regime under a changing climate was mechanistically
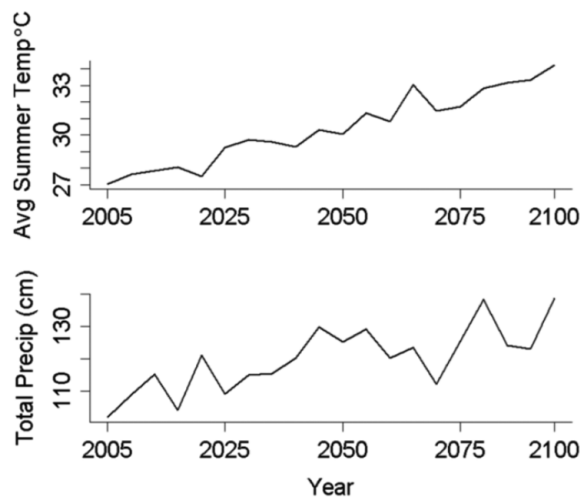
Fig. 3. Average temperature (top) and precipitation (bottom) for the summer months (June, July and August) in the A2 climate scenario, which was derived from Hadley Community Model 3 global circulation model.

simulated through altered fire weather conditions (see below), such that fire effects are an emergent property of climate and current levels of fragmentation. See Supplement, DFS inputs for the complete list of model input parameters.

*Climate change data*

Both the Century extension and the DFS extension are climate-dependent, and it was necessary to develop consistent climate data that would feed directly into both extensions. Our baseline climate scenario was based on 30-year (1961–1990) monthly averages from the US EPA Center for Exposure Assessment Modeling (www.epa.gov/ceampubl). Our climate change scenario was derived from the HadCM3 General Circulation Model (http://www.ipcc-data.org/). HadCM3 projects average minimum and maximum temperatures and average precipitation on a monthly basis to the year 2100. Over the course of the projected 100 years, temperatures steadily increased with a 7.6°C increase in maximum summer temperature and a 5.1°C increase in minimum winter temperature (Fig. 3). Precipitation was more variable than temperature from year to year across the 100 year projection but generally increased. There was also a shift in seasonality of precipitation with annual peaks

shifting from August in the year 2000 to November in the year 2100. Because the Century extension operated at a 5-year time step, we calculated monthly mean and standard deviation for minimum temperature, maximum temperature and precipitation over each 5-year period in the HadCM3 projection.

The DFS extension requires daily weather to compute fire weather variables for estimating fire rate of spread and fire severity. For current-day simulations, local meteorological records can be used for this purpose, but for climate change simulations, daily weather must be generated to match the predicted climate. Down-scaling monthly GCM projections to a daily time step required the creation of daily minimum temperature, maximum temperature, and precipitation from monthly projections. We used a stochastic weather generator, LARS-WG (Semenov and Barrow 1997) to generate this dataset. LARS-WG requires daily and monthly reference datasets. Daily meteorological inputs were acquired from the weather station at the Atlantic City airport. Monthly data were provided by the HadCM3 projections. LARS-WG combines HadCM3 monthly precipitation and temperature anomalies (calculated as the difference between the observed climate averages and the HadCM3 projections) and the sequences of wet and dry days found in the daily reference dataset to simulate daily precipitation and temperature (Semenov and Barrow 1997).

To validate our down-scaled daily climate data, we used LARS-WG to simulate current day daily weather using the weather station data as above and monthly meteorological inputs (minimum and maximum temperature, precipitation) from the US EPA Center for Exposure Assessment Modeling (www.epa.gov/ceampubl). The results showed that temperature and the periodicity of dry and wet spells were in general agreement with our meteorological reference dataset. LARS-WG daily precipitation predictions were rescaled to match monthly total precipitation projections from HadCM3.

Finally, for each 5-year DFS time step, we used LARS-WG to generate a 30 years of daily data based on HadCM3 output. A 30-year dataset (rather than a 5-year dataset) was necessary to maximize the probability that the LARS-WG generated meteorological data matching the
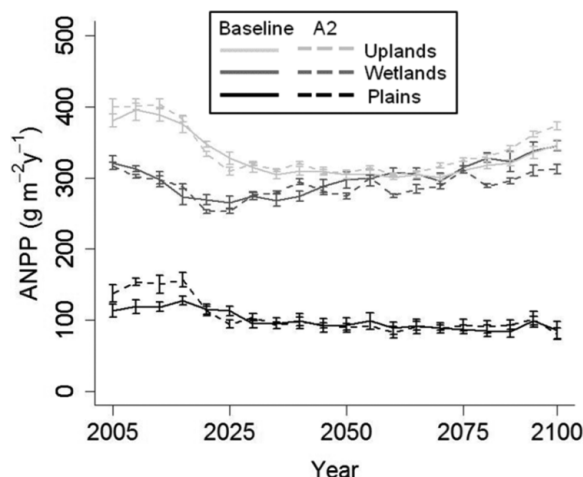
Fig. 4. Aboveground net primary productivity (ANPP) for baseline and A2 climate scenarios in three principle land types, 'pine plains', 'wetlands' and 'uplands', in the NJ pine barrens. Units are g C m$^{-2}$ yr$^{-1}$. Each year is the average of five model replicates with corresponding standard error bars.

variability of conditions present in the reference data, as suggested by Semenov and Barrow (1997). FWI was calculated for this 30-year dataset and for each simulated wildfire, daily fire weather was randomly selected from this large dataset (Sturtevant et al. 2009). Given the lack of significant trend in meridional or zonal wind speed in the HadCM3 output for the study area, we assumed that wind speed and direction did not change significantly for our study period. We assigned wind speed and direction data for each day in the fire weather dataset by randomly selecting a speed-direction pair within each season from the daily reference dataset. Wind direction and speed were linked together in order to preserve existing relationships between direction and speed. The DFS extension also requires estimates of relative humidity (RH) to calculate a daily Fire Weather Index (Sturtevant et al. 2009). We estimated relative RH by assuming that the minimum temperature is equal to dewpoint (e.g., Running et al. 1987); the correlation between reference data and estimates was acceptable ($R^2 = 0.76$).

## Results

The uplands and wetlands had a different temporal pattern in simulated aboveground net primary productivity (ANPP) as compared to the plains (Fig. 4). ANPP in the uplands and wetlands initially declined under both climate scenarios due to age-related decline in productivity (sensu Gower et al. 1996; data not shown). ANPP increased over the last 75 years in the uplands and wetland due to continued wildfires that generated a broad mosaic of forest ages over time, reducing the effect of forest age. Over the last 25 years, ANPP in the uplands increased relative to the baseline climate whereas wetland ANPP declined relative to the baseline climate. By comparison, ANPP modestly declined in the plains over the 100 year simulation regardless of climate scenario. As the plains have consistently burned since the cessation of extensive logging, forest age had minimal effect on ANPP.

Above- and belowground live carbon for the upland and plains ecoregions gradually increased in the baseline climate scenario until year ~2050 when it stabilized (Fig. 5a). Although the plains had higher live biomass for a period under the A2 climate, the difference was minimal by year 2100 (Fig. 5a); neither detrital C nor SOC were substantially different in the plains (Fig. 5b, c). After year 2070, upland ecoregions had lower detrital C and SOC under climate change (Fig. 5b, c), despite higher ANPP, indicating increased heterotrophic respiration. Wetlands had markedly lower live C, detrital C, and SOC under climate change after 2070 (Fig. 5).

Under both the baseline and A2 climate scenarios, the rate of carbon accumulation slowed over the course of 100 years, indicating reduced carbon uptake (Fig. 6). The wetlands shifted from being strong C sinks to being C neutral with climate change. Total carbon accumulation (vegetation and soil combined, Tg) reached steady-state in the uplands after 2020 in the baseline and A2 climate change scenarios. The plains had generally similar and low total C for both climate scenarios. Total carbon was not substantially different between climate scenarios in the uplands and plains.

Fire frequency varied across the landscape and explained about 10% of the variation in ANPP ($R^2 = 0.095$; $p < 0.001$) in the baseline scenario. Notably, the relationship was weakest ($R^2 = 0.07$) in the plains. However, climate change had no significant effect on fire severity. Nor was percent
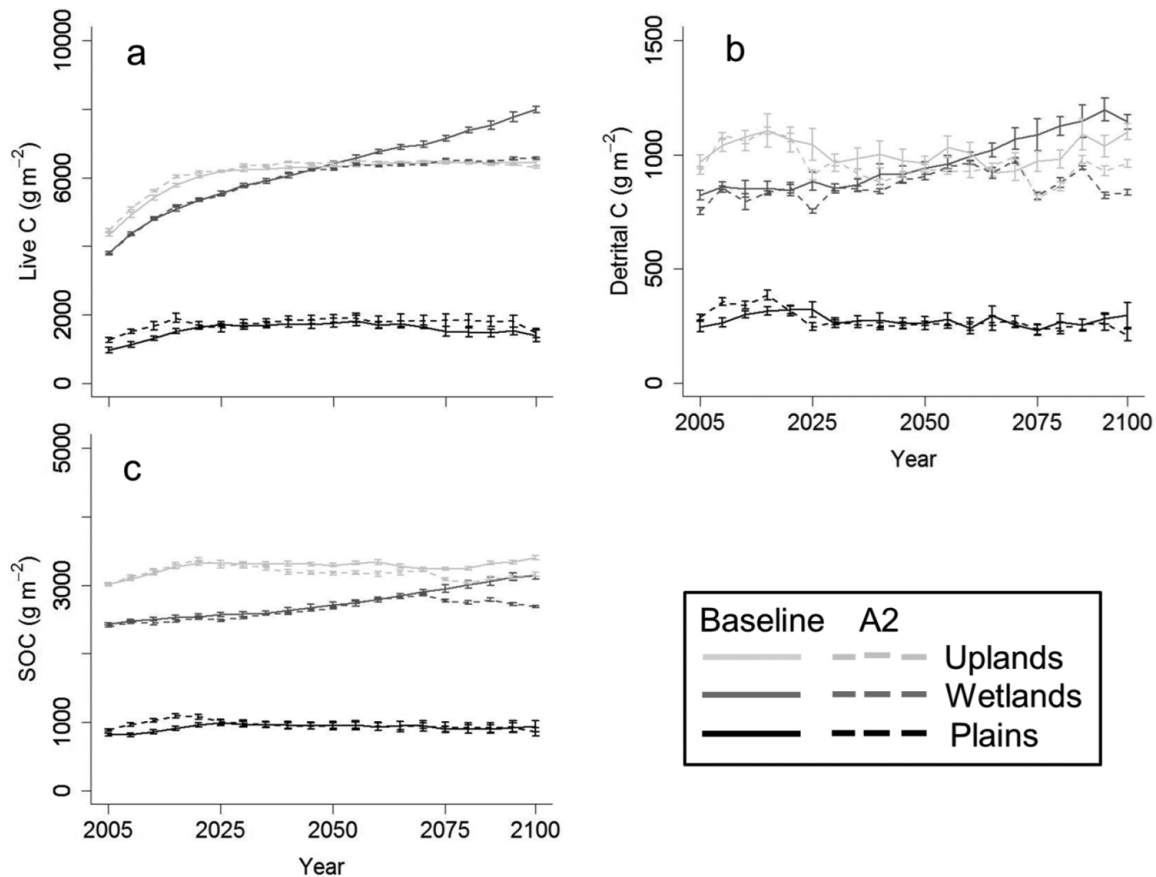
Fig. 5. Total live carbon (includes above- and belowground live carbon) (a), detrital carbon (b), and soil organic carbon (SOC) (c) for baseline and A2 climate scenarios in three principle land types, 'pine plains', 'wetlands' and 'uplands', in the NJ pine barrens. Units are g C m$^{-2}$. Each year is the average of five model replicates, with corresponding standard error bars.

area burned significantly different between the two climate scenarios (data not shown). Though climate change increased air temperature, the FWI did not significantly increase.

How individual tree species responded to climate change varied by edaphic properties. We examined the aboveground biomass (AGB) of the six dominant tree species in the NJPB, by ecoregion and by climate scenario (Fig. 7). Pitch pine had higher biomass with climate change in all ecoregions except the plains. This positive response to climate change in the upland/wetland forests was also observed in white oak, chestnut oak, and black oak. Atlantic white cedar, which occurred primarily in the wetlands, consistently declined in response to climate change in the three wetland ecoregions. The

biomass of swamp tupelo, another wetland species, decreased in two of the three wet ecoregions.

The probability of establishment ($P_{EST}$)—which is a function of soils and climate—was also sensitive to climate change (data not shown). The $P_{EST}$ of the most abundant species on the landscape, pitch pine, declined dramatically, falling from as high as >80% in some ecoregions, to zero in all ecoregions by the year 2060. Conversely, hardwood $P_{EST}$ increased over the course of the 100 year simulation, with the exception of red maple, which declined. The $P_{EST}$ of shortleaf pine and blackjack oak increased most under the A2 scenarios, increasing by an average of ~45%; these were the only two species to show increases of $P_{EST}$ in all ecoregions over
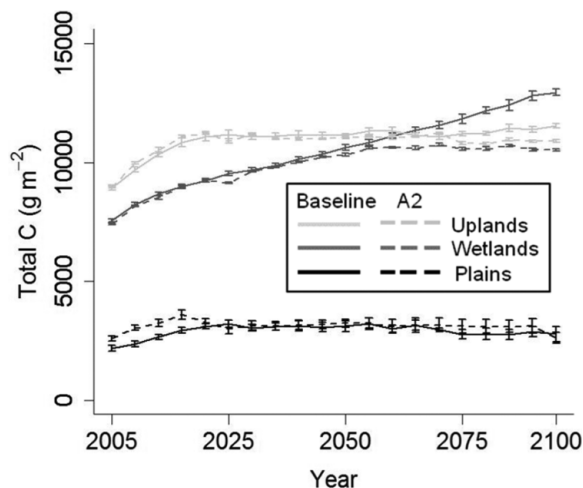
Fig. 6. Total carbon (Tg) for three general forest types, 'pine plains', 'wetlands' and 'uplands', in our study area under baseline and A2 climate scenarios.

the course of the 100 years. Neither of these species constitutes a substantial percentage of overall biomass in any ecoregion and neither species gained a significant amount of biomass over the course of the 100 year simulation. Estimated $P_{EST}$ of white oak, the most abundant oak species, declined in every ecoregion, falling from 40% to zero or near zero in many ecoregions by year 90.

## Discussion

The goal of our research was to understand carbon dynamics as a function of climate, disturbance, soil formation and heterotrophic respiration, and shifting tree species composition in a system characterized by a complex land use history, diverse soils, and a diverse overstory. Therefore we simulated the interactive regional effects of climate change, including the effects on fire, carbon dynamics, and species composition across the New Jersey Pine Barrens. These results demonstrate that the effects of climate change on total forest carbon may be substantial with potentially large changes in productivity, net ecosystem production, live carbon, and detrital carbon. The magnitude and direction of the responses were strongly dependent on soil type and overstory tree species composition.

Fire frequency was correlated with ANPP

although the effect of fire frequency on ANPP was lowest in the pine plains, which are dominated by fire-adapted vegetation (Scheller et al. 2011b). Climate change had no effect on the Fire Weather Index (FWI), wildfire spread, or severity due to higher overall precipitation and fewer prolonged droughts later in our simulations (Fig. 3). This differs from previous studies showing that fire increases with climate change, though these studies have generally been conducted in the western US and Canada (e.g., Westerling et al. 2006, Wotton et al. 2010). Wildfire is strongly constrained by fragmentation (Luque et al. 1994) and fire suppression in the NJPB (Forman and Boerner 1981, Scheller et al. 2008), limiting the potential for wildfire to increase with climate change. Likely, only a substantial increase in FWI could create conditions leading to substantially higher spread rates and larger fires. Nevertheless, wildfire was a large source of variation in our simulations.

The divergent response of ANPP, among ecoregions and between climate scenarios, was due to the interactions between the dominant tree species, temperature, and soil water holding capacity. Temperatures steadily rose throughout the A2 climate scenario which affected both photosynthesis via optimal growth parameters and available soil moisture via increased evapotranspiration. As an example, a single cohort of pitch pine growing in an upland ecoregion was more water limited under climate change after year 2050 (a lower growth modifier), although the effect was offset by reduced temperature limitation of similar magnitude (Fig. 8); no other growth modifiers changed substantially. In contrast, the ANPP of a cohort of Atlantic white cedar—a moisture sensitive species—growing in wetland soils became substantially more water limited under the A2 scenario (Fig. 8). As a result, Atlantic white cedar (and swamp tupelo) declined despite reduced temperature limitations (Fig. 7). However, the AGB decline of Atlantic white cedar and swamp tupelo was partially offset by increased oak growth in the wetlands (Fig. 7). Finally, as an example of a positive response to climate change, a black oak cohort growing on upland soils became marginally more water limited but substantially less temperature limited (Fig. 8). In general, the ANPP response to climate change was relatively modest
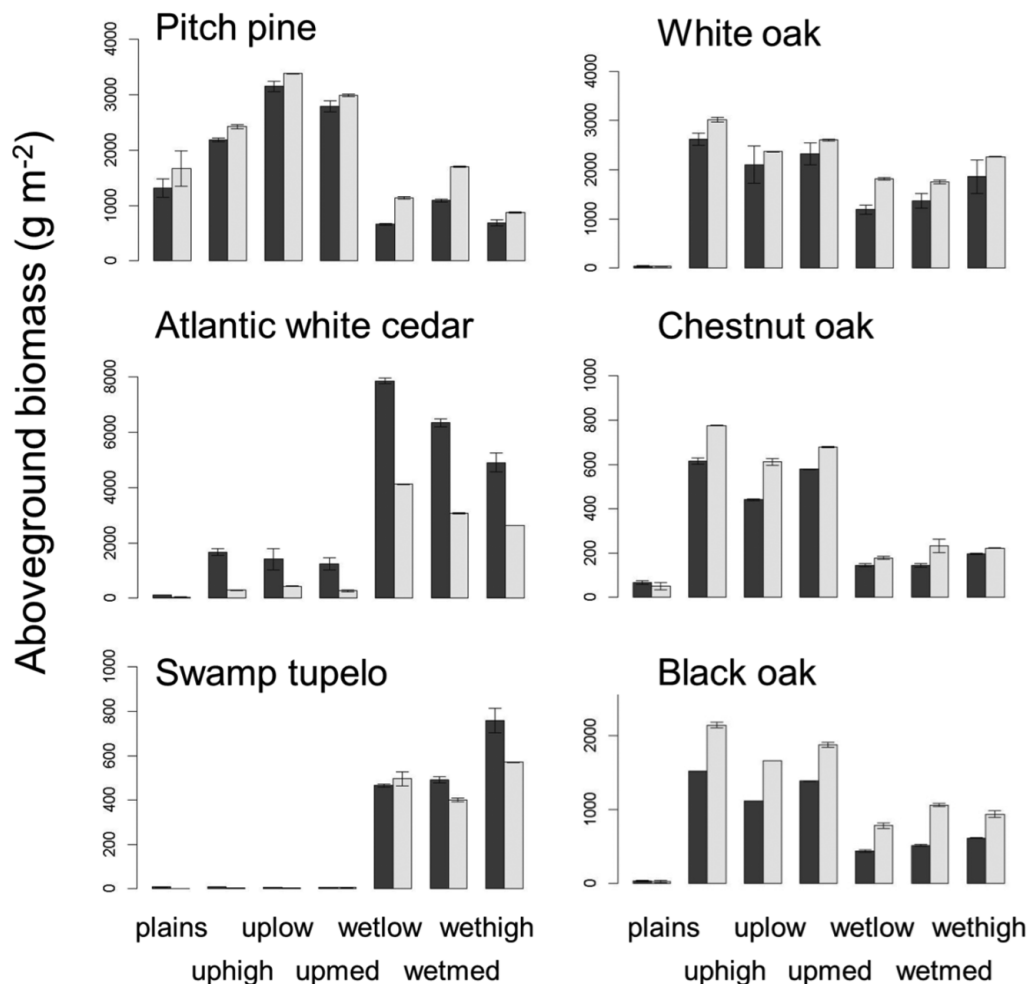
Fig. 7. Comparison of above ground live biomass (g m$^{-2}$) of the six dominant species in the NJ pine barrens at year 100 of baseline (dark grey) and A2 climate scenarios (light grey) for seven modeled ecoregions. All five functional species groups are represented by at least one species. See Supplement, Century inputs for ecoregion parameters and definitions.

primarily because higher moisture limits were offset by lower temperature limits.

Soil organic carbon increased modestly in the uplands and wetlands due to detrital inputs (Scheller et al. 2011a). Climate change had relatively minimal effect on SOC although there was a modest decline in wetland and upland SOC after 2070. Our live C, detrital C, and SOC estimates are substantially lower than our previous estimates (Scheller et al. 2011b). This is due in part to a more comprehensive calibration against empirical data. Although our calibration to flux tower data was lower (adjusted r$^2$ = 0.66 vs. 0.89), our initial SOC values are now much closer to the

values derived from SSURGO (Scheller et al. 2011b; see Supplement, Century inputs). Changes in our results also reflect our improved representation of N dynamics.

Our SOC estimates do not support the hypothesis that climate change will stimulate production more than heterotrophic respiration, resulting in a net accumulation of soil carbon (Thornley and Cannell 2001). However, our wetland results support the hypothesis that SOC will decrease with climate change due to lower growth (Fig. 4) and higher decomposition at higher temperatures (e.g., Knorr et al. 2005, Davidson and Janssens 2006; Fig. 5c). Neverthe-
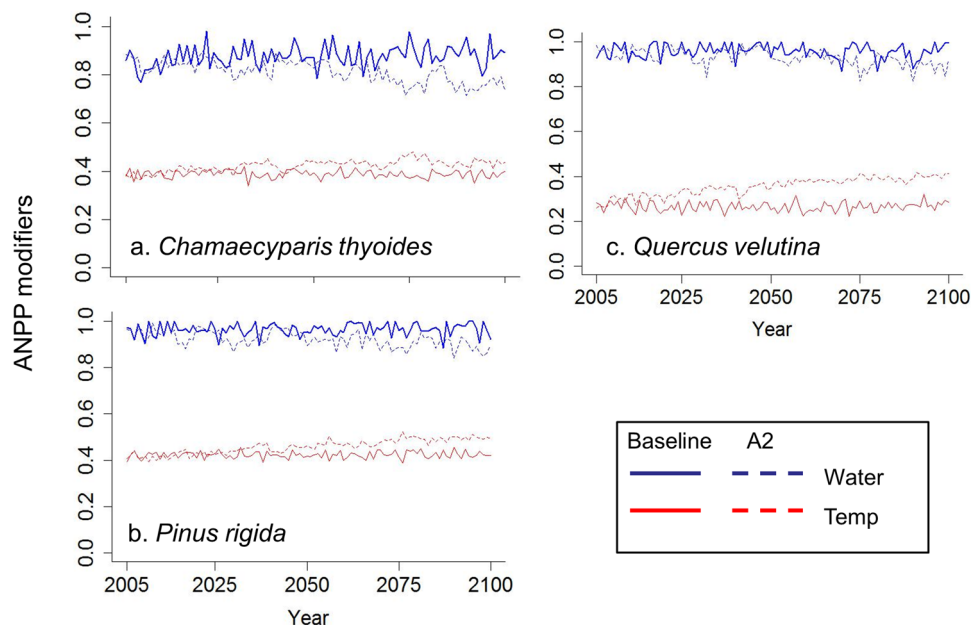
Fig. 8. Annual water and temperature limitations to ANPP for (a) Atlantic white cedar (wetland soils), (b) pitch pine (upland soils), and (c) black oak (upland soils). ANPP limitations were calculated using a single-cell simulation initialized with a 60 year old pitch pine or Atlantic white cedar cohort in an upland or wetland ecoregion, respectively. Each modifier is successively multiplied by the maximum monthly ANPP (see Supplement, Century inputs) and other limitations not depicted (leaf area index, ABG carrying capacity, nitrogen).

less, there is large model uncertainty when simulating long-term changes in SOC (Schmidt et al. 2011) and our estimates are predicated on model assumptions and model calibration. The complex constituency of soil organic matter makes it difficult to determine how SOC will respond to climate change because the fractions differ in their responsiveness to changes in temperature and precipitation (Trumbore 2000). More research is needed to determine how best to simulate soil organic matter and its response to climate change, knowing that our current approach may be too simplistic (Davidson and Janssens 2006, Schmidt et al. 2011).

Our overall C trajectories do not exhibit any consistent trend among ecoregions (Figs. 4–7). Given the minimal climatic variation across the NJPB and lack of substantial wildfire change, soil water holding capacity, soil moisture, and species composition therefore must explain the divergent carbon dynamics among land types under the A2 climate scenario. Previous research demonstrated a bifurcation of carbon response with increased

growth and biomass at higher soil water holding capacity (Pastor and Post 1988) but our results suggest the opposite. Wetlands switched from a strong carbon sink to being relatively carbon neutral (Fig. 6). In the wetlands, many dominant tree species are relatively moisture-sensitive (Figs. 7 and 8), resulting in reduced ANPP and roughly equivalent heterotrophic respiration estimates. This highlights the need to consider biological lags when projecting near-term climate change effects and to not assume climate equilibrium species composition. However, wetlands were our least well calibrated ecoregion due to the absence of flux towers in these forests. Given the substantial potential capacity for wetland C sequestration, future studies should focus on improving our understanding of carbon dynamics in wetland forests.

Climate change is only one process driving forest change in the NJPB and our approach excluded many by necessity. Residential and commercial development continues to fragment the remaining contiguous forested areas (Drum-

mond and Loveland 2010). As development continues, any gains in C may be lost. As a comparison, Thompson et al. (2011) found that housing development explained a larger portion of projected aboveground biomass variance in Massachusetts than either climate change or harvesting. Pan et al. (2009) estimated that changing atmospheric chemistry (including $CO_2$, $O_3$, and N deposition) has had a much larger effect than climate warming over the past century on net primary productivity. Although we incorporated N deposition (Scheller et al. 2011b), we did not consider the effects of elevated $CO_2$ and $O_3$; however, the two effects are offsetting to some degree (Isebrands et al. 2001). Future research will consider the combined effect of climate change, wildfire, and insect outbreaks due to the widespread gypsy moth (*Lymantria dispar* L.) and the more recently introduced Southern Pine Beetle (*Dendroctonus frontalis*) on this ecosystem.

Our projections depict large variation among model replicates, primarily due to stochastic wildfire events, emphasizing the role of uncertainty in reducing our ability to project change with any real precision. Our model uncertainty is further exacerbated by the absence of several key processes, including insect defoliation (Clark et al. 2010), deer browsing, and continuing fragmentation due to housing development (Lathrop and Kaplan 2004).

In summary, our projections uniquely combine a multitude of processes necessary to forecast climate change effects on carbon at a regional scale, including climate-sensitive disturbance, shifts in tree species composition with associated physiological properties, and soil dynamics that respond to changing disturbances and species composition. Our simulations suggest that continued total C accrual may be hampered by climate change in wetlands, which could potentially sequester the most carbon (Fig. 6). Despite these limitations, our approach allowed us to learn about the potential consequences of climate change based on an empirical foundation of field and flux tower observations (Clark et al. 2010, Clark et al. 2011).

## Acknowledgments

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## SUPPLEMENTAL MATERIAL

### SUPPLEMENT

Input data required for running simulations in LANDIS-II (*Ecological Archives* C003-011-S1).