



Social and biophysical determinants of future forest conditions in New England: Effects of a modern land-use regime

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ABSTRACT

The future forests of eastern North America will be shaped by at least three broad drivers: (i) vegetation change and natural disturbance patterns associated with the protracted recovery following colonial era land use, (ii) a changing climate, and (iii) a land-use regime that consists of geographically variable rates and intensities of forest harvesting, clearing for development, and land protection. We evaluated the aggregate and relative importance of these factors for the future forests of New England, USA by simulating a continuation of the recent trends in these drivers for fifty-years, nominally spanning 2010 to 2060. The models explicitly incorporate the modern distribution of tree species and the geographical variation in climate and land-use change. Using a cellular land-cover change model in combination with a physiologically-based forest landscape model, we conducted a factorial simulation experiment to assess changes in aboveground carbon (AGC) and forest composition. In the control scenario that simulates a hypothetical absence of any future land use or future climate change, the simulated landscape experienced large increases in average AGC—an increase of 53% from 2010 to 2060 (from 4.2 to 6.3 kg m⁻²). By 2060, climate change increased AGC stores by 8% relative to the control while the land-use regime reduced AGC by 16%. Among land uses, timber harvesting had a larger effect on AGC storage and changes in tree composition than did forest conversion to non-forest uses, with the most pronounced impacts observed on private corporate-owned land in northern New England. Our results demonstrate a large difference between the landscape's potential to store carbon and the landscape's current trajectory, assuming a continuation of the modern land-use regime. They also reveal aspects of the land-use regime that will have a disproportionate impact on the ability of the landscape to store carbon in the future, such as harvest regimes on corporate-owned lands. This information will help policy-makers and land managers evaluate trade-offs between commodity production and mitigating climate change through forest carbon storage.

1. Introduction

Whether regional socio-ecological systems can provision needed services into the future will not be determined by any single driver, but will instead be the product of integrated human and natural systems operating at local to global scales (Liu et al., 2013, 2015; Dearing et al., 2014). The interconnectedness of these systems, their complexity, and the many irreducible uncertainties involved precludes attempts to predict their precise future state (Lambin et al., 2001; Rudel et al., 2005; Liu et al., 2007; Lambin and Meyfroidt, 2010). Nonetheless, efforts to disentangle and understand the relative, aggregate, and interactive impacts of the major drivers of ecological change are critically needed to inform environmental policy and decision-making (Dearing et al., 2010). Throughout much of eastern North America, dense human

populations are embedded into a forest-dominated landscape that is controlled by hundreds of thousands of private landowners, including large blocks of corporate-owned land and millions of smaller woodlots. There is no centralized authority to regulate land use; instead, land-use policies are geographically fragmented and loosely determined by state, regional, and municipal policies and planning entities. Land-use decisions are driven by individual social and economic factors (Kittredge, 2004). The objectives and behaviors of landowners are diverse resulting in large differences in their impact on the landscape (Silver et al., 2015; Field et al., 2017; Thompson et al., 2017a). For example, over a fifty-year period, some forested parcels might be subject to multiple partial harvests, while a neighboring parcel could be developed for a house lot, and another may be permanently protected from any future land use. In aggregate, the mosaic of landowners largely determine the

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characteristics and ecological impacts of the forest land-use regime, which consists of a geographically varying pattern of timber harvesting, forest conversion to development, and permanent land protection from future development. In the United States (U.S.), developed land is the most rapidly expanding land-cover class while forest land is the most rapidly declining (Sleeter et al., 2013). Forests converted to developed uses result in large reductions in AGC. The six New England states have lost more than 350,000 ha of forest cover to commercial, residential, and energy (transmission lines, pipelines, solar arrays, etc.) development, since 1985. Spatially, this represents between 0.02% and 0.66% lost annually within the U.S. Census Bureau's Core Base Statistical Areas (CBSA) (Olofsson et al., 2016; Thompson et al., 2017b), marking an abrupt reversal of a 150-year trend of forest expansion. The vast majority of forest loss has been to rural or low-density development (94%) and much smaller fraction to urban or high-density development (5%). In the same period, there have been negligible transitions from developed or agricultural cover to forest cover (Olofsson et al., 2016; Thompson et al., 2017b). Forest loss is concentrated in suburban areas, particularly around the largest cities. Forest conversion to development results in a permanent loss of carbon storage and future sequestration potential (Jeon et al., 2008; Woodall et al., 2015; Reinmann et al., 2016), and is the primary cause of habitat loss and fragmentation and the associated declines in biodiversity (Rands et al., 2010; Pereira et al., 2010). Terrestrial forest carbon is a critical stock in the global climate system. Globally, land-cover change (e.g., deforestation where forests are converted to non-forest) and forest management (e.g., timber harvesting where logging assumes successful regeneration) reduces terrestrial carbon stocks from their potential by approximately 50% each, however spatial large variation exists between biomes (Erb et al., 2018; Curtis et al., 2018). Timber harvesting in New England is a less intense and ephemeral form of land use than deforestation, but harvesting is much more widespread and exerts significant impacts on forest composition and forest age distribution (Brown et al., 2018). Indeed, while forestry is not a major part of the region's economy, harvest is still a larger cause of mature tree mortality in northeastern U.S. forests than all other causes—natural and anthropogenic—combined (Canham et al., 2013). The frequency of harvests varies markedly by owner class, with 3.6% of corporate-owned forest, 2.9% of private woodland owners, and just 1.5% of publicly owned forest subject to some level of harvest per year (Thompson et al., 2017a). While commercial harvesting does occur in populated suburban areas, it is far more frequent and more intense in rural areas with high forest cover and lower average incomes (Colgan et al., 2014; Kittredge et al., 2017). Most harvests in northeastern U.S. forests only remove a portion of the total available biomass (Thompson et al., 2017a; Brown et al., 2018), but nonetheless alter tree composition and carbon dynamics (Birdsey et al., 2006; Hompson et al., 2011; Woodall et al., 2011). Land protection is also an important component of the regional land-use regime. In New England, 23% of the land is legally protected from development, and half of that has been protected in the past 25-years (Meyer et al., 2014; Foster et al., 2017). Most of these protected forests remain open to timber harvesting (Foster et al., 2017). Seventy percent of land protected since 1990 is privately owned and has been conserved using conservation easements. A distinct spatial pattern exists within the existing protected lands; the largest protected areas occur in rural northern New England where they continue to be managed for timber while southern New England contains tens of thousands of small protected parcels serving multiple uses (Foster et al., 2017). The land-use regime in New England interacts with naturally dynamic forest ecosystems that are still recovering from nineteenth century land use. The region's forests continue to grow and trend toward mature, late successional, long-lived, and shade tolerant species (Thompson et al., 2013; Eisen and Barker Plotkin, 2015). The long-term accrual of carbon associated with forest development is expected to continue for a century or more (Albani et al., 2006; Duveneck et al., 2017; Wang et al., 2017). Simulations suggest that climate change will have limited direct

effects on forest composition in New England (Duveneck et al., 2017; Liang et al., 2017), but will enhance productivity due to longer growing seasons and greater CO₂ concentrations (Duveneck and Thompson, 2017). This trend could be altered if climate change interacts with disturbances (e.g., insect defoliation, and/or wind damage). Nonetheless, climate change will both directly and indirectly interact with land-use regimes to shape future forests. For example, climate mitigating energy policies may result in more forest land converted to land dedicated to solar or wind energy production; or tree mortality induced by the interaction of stress and insect or pathogen impacts may stimulate increased harvesting of live trees during salvage or pre-salvage operations. A growing concern exists that global change, the combination of climate change a changing land-use regime, and a changing natural disturbance regime will threaten ecosystem function and be more impactful than climate change alone (Lambin et al., 2001; Ordóñez et al., 2014). These interactions have been identified as crucial areas of study to inform policy-makers (Arneeth et al., 2014; Mayer et al., 2016). In this paper we examine the forests of New England, USA as a regional socio-ecological system to understand the aggregate and relative importance of multiple climate and land-use change drivers for determining the future condition of the region. We simulated a continuation of the modern land-use regime—i.e. the observed frequency, geography, and intensity of dominant land uses (Watson et al., 2014; Ramankutty and Coomes, 2016)—in combination with anticipated climate change over a multi-decadal timeframe to determine their impacts on forest carbon, and composition. By projecting the modern land-use regime, we establish a baseline scenario and an assessment of multiple global change drivers that are being superimposed on an inherently dynamic system. We coupled a dynamic vegetation model with a cellular land-cover change model to address the following questions: Which components of the modern land-use regime (i.e., land protection, land development, and timber harvesting) will be most influential on future forest carbon, and species composition? What is the spatial configuration of the modern and projected future land-use regime and resulting forest ecosystem condition? Where geographically and within what forest types will the modern land-use regime have the largest effects on forest pattern and process? Understanding the drivers and interactions of the current land-use regime can inform both local and global decision-making affecting future land use (Mather, 1992; Coulston et al., 2015).

2. Methods

2.1. Study area and analytical approach

We explored the effects of the modern land-use regime in New England, a six state (Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, and Connecticut) region in the northeast U.S. (Fig. 1). New England is among the most forested and most densely populated parts of the U.S. The region includes a gradient of boreal tree species in the north to temperate species in the south with forest covering approximately 76% of the total land area. The region is characterized by diverse soils (SSURGO Soil Survey Staff, 2011), climate (Daly and Gibson, 2002), forest types (Duveneck et al., 2015), land owners (Butler et al., 2016), and land uses (Schleeweis et al., 2013; Olofsson et al., 2016). Private woodland owners (i.e., non-corporate or family forest owners) control 65% of New England forests comprising > 800,000 small parcels (200,000 > 2.5 ha) (Butler et al., 2016). Other dominant land owner groups include: private corporate (19%), Federal (4%), State (8%), non-governmental private (2%), and tribal (2%) (Fig. 1). Mean annual temperatures of 3–10 °C follow latitudinal and elevational gradients. Mean annual precipitation ranges from 79 to 255 cm with greater precipitation at higher elevations (Daly and Gibson, 2002). Our analytical approach integrates two spatially interactive simulation models (Fig. 2). We used a forest landscape model to simulate forest growth and succession and timber harvesting and a cellular automata

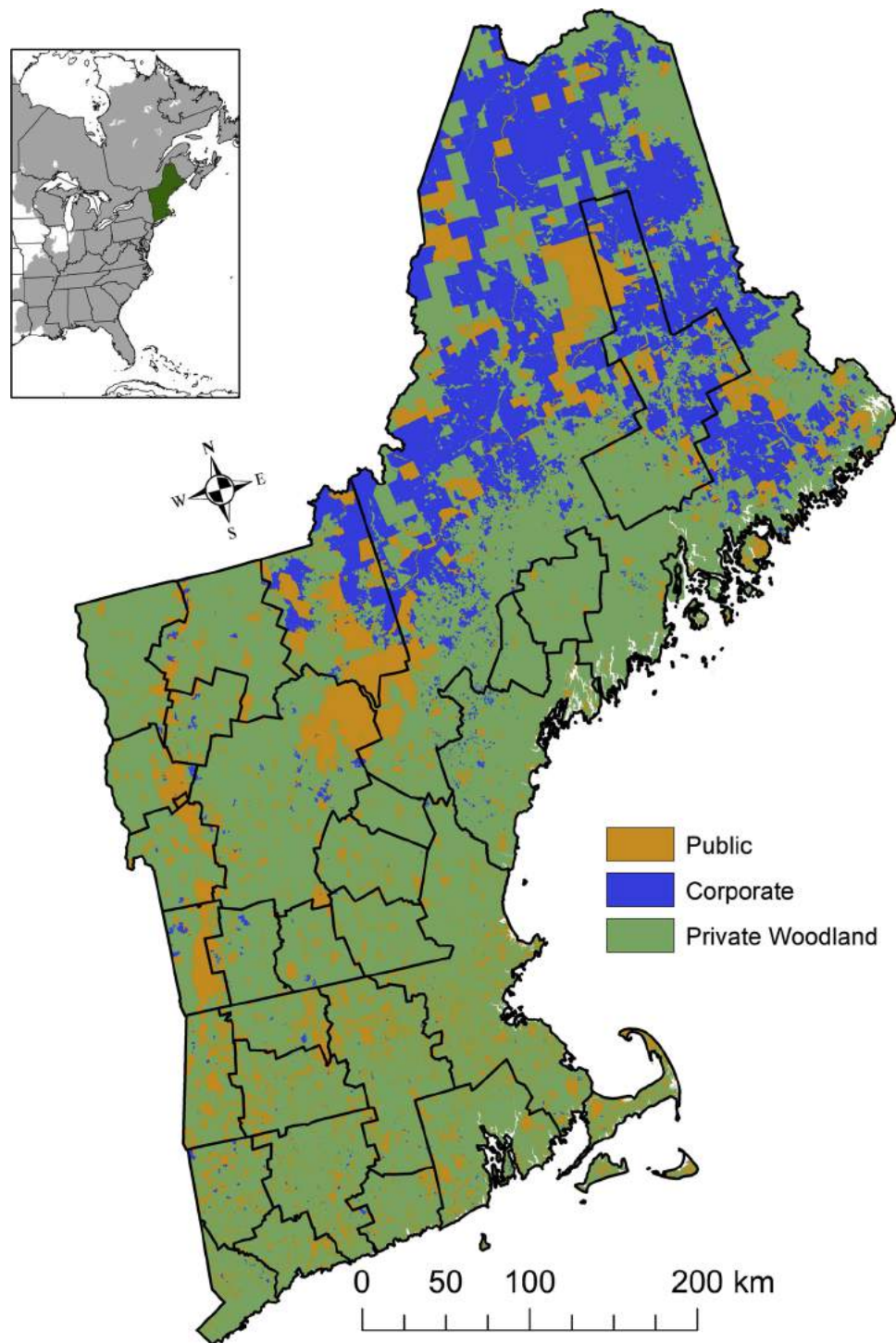


Fig. 1. New England landowner map (colored polygons) of study area within sub-regions (black lines). Call-out indicates landscape (green) within northeastern North America (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

land-cover model to simulate land-cover change (e.g., change of forest to development) and land protection (e.g. conservation status). See below for details regarding the simulation methods. We conducted a simulation experiment to quantify the individual and aggregate impacts of a continuation in the recent trends of climate change, forest conversion to development, forest harvesting, and land protection spanning the period from 2010 to 2060. The effects of each of these drivers was determined by comparing to a “control” scenario that included only projected forest growth across the landscape (i.e., the “potential” future landscape) in the absence of any land use, land conversion or climate

change. In a factorial design, we simulated the drivers individually and in all possible combinations (Table 1). For each treatment combination, we assessed differences in aboveground carbon (AGC) which we assumed was $\frac{1}{2}$ of aboveground biomass (AGB) to characterize changes in aboveground structure. Within forest types, land owner types (as explained below), and New England states, we report differences from the control scenario at simulation year 2060. To assess tree species community change, we assessed the composition of 32 dominant tree species and then highlighted the changes in the ten most abundant species currently on the landscape.

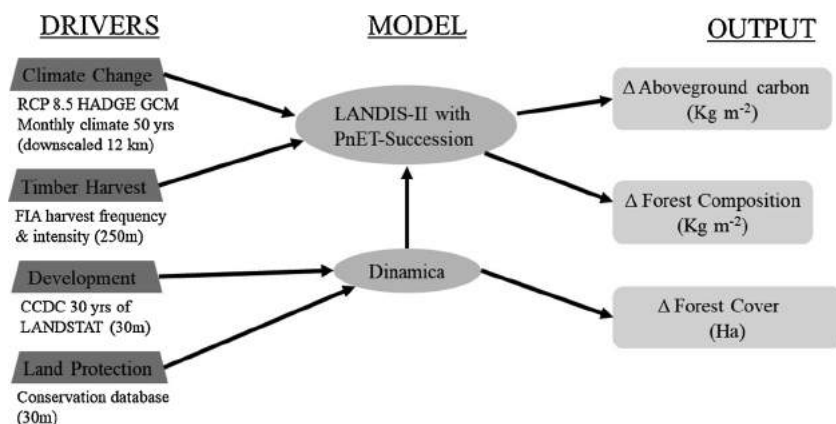


Fig. 2. Conceptual framework illustrating our simulation approach. The diagram represents some of the multiple drivers of land-use change including data sources and spatial resolution. Additional model variables are described in methods. The drivers are spatial variables in the models which affect the outputs.

Table 1
Climate and land-use scenarios used to evaluate the modern land-use regime in New England.

SCENARIO	CLIMATE	LAND USE
Control	Static Climate	No land use
Static_Dev	Static Climate	Forest loss to development
Static_Harv	Static Climate	Timber harvesting
Static_HarvDev	Static Climate	Development & timber harvesting
ClimateChange_NoLU	Climate Change	No land use
ClimateChange_Dev	Climate Change	Forest conversion to development
ClimateChange_Harv	Climate Change	Timber harvesting
ClimateChange_HarDev	Climate Change	Development & timber harvesting

2.2. Simulating forest growth and succession

We simulated forest dynamics using the LANDIS-II v6.2 forest landscape modeling framework (Scheller et al., 2007). The LANDIS-II core model tracks spatial processes, including seed dispersal and disturbance, and integrates the inputs and outputs of additional model extensions. Trees are grouped into species × age cohorts. We used the PnET-Succession extension to LANDIS-II (v2.1.1, (de Bruijn et al., 2014d)) to simulate tree species growth and succession of 32 species within 250 m pixels. PnET-Succession is based on the PnET-II ecophysiological model (Aber et al., 1995) and uses a mechanistic ‘first principals’ approach to modeling forests response to changing environments. PnET-Succession simulates photosynthesis and the accumulation of biomass based on available light, water, temperature, and competition through vertical layers in the canopy. Cohort AGB is used as a surrogate for canopy height to simulate canopy layers. Competition among cohorts is simulated by partitioning incoming light through multiple canopy layers. Biomass growth is further affected by available soil water, which is balanced based on precipitation, transpiration, evaporation, runoff, and percolation. In addition, growth increases with foliar N, and atmospheric CO₂ concentration, and decreases as cohorts near their longevity age or depart from optimal temperature. Establishment of new cohorts is controlled stochastically based on distance from a seed source, soil water, and subcanopy light. The parameterization of the modeling framework for New England, including calibration, validation, and sensitivity analyses have been described previously (McKenzie et al., in review; Duveneck and Thompson, 2017; Duveneck et al., 2017; Liang et al., 2017). One limitation of LANDIS-II/PnET-Succession is that spin-up of initial communities does not include prior disturbance or land use. Therefore, the model tends to over-predict initial stand biomass. To correct for this, we adjusted the landscape biomass based on the National Biomass and Carbon Dataset (Kelldorfer et al., 2013). We initialized forest structure and

composition information using a near-neighbor imputation of forest inventory plots (Bechtold and Patterson, 2005; Duveneck et al., 2015). We simulated one replicate of each scenario. This decision was based on our experience with this model, which has shown that, without large disturbances, the small-scale stochastic components within the model stabilize to their average when measured at watershed to landscape scales (Duveneck et al., 2017; Liang et al., 2017). Simulations using a ‘static’ climate (i.e., no climate change) projected a continuation of current climate using monthly temperature and precipitation information provided by PRISM (Daly and Gibson, 2002) based on the period from 1981–2013. Climate change scenarios employed the Regional Concentration Pathway (RCP) 8.5 emission scenario (IPCC, 2013) as simulated by to the Hadley Global Environment Model v.2-Earth System (HADGE) Global Circulation Model (GCM) downscaled and obtained from the USGS Geo Data Portal (Stoner et al., 2013). We chose the RCP 8.5 emission scenario because it represents the highest emissions scenario published by the IPCC, however, observed CO₂ emissions already exceed the RCP 8.5 trajectory (Friedlingstein et al., 2014). We chose the HADGE GCM because it has been shown to simulate historical climate in the northeast accurately (Sillmann et al., 2013). For comparisons of this representation of climate change in New England to other GCMs, see (Duveneck and Thompson, 2017).

2.3. Land uses

2.3.1. Harvesting

We simulated timber harvesting in LANDIS-II using Biomass Harvest v.3.2 extension (Gustafson et al., 2000), which simulates user defined harvest prescriptions within spatially explicit owner-type group areas (Fig. 1). Multiple harvest prescriptions were developed that dictated the patch size and percent of biomass removed as a function of tree species and ages present on a site. The frequency that each prescription was applied to the landscape varied by owner group and was based on average harvest rates and intensities observed in previous analyses of Forest Inventory and Analysis (FIA) database (Bechtold and Patterson, 2005; Thompson et al., 2017a). The harvest frequency rates included a large variation in harvest intensity. Most harvest events in New England remove less than 20% of the basal area (Thompson et al., 2017a; Brown et al., 2018). Harvest preference by species is largely dependent on region and in some cases, ownership. For example, corporate lands, harvest a large amount of spruce-fir species especially in northern New England where those species are more dominant; white pine and several species of oak, predominately, northern red oak, is preferentially harvested by private woodland owners in southern New England where those species are more dominant (Thompson et al., 2017a). Based on an analyses of FIA data (Belair and Ducey 2018; Thompson et al., 2017a) and consultation with several forestry experts, we developed a range of

Table 2
Land-cover reclassification used in this study based on existing classifications from Continuous Change Detection and Classification (CCDC) (Olofsson et al., 2016), and National Land Cover Database (NLCD) (Wickham et al., 2013).

OUR CLASSIFICATION	CCDC	NLDC
Low Density Development	Low Density Residential	Developed Open Space Developed Low Intensity Developed Medium Intensity
High Density Development	High Density Residential Commercial/Industrial	Developed High Intensity
Forest	Mixed Forest Deciduous Broadleaf Forest Evergreen Needleleaf Forest Woody Wetland	Mixed Forest Deciduous Forest Evergreen Forest Woody Wetland Shrub/Scrub
Agriculture	Agriculture	Pasture/Hay Cultivated Crops
Other	Bare Herbaceous / Grassland Wetland Water	Barren Land (Rock/Sand/Clay) Emergent Herbaceous Wetlands Open Water Perennial Ice/Snow

harvest prescriptions (Appendix I, Table 1) that include a range of harvest intensities from light intensity thinning to high intensity clear cutting and partitioned these prescriptions to the frequency rates for each landowner group. We then validated the frequency and intensity of simulated harvest throughout New England (Appendix I, Fig. 1).

2.3.2. Forest conversion to development

We simulated forest loss to developed uses using the Dinamica cellular land-cover model, parameterized with the rates and spatial patterns observed between 1990 and 2010 (Thompson et al., 2017b). We used time series of 30 m resolution land-cover maps described by Olofsson et al. (Olofsson et al., 2016) using Continuous Change Detection and Classification (CCDC) methods. We focused our analysis on the land uses classified by Olofsson et al. (2016), and where data were not available, the National Land Cover Database (NLCD) (Wickham et al., 2013). We then simplified these classifications into two types (Table 2). Low Intensity Development (LD) is defined as areas of urban or residential development with impervious surface areas from 0% to 50%. High Intensity Development (HD) is defined as areas of urban or residential development with impervious surface areas from 50% to 100%. We simulated conversions between the dominant components of the recent land-use regime (Table 3). While additional land-use transitions occurred during the recent land-use regime (e.g., from agriculture to forest), they represented minor components (Olofsson et al., 2016), and were not included in our scenario of recent trends. For areas in New England where spatial data were not present, (i.e., northern Maine, southern Connecticut, and northwestern Vermont), or was unclassified due to ongoing change (< 1% of pixels), we used classified pixels from the NLCD (Wickham et al. 2013). Unlike harvest areas that were based on landowner type groups, we captured the spatial variation in land-use conversions by delineating 32 sub-regions (Fig. 1). Sub-regions follow Census Bureau defined Core Base Statistical Areas (CBSA) which collectively represent both Census Metropolitan and Micropolitan statistical areas and were used on previous land-use research in New England (Thompson et al., 2017b). There are 27 CBSAs in New England, however not all of New England is covered by a CBSA. In addition to 27 CBSA's we added five rural regions to fill the gaps, for a total of 32 unique and exhaustive sub-regions. Within sub-regions, conversion rates and patch parameters were based on geographic units where economic factors most associated with rates and patterns of conversion were homogenous. We used the Dinamica Ego land-use change model v 2.4.1 (Soares-Filho et al., 2002). Dinamica is capable of multi-scale stochastic simulations that incorporate spatial feedbacks.

Table 3
Land use transitions simulated under recent trends scenario. LD = low Density, HD = High Density.

FROM	TO			
Forest	Agriculture	LD Development	HD Development	Land Protection
Agriculture		LD Development	HD Development	
LD Development			HD Development	

Dinamica uses a weights-of-evidence (WoE) method to set transition probabilities for every pixel. The WoE approach uses a modified form of Bayes theorem of conditional probability (Goodacre et al., 1993; Bonham-Carter, 1994) to calculate weights for each spatial variable independent of a combined solution (Soares-Filho et al., 2002). ‘Distance to the nearest developed land’ was the strongest predictor of forest loss to development for most sub-regions. ‘Population density’ and ‘distance to roads’ were frequently ranked as the second strongest predictor variables, with a clear geographic pattern of ‘population density’ being stronger in southern New England and ‘distance to roads’ being stronger in northern New England. ‘Wetlands’ had more influence in sub-regions along the coast whereas the ‘slope’ of the land was more important in the mountainous northern and western sub-regions. For a more detailed explanation of the parameterization of Dinamica Ego, see Thompson et al. (Thompson et al., 2017b).

2.3.3 Land Protection

We simulated a continuation of the recent trends in land protection using the same cellular land-cover change model (Dinamica Ego) that we used to simulate development. Here we define land protection as a forest area where development is prohibited by law. We set unique rates and patch parameters for each of the 32 sub-regions using the observed trend in the period spanning 1990 to 2010 (Foster et al., 2017). This provided the spatial variability of projecting few large conservation blocks in northern New England and numerous smaller patches in southern New England. Indeed, during the reference period, just 38 large timberland easements in northern New England accounted for half of the 3.6 million ha protected, while the remaining half are distributed across > 17,000 diverse protected areas. Dinamica Ego’s WoE method was used to set transition probabilities for the ‘forest to land protection’ transition using the same suite of spatial variables described previously. ‘Distance to the nearest developed land’ and ‘distance from roads’ were found to be the strongest predictors of land protection. Across most sub-regions the areas farthest away from roads or development had the highest probability of transitioning from unprotected to protected land.

2.3.3. Linking land uses to forest change

To link the simulations of forest loss to the simulations of forest growth and harvesting, we resampled the 30 m land-use change outputs from Dinamica at each time-steps to the 250 m resolution required of the computationally demanding forest growth model. For each time-step following spin-up, and for each 250 m pixel, we calculated the cumulative percent of 30 m pixels converted from one land use to another. This allowed us to simulate partial conversion of 250 m pixels

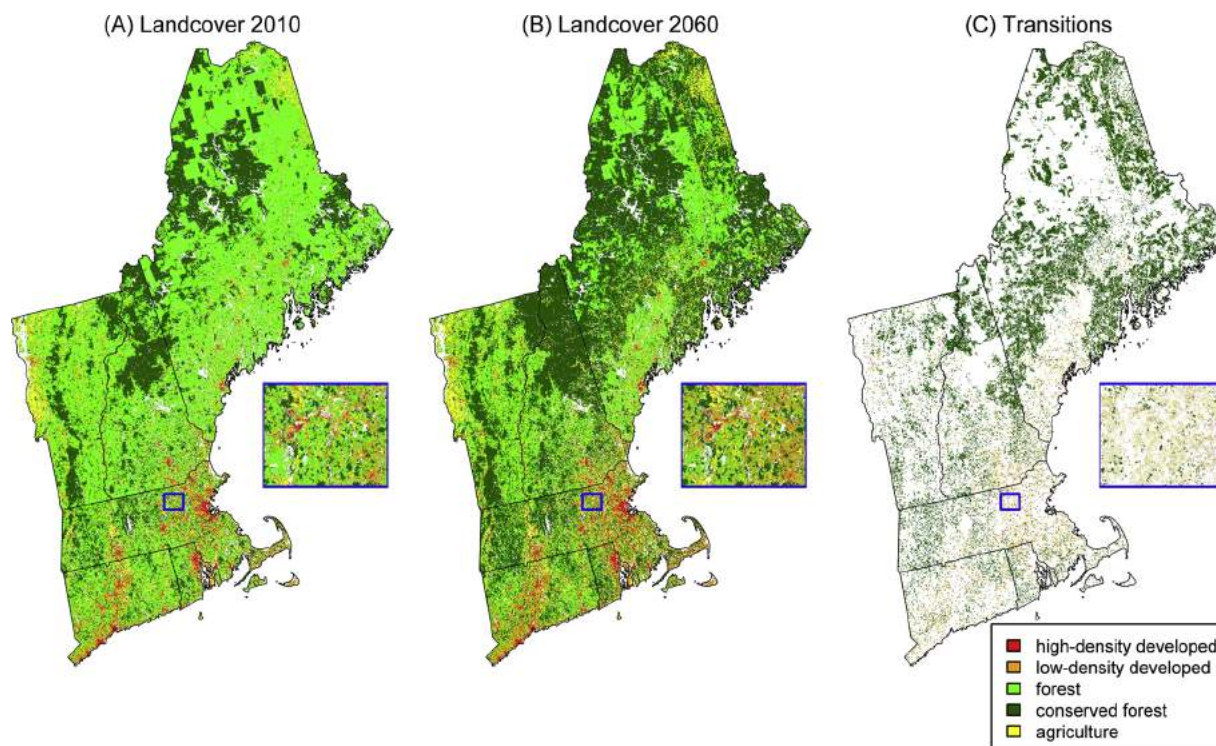


Fig. 3. Initial and simulated future land cover in New England. A) 2010 land cover; B) 2060 land cover; and C) transition patches between 2010 and 2060. Inset maps indicate referenced zoomed-in area.

based on the finer 30 m resolution. For the development scenarios, we simulated forest to development loss by subtracting the development percent of each pixel from layers of total AGC, and species AGC at each time-step. This allowed spatial and temporally explicit simulation of development incorporated in the forest succession scenario. For forest to agriculture, we assumed that conversion would result in a 100% removal of forest. For forest to low- and high-density development we assumed that 50%, and 94% of the forest AGC would be removed, respectively. We based these percentages on the proportion of impervious surface within these classes (Olofsson et al., 2016). This partial reduction in carbon following conversion accounted for some forest remaining in a developed landscape, which may be an important contributor to future carbon sequestration (Reinmann et al., 2016). **3.0**

3. Results

3.1. Spatial extent and configuration of the modern land use regime

At the start of the simulations (i.e., initial conditions), 76% of New England land cover is forest (130,694 km²), 1% is high-density development (2115 km²) and 8% is low-density development (11,977 km²) (Fig. 3A). After projecting recent trends in land use for 50 years with Dinamica, forests cover was reduced by 4% to 125,065 km², high-density development increased 28% to 2700 km², and low-density development increased 38% to 16,520 km² (Fig. 3B). Most forest lost to high-density development occurred in close proximity to existing high-density development in southern New England (Fig. 3C). Northern New England, in contrast, experienced little forest loss, although low-density development did perforate forest cover throughout New England. Protected forests expanded from 26% of the New England forested landscape (34,014 km²) in 2010, to 59% (74,086 km²) in 2060. Spatially the largest increase in future protected area occurred in northern New

England, where very large forestry conservation easements were simulated, emulating the recent trends in conservation (Fig. 3). Conversely, areas with the lowest proportion of new protected land were in areas with the highest proportion of developed land.

3.2. Climate and land-use effects on carbon stocks

In the hypothetical absence of land use or climate change, AGC in our simulations increased 53%, from 4.2 kg m⁻² at the start of the simulation (Figs. 4A, 5) to 6.3 kg m⁻² at year 2060. Climate change initially increased AGC storage less than this control scenario, but exerted a positive effect after 2040 (Fig. 5). Less initial AGC accumulation under climate change was due to reduced summer season growth associated with greater respiratory demand. After 2040, the effect of longer growing seasons compensates for summer respiration, as described in Duveneck and Thompson (2017). Compared to initial conditions, by year 2060, the climate change scenario increased average AGC by 65% (Fig. 4B) to 6.8 kg m⁻² (Figs. 4E, and 5). By year 2060, climate change increased carbon density by 12% (0.5 kg m⁻²) relative to the hypothetical control scenario with no climate or land-use change. Regional net carbon accumulation over the 50-year simulation was still positive, even when including a continuation of the recent trends in land use. Compared to initial conditions, much of the landscape continued to accumulate additional AGC as land-use activities resulting in reductions were infrequent relative to the size of the landscape (Fig. 4C and F). However, compared to the control, harvesting reduced average AGC by 14%, while forest loss to development reduced average AGC by 3%. The combined effects of development and harvesting (which on some sites was co-located) reduced average AGC by 16%, compared to the control. The net reduction in AGC from land-use were moderated when also simulating the growth enhancing effects of climate change. Together, harvesting (decreasing) and climate change (increasing)

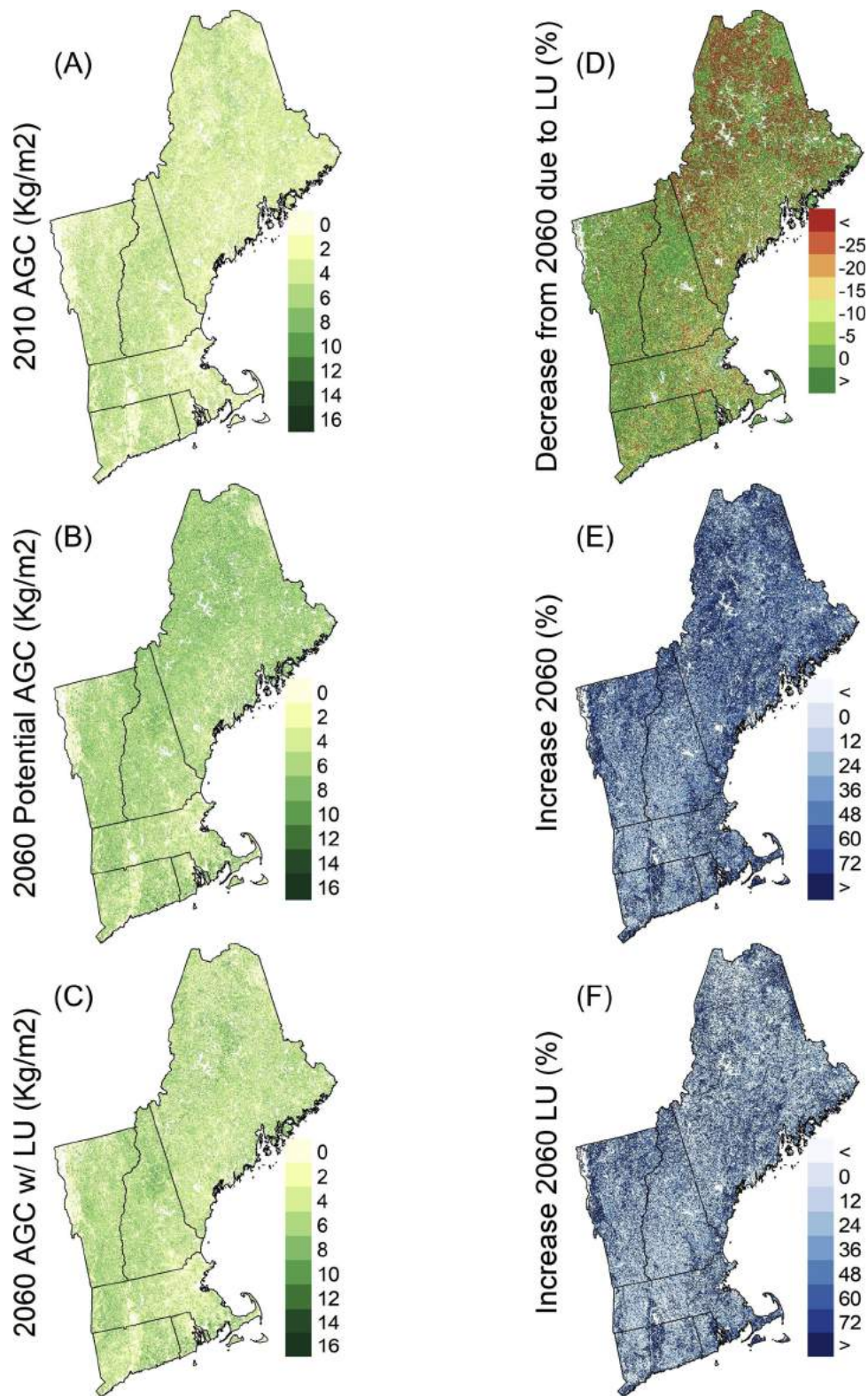


Fig. 4. New England maps of: (A) AGC at year 2010; (B) AGC at year 2060 without land use; (C) AGC at year 2060 with land use; (D) percent change in AGC with land use at year 2060 from year 2060 without land use; (E) percent change in AGC without land use at year 2060 from year 2010; (F) percent change in AGC with land use at year 2060 from year 2010. All 2060 map results include climate change.

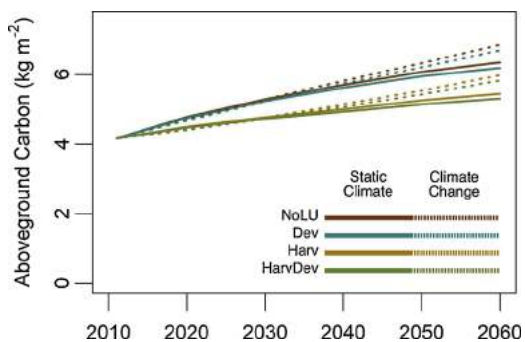


Fig. 5. Mean AGC density (kg m^{-2}) across New England as resulting from eight scenarios that include two climate scenarios (with change and without) and four separate land-use scenarios (Table 1).

resulted in a net 6% decrease in average AGC compared to the control scenario at year 2060, while development (which resulted in a relatively small reduction) and climate change increased average AGC by 5% (Fig. 5). In aggregate, the effects of climate change, harvesting, and development resulted in 8% less AGC in 2060 relative to the control scenario with no global change drivers. Spatially, the largest differences in AGC between the recent trends scenario and the control were in the northern part of the region (Fig. 4D) and were related to harvesting.

Over the 50-year simulation, harvest intensity varied resulting in between 0.03 and 2.2 kg m^{-2} of removed AGC across sub-regions under the static climate scenario. Removed AGC was slightly higher when climate change was also simulated (i.e., between 0.03 and 2.3 kg m^{-2} across sub-regions) because more AGC was available for harvest (Fig. 6). Likewise, harvest frequency varied across the landscape. Within the harvest scenarios, 79% of sites were never harvested, 15% of sites were harvested at least once, 5% at least twice, and 1% at least

three times. Compared to harvesting, development intensity resulted in less removed AGC, ranging from 0.03 to 0.5 kg m^{-2} within sub-regions under either climate scenario over the 50-year simulation (Fig. 6). However, at the site (i.e., cell) scale, development resulted in the permanent removal of up to 100% of the AGC. The spatial pattern of harvest frequency varied inversely from development (i.e., there was greater harvest area simulated in rural northern New England compared to southern New England where more development occurred).

3.3. Variation in the land-use regime

Among owner groups (Fig. 1), corporate lands were the furthest from their hypothetical carbon potential at 2060. This difference was almost entirely due to timber harvest (Fig. 7A). In fact, 68% of the total land-use effect on New England AGC stores is a result of the harvest regime on corporate lands. These impacts notwithstanding, corporate lands still experienced a net 4% gain in average AGC when assuming climate and land-use change, which emphasizes the strength of forest growth and recovery in the region. Within corporate lands, forests experienced average reductions of 35% compared to the hypothetical control under harvesting, development, and climate change. Private woodlands, compared to the control at year 2060, experienced a net 8% average reduction in AGC under harvesting, development, and climate change. Public land, in contrast, experienced almost no development and less harvesting; this led to a 1% increase in public land carbon density compared to the control at year 2060 (Fig. 7A). Development alone resulted in relatively minor reductions to AGC within owner groups compared to the control with the largest reductions in private woodland forests (3%). Compared to initial conditions, all six New England states increased AGC stores under all scenarios. The combined influence of harvesting, development, and climate change in Maine, New Hampshire, Vermont, and the combined southern New England states increased average AGC by 42%, 37%, 46%, and 33%,

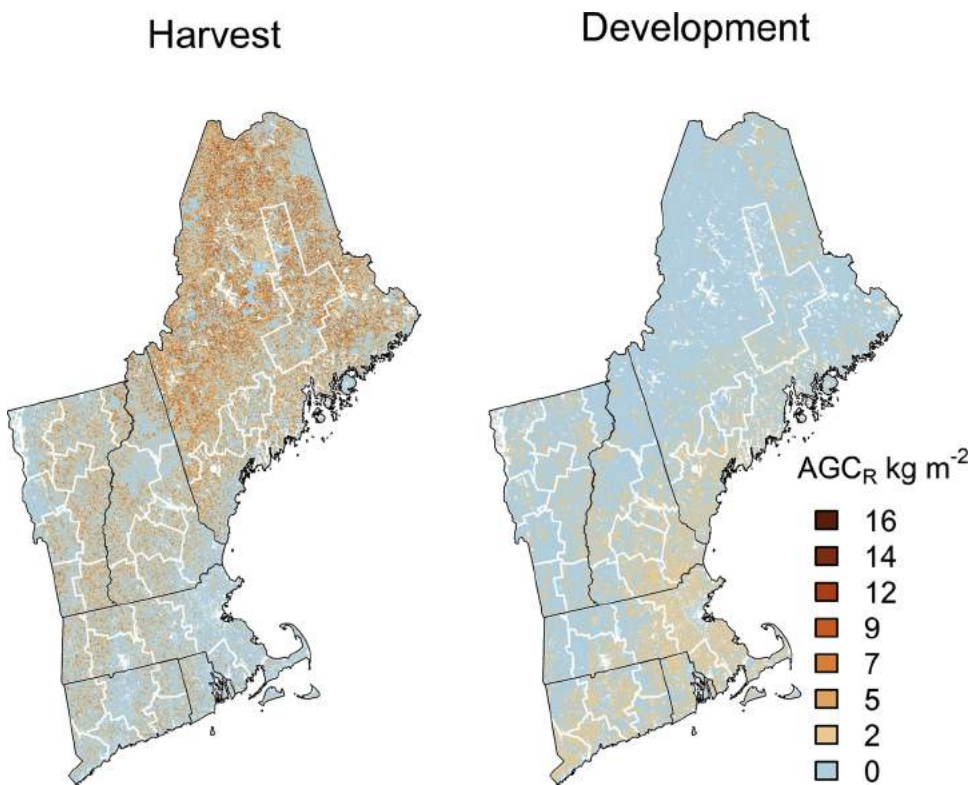


Fig. 6. Map of land-use intensity from harvesting and development. Land-use intensity represents cumulative removals from 2010 to 2060 under the climate change scenario. Sites that were not affected by each respective land use are represented in blue. White and black lines delineate sub-region and state boundaries, respectively. $\text{AGC}_R = \text{Aboveground Carbon Removed} (\text{kg m}^{-2})$.

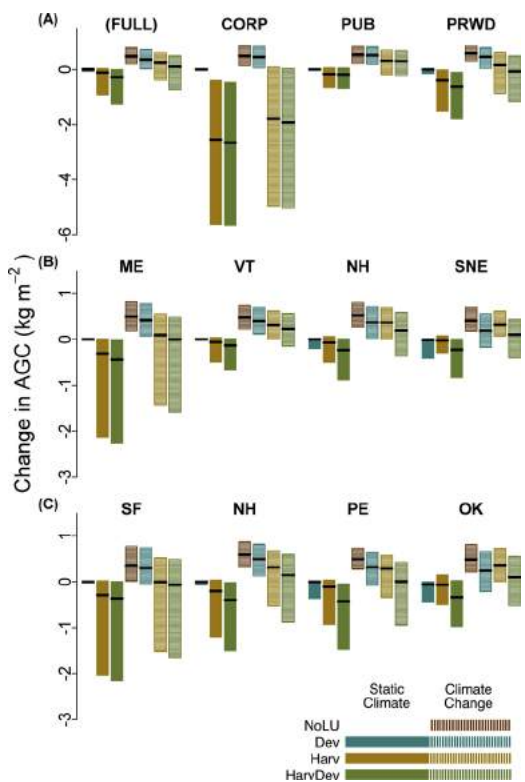


Fig. 7. Boxplots showing change in AGC within each scenario compared to the control (i.e., landscape potential with no land use nor climate change) at year 2060 aggregated within: A) ownership groups (FULL = full New England landscape, CORP = corporate, PUB = public, PRWD = private woodlands); B) New England states (ME = Maine, VT = Vermont, NH = New Hampshire, SNE = Southern New England (Rhode Island, Connecticut and Massachusetts)); and C) forest types (SF = spruce-fir, NH = northern hardwoods, PE = pine, OK = oak). Black line in box plots indicate the median, and the colored boxes show the 25th and 75th quartile range of all pixels within each spatial group. Seemingly missing scenario box plots indicate little or no change from the control scenario.

respectively. Compared to the control in the year 2060, Maine experienced the largest reduction in AGC (14%) due to harvesting, development, and climate change. AGC reductions in Maine were largely due to harvesting on corporate lands (Fig. 1). New Hampshire, Vermont, and

the combined southern states each experienced a net AGC loss of 2%, 1%, and 2%, respectively compared to the control at year 2060 under harvesting, development, and climate change. In southern states, development and harvesting resulted in approximately the same average reduction in AGC density compared to the hypothetical control at year 2060; whereas, harvesting alone had a larger effect than development alone in northern states (VT, NH, ME) (Fig. 7B). Compared to initial conditions, the combination of harvesting, development, and climate change resulted in an increase in AGC within all forest types (i.e., 46%, 40%, 36%, and 5% in the spruce-fir, northern hardwoods, pine, and oak forest types, respectively). Compared to the control scenario at year 2060, climate change increased mean landscape AGC in all forest types. Specifically, climate change resulted in a 10% increase in oak, 9% increase in northern hardwoods, 8% increase in pine and 5% increase in spruce-fir (Fig. 7C). The combination of harvesting, development, and climate change resulted in reductions in all forest types compared to the control scenario; specifically, there was a 14% reduction in spruce-fir, 9% reduction in pine, 7% reduction in northern hardwoods, and 1% reduction in oak.

3.4. Land-use effects on species composition

The control scenario at year 2060, with the no climate or land-use change, resulted in substantial changes to species abundance (i.e., mean AGC by species), but only modest changes to their relative abundance. Compared to initial conditions, species specific average AGC increased 0.56 kg m⁻² in red maple (*Acer rubrum*), 0.26 kg m⁻² in sugar maple (*A. saccharum*), 0.21 kg m⁻² in balsam fir (*Abies balsamea*), 0.21 kg m⁻² in eastern hemlock (*Tsuga canadensis*), and 0.22 kg m⁻² in red spruce (*Picea rubens*) (Fig. 8, Appendix I, Table 2). Many of these species are fast growing (e.g., red maple) or shade tolerant (e.g., eastern hemlock, and balsam fir). The AGC of red oak (*Quercus rubra*) decreased by 0.07 kg m⁻² under the control scenario from 2010 to 2060 as it was outcompeted by other species for growing space. Compared to the control scenario at 2060, climate change resulted in greater AGC density of red maple by 0.23 kg m⁻² but resulted in minor effects to other species. Additional effects are expected beyond 2060 as climate change intensifies (Duveneck et al., 2017; Wang et al., 2017). At a regional scale, forest loss to development had little effect on relative species composition because development removed equal proportions of species within sites (Fig. 8; Appendix I, Table 2). Development did affect species composition for some minor species growing in southern New England where more development occurred. For example, compared to the control scenario at year 2060, black oak (*Quercus velutina*) which is

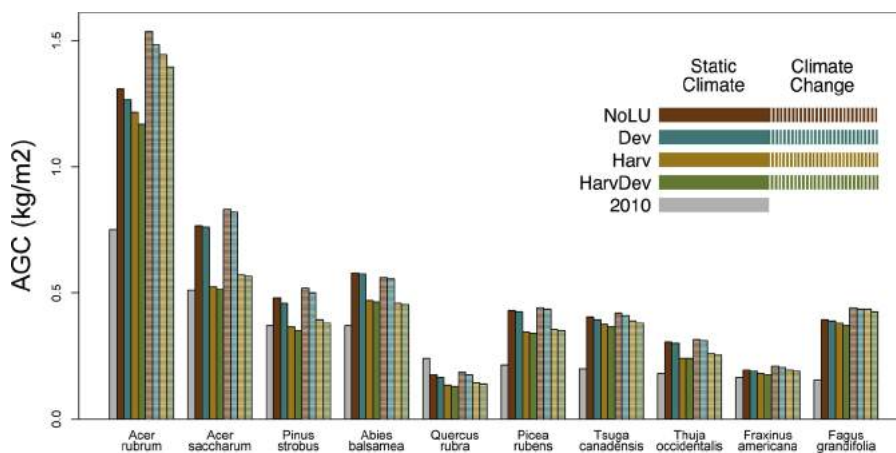


Fig. 8. Mean landscape AGC (kg m⁻²) of the ten most abundant species at year 2010 and within each scenario at year 2060.

more dominant in the southern part of the landscape resulted in almost no difference in AGC under the harvest scenario while development resulted in a reduction of 0.01 kg m^{-2} (Appendix I, Table 2). In contrast, balsam fir, which grows predominately in the north where very little development occurred, was largely immune to the effects of development (Fig. 8). Analogous to total AGC, timber harvesting had a larger effect on species AGC than development. Specifically, harvesting, with and without climate change resulted in losses to commercially valuable species. For example, compared to the control scenario at year 2060, harvesting alone resulted in average AGC reductions of 31% in sugar maple (0.24 kg m^{-2}), 24% in white pine (0.12 kg m^{-2}), 23% in red oak (0.04 kg m^{-2}), and 20% reduction in red spruce (0.09 kg m^{-2}) (Fig. 8, Appendix I, Table 2). In contrast, red maple which is among the most abundant species on the landscape but is less commercially valuable lost only 7% (0.10 kg m^{-2}) from harvesting, compared to the control scenario.

4. Discussion

4.1. New England forests are likely to be a persistent carbon sink

While land use reduced forest carbon stocks relative to their potential, our simulations suggest that if recent trends continue New England forests will, on net, continue to accrue carbon over the next 50-years. Our findings are consistent with other studies that suggest an even longer time horizon of continued forest carbon accrual in New England (Brown et al., 2018). The size of the regional carbon stock in our simulations was bolstered by the growth enhancement effects of climate change, including longer growing seasons and CO_2 fertilization. Carbon stores increased throughout the region; overall, 80% of the landscape had more carbon in 2060 than at the start of the simulation in 2010, despite ongoing harvesting, and forest loss to development. For comparison, in the absence of land use, 92% of the region had larger carbon stores in 2060. This analysis is focused on live aboveground forest carbon and does not account for the fate of harvested wood. It is important to note that the carbon in harvested wood has multiple fates that affect its contribution to global warming (Smith et al., 2006; Fahey et al., 2010). A large proportion of harvested wood from this system is short-lived—e.g., pulp and biomass fuel—and is quickly converted to CO_2 and returned to the atmosphere. Some is stored in durable products and contributes to long-term carbon storage. Finally, some harvested wood is not utilized at all, but is left on site to decompose. A complete carbon life-cycle analysis was outside the scope of this project, but represents an important opportunity for future research.

4.2. Ownership and geography

The region's ownership mosaic has large implications for the future of forest carbon stocks. AGC is strongly affected by the greater frequency and intensity of timber harvest on corporate-owned land, as compared to private woodlots or publicly owned forest. The ownership patterns underscore regions that could be targeted for increased conservation and carbon sequestration projects. Specifically, intensive harvesting in northern New England, where most corporate lands exist resulted in large losses to AGC. As with corporate timberlands globally, forest ownership patterns in this part of New England are changing rapidly (Cashore et al., 2014). In the past twenty years, more than 10 million hectares of New England forests were divested by traditional timber or wood products companies selling to Timber Investment Management Organizations (TIMOs) and Real Estate Investment Trusts (Daigle et al., 2012; Shifley and Moser, 2016; Thompson et al., 2017a).

Traditional forest management companies often had long planning horizons, which were needed to ensure supply to their nearby mills. In contrast, harvest planning by TIMOs and REITs is more influenced by global-scale markets and investor rate of return on 10-year time horizons. As such, there is great concern that the transfer of corporate forests to TIMOs and REITs could lead to abrupt land-use changes that could transform the structure and dynamics of the region and result in even greater losses of forest carbon. Globally, over the last two decades, permanent forest loss to development represented a relatively minor fraction (0.6%) of the total forest reductions associated with forestry, wildfire, and shifting agriculture. However, the majority of forest loss to urban development (> 66%) occurred in the Eastern United States (Curtis et al., 2018). In our simulations, Southern New England forests, dominated by private woodland forests received less harvesting pressure but were more likely to transition to developed sites. Specifically, southern sites near cities (e.g., Boston) are the most vulnerable to development and will experience the greatest loss of forest carbon to development under a future scenario, assuming a continuation of recent trends. Forest conversion to development has a greater impact than harvesting at a site scale, but since conversion affects a much smaller area, the regional effects of development are a fraction of harvesting. However, because developed sites do not recover their carbon, the impacts of developed sites will compound over time. The patterns we observed in the New England socio-ecological system related to the importance of forest management relative to forest loss for carbon stores are in many ways consistent with those observed or modeled at the scale of the continental US (Schleeweis et al., 2013), and the globe (Erb et al., 2018; Curtis et al., 2018).

4.3. Management implications

There is a striking discordance in the regional pattern of land protection and land development. Although simulated land protection restricted where development could occur, protection and development were not mutually exclusive within sub-regions in New England. Generally, high development rates occurred where low land protection rates occurred, and high land protection rates occurred where low development pressure occurred. Rather than suggest that land protection is not occurring where it would be most effective to reduce development, we recognize that conservation priorities exist based on lands that are not immediately under development threat. For example, conservation priorities include areas with high diversity potential (Anderson and Ferree, 2010), areas producing extra valuable ecosystem services (Postel and Thompson, 2005) and lands whose development rights have become available on the market (Foster et al., 2017). Nevertheless, the dichotomy between conservation and development patterns has large implications for assessing the priority to protect land where a threat of future development exists. Although this concern has been identified globally (Hoekstra et al., 2005), our sub-unit level of analysis in New England provides an important scale to manage conservation priorities.

Generally, development trends are higher within areas where timber harvesting rates are low, which, like land protection, limited the interaction between timber harvesting and development. This pattern has been observed along rural to urbanizing gradients throughout North America (e.g., (Wear et al., 1999; Kittredge et al., 2017)). However, there also may be interactions between forest conditions and development patterns that we were not able to simulate. For example, Puhlick et al. (2017) indicate that poorly stocked stands have a greater probability of conversion for development. Greater carbon density generally results in higher value forest land which can disincentivize

development. Greater carbon density, therefore may be directly valuable by both sequestering more carbon for climate mitigation for example, and indirectly valuable in incentivizing land owners to keep their forests as forests (Publick et al., 2017). Furthermore, greater carbon density can be managed for through forest silviculture practices (Puettmann, 2011).

4.4. Limitations and alternative scenarios

Large uncertainty exists in the future New England land-use regime. Our results are not meant to be interpreted as predictions; rather they represent a single plausible scenario based on the continuation of recent trends of land use as they interact with natural forest processes and projected climate change. What manifests as the future land-use regime will depend on difficult-to-predict global to local socio-ecological factors (Lambin et al., 2001; Rudel et al., 2005; Lambin and Meyfroidt, 2010). To help understand some potential alternative pathways, we have co-designed a suite of alternative land-use scenarios with stakeholders from throughout New England (McBride et al., 2017). We will soon be incorporating those scenarios into this simulation framework so we can compare a continuation of the recent trends to a set of alternatives, which many stakeholders have agreed are important to consider.

Uncertainty about the future landscape is not limited to land use. There are processes that we did not include but will almost certainly have large effects of future forests. Insects and other pathogens are already altering future forest composition and carbon (Orwig et al., 2002; Albani et al., 2010; Lovett et al., 2016); atmospheric nitrogen deposition is declining as a result of pollution controls and is causing a unknown but potentially significant decline in forest growth (Templer et al., 2012); and tree species may acclimate to warmer temperatures in novel ways (Reich et al., 2016).

We selected PnET-Succession because of its ability to mechanistically simulate variation in net primary production among species and through multiple canopy layers as tree cohorts respond to changes in climate. In addition, the PnET family of models, including PnET-Succession, has been calibrated, validated, and widely used within New England (Aber and Federer, 1992; Ollinger et al., 1998; Duveneck and Thompson, 2017). The focus of this research was on changes in AGC and species composition, therefore, the additional state-variables provided by PnET-Succession were not reported here (e.g., net primary productivity, respiration, transpiration), but have been explored previously (McKenzie et al., in review; Duveneck and Thompson, 2017; Duveneck et al., 2017).

In addition to local factors, precise global climate change is hard to predict and largely uncertain. To aide interpretability, the climate change results we presented here are based on a single climate change model and a single (high) emission scenario. Ultimately, the effect of average changes in temperature and precipitation on future forest productivity may be a tradeoff between longer growing seasons that increase productivity, and warmer summers that increase respiration (Duveneck and Thompson, 2017). Changes to the magnitude and frequency of climate extremes (e.g., hurricanes, ice storms, droughts) and climate-related tipping points remain a major unknown factor with the potential to drive regional forest dynamics. For example, changes to the amount and timing of snow-pack and frozen ground may greatly affect

forest management activities. For this analysis we simulated just 50 years of future climate; but it should be noted that the effects of climate change are widely projected to increase dramatically beyond 50 years (Duveneck and Thompson, 2017; Wang et al., 2017; Janowiak et al., 2018).

Coupling our understanding of land-use change and climate change is critical to assess future ecosystem services, policies, and adaptation strategies (Arnell et al., 2014). Understanding the drivers and interactions of recent land-use transitions can inform both local and global behavior affecting future land use (Mather, 1992). Although our results demonstrate the value in exploring the current land-use regime on future conditions, others note that rapid changes in land use may not follow trajectories based on recent trends (Ramankutty and Coomes, 2016). For example, the large effect of harvesting on the future land-use regime was based on the observed harvest intensity and frequency within recent forest inventories. This rate and intensity of harvesting may not represent the future land-use regime. Furthermore, future carbon trajectories may indeed benefit from adaptive management approaches, where for example species composition is intentionally adjusted based on projections of a changing climate (e.g., Duveneck and Scheller, 2015).

5. Summary and implications

Even in the hypothetical absence of future land use and climate change, New England forests would change dramatically during the next 50-years. The persistent legacy of nineteenth century land use would continue to drive large gains in AGC accumulation and a slow transition to shade tolerant long-lived tree species. Of course global change, specifically the combination of climate and land-use change, will be a major driver of change in New England's and its effects will be superimposed on this inherently dynamic system. A continuation of recent trends in climate and land-use will result in a large difference between the potential and the realized carbon stocks, and their effects will be spatially heterogeneous. Climate change will enhance carbon stores while land use will reduce them. On net, our simulations result in a decrease of forest carbon by 16%, relative to their potential. It is land use, not climate change, that has the greatest influence on carbon dynamics in New England over the next 50 years. Despite not being a significant part of the region's economy, timber harvesting is projected to have a greater impact on carbon stocks and species composition than forest loss to development. Indeed, most of the total land-use impacts on carbon (68%) occur on the corporate-owned forest, which make up than one-quarter of region. This presents a significant opportunity for policy-makers and conservationists to focus their analyses of trade-offs and future conservation efforts on the areas where their efforts are likely to have the greatest impact.

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Appendix A

See Fig. A1

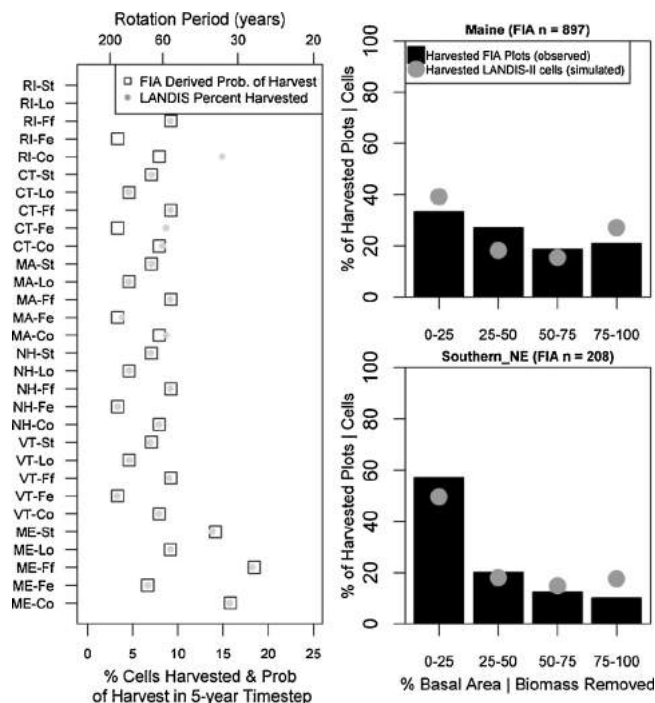


Fig. A1. Calibration of harvest frequency and intensity (Left); Frequency of harvest by state and owner classes within Forest Inventory and Analysis (FIA) plots. Squares represent FIA derived probability of harvest, dots represent simulated frequency of pixels harvested within each group. (Right); Intensity of harvest by Maine and southern New England (all other New England states). Bars represent harvest intensity (i.e., percent basal area removed) derived from repeat measured FIA plots. Dots represent simulated intensity of pixels (i.e., percent biomass removed by harvest).

See Tables A1 and A2

Table A1

Percent of each major harvest prescription used by area partitioned within each New England state.

STATE	CLEARCUT	SHELTERWOOD	HIGH-GRADE	THINNING
CT	6	14	22	59
MA	6	13	20	62
ME	22	14	15	49
NH	9	13	20	57
RI	6	13	21	60
VT	7	13	21	59

Table A2
Mean landscape AGC (kg m^{-2}) of individual species at year 2010 and within each scenario at year 2060.

SPECIES	2010	2060; Static Climate; No Land Use	2060; Static Climate; Development	2060; Static Climate; Harvest	2060; Static Climate; Harvest & Development	2060; Climate Change; No Land Use	2060; Climate Change; Development	2060; Climate Change; Harvest	2060; Climate Change; Harvest & Development
<i>Acer rubrum</i>	0.75	1.31	1.27	1.22	1.17	1.54	1.49	1.45	1.40
<i>Acer saccharum</i>	0.51	0.77	0.76	0.53	0.52	0.83	0.82	0.57	0.57
<i>Pinus strobus</i>	0.37	0.48	0.46	0.37	0.35	0.52	0.50	0.40	0.38
<i>Abies balsamea</i>	0.37	0.58	0.58	0.47	0.47	0.56	0.56	0.46	0.46
<i>Quercus rubra</i>	0.24	0.18	0.17	0.14	0.13	0.19	0.18	0.15	0.14
<i>Picea rubens</i>	0.22	0.43	0.43	0.35	0.34	0.44	0.44	0.36	0.35
<i>Tsuga canadensis</i>	0.20	0.41	0.40	0.38	0.37	0.42	0.41	0.39	0.38
<i>Thuja occidentalis</i>	0.18	0.31	0.30	0.24	0.24	0.32	0.31	0.26	0.26
<i>Fraxinus americana</i>	0.17	0.20	0.19	0.18	0.18	0.21	0.21	0.20	0.19
<i>Fagus grandifolia</i>	0.16	0.40	0.39	0.38	0.37	0.44	0.44	0.44	0.43
<i>Betula alleghaniensis</i>	0.13	0.16	0.16	0.12	0.12	0.17	0.17	0.13	0.13
<i>Betula papyrifera</i>	0.11	0.11	0.11	0.12	0.11	0.12	0.12	0.13	0.13
<i>Quercus velutina</i>	0.11	0.06	0.06	0.06	0.06	0.07	0.06	0.06	0.06
<i>Populus tremuloides</i>	0.09	0.04	0.04	0.05	0.05	0.04	0.04	0.05	0.05
<i>Picea mariana</i>	0.08	0.13	0.13	0.10	0.10	0.14	0.14	0.11	0.11
<i>Picea glauca</i>	0.07	0.13	0.13	0.11	0.11	0.14	0.14	0.11	0.11
<i>Quercus alba</i>	0.06	0.13	0.12	0.12	0.11	0.14	0.13	0.13	0.13
<i>Prunus serotina</i>	0.06	0.12	0.11	0.12	0.11	0.13	0.13	0.13	0.13
<i>Betula lenta</i>	0.05	0.06	0.06	0.06	0.06	0.07	0.06	0.07	0.06
<i>Populus grandidentata</i>	0.04	0.02	0.02	0.03	0.03	0.02	0.02	0.03	0.03
<i>Larix laricina</i>	0.04	0.06	0.06	0.06	0.06	0.07	0.07	0.06	0.06
<i>Pinus rigida</i>	0.04	0.08	0.08	0.08	0.07	0.09	0.08	0.09	0.08
<i>Pinus resinosa</i>	0.04	0.07	0.07	0.06	0.06	0.07	0.07	0.07	0.06
<i>Carya glabra</i>	0.03	0.04	0.04	0.04	0.03	0.04	0.04	0.04	0.04
<i>Fraxinus nigra</i>	0.02	0.04	0.04	0.04	0.04	0.05	0.05	0.05	0.05
<i>Quercus coccinea</i>	0.02	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
<i>Populus balsamifera</i>	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
<i>Tilia americana</i>	0.01	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.03
<i>Quercus prinus</i>	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.01
<i>Ulmus americana</i>	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
<i>Betula populifolia</i>	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
<i>Ostrya virginiana</i>	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01

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