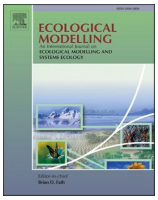
Ecological Modelling 456 (2021) 109657

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Projecting complex interactions between forest harvest and succession in the northern Acadian Forest Region

Erin Simons-Legaard, Conceptualization;Methodology;Validation;Formal analysis;Writing – original draft;Funding acquisition [a, b,*], Kasey Legaard, Conceptualization;Software;Data curation;Writing – review & editing;Funding acquisition [a, b], Aaron Weiskittel, Conceptualization;Methodology;Writing – review & editing;Funding acquisition [a, b]

[a] School of Forest Resources, University of Maine, Orono, ME 04469, USA
[b] Center for Research on Sustainable Forests, University of Maine, Orono, ME 04469, USA

ARTICLE INFO

Keywords:
Aboveground biomass
Forest composition
Forest landscape model
LANDIS-II
Northeast USA
Timber harvest

ABSTRACT

Preventing declines of native and historically-abundant tree species is an important aspect of sustainable forest management, but predicting future forest composition is challenging when succession does not tend to follow a well-defined path. We evaluated the implications of site-level interactions between timber harvesting and forest succession on the regional landscape dynamics of the complex and species-rich northern Acadian Forest Region. Our expectation was that forest composition would trend away from long-lived and shade-tolerant species, because rates of landscape disturbance from timber harvesting are high relative to historic rates of natural disturbance. We used a novel modeling approach that combined Landsat-derived time series of forest disturbance to inform realistic simulations of timber harvesting across many individual commercial forest landowners using LANDIS-II, and evaluated changes in tree species' distributions and abundance with and without harvesting. Detailed descriptions of initial forest conditions were derived from maps of relative tree species abundance, developed using Landsat satellite imagery, regional inventory data, and an innovative machine learning algorithm. If recent harvest rates persist, simulations suggest timber harvesting will generally be sustainable in our study area; however, projected rates of site-level species turnover were high, predominantly favoring species that were less abundant under the region's natural disturbance regime. As a result, broad-scale patterns of projected species co-occurrence shifted, destabilizing important regional forest types. Our results highlight both the region's capacity for forest growth and the importance of accurately capturing the local effects of land management when projecting forested regions dominated by commercial ownership.

1. Introduction

Managing for tree species that are native and historically dominant to a region is an important aspect of sustainable forest management (Amos-Binks et al., 2010). In contrast, there is growing evidence that extensive or selective harvesting has contributed to an "unmixing" or homogenization of many of the mixed conifer-deciduous forests of the northern U.S. and southern Canada (Amatangelo et al., 2011; Boucher et al., 2009; Hanberry et al., 2013). In these situations, long-lived, shade-tolerant conifers associated with late succession are usually the losers, while less shade-tolerant, typically broad-leaved trees associated with early succession are often the winners. In the mixed Laurentian forests of the Great Lakes-St. Lawrence region, for example, many areas historically dominated by site limited conifers like eastern hemlock (*Tsuga canadensis*) have shifted towards dominance by adaptable hardwoods such as red maple (*Acer rubrum*) following high-intensity harvesting (Amatangelo et al., 2011; Boucher et al., 2009). These regional shifts in species composition coupled with a reduction in forest diversity threaten forest resilience, particularly in landscapes facing a complex assembly of threats (e.g., climate change, insect outbreaks, invasive species) (Messier et al., 2019). Predicting how harvesting will influence succession, thereby making it possible to avoid unwanted species shifts, can be a significant challenge for forest managers, however, particularly when they are reliant on natural

---

* Corresponding author.
E-mail address: erin.simons@maine.edu (E. Simons-Legaard).

https://doi.org/10.1016/j.ecolmodel.2021.109657
Received 12 October 2020; Received in revised form 17 June 2021; Accepted 18 June 2021

regeneration and the conditions that ensure self-replacement of desired species are limited (Gould et al., 2005; Taylor et al., 2009).

Within the Acadian Forest Region (AFR) of northeastern U.S., longitudinal studies suggest that maintaining some native conifers in northern mixedwood forests will be challenging even with targeted or intensive management (Bataineh et al., 2013; Olson and Wagner, 2010). Although the AFR shares many tree species in common with the Great Lakes-St. Lawrence region, an important distinguishing feature of the AFR is the presence of red spruce (*Picea rubens* Sarg.). Pre-settlement forests in Maine, for example, were dominated by red spruce and other long-lived conifers (e.g., eastern hemlock), which often also occurred in mixedwood associations with shade-tolerant hardwoods such as sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*) (Mosseler et al., 2003). Historically, stand dynamics were driven by windfall and the creation of small canopy gaps. Gap-creating wind events occurred with a return interval of approximately 100 years; large or catastrophic disturbances were rare (i.e., >1, 000 year return interval) (Lorimer, 1977; Seymour et al., 2002). As a consequence, shorter-lived shade tolerant species (e.g., balsam fir, *Abies balsamea*) or shade intolerant species (e.g., paper birch, *Betula papyrifera*), although occasionally in high abundance, occurred predominantly in the understory (Mosseler et al., 2003). In recent decades, however, those types of species have become increasingly abundant as rates of landscape disturbance, now driven primarily by timber harvesting, have increased.

Statistical and empirically-derived models are a commonly used tool in forest planning, but planning for novel environmental and forest conditions will require more dynamic tools capable of large-scale application. Although generally developed for research purposes, forest landscape models (FLMs) are increasingly being used for decision support because they can simulate forest response to changing conditions (Gustafson et al., 2011). FLMs that are phenomenological and stochastic are particularly well-suited to application to forest systems in which succession at a given site does not tend to follow a well-defined path, but rather has many potential endpoints. Previous studies of regional forest dynamics using an FLM have included the AFR (Duveneck et al., 2017; Duveneck and Thompson, 2019; Wang et al., 2017), but in each the effects of timber harvesting were either ignored, in lieu of focusing on climate change, or generalized based on broad-scale information about harvest rates (Harris et al., 2016). Tim- ber harvesting is, however, the dominant forest disturbance factor in northeastern forests (Brown et al., 2018) and in the U.S. The spatial resolution of the projections was also coarse (250 m or 270 m). Forest projections that discount the spatially-varied and temporally dynamic effects of timber harvesting in northeastern forests, particularly those areas dominated by commercial forestlands, potentially obscure important details about local feedbacks, as well as cross-scale interactions, affecting regional processes.

The goal of our study was to better understand the regional implications of local interactions between timber harvesting and forest succession for the AFR. Our primary research objectives were to use a novel implementation of the LANDIS-II FLM to expressly emulate recently observed harvest rates and patterns across individual landowners in Maine, and to project cumulative changes in future tree species' distributions and abundance stemming from land use and forest dynamics. Regionally, Maine has the highest harvest rates in the AFR (Brown et al., 2018; Canham et al., 2013; Duveneck and Thompson, 2019). In northern Maine, land is almost entirely owned by commercial forest companies, and forest management is almost entirely dependent on partial harvesting and natural regeneration (Bataineh et al., 2013; Brissette, 1996; Canham et al., 2013). Locally, the median annual harvested area in that region is approximately 2% with substantial spatiotemporal variation between landowners, which has resulted in distinct landscape-scale patterns associated with forest composition and age (Legaard et al., 2015). Our expectation was that under the current forest management regime total live aboveground biomass would remain relatively steady but species relative abundances would change, with a decline in long-lived, shade-tolerant species such as red spruce (Olson and Wagner, 2010).

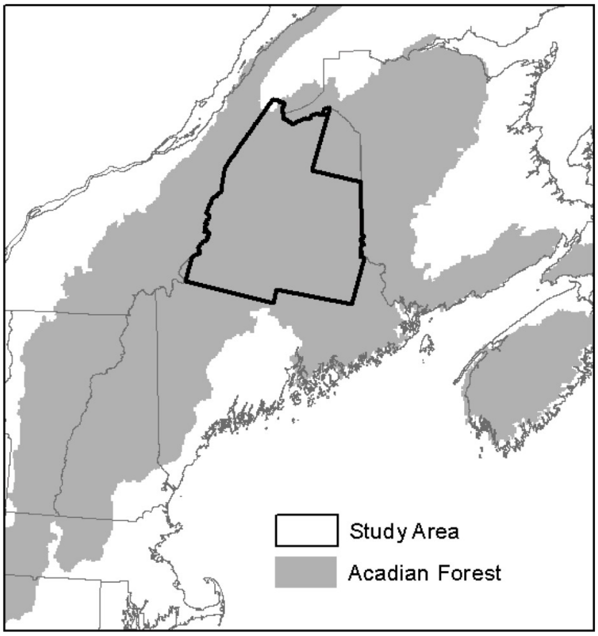


Fig. 1. 30,760 km^2 study area located in the Acadian Forest Region (AFR) of the northeastern U.S. AFR boundary obtained from Olson et al., (2001).

2. Methods

2.1. Study area

We evaluated land use and forest dynamics across a study area that encompassed approximately 30,760 km^2 of the AFR in Maine (67.76−70.61° E, 45.16−47.44° N; Fig. 1). Virtually all forestland in this area is considered commercially productive and approximately 90% is private, primarily owned by large (>40 km^2) landowners with highly contrasting management objectives, including industrial forest products companies, family-owned corporations, and investment entities. Small forest landowners (also known as family forests) are few in this region of Maine. Parcels owned by the State (managed or held in reserve) also occurred in this area, including Maine's largest forest reserve, Baxter State Park (847 km^2). Population density (0−65 people/km^2) and urban or residential development are all exceptionally low throughout this region (McWilliams et al., 2005).

Climate in this region is characterized by warm, humid summers and cold, snowy winters. Erosion and glaciation have shaped the topography, which is mostly flat or rolling with elevations ranging from sea level to over 1,500 m (Seymour, 1995). Maine is covered by an extensive network of rivers, streams, lakes, swamps and wetlands. Forest type distributions are generally associated with topographically related climate and soil gradients (Seymour, 1995). Commonly occurring tree species include: balsam fir (*Abies balsamea*), white (*Picea glauca*), red (*P. rubens*), and black (*P. mariana*) spruce, white pine (*Pinus strobus*), white (*Betula papyrifera*) and yellow (*B. alleghaniensis*) birch, red (*Acer rubrum*) and sugar (*A. saccharum*) maple, and American beech (*Fagus grandifolia*). Tree advance regeneration is often highly abundant in this region with high species richness, high stem densities, and limited effects of herbivory (Bose et al., 2016)

2.2. Forest landscape model

We modeled forest change using LANDIS-II version 6.0. LANDIS-II and its predecessor LANDIS have both been described extensively in the literature (Mladenoff et al., 1996; Mladenoff and He, 1999; Mladenoff, 2004; Scheller and Mladenoff, 2004; Scheller et al., 2007). LANDIS-II is a raster-based forest landscape model; a landscape is represented by a grid of cells aggregated by user-defined ecoregions. The successional processes of tree establishment, growth, and mortality are simulated for each cell at the level of tree cohorts characterized by species and age. Multiple cohorts can be present in a cell and inter-cohort competition is driven by life history attributes (e.g., shade tolerance, longevity, regeneration strategy). Cells are spatially linked by the processes of seed dispersal and disturbance.

The LANDIS-II software system is composed of a core program and user-selected extensions that have been developed to simulate a variety of disturbances. We used the Biomass Succession extension (version 3.1.1) (Scheller and Mladenoff, 2004) to simulate succession, the Biomass Harvest extension (version 2.1) (Gustafson et al., 2000) to simulate timber harvesting, and the Base Wind (Scheller and Mladenoff, 2004) to simulate wind events. Extensions can be run with different temporal intervals; we used a 5-year time step for all. Based on past experience and a global sensitivity analysis of LANDIS-II (Simons-Legaard et al., 2015), a novel formulation of parameterizing and initialization was used to ensure robust model behavior, as described below.

2.3. Model initialization

LANDIS-II requires as part of its initialization two input maps, ecoregions and initial forest conditions, and accompanying text files. For both ecoregions and initial conditions, we used observations and measurements collected at US Forest Service (USFS) Forest Inventory and Analysis (FIA) field plots within our study area (2006–2010; $n = 1{,}521$) as reference data. We derived our ecoregions from a combination of climate zones delineated by Briggs and Lemin (1992) and DEM-derived slope to capture the effects of relative landscape position on individual species establishment (See Section 2.4.1). The majority of FIA plots in our study area are categorized as mesic, occurring either in flat lowlands (Condition Table; Physiographic class code or PHYSCLCD = 21) or hilly upland areas (PHYSCLCD = 22). Percent slope is recorded for each subplot (Subplot Table), and to identify a threshold slope to use for classifying all forest within our study area as lowland or upland, we calculated the value at which histograms of slope grouped by the two PHYSCLCD categories intersected (i.e., ~5% slope). We combined our upland/lowland delineation with the 3 major climate zones associated with our study area for a total of 6 ecoregions.

Initial forest conditions are provided by the user in the form of a thematic map and associated text file, which LANDIS-II uses to populate each cell with information about species presence and forest age. For each cell, we determined which species were present in high relative abundance using maps of percent biomass (live aboveground). Percent biomass ca. 2010 was modeled and mapped for each of the 13 most abundant species in our study area (Supplementary Table 1). Following the methods of Legaard et al. (2020), predictive models were constructed for each species using support vector machines (SVMs) with model specification determined by a multi-objective genetic algorithm (GA) designed to simultaneously minimize total prediction error and systematic error. Estimates of percent biomass from FIA plots were used as reference and potential predictor variables included spectral variables from Landsat Thematic Mapper (TM) images acquired throughout the growing season (i.e., late April through mid-October); terrain variables generated from the National Elevation Dataset and National Hydrography Dataset; and climatological variables obtained from the USFS Rocky Mountain Research Station (Rehfeldt, 2006). Using the cross-validation procedure described by Legaard et al. (2020), RMSE (root mean squared error) and systematic RMSE for the final models ranged from 4–17% and 0.5–3%, respectively, across species. From the 13 percent biomass maps we 1) identified the 3 most abundant species for each cell, 2) rescaled percent abundances for those 3 species to sum to 100%, and 3) assigned cohorts to species based on relative abundance (i.e., 1–33% = 1 cohort, 33–66% = 2 cohorts, and 66–100% = 3 cohorts). If, for example, after rescaling the relative abundances of the top 3 species in a given cell were 60%, 30%, and 10%, they were assigned 2, 1, and 1 cohort(s), respectively. This strategy ensured that cohort assignment to a cell represented relative species abundance based on empirical data, maintained dominant patterns of species co-occurrence, and resulted in a total number of cohorts that was computationally tractable for simulations.

We assigned age(s) to each species cohort based on disturbance history and FIA plot data. Forest disturbance and % basal area removal were mapped for our study area from 1973 to 2010 in 2–4 year intervals using the same modeling framework that produced the percent biomass maps (Legaard, 2018). Reference data were obtained from visual interpretation of satellite images and air photos (disturbance occurrence) and from re-measured FIA plots (% basal area removed). Potential predictor variables were derived from Landsat Multispectral Scanner (MSS) and TM images. User's and producer's accuracies ranged from 86–92% and 78–87%, respectively, across the intervals. For cells that had received a stand-replacing harvest, which we defined as ≥70% basal area removal, age was assigned based on time since harvest (i.e., 5–40 years old). For the remaining cells, which were a combination of cells with no history of harvest 1973–2010 and those that had received a partial harvest (i.e., harvest resulting in <70% biomass removal at the cell level), we assigned overstory age randomly to contiguous neighborhoods in conformance with the age distribution for FIA plots in our study area with stand age >40 years old. Finally, for a given species we assigned understory cohorts randomly to the subset of cells in which a species occurred based on the proportion of FIA plots with >2.54 cm (1 inch) trees of a given species that also had seedlings of that species. A spatial resolution of 30 m was retained throughout the mapping processes; ultimately, the total number of unique combinations of species/age cohorts (i.e., initial communities) modeled was 9,273.

2.4. Model parameterization and calibration

2.4.1. Succession

For each species, LANDIS-II users must also provide values for general life history characteristics as well as growth-related parameters to model succession and live aboveground biomass (AGB) with the Biomass Succession extension. We derived species-specific values for life history traits from the peer-reviewed literature including previous LANDIS-II studies. With respect to growth, AGB for a cohort is modeled as a function of annual net primary productivity (ANPP) and mortality (Scheller and Mladenoff, 2004). Sensitivity analyses have determined that predictions of AGB using Biomass Succession are most sensitive to the parameters maximum ANPP ($ANPP_{max}$) and maximum aboveground biomass (B_{max}) (Scheller and Mladenoff, 2004; Simons-Legaard et al., 2015; Thompson et al., 2011). We determined $\mathrm{B_{max}}$ for each species from USFS FIA plot data by first calculating total plot biomass and then identifying the maximum value for the subset of plots where a given species was one of the top three most abundant.

We used the process-based PnET-II model (Aber et al., 1995) to derive $\mathrm{ANPP_{max}}$ for each of our ecoregions in a manner similar to previous LANDIS-II studies (e.g., Scheller and Mladenoff, 2004; Scheller et al., 2008; Thompson et al., 2011). PnET-II is a forest carbon and water balance model that predicts monthly changes in whole canopy photosynthesis and estimates live ANPP (foliar and wood). We used species-specific estimates of foliar nitrogen concentrations (mg N $\mathrm{g^{-1}}$ leaf) and specific leaf mass for our 13 species (Supplementary Table 1), and for other parameters used generic values for northern hardwood, spruce-fir, and pine (Aber et al., 1995; Ollinger and Smith, 2005). Climate inputs into PnET-II include monthly averages for maximum/minimum temperatures, precipitation, and photosynthetically active radiation (PAR). We generated 100 random points within each of our ecoregions and extracted monthly values for temperature and precipitation from 30-year normal PRISM maps. We used the open source software SAGA-GIS (http://www.saga-gis.org/) to calculate monthly insolation values for each of the points and converted those values to PAR (umoles m^{-2} sec^{-1}). We then ran PnET-II for each point and each species to estimate species-specific $ANPP_{max}$ values for each ecoregion.

In the absence of disturbance, the Biomass Succession model assumes that an equilibrium condition will develop over time as annual age-related mortality increases and eventually offsets annual growth as a cohort approaches B_{max}. Two shape parameters interact with $ANPP_{max}$ and B_{max}; the *growth shape parameter* (*r*) determines the age at which a species achieves $ANPP_{max}$ and the *mortality shape parameter* (*d*) expresses the relationship between age-related mortality and B_{max} as a cohort nears its longevity age. These shape parameters, which range from 0-1.0 (*r*) and 5-25 (*d*), have no empirical basis but can used be to express relative differences in life history strategies between species (e.g., faster growth by less-shade tolerant species in a high light environment). Projections of aboveground biomass, particularly initial biomass and in the first few simulated intervals, can be especially sensitive to small changes in *r* (Thompson et al. 2011; Simons-Legaard et al., 2015) so we adopted a conservative approach, ultimately setting *r* (0.62-0.87) and *d* (9-15) over a relatively narrow range across species. Finally, the model includes an additional calibration parameter (i.e., *Spin-up mortality* fraction) that can be used to modify AGB estimation during the model spin-up phase to better align initial estimates with available reference data. We incrementally increased this parameter from zero, with the goal of matching the total AGB projected at year 0 to the estimate for our study area calculated from FIA data (2006–2010).

In addition to cohort growth, LANDIS-II models the establishment of new cohorts. Any reproductively mature cohort within a user-specified neighborhood can act as a potential seed source, but the probability of successful dispersal to a cell declines rapidly with distance from source (Mladenoff and He, 1999; Ward et al., 2005). Given a seed source, the likelihood of success is determined by a species' shade tolerance and the *probability of establishment* (P_{est}) as specified by the user. P_{est} ranges from 0.01–1 and can be varied by ecoregion (He et al., 1999; Mladenoff and He, 1999). We estimated P_{est} separately for lowland and upland forest, as defined in the ecoregion map (See Section 2.3), by comparing the number of FIA plots with seedlings of a given species to the number of plots with seedlings and 2.54 cm (1 inch) saplings of that species.

To evaluate our initialization, parameterization and calibration of the Biomass Succession extension, we performed a multi-scale comparison of biomass estimates from FIA data (2006–2010) to LANDIS-II predictions at year 0. The FIA sampling design provides approximately one sample location every 2,428 ha (or 6,000 ac) across the U.S. We first generated a tessellated dataset of 2,428 ha squares overlapping our study area in ArcMap and then identified the FIA plot nearest to each square's center. For each square, we estimated total AGB based on the identified FIA plot (scaled to the 2,428 ha square) and compared it to total AGB predicted by LANDIS-II for the same area (i.e., summing the 30 m cell-level predictions within the 2,428 ha square). We then systematically combined neighboring squares (3 × 3, 6 × 6, 12 × 12, 24 × 24) into square areas of increasing size (21,852 ha, 87,408 ha, 349,632 ha, 1,398,528 ha), and compared FIA and LANDIS-II estimates at each scale using a Pearson's correlation coefficient. Finally, we compared the relative abundance at year 0 for the 13 species between FIA and LANDIS-II for the study area. Although it is relatively common to compare LANDIS-II predictions to FIA plot data, comparisons are generally only made at the level of the individual plot or the entire study area, which can obscure scale-dependent patterns of disagreement.

2.4.2. Disturbance

Calibration of disturbance extensions generally focuses on relevant literature for the region of interest to specify disturbance characteristics such as frequency, size, and intensity. For example, we calibrated the Base Wind extension to simulate a 0.1% rate of annual area disturbed by small to moderate wind events (Lorimer, 1977; Lorimer and White, 2003; Seymour et al., 2002). When calibrating the Biomass Harvest extension, previous studies including the AFR have used regional estimates of harvest rates derived from FIA plot data (Duveneck and Thompson, 2019; Wang et al., 2017). In contrast, we were able to use the local, spatially-explicit information provided by the Landsat forest disturbance time series developed for our study area. For this, we first delineated management units based on a map of land ownership boundaries ca. 2010, which encompassed >500 parcels and >80 landowners. Ownerships ranged in size from <1 km^2 to 4,162 km^2. In addition to commercially-managed forest, our study area included ~179,000 ha of publicly- or privately-owned forest managed as preserves and ~82,000 ha of forest we identified as inaccessible or ineligible for timber harvest due to elevation or slope based on current state regulations. We then estimated the annual area harvested for each landowner based on the observed harvest areas in the three most recent intervals (i.e., 2001–2004, 2004–2007, 2007–2010) in the forest disturbance times series. Estimated rates varied widely between landowners, ranging from <1% to 8.2% of forested area per year, with a study-wide average of 2.2% (SD=1.6%). Based on each landowner's average harvest rate, the resulting cumulative target area was 768,379 ha to be harvested every 10 years.

Harvesting in LANDIS-II is based on control of harvest area, not volume. Harvest area targets for each landowner in our modeled system were assigned to two prescriptions: "clearcut" or "partial harvest." Partial harvesting represents >90% of the harvests in Maine, according to self-reporting by Maine landowners to the Maine Forest Service (Maine Forest Service 2020). We designed our partial harvest prescription to be variable in intensity based on a post-harvest survey in our study area by Rice et al. (2012), which determined that on average the area of a partial harvest is comprised of 35% complete overstory removal (predominantly in trails and landings) and 45% partial overstory removal. Our partial harvest prescription was implemented as a 2-stage harvest across consecutive periods. Selected stands first received a patch cut treatment (to approximate trails) targeting 40% of the stand area, followed in the next period by a uniform selection cut of the remaining stand area, with removals targeting primarily older cohorts. The clearcut prescription was designed to remove all but seedlings. Clearcuts were only assigned to a portion of landowners with a recent history of conducting stand-replacing harvests. We also calibrated target rates to maintain an annual average clearcut rate across ownerships of approximately 4% in accordance with annual landowner harvest reports to the Maine Forest Service (Maine Forest Service 2020). When identifying "stands" for use in the Biomass Harvest extension our minimum mapping unit was 9 cells, or approximately 1 ha.

2.5. Scenario design and data analysis

We simulated forest growth and succession with and without timber harvesting. Our start date was 2010 based on the initialization data. Total duration for simulations with timber harvesting was 50 years, reflecting a typical strategic planning horizon in our region. Total duration for simulations without timber harvesting (i.e., succession only) was 150 years. We compared results between simulations with and without timber harvesting at 50 years. For simulations without timber harvesting we also compared results at year 50 to year 150 to further verify our calibration of the Biomass Succession extension regarding the longer-term outcomes of competitive species interactions and to better understand the effects of harvesting on AGB dynamics. Our expectation was that if the model was parameterized and calibrated appropriately for our forest system, the relative abundance of less shade tolerant species would decline over time in simulations without timber harvesting. All simulations included wind disturbance.

LANDIS-II models stochasticity in some of the successional (e.g., dispersal and cohort establishment) and disturbance (e.g., stand selection for wind damage or harvest) processes. We replicated each scenario

Table 1
Comparison of total live aboveground biomass ca. 2010 estimated from LANDIS-II projections (year 0) with USFS Forest Inventory and Analysis plot data (2006–2010) at 5 nested scales, including neighborhood size, area (ha) of square sample unit, number of samples (n), Pearson's correlation coefficient (ρ) between estimates, as well as average ($\overline{x}$) and standard deviation (σ) of aboveground live biomass (teragrams) for each dataset at each scale.

				LANDIS-II		FIA	
Neighborhood Size	Area	n	ρ	$\overline{x}$	σ	$\overline{x}$	σ
1 × 1	2,428	1,407	0.16	0.18	0.04	0.16	0.10
3 × 3	21,852	155	0.43	1.50	0.28	1.33	0.43
6 × 6	87,408	49	0.87	5.09	1.76	4.50	1.74
12 × 12	349,632	14	0.96	17.69	6.66	15.76	6.24
24 × 24	1,398,528	4	0.98	61.93	17.31	55.15	15.86

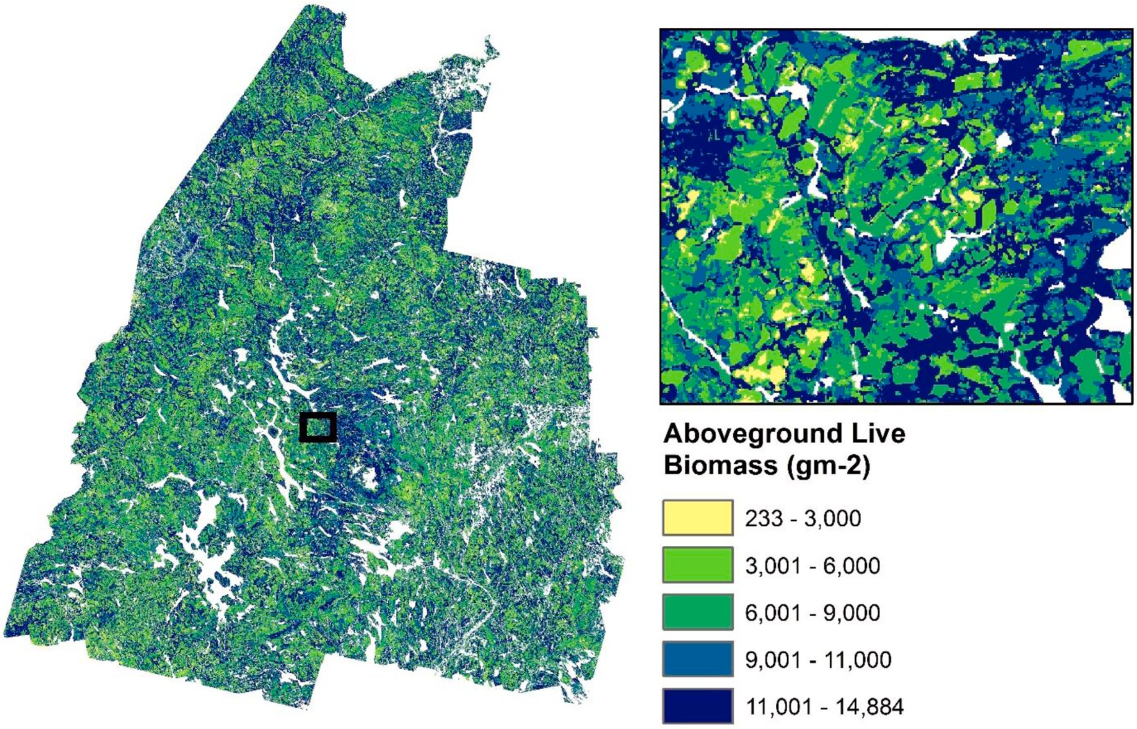


Fig. 2. Simulated distribution of aboveground live biomass ca. 2010 based on initial forest conditions derived from maps of relative tree species abundance and forest disturbance history developed using Landsat satellite imagery and USFS Forest Inventory and Analysis plot data. Inset area (bold outline) references zoomed-in example map.

ten times and evaluated variance in modeled outcomes. For each scenario, we used maps of AGB (g/m^2) output by LANDIS-II at each time step to calculate projected changes in species AGB and total AGB summed across species (AGB$_{total}$). We used the Output Biomass Reclass extension to classify sites based on species dominance and compared initial spatial patterns to projected spatial patterns to evaluate species turnover. We also developed forest type maps and calculated the changes in forest area by type. Forest was classified as: spruce-fir (≥75% AGB$_{total}$ composed of balsam fir or spruce *sp.*), spruce-fir mixed (≥50% AGB$_{total}$ and <75% AGB$_{total}$ composed of balsam fir or spruce *sp.*), maple-beech-birch (≥75% AGB$_{total}$ composed of sugar maple, yellow birch, or American beech), maple-beech-birch mixed (≥50% AGB$_{total}$ and <75% AGB$_{total}$ composed of sugar maple, yellow birch, or American beech), other hardwoods (≥75% AGB$_{total}$ composed of red maple, paper birch, or white ash), other softwoods (≥75% AGB$_{total}$ composed of eastern hemlock, northern white cedar, or white pine), or mixed species. Finally, for simulations that included harvesting we calculated harvested area and compared to assigned targets.

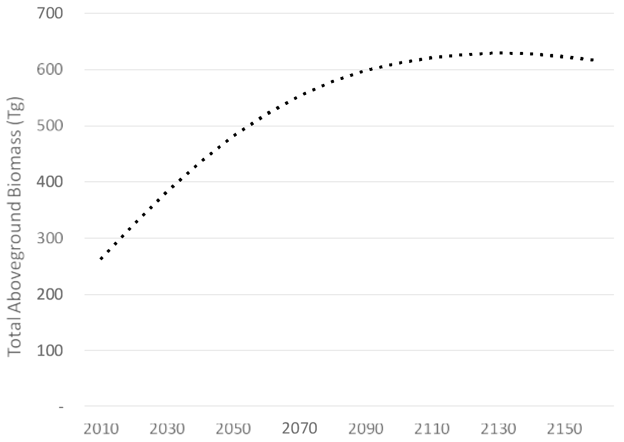


Fig. 3. Projected total (Tg) live aboveground aboveground biomass, simulated without timber harvesting 2010–2160. Complete set of 10 model runs are displayed but results are highly overlapping because of low variation (CV range 0.01–0.02%) between runs.

3. Results

Pearson's correlation between LANDIS-II predictions at year 0 (i.e., 2010) and total live aboveground biomass (AGB$_{total}$) estimated from FIA

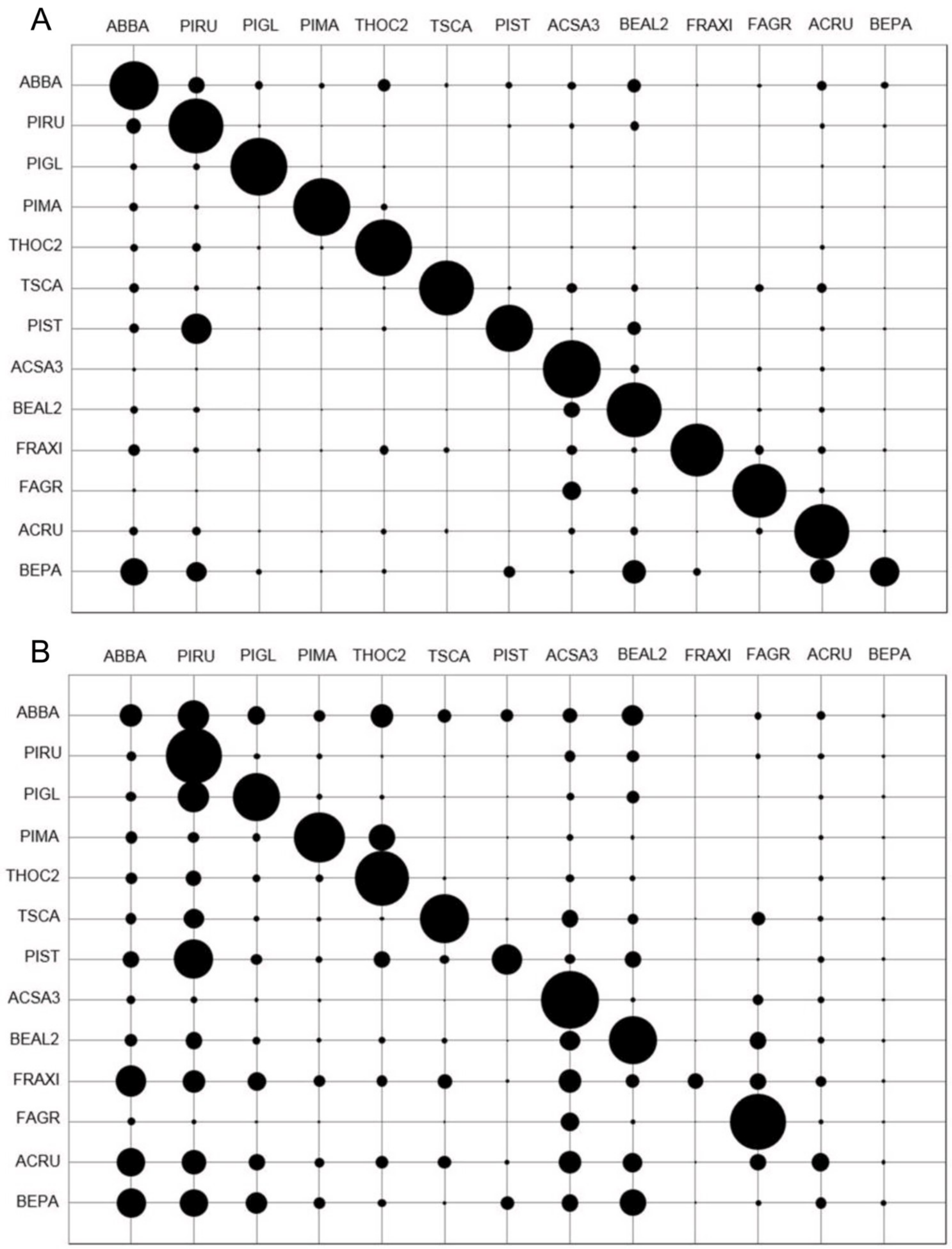


Fig. 4. Turnover in site dominance between all pairs of species[1] after A) 50 and B) 150 years without timber harvesting in the Acadian Forest Region of northern Maine. Size of the filled circle provides a relative measure averaged across 10 model runs; a larger circle indicates more site turnover from the species on the vertical axis to the species on the horizontal axis. For example, the circle at bottom left corner represents the turnover of sites dominated by paper birch (BEPA) in 2010 to dominance by balsam fir [1]Balsam fir (*Abies balsamea* ABBA), red spruce (*Picea rubens* PIRU), white spruce (*Picea glauca* PIGL), black spruce (*Picea mariana* PIMA), northern white cedar (*Thuja occidentalis* THOC2), eastern hemlock (*Tsuga canadensis* TSCA), eastern white pine (*Pinus strobus* PIST), sugar maple (*Acer saccharum* ACSA3), yellow birch (*Betula alleghaniensis* BEAL2), white ash (*Fraxinus americana* FRAXI), American beech (*Fagus grandifolia* FAGR), red maple (*Acer rubrum* ACRU), paper birch (*Betula papyrifera* BEPA).

field plots increased with area, achieving $\rho = 0.87$ at the intermediate scale of 87,408 ha (Table 1). At the scale of our study area, LANDIS- II estimated 262.06 Tg ca. 2010 based on initial forest conditions, which was within 0.04% of the $\text{AGB}_{\text{total}}$ estimated from FIA plot data for our study area (262.16 Tg). At the cell level, estimates of AGB ranged widely across our study area (233–14,884 g/m^2). Spatial patterns were generated by variation in forest age and dominant species composition (Fig. 2). Patches of lower AGB tended to occur in areas of regenerating forest (<40 years old), whereas patches of high AGB occurred in areas of residual or reserved mature forest. Species relative abundances estimated for the study area at year 0 using maps of species biomass from LANDIS-II were ±2% for all species compared to estimates from FIA plot data (Supplementary Table 2).

Simulations of forest growth without timber harvesting suggest that forest in our study area could accumulate twice as much live aboveground biomass within 50-60 years (Fig. 3). Beyond 2070 the simulated rate of accumulation slowed, with $\text{AGB}_{\text{total}}$ reaching a maximum of 629.4 Tg ca. 2130 before declining. Variability in projected estimates of $\text{AGB}_{\text{total}}$ was very low (CV range 0.01– 0.02%) between replicates and across intervals (Supplementary Table 3).

After 50 years without timber harvesting, projections suggest species would generally maintain their current patterns of site dominance (Fig. 4A), with the exception of paper birch (BEPA) and to a lesser extent white pine (PIST). Sites currently dominated by paper birch were projected to transition to more shade tolerant species, including balsam fir (ABBA), red spruce (PIRU), yellow birch (BEAL2), and red maple (ACRU). Approximately equal site turnover rates between balsam fir and red spruce were projected, in contrast to red spruce and white pine, for which red spruce was projected to gain dominance at many more sites. Other notable trends included increasing site dominance of sugar maple (ACSA3) and yellow birch at sites currently dominated by a variety of northern conifers and hardwoods. After 150 years without timber harvesting a greater magnitude of site turnover was projected, with patterns generally favoring more shade tolerant species (Fig. 4B). Site dominance by the less shade tolerant hardwoods (i.e., red maple, paper birch, and white ash (FRAXI)) was projected to decline. The decline in site

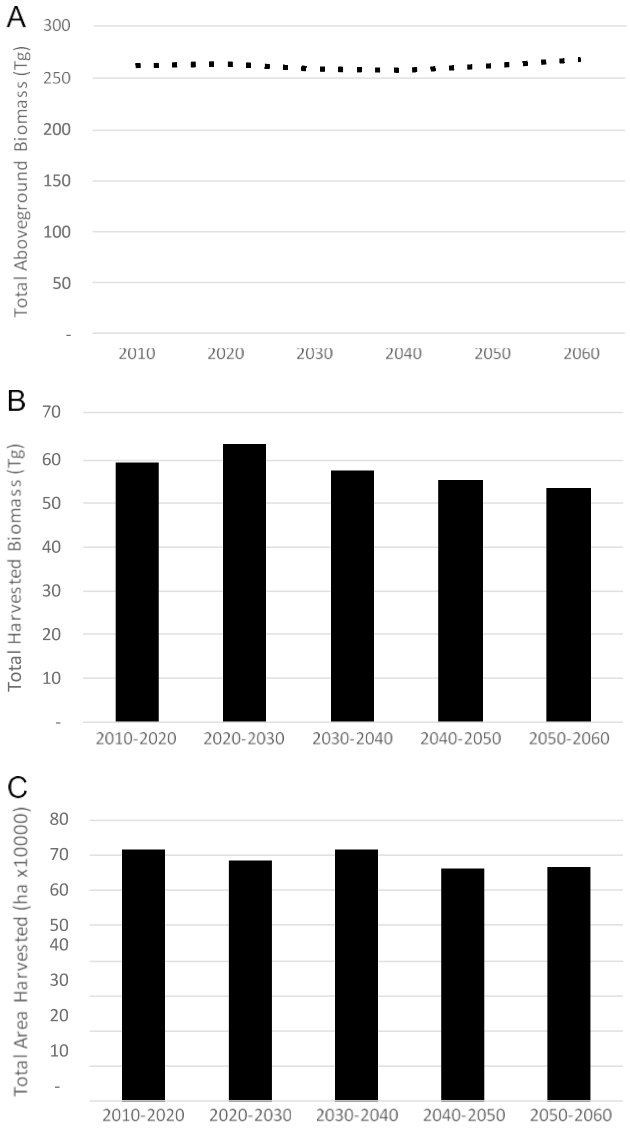


Fig. 5. Projected A) total live aboveground aboveground biomass (Tg) with timber harvesting 2010−2060, and associated projections of B) total harvested live aboveground biomass (Tg) and C) total harvested area (hectares) during each 10-year period between 2010 and 2060, averaged across 10 model runs. Note the complete set of 10 model runs are displayed in A, but lines are highly overlapping because of low variation (CV range 0.02−0.03%) between runs.

dominance by white pine was also projected to continue. Despite its high shade tolerance, maintenance of site dominance by balsam fir was projected to decline as sites transitioned to longer lived species, primarily red spruce. Nonetheless, turnover favoring balsam fir was projected to occur at sites currently dominated by a variety of species.

Emulating average landowner harvest rates, simulations suggested forest growth will generally replace biomass removals from harvesting. AGB_{total} was projected to be relatively stable at approximately ±2% of the initial estimate from 2010−2060 (Fig. 5A). Average g/m^2 of AGB increased 2.5% between 2010 and 2060. As with the no-harvest scenario, variability of AGB_{total} was very low (CV range 0.02−0.03%) between replicates and across intervals (Supplementary Table 4). Harvested biomass ranged from a maximum of 64 Tg during the second harvest period (2020−2030) to a minimum of 54 Tg during the last harvest period (2050-2060) (Fig. 5B; Supplementary Table 5). Harvested area simulated for each 10-year period averaged 685,482 ha (Fig. 5C) with limited variability (STD ± 22,684 ha or ±3.3%) across periods and runs (Supplementary Table 6), consistently lower than the 10-year target area of 768,379 ha.

Simulations suggested that continued timber harvesting would benefit specific species (Fig. 6) compared to the no harvest scenario after 50 years (Fig. 4A). Most notably, paper birch was projected to maintain site dominance to a greater degree, and many more sites were projected to transition to dominance by balsam fir or paper birch. Site dominance by red spruce was projected to increase at a variety of sites, but it was projected to be less successful maintaining dominance at sites where it is currently the most abundant. Species projected to be notably less successful at maintaining or gaining site dominance compared to the no harvest scenario included northern white cedar (THOC2), eastern hemlock (TSCA), and white ash. Although both maples benefitted from timber harvesting, turnover favored red maple to a greater degree than sugar maple.

Projections ultimately suggested that the cumulative effects of spatial interactions between timber harvesting and forest succession on species co-occurrence would be changes in the regional extent of forest types, including a loss of northern hardwood forest (Table 2). In 2010, the most prevalent forest type in our study area was mixed (28%); spruce-fir forest and maple-beech-birch forest each comprised 18% of the forested area. Both were broadly distributed across the study area, with localized spatial patterns associated with topography and landscape position (Fig. 7A). By 2060, the extent of maple-beech-birch forest was projected to decline 31%; in contrast, spruce-fir forest was projected to increase 7%. Maple-beech-birch mixed forest was also projected to decline (-12%) compared to an increase in spruce-fir mixed forest (33%), which expanded its footprint broadly, particularly along edges between spruce-fir and maple-beech-birch forest (Fig. 7B). Other hardwood forest was projected to increase 12%, whereas other conifer, which had the least extent ca. 2010, was projected to decline 53% by 2060.

4. Discussion

Spruce trees were once the dominant feature of Maine's forests and beyond (Cogbill et al., 2002). Witness tree data tells a clear story of the importance of spruce, which as a group were nearly twice as abundant as any other tree species statewide prior to the 1850s, and other long-lived conifers (e.g., eastern hemlock) and shade-tolerant hardwoods (e.g., yellow birch and American beech) (Barton et al., 2012). Since then the relative abundance of many of those species has changed considerably, with a general pattern of heavily-utilized species associated with late-successional forest decreasing in abundance. Our projections demonstrated that shifts in forest composition will be an ongoing consequence of contemporary timber harvesting in Maine.

In the absence of timber harvesting, forests in the northern AFR would begin to shift back towards their historic composition. With increasing shade, the less shade-tolerant hardwoods like red maple and paper birch would decline (Fig. 4), eventually outcompeted and replaced by northern hardwoods (sugar maple, yellow birch, or American beech) or northern conifers (balsam fir or spruce). Without harvesting pressure, the balance of site turnover between balsam fir and red spruce would eventually shift towards the longer-lived spruce. Although it is not as numerous as it once was, red spruce regeneration and growing stock are still relatively abundant and well-distributed across the landscape (McCaskill et al., 2011). Nonetheless, balsam fir is a highly aggressive competitor in this system and its abundance will likely remain elevated relative to presettlement for a considerable time given its wide distribution, slowing its replacement by species that were historically more abundant.

Under the considerably more likely scenario of ongoing timber harvesting, and assuming recent harvest rates and practices persist, forest composition will generally continue to shift away from presettlement conditions. Results support the conclusion of empirical studies in the AFR that higher disturbance intensity favors establishment of species better adapted to higher light conditions (Bataineh et al., 2013; Olson and Wagner, 2010). In this forest system, although pre-harvest

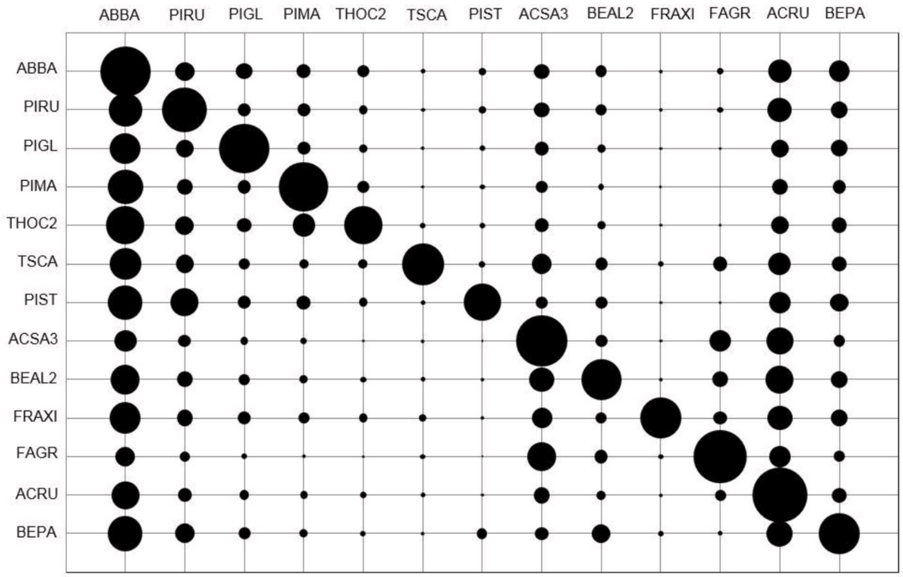


Fig. 6. Projected turnover in site dominance between all pairs of species after 50 years of timber harvesting (2010–2060) in the Acadian Forest Region of northern Maine. Size of the filled circle provides a relative measure of turnover from the species on the vertical axis to the species on the horizontal axis, averaged across 10 model runs. See Figure 4 for species codes and additional information.

Table 2
Area (ha) and percent of forested area (% forest) for each forest type ca. 2010 based on initial conditions and ca. 2060 from LANDIS-II projections of 50-years of timber harvesting, averaged across 10 model runs.

Forest type	2010 ha	% forest	2060 ha	% forest
Spruce-Fir	542,922	18%	581,351	19%
Spruce-Fir Mixed	428,214	14%	570,973	19%
Mixed	860,718	28%	827,087	28%
Maple-Beech-Birch	540,349	18%	373,864	12%
Maple-Beech-Birch Mixed	370,316	12%	330,974	11%
Other Hardwood	254,426	8%	285,171	9%
Other Conifer	77,309	3%	35,971	1%

canopy composition is generally the best, albeit still relatively weak, predictor of regeneration composition, within-stand variability is high and developmental pathways tend to migrate away from pre-harvest composition. In the context of our study, the 2.2% annual rate of landscape disturbance generated by timber harvesting across our study area is clearly high enough to favor species that are better adapted to regeneration and rapid growth in more open conditions compared to the 0.1% wind-driven rate of disturbance that characterizes the region's natural disturbance regime (Lorimer, 1977; Seymour et al., 2002). Our study further suggests that shifts in individual tree species distribution and abundance post-harvest will drive broad-scale changes in patterns of species co-occurrence and co-dominance. As a result, the positive feedbacks that reinforce self-replacement and the perpetuation of regional forest types may weaken. In this respect, the northern conifer type (i.e., spruce-fir) was more resistant than the northern hardwood type (i.e., maple-beech-birch), which was projected to decline by 31%. For the spruce-fir species, changes in species dominance were typically within group (e.g., balsam fir to spruce, not balsam fir to hardwood species), so did not result in a change of forest type. In contrast, northern hardwood species were more frequently replaced by species associated with a different forest type (e.g., balsam fir or red maple), driving changes away from the maple-beech-birch type (Table 2).

Notwithstanding changes in species abundance, our results suggest that timber harvesting will generally be sustainable in northern Maine. AGB was projected to be relatively stable 2010–2060 at ±2% of the initial estimate (Fig. 5); average g/m^2 of AGB increased 2.5% between 2010 and 2060. These results contrast with recent LANDIS-II projections by (Duveneck and Thompson, 2019) suggesting that removals from timber harvesting will exceed forest growth, causing a (14%) decline of average g/m^2 of AGB in Maine by 2060 under the current climate. One likely cause for the difference in the simulated effects of harvesting on AGB was the higher rate of annual harvest (~3.2%) as well as the higher rate of clearcutting as a percent of harvested area (45%) that Duveneck and Thompson (2019) projected for commercial forests owned by corporations in Maine, compared to our 2.2% and 4%, respectively. It is also important to note that a different LANDIS-II succession extension (PnET-Succession) was used, which may have resulted in lower projected growth rates relative to our projections using Biomass Succession (de Bruijn et al. 2014). Both the spatial and thematic resolution of the map of initial forest conditions Duveneck and Thompson (2019) used were also lower. The cell size of their input map was 250 m compared to our 30 m, and the number of initial communities in the area overlapping our study area was 2,257 compared to 9,273 in our initial communities map. LANDIS-II projections are almost certainly sensitive to these differences in input conditions, as was demonstrated by Liang et al. (2013) for LANDIS, which has important implications if projections are to meaningfully inform future place-based forest policy. Policy makers working from the assumption that future carbon stocks would be stable in the absence of additional stressors such as climate change or insect outbreaks can focus on addressing those stressors, rather than considering additional regulation of timber harvesting to ensure basic sustainability.

A common approach to producing the map of initial forest conditions required by LANDIS-II, which includes tree species and forest age for every cell, is nearest neighbor imputation (e.g., Gradient Nearest Neighbor (GNN)) using a reference dataset such as FIA plot data (e.g., Dijak, 2013; Duveneck et al., 2015; Scheller et al., 2008). Values are assigned to each pixel within the mapped area by averaging reference observations from a set of similar pixel locations, with similarity determined by spectral or environmental predictors. Nearest neighbor methods are convenient in that they can be used to populate pixels with an entire suite of observations obtained at reference plot locations, and as a result are able to produce reliable community-level outcomes (Henderson et al., 2014; Ohmann and Gregory, 2002). However, predictive accuracy for individual species can be low and subject to strong attenuation bias that causes considerable underestimation where

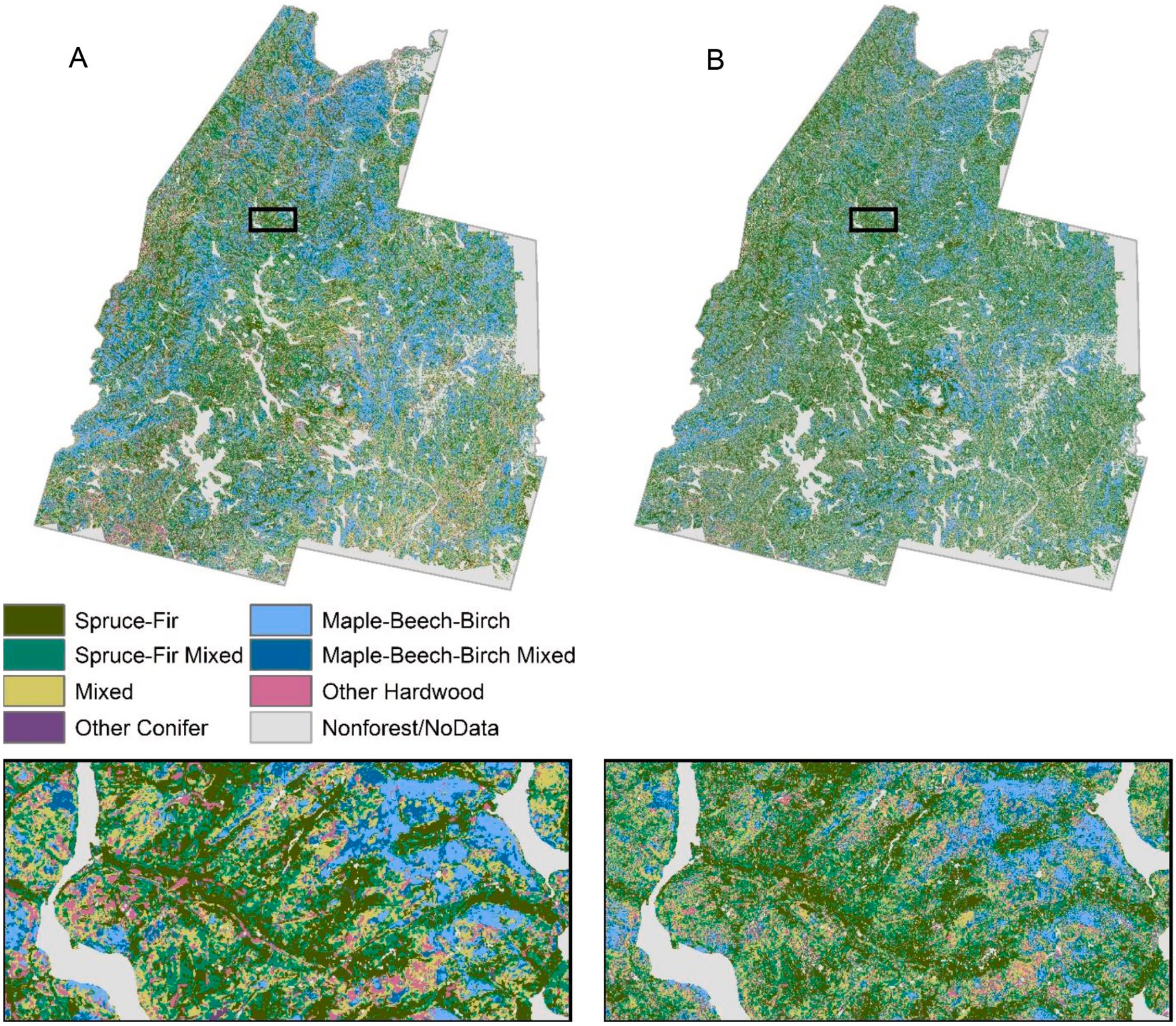


Fig. 7. Simulated distribution of major forest types A) ca. 2010 based on initial forest conditions, and B) ca. 2060 from an example run with timber harvesting. Inset areas (bold outlines) reference zoomed-in maps.

observed relative abundance is high and overestimation when relative abundance is low (Legaard et al., 2020). In comparison, the mapping strategy underlying our initialization map, which is based on a multi-objective machine learning algorithm, reduces the attenuation bias that leads to systematic error while simultaneously maintaining high overall accuracy. As demonstrated by Legaard et al. (2020), this approach is capable of achieving lower total error for individual species (9-44% reduction of RMSE relative to GNN) and much lower systematic error (40−69% reduction of systematic RMSE relative to GNN), while also reproducing observed frequencies of species dominance/codominance to a level approaching that of the GNN method (i.e., 6% maximum absolute difference between observed and predicted frequencies of dominance/codominance, compared to 4% for GNN). On the basis of maps generated using those methods, we were able to obtain estimates of initial biomass and species relative abundance for the study area from LANDIS-II that compared very well to FIA plot data. More importantly, our scaled comparison (Table 1) demonstrated that our AGB estimates are robust at scales relevant to landscape-scale forest management.

FLMs like LANDIS-II were designed to simulate forest dynamics as emergent properties of process interactions (Gustafson, 2013). Rather than being based on predetermined pathways that follow observed patterns of community assembly, empirical data are used to define relationships that drive tree growth and competition. The strength of a FLM lies in its lack of determinism and its ability to model ecological interactions in both space and time across large areas. As we observed, however, and has been previously noted (e.g., Thompson et al., 2011; Duveneck et al., 2014), outcome variability between replicates of a particular scenario tends to be low. With respect to simulations without harvesting, 150 years may not have been long enough for divergence to occur between runs given that our forest is predominantly mid-successional at present and many of the tree species are long-lived (Xu et al., 2009). We expected higher variability between replicates under the harvest scenario because of the added disturbance, particularly given the variation in annual harvest rate across owners (i.e., from <1% to 8%). The lack of variation (CV range 0.03−0.04%), however, suggests that there was a high degree of similarity in which stands were selected for harvest between runs, and little variability in which species established in a given harvested area. In effect, over the course of each model run, all forest available for harvest was harvested at some point. It is important to also note that simulated area harvested was also consistently lower (6−16% across runs) than our prescribed targets; thus, our projections should be considered optimistic. Having knowledge of the degree to which LANDIS-II simulations of harvesting adhered to prescriptions and produced intended outcomes is an important, but rarely reported detail for interpreting projection results, particularly when comparing outcomes from alternative forest management strategies.

Our goal was to model local, landscape, and regional forest dynamics across the large working forest of the northern AFR. Although our results were based on the best available information about timber harvesting rates and patterns in this region, projections may not represent the future land-use regime in a changing climate. Increasing CO_2 and a longer growing season are expected to boost forest productivity in the AFR (Wang et al., 2017; Duveneck and Thompson, 2019), but effects will vary by species, which may influence foresters' decisions about which species to target as growing stock. Nonetheless, because timber harvesting is the dominant disturbance factor regionally (Brown et al., 2018) and nationally (Harris et al., 2016), we saw value in an exclusive focus on land use, as others in our region have focused on projecting climate change and forest growth in the absence of land use (Duveneck et al., 2017). This also provided an opportunity to compare different study designs across a common area, which suggested important influences of input data resolution on projection outcomes and insights into the limits to which a forest landscape model can be used to inform forest managers and policy makers in a large commercial landscape.

In this study, we also did not consider other disturbances that may become increasingly important in the AFR, specifically forest insects. Eastern spruce budworm (*Choristoneura fumiferana* Clem.) is a native defoliator that infests Maine and Atlantic Maritime Canada on average every 30–50 years, causing widespread defoliation, growth reduction, and mortality of balsam fir and spruce trees (MacLean, 1980; Morin et al., 2007). Rapidly expanding patterns of defoliation in Quebec and increasing trap catches of spruce budworm moths in Maine suggest that outbreak conditions may emerge in the next few years. Dymond et al. (2010) projected that spruce budworm could cause the forests of eastern Quebec to switch from a carbon sink to a carbon source. Our future simulation studies will include the effects of spruce budworm, and potentially other native (e.g., Pine bark adelgid *Pineus strobi*) or emerging invasive defoliators (e.g., Hemlock wooly adelgid *Adelges tsugae*), in concert with the effects of climate change on tree productivity and establishment.

5. Conclusions

Our projections agreed with empirical studies (Bataineh et al., 2013; Olson and Wagner, 2010) indicating that species in our system which are better suited to more frequent or higher intensity disturbances (e.g., balsam fir, red maple, and paper birch) and which have become more abundant in recent decades (McCaskill et al., 2011) will continue to benefit from timber harvesting. As a result, broad-scale patterns of species co-occurrence will likely shift, challenging the persistence of important regional forest types such as northern hardwood forest characterized by sugar maple, yellow birch, and American beech. Forest management that promotes regeneration of long-lived species such as red spruce and sugar maple will benefit ecosystem stability in the AFR. Overall, we conclude that forest landscape models such as LANDIS-II when carefully parameterized and initialized can provide valuable information at relevant scales for working forests concerning their future resistance and resilience to changes in species composition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work was supported by the U.S. Carbon Cycle Science Program funded jointly by NASA and USDA National Institute of Food and Agriculture (2011-67003-30351), by the National Science Foundation Dynamics of Coupled Natural and Human Systems Program (DEB-1313688) and EPSCoR Program (RII-1920908), and by the Northeastern States Research Cooperative through funding made available by the USDA Forest Service. Confidential coordinates of Forest Inventory and Analysis (FIA) field plots were made available through a collaborative agreement with the USDA Forest Service Northern Research Station FIA Program (FS Agreement No. 2014-MU-11242305-055). We thank Elizabeth Burrill for assistance in obtaining and working with FIA spatial data. We also thank our two anonymous reviewers for their thoughtful comments.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2021.109657.

References

Aber, J.D., Ollinger, S.V., Federer, C.A., Reich, P.B., Goulden, M.L., Kicklighter, D.W., Melillo, J.M., Lathrop Jr., R.G., 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. Climate Research 5, 207–222.

Amatangelo, K.L., Fulton, M.R., Rogers, D.A., Waller, D.M., 2011. Converging forest community composition along an edaphic gradient threatens landscape-level diversity. Diversity and Distributions 17 (2), 201–213.

Amos-Binks, L.J., MacLean, D.A., Wilson, J.S., Wagner, R.G., 2010. Temporal changes in species composition of mixedwood stands in northwest New Brunswick: 1946–2008. Can. J. For. Res. 40 (1), 1–12.

Barton, A.M., White, A.S., Cogbill, C.V., 2012. The Changing Nature of the Maine Woods (Vol. 2). University of New Hampshire Press.

Bataineh, M., Kenefic, L., Weiskittel, A., Wagner, R., Brissette, J., 2013. Influence of partial harvesting and site factors on the abundance and composition of natural regeneration in the Acadian Forest of Maine. USA. Forest Ecology and Management 306, 96–106.

Bose, A.K., Weiskittel, A., Wagner, R.G., Kuehne, C., 2016. Assessing the factors influencing natural regeneration patterns in the diverse, multi-cohort, and managed forests of Maine, USA. Journal of Vegetation Science 27 (6), 1140–1150.

Boucher, Y., Arseneault, D., Sirois, L., Blais, L., 2009. Logging pattern and landscape changes over the last century at the boreal and deciduous forest transition in Eastern Canada. Landscape Ecology 24 (2), 171–184.

Briggs, R.D., Lemin Jr., R.C., 1992. Delineation of climatic regions in Maine. Can. J. For. Res. 22 (6), 801–811.

Brissette, J.C., 1996. Effects of intensity and frequency of harvesting on abundance, stocking and composition of natural regeneration in the Acadian forest of eastern North America. Silva Fennica 30, 301–314.

Brown, M.L., Canham, C.D., Murphy, L., Donovan, T.M., 2018. Timber harvest as the predominant disturbance regime in northeastern U.S. forests: effects of harvest intensification. Ecosphere 9 (3), e02062.

Canham, C.D., Rogers, N., Buchholz, T., 2013. Regional variation in forest harvest regimes in the northeastern United States. Ecol. Appl. 23 (3), 515–522.

Cogbill, C.V., Burk, J., Motzkin, G., 2002. The forests of presettlement New England, USA: spatial and compositional patterns based on town proprietor surveys. J. Biogeogr. 29 (10–11), 1279–1304.

de Bruijn, A., Gustafson, E.J., Sturtevant, B.R., Foster, J.R., Miranda, B.R., Lichti, N.I., Jacobs, D.F., 2014. Toward more robust projections of forest landscape dynamics under novel environmental conditions: Embedding PnET within LANDIS-II. Ecol. Modell. 287, 44–57.

Dijak, W., 2013. Landscape Builder: software for the creation of initial landscapes for LANDIS from FIA data. Computational Ecology and Software 3 (2), 17–25.

Duveneck, M.J., Thompson, J.R., 2019. Social and biophysical determinants of future forest conditions in New England: Effects of a modern land-use regime. Global Environmental Change: Human and Policy Dimensions 55, 115–129.

Duveneck, M.J., Thompson, J.R., Gustafson, E.J., Liang, Y., de Bruijn, A.M.G, 2017. Recovery dynamics and climate change effects to future New England forests. Landscape Ecology 32 (7), 1385–1397.

Duveneck, M.J., Thompson, J.R., Wilson, B.T., 2015. An imputed forest composition map for New England screened by species range boundaries. Forest Ecol. Manag. 347, 107–115.

Dymond, C.C., Neilson, E.T., Stinson, G., Porter, K., MacLean, D.A., Gray, D.R., Campagna, M., Kurz, W.A., 2010. Future Spruce Budworm Outbreak May Create a Carbon Source in Eastern Canadian Forests. Ecosystems 13 (6), 917–931.

Gould, P.J., Steiner, K.C., Finley, J.C., McDill, M.E., 2005. Developmental Pathways following the Harvest of Oak-Dominated Stands. Forest Science 51 (1), 76–90.

Gustafson, E.J., 2013. When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. Landscape Ecology 28 (8), 1429–1437.

Gustafson, EJ., Shifley, S.R., Mladenoff, D.J., Nimerfro, K.K., He, H.S., 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. Can. J. For. Res. 30 (1), 32–43.

Gustafson, E.J., Sturtevant, B.R., Shvidenko, A.Z., Scheller, R.M., 2011. Using landscape disturbance and succession models to support forest management. In: Li, C., Lafortezza, R., Chen, J. (Eds.), Landscape Ecology in Forest Management and Conservation. Springer, pp. 99–118.

Hanberry, B.B., Palik, B.J., He, H.S., 2013. Winning and losing tree species of reassembly in Minnesota's mixed and broadleaf forests. PLoS One 8 (4), e61709.

Harris, N.L., Hagen, S.C., Saatchi, S.S., Pearson, T.R.H., Woodall, C.W., Domke, G.M., Braswell, B.H., Walters, B.F., Brown, S., Salas, W., Fore, A., Yu, Y., 2016. Attribution of net carbon change by disturbance type across forest lands of the conterminous United States. Carbon Balance Manage. 11 (1), 24.

He, H.S., Mladenoff, D.J., Crow, T.R., 1999. Linking an ecosystem model and a landscape model to study forest species response to climate warming. Ecol. Modell. 114 (2), 213–233.

Henderson, E.B., Ohmann, J.L., Gregory, M.J., Roberts, H.M., Zald, H., 2014. Species distribution modelling for plant communities: stacked single species or multivariate modelling approaches? Appl. Veg. Sci. 17 (3), 516–527.

Legaard, K.R., 2018. New Approaches to Mapping Forest Conditions and Landscape Change from Moderate Resolution Remote Sensing Data across the Species-Rich and Structurally Diverse Atlantic Northern Forest of Northeastern North America. University of Maine, Orono, Maine. PhD.

Legaard, K.R., Sader, S.A., Simons-Legaard, E.M., 2015. Evaluating the impact of abrupt changes in forest policy and management practices on landscape dynamics: analysis of a Landsat image time series in the Atlantic Northern Forest. PLoS One 10 (6), e0130428.

Legaard, K., Simons-Legaard, E., Weiskittel, A., 2020. Multi-Objective Support Vector Regression Reduces Systematic Error in Moderate Resolution Maps of Tree Species Abundance. Remote Sensing 12 (11), 1739.

Liang, Y., He, H.S., Fraser, J.S., Wu, Z., 2013. Thematic and spatial resolutions affect model-based predictions of tree species distribution. PLoS One 8 (7), e67889.

Lorimer, C.G., 1977. The Presettlement Forest and Natural Disturbance Cycle of Northeastern Maine. Ecology 58 (1), 139–148.

Lorimer, C.G., White, A.S., 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. Forest Ecol. Manag. 185 (1), 41–64.

MacLean, D.A., 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: a review and discussion. For. Chron. 56 (5), 213–221.

Maine Forest Service, 2020. 2018 Silvicultural Activities Report. Department of Agriculture, Conservation and Forestry, Maine Forest Service, Forest Policy and Management Division, Augusta, Maine, USA.

McCaskill, G.L., McWilliams, W.H., Barnett, C.J., Butler, B.J., Hatfield, M.A., Kurtz, C.M., Morin, R.S., Moser, W.K., Perry, C.H., Woodall, C.W., 2011. Maine's forests 2008. Resour. Bull. NRS- 48. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station.

McWilliams, W.H., Butler, B.J., Caldwell, L.E., Griffith, D.M., Hoppus, M.L., Laustsen, K. M., Lister, A.J., Lister, T.W., Metzler, J.W., Morin, R.S., Sader, S.A., Stewart, L.B., Steinman, J.R., Westfall, J.A., Williams, D.A., Whitman, A., Woodall, C.W., 2005. The forests of Maine: 2003. Resour. Bull. NE-164. US Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA.

Messier, C., Bauhus, J., Doyon, F., Maure, F., Sousa-Silva, R., Nolet, P., Mina, M., Aquilué, N., Fortin, M.-J., Puettmann, K., 2019. The functional complex network approach to foster forest resilience to global changes. Forest Ecosystems 6 (1), 21.

Mladenoff, D.J., 2004. LANDIS and forest landscape models. Ecol. Modell. 180 (1), 7–19.

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

Mladenoff, D.J., Host, G.E., Boeder, J., Crow, T.R., 1996. LANDIS: A spatial model of forest landscape disturbance,succession and management. In: Goodchild, M.F., Seyaert, L.T., Parks, S. (Eds.), GIS and Enviornmental Modeling: Progress and Research Issues. GIS World Books, pp. 175–180.

Morin, H., Jardon, Y., Gagnon, R., 2007. Relationship between spruce budworm outbreaks and forest dynamics in eastern North America. Plant Disturbance Ecology. Elsevier, pp. 555–577.

Mosseler, A., Lynds, J.A., Major, J.E., 2003. Old-growth forests of the Acadian Forest Region. Environmental Review 11 (S1), S47–S77.

Ohmann, J.L., Gregory, M.J., 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest-neighbor imputation in coastal Oregon, USA. Can. J. For. Res. 32 (4), 725–741.

Ollinger, S.V., Smith, M.-L., 2005. Net Primary Production and Canopy Nitrogen in a Temperate Forest Landscape: An Analysis Using Imaging Spectroscopy, Modeling and Field Data. Ecosystems 8 (7), 760–778.

Olson, M.G., Wagner, R.G., 2010. Long-term compositional dynamics of Acadian mixedwood stands under different silvicultural regimes. Can. J. For. Res. 40 (10), 1993–2002.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on Earth. Bioscience 51, 933–938.

Rehfeldt, G.E. (2006). A Spline Model of Climate for the Western United States. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA.

Rice, B., Wagner, R.G., Weiskittel, A., 2012. Residual conditions of 50 partially harvested stands in northern Maine. University of Maine Cooperative Forestry Research Unit.

Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J., Mladenoff, D.J., 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecol. Modell. 201 (3), 409–419.

Scheller, R.M., Mladenoff, D.J., 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. Ecol. Modell. 180 (1), 211–229.

Scheller, R.M., Van Tuyl, S., Clark, K., Hayden, N.G., Hom, J., Mladenoff, D.J., 2008. Simulation of forest change in the New Jersey Pine Barrens under current and pre-colonial conditions. Forest Ecol. Manag. 255 (5), 1489–1500.

Seymour, R.S., 1995. The northeastern region. Regional Silviculture of the United States 3, 31–79.

Seymour, R.S., White, A.S., Philip, G.M., 2002. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. Forest Ecology and Management.

Simons-Legaard, E., Legaard, K., Weiskittel, A., 2015. Predicting aboveground biomass with LANDIS-II: A global and temporal analysis of parameter sensitivity. Ecol. Modell. 313, 325–332.

Taylor, A.R., Chen, H.Y.H., Van Damme, L., 2009. A Review of Forest Succession Models and Their Suitability for Forest Management Planning. Forest Science 55 (1), 23–36.

Thompson, J.R., Foster, D.R., Scheller, R., Kittredge, D., 2011. The influence of land use and climate change on forest biomass and composition in Massachusetts, USA. Ecological Applications: A Publication of the Ecological Society of America 21 (7), 2425–2444.

Wang, W.J., He, H.S., Thompson, F.R., Fraser, J.S., Dijak, W.D., 2017. Changes in forest biomass and tree species distribution under climate change in the northeastern United States. Landscape Ecology 32 (7), 1399–1413.

Ward, B.C., Mladenoff, D.J., Scheller, R.M., 2005. Simulating Landscape-Level Effects of Constraints to Public Forest Regeneration Harvests due to Adjacent Residential Development in Northern Wisconsin. Forest Science 51 (6), 616–632.

Xu, C., Gertner, G.Z., Scheller, R.M., 2009. Uncertainties in the response of a forest landscape to global climatic change. Global Change Biol. 15 (1), 116–131.