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Timber harvest as the predominant disturbance regime in northeastern U.S. forests: effects of harvest intensification

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Citation: Brown, M. L., C. D. Canham, L. Murphy, and T. M. Donovan. 2018. Timber harvest as the predominant disturbance regime in northeastern U.S. forests: effects of harvest intensification. Ecosphere 9(3):e02062. 10.1002/ecs2.2062

Abstract. Harvesting is the leading cause of adult tree mortality in forests of the northeastern United States. While current rates of timber harvest are generally sustainable, there is considerable pressure to increase the contribution of forest biomass to meet renewable energy goals. We estimated current harvest regimes for different forest types and regions across the U.S. states of New York, Vermont, New Hampshire, and Maine using data from the U.S. Forest Inventory and Analysis Program. We implemented the harvest regimes in SORTIE-ND, an individual-based model of forest dynamics, and simulated the effects of current harvest regimes and five additional harvest scenarios that varied by harvest frequency and intensity over 150 yr. The best statistical model for the harvest regime described the annual probability of harvest as a function of forest type/region, total plot basal area, and distance to the nearest improved road. Forests were predicted to increase in adult aboveground biomass in all harvest scenarios in all forest type and region combinations. The magnitude of the increase, however, varied dramatically—increasing from 3% to 120% above current landscape averages as harvest frequency and intensity decreased. The variation can be largely explained by the disproportionately high harvest rates estimated for Maine as compared with the rest of the region. Despite steady biomass accumulation across the landscape, stands that exhibited old-growth characteristics (defined as ≥300 metric tons of biomass/hectare) were rare (8% or less of stands). Intensified harvest regimes had little effect on species composition due to widespread partial harvesting in all scenarios, resulting in dominance by late-successional species over time. Our analyses indicate that forest biomass can represent a sustainable, if small, component of renewable energy portfolios in the region, although there are tradeoffs between carbon sequestration in forest biomass and sustainable feedstock supply. Integrating harvest regimes into a disturbance theory framework is critical to understanding the dynamics of forested landscapes, especially given the predominance of logging as a disturbance agent and the increasing pressure to meet renewable energy needs.

Key words: biomass energy; disturbance regimes; forest composition; forest structure; harvest regimes; logging; northeastern United States.

Received 26 April 2017; revised 18 September 2017; accepted 25 September 2017. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

Harvesting is the leading source of canopy tree mortality in forests of the northeastern United States. It comprises more than half of all mortality (on a volume basis), making logging the predominant disturbance—natural or anthropogenic—affecting forest ecosystems in the region (Canham et al. 2013). Current harvest regimes are dominated by partial harvesting (Canham et al. 2013) in contrast to previous decades in which clearcutting was the most common silvicultural system (Kelty and D'Amato 2006, Masek et al. 2011).

Classical disturbance theory was developed to describe natural disturbances (Pickett and White 1985), but it is also a useful framework for studying anthropogenic disturbances such as logging (Oliver and Larson 1996, Seymour et al. 2002). As with natural disturbances like windthrow and fire, logging varies widely in terms of frequency and intensity. For instance, low-intensity wind storms occur at much higher frequencies (decades) than catastrophic events (centuries to millennia; Canham and Loucks 1984), just as low-intensity logging occurs at higher frequencies than clearcutting (Seymour et al. 2002, Canham et al. 2013). Logging and natural disturbances can both be highly selective in mortality by species and size (Canham et al. 2001, 2013, Papaik and Canham 2006). In a recent paper, Canham et al. (2013) quantified current harvest regimes in terms of logging frequency and intensity by species and size within the northeastern United States. The statistical characterization of the harvest regimes represented the aggregate of stand-scale management across the landscape, just as natural disturbance regimes are characterized by the cumulative effect of individual disturbances (Pickett et al. 1989, Seymour et al. 2002).

Importantly, logging also differs from natural disturbance. Foremost, logging is driven by a wide range of socioeconomic factors and human decisions (Puettmann et al. 2009, Thompson et al. 2017). There are more than 2 million forest landowners in the northeastern United States (USDA Forest Service 2016*b*), and each landowner decides whether, when, and how to manage their forests. Roughly half of current owners have logged their forests during their tenure for reasons including improving remaining stock, personal use of wood, increasing recreation and hunting opportunities, and financial gain (USDA Forest Service 2016*b*). Logging regimes can also vary dramatically over short periods of time in response to market forces. For example, federal timber sale restrictions in the western United States accounted for an increase in private forest land harvest in the southern United States during the late 1980s and 1990s (Wear and Murray 2004), and harvest rates in the northeastern United States dropped significantly in response to the economic downturn in 2008.

Recent calls for increasing the use of forest biomass as a feedstock for the renewable energy industry underscore the importance of examining the effects of variation in the frequency and intensity of harvest on landscape-scale forest structure and composition. Many states are setting progressive renewable energy goals to increase energy independence and reduce carbon emissions (Energy Independence and Security Act 2007, Biomass Energy Resource Center 2013, Energy Information Administration 2015). For example, Vermont has set a goal of meeting 90% of the state's energy needs through renewables by the year 2050 (Vermont Comprehensive Energy Plan 2016), while New York aims to meet 50% of its electricity needs by the year 2030 from renewable energy (New York State Energy Plan 2015). New Hampshire is the first state in the region to require that a portion of its Renewable Portfolio Standard is met through thermal energy, and expects to increase forest bioenergy to achieve that goal (Hunter 2014). Despite these goals, the benefits of increasing timber harvest to meet energy needs are still being debated (IPCC 2014).

How would intensification of harvest affect both biomass feedstock supply and forest structure and composition in the region? Preliminary assessments by all four northern forest states (New York, Vermont, New Hampshire, and Maine), which are collectively 71% forested, have concluded that more intensive harvest regimes could yield additional sustainable feedstock supply (Maine Forest Service 2010, New Hampshire Department of Resources and Economic Development 2010, New York State Department of Environmental Conservation 2010, Vermont Agency of Natural Resources 2010). More detailed forest bioenergy assessments in different portions of this region have resulted in similar findings; however, the predicted amount of feedstock that can be harvested sustainably varies considerably due to differing assumptions concerning technology, forest utilization, market forces, and available forest land base (Sherman 2007, Castellano et al. 2009, Biomass Thermal Energy Council 2010, Buchholz et al. 2011, Wojnar 2013).

These analyses, however, typically represent static analyses based on growth and yield from the current mix of forests within the landscape of a defined region, without considering the effects of changes in harvest regimes on the future composition, structure, and productivity of the forest landscape. In the analyses presented here, we use data from the U.S. Forest Service's Forest Inventory and Analysis Program (FIA; USDA Forest Service 2016*a*) to characterize current harvest regimes for different regions and forest types across the northern forest states of New York, Vermont, New Hampshire, and Maine. The harvest regimes are then implemented in SORTIE-ND, an individual-based model of forest dynamics (www.sortie-nd.org), to explore the effects of the current harvest regimes and five alternative harvest scenarios over the next 150 yr. The model is initialized using current inventory data from existing FIA plots, which allows us to develop regional-scale predictions of the consequences of different harvest scenarios for forests in the region. Our analyses thus address two broad questions: (1) "What are the current harvest regimes in different regions and forest types within New York, Vermont, New Hampshire, and Maine?" and (2) "What are the effects of harvest intensification on biomass feedstock supply and long-term forest structure and composition over the next 150 yr?"

METHODS

Study area

The study area includes all forest land in the states of New York, Vermont, New Hampshire, and Maine, which covers approximately 71% of the four-state region. Forest Inventory and Analysis defines forest land as land that has at least ten percent live crown cover of trees of any size or past evidence of such a condition (USDA Forest Service 2016*a*). Forest types in the region range from high elevation spruce–fir forests to oak–hickory forests; northern hardwood–conifer forests are the most widespread forest type. The temperate climate is diverse and characterized by warm summers and cold, frozen winters. Boreal conditions to the north and coastal conditions to the east influence temperature and precipitation patterns. Land ownership patterns are dominated by private woodland owners (80% of forest land), and while most of these owners are non-corporate (70%), industrial owners retain significant acreage particularly in Maine (Thompson et al. 2017).

Analysis of regional variation in forest harvest regimes

Our analysis of regional variation in northern forest harvest regimes is an extension of statistical models developed by Canham et al. (2013). We used data from FIA plots from New York, Vermont, New Hampshire, and Maine that were censused at least two times using the new national standard plot design (Woudenberg et al. 2010) and were available for harvest, meaning not legally protected according to either FIA records or a more thorough secured lands database compiled by The Nature Conservancy (n = 4582; Table 1; Anderson and Olivero Sheldon 2011). Each FIA plot is classified by forest type; we grouped the plots into five main forest types for analysis: aspen–birch, bottomland, northern hardwood–conifer, oak–hickory, and spruce–fir. Because evidence suggests harvest rates in Maine are greater than the rest of the study area (Buchholz et al. 2011, Canham et al. 2013), we divided northern hardwood–conifer forests into two regions: Maine and a combined region of New York, Vermont, and New Hampshire. This resulted in six total forest type and region combinations.

For each of the six forest type/regions, we quantified two components of the harvest regime: (1)

Table 1. Characteristics of the forest inventory and analysis plots (USDA Forest Service) used to initialize SORTIE-ND model runs (n = 5000).

State	Total plots	Aspen–Birch	Bottomland	Northern Hardwood–Conifer	Oak–Hickory	Spruce–Fir	Average remeasurement period (year)	Percent protected plots
ME	2564	311	55	1225	103	870	4.96	3.79
NH	396	20	10	256	86	24	6.50	5.30
NY	1551	64	127	983	307	70	7.97	15.23
VT	489	31	9	391	21	37	6.33	12.47

the annual probability that a plot was harvested, and (2) the total amount of basal area removed (BAR), if a plot was harvested. In the simplest statistical model, the annual probability of harvest and the fraction of BAR, if harvested, were assumed to vary solely as a function of the forest type/region and stand basal area. Following Canham et al. (2013), we described the probability that a plot was harvested during a census interval as:

$$\mathrm{Prob}\left(\mathrm{harvest}_{ij}\right) = 1 - \left[a_j\, e^{-m_j X_{ij}^{b_j}}\right]^{N_i} \tag{1}$$

where X_{ij} was adult tree basal area (m^2/ha) at the beginning of the census interval in the ith plot of the jth forest type/region, N_i was the census interval (in years) for that plot, and a_j, m_j, and b_j were estimated forest type/region-specific parameters.

The mean percent of BAR if a plot was logged during the census interval was also fit using an exponential model:

$$\mathrm{BAR}_{ij} = \alpha_j e^{-\mu_j X_{ij}{}^{\beta_j}} \tag{2}$$

where again X_{ij} was adult tree basal area (m^2/ha) at the beginning of the census interval in the ith plot of the jth forest type/region, and α_j, μ_j, and β_j were estimated forest type/region-specific parameters. The β_j parameter allows a flexible form, but tests indicated that the data were best fit with a simple negative exponential form in which the β_j parameter was dropped.

There are clearly many other factors that influence landowner decisions whether to harvest, and with what intensity or silvicultural system (Butler et al. 2010). We tested a number of alternate models in which terms in Eqs. 1 and 2 were modified to take into account a suite of socioeconomic and biophysical aspects of the plot location. These included (1) distance to the nearest improved road (as measured in feet by seven classes defined by FIA: ≤100, 101–300, 301–500, 501–1000, 1001–2640, 2641–5280, and >5280), (2) local population density at the county or smaller census tract scale, (3) land protection status, specifically presence of an easement that prevented development but allowed resource extraction, and (4) parcel size. Both land protection status and parcel size were assessed for a subset of the FIA plots, using a data layer compiled by The Nature Conservancy that covered roughly two-thirds of the region. Details of the modifications to test effects of population density, land protection status, and parcel size are given in Appendix S2. Based on visual examination of the data, road distance altered the probability of harvest but not the intensity when harvested. Thus, the model incorporating road distance replaced the intercept parameter a_j in Eq. 1 with a vector of seven parameters for each forest type/region, representing the seven road distance classes. Our strategy for model comparison was to first examine raw data to determine whether there was variation in either harvest frequency or intensity as a function of any one of these factors, and then to test alternate models in which a factor was incorporated in one or more of the terms in the model.

As in Canham et al. (2013), the functions for probability of harvest and intensity if harvested were fit simultaneously using maximum-likelihood methods. The analysis is effectively a mixture of a Bernoulli trial (whether or not a plot was harvested), and a gamma-distributed likelihood function to characterize the percent of BAR, if harvested. We solved for the maximum-likelihood values of the parameters for both parts of the model using global optimization in the *likelihood* package in R version 3.1.1 (R Core Team 2014, Murphy 2015).

Development and implementation of alternate harvest regime scenarios

We developed six harvest scenarios that varied in magnitude and frequency of harvest (Table 2). The first scenario represents the current harvest regime characterized by the analyses described above, without any influence of climate change (current harvest). Given the inevitability of climate change, all other scenarios incorporate a nominal climate change based on regional climate assessments and IPCC scenarios (Horton et al. 2014). The climate change scenarios assumed that mean annual temperature increased linearly 3°C over the next 100 yr (and then stabilized), with a 10% increase in total annual precipitation over the same time period (Appendix S1). The second scenario is the current harvest regime with this climate change (current harvest + climate). The third scenario increases average harvest intensity by 50% (current harvest + climate + intensity). The fourth scenario increases the frequency of harvests by 75%, keeping the current distribution of harvest intensity (current harvest + climate + frequency).

Table 2. Harvest scenario descriptions.

Harvest scenario name	Harvest scenario definition
Current harvest	The current harvest regime characterized as a function of forest type/region, total plot basal area, and distance to the nearest improved road
Current harvest + climate	The current harvest regime plus a change in climate conditions that includes a 3°C increase in mean annual temperature and a 10% increase in total annual precipitation over the next 100 yr
Current harvest + climate + intensity	The current harvest regime plus climate change and a 50% increase in average harvest intensity
Current harvest + climate + frequency	The current harvest regime plus climate change and a 75% increase in harvest frequency
Current harvest + climate + intensity + frequency	The current harvest regime plus climate change, a 50% increase in average harvest intensity, and a 100% increase in harvest frequency
No harvest	A no harvest scenario plus climate change

The fifth scenario increases average harvest intensity by 50% and harvest frequency by 100% (current harvest + climate + intensity + frequency). For reference, a sixth scenario included no harvests (no harvest).

To increase the frequency of harvest over current levels, we adjusted the a and m parameters in Eq. 1 for each forest type/region and road distance category as follows:

$$a' = a - (x \times (1 - a)) \qquad m' = m \times (1 + x)$$

where x is the proportion by which to increase harvest (e.g., 0.75 in the case of a 75% increase in harvest frequency). To increase the average intensity of a harvest regime, we shifted the observed distribution of harvest intensity by forest type/region upwards so that the average harvest intensity increased by the desired amount, but the approximate shape of the distribution of harvest intensity was maintained (details in Appendix S1).

Simulation of forest dynamics with SORTIE-ND

We implemented the six harvest scenarios in SORTIE-ND (Coates et al. 2003, Uriarte et al. 2009, Forsyth et al. 2015), a spatially explicit individual-tree forest stand model that tracks the recruitment, growth, and mortality of all individual seedlings, saplings, and adult trees over time. The model has been parameterized from FIA data for the 50 most common tree species in the eastern United States (Canham and Murphy 2016*a*, *b*, 2017). Only 30 of the species are common in our study region and were used in our simulations (Appendix S1).

The structure of the model, including details on all behaviors in the model, and the statistical analyses used to parameterize behaviors for each of the species are described in Appendix S1. A single scenario consists of 5000 separate runs of the model, with each run representing the predicted dynamics of a 4-ha stand initialized using the current structure and composition of one of 5000 randomly selected FIA plots within the study region (Fig. 1). Because FIA plots are themselves a randomly selected representative sample of forest land, output from the model, in aggregate, can be considered representative of the expected changes in the condition in forests across the landscape. The attributes of the FIA plots (e.g., state, forest type) can also be used to stratify and interpret variation in model predictions. Seedlings, saplings, and adult trees from the individual FIA plots are counted and categorized by species and size class and scaled to number per hectare to initialize the 5000 individual SORTIE-ND runs (Fig. 1a). Each plot in every scenario except current harvest is assigned the climate change regime described above. Current mean annual temperature and precipitation data for each plot were extracted using bilinear interpolation from 800-m resolution PRISM climate data (Parameter-elevation Regression on Independent Slopes Model; http://www.prism.oregonstate.edu/) using true plot locations obtained under a security memorandum with the U.S. Forest Service. The climate data are combined with data on topography (for solar radiation calculations) and soil water storage capacity (from USDA soil databases) to calculate annual water deficits for each plot in each year. Given the environmental conditions of each plot over time, SORTIE-ND then implements a sequence of behaviors, including the harvest

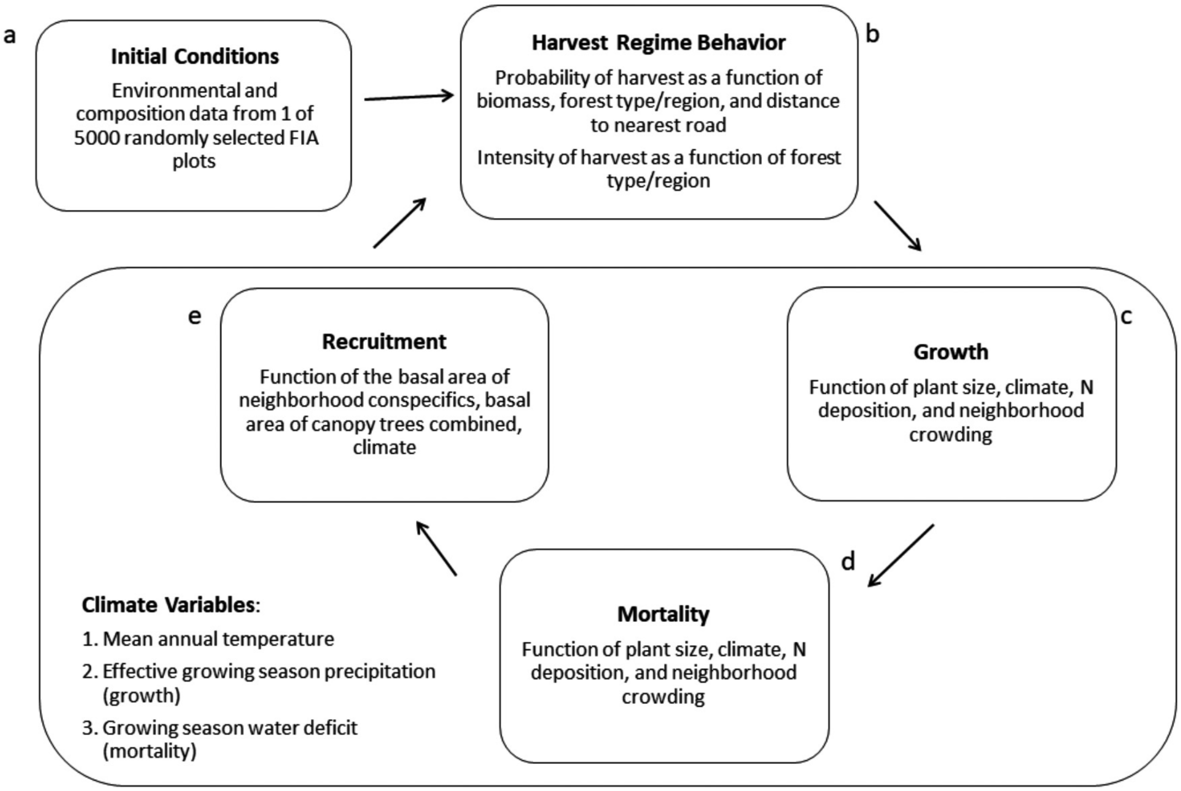

Fig. 1. Schematic diagram of the SORTIE-ND forest simulation model. A detailed description of the model structure and parameterization is provided in Appendix S1.

regime (described above; Fig. 1b), tree growth (Fig. 1c), adult and sapling natural mortality (Fig. 1d), and seedling recruitment (Fig. 1e), and outputs detailed metrics on stand structure and composition, as well as harvest rates by species and size, annually for 150 yr.

*Growth.—*Individuals that are not harvested in a timestep grow according to plot environmental and biotic conditions. Adult and sapling diameter growths are calculated as the average potential growth a tree can attain (cm/year), adjusted by several climate and neighborhood competition variables that limit tree growth (Fig. 1c). Tree size (Canham et al. 2006, Kunstler et al. 2009), precipitation, temperature, crowding (Canham et al. 2006), and nitrogen deposition (Thomas et al. 2010) are all factors that have the potential to limit adult and sapling growth, depending on species (details in Appendix S1). Parameter values are reported in Canham and Murphy (2016*a*) and based on empirical analyses of FIA data. There is no direct measurement of seedling growth in FIA data so sapling growth rates are applied to seedlings as well.

*Natural mortality.—*There are three different natural mortality behaviors that apply to different tree age classes: (1) adult and sapling mortality, (2) seedling mortality, and (3) size-dependent large tree mortality (which increases mortality in very large trees; Fig. 1d). Adult and sapling mortality is a function of climate, neighborhood competition, and nitrogen deposition, where the potential survival for each individual is reduced by variables that were observed to significantly reduce survivorship in analysis of FIA data, including tree size, soil water deficit, temperature, crowding, and nitrogen deposition (Canham and Murphy 2017). The seedling mortality behavior applies to seedlings of all species and is a function of mean annual temperature, soil water deficit, and total adult basal area within a 10 m radius circle (details in Appendix S1). All parameter values are derived from empirical analyses of FIA data (Canham and Murphy 2016*a*, *b*, 2017). Lastly, a size-dependent logistic mortality function imposes an increased mortality in very large trees. This is necessary because FIA data contain too few large trees to estimate mortality rates for large trees (Canham and Murphy 2017).

*Recruitment.—*Seedling recruitment is spatially explicit in the model and is a function of the total basal area of conspecific adult trees within a 10 m radius neighborhood. The recruitment functions were parameterized using FIA data (Canham and Murphy 2016*b*). SORTIE-ND then applies a temperature-dependent colonization function to allow for establishment of seedlings when no adults are currently present in the plot (e.g., due to bath rain of seeds where no parents are present; Fig. 1e; details in Appendix S1).

Results

Analysis of regional variation in forest harvest regimes

The basic statistical model for the harvest regime characterized the annual probability of harvest and the intensity of harvest each as a function of forest type/region and total plot basal area. Of the four socioeconomic predictors examined, there was only strong support for including distance to the nearest improved road in the final model (Appendix S2). The average annual probability of harvest increased steadily with increasing plot basal area across all forest types/regions (Fig. 2A). Northern hardwood–conifer forests in Maine had the highest probability of annual harvest, followed by aspen–birch and spruce–fir forests, both of which are located predominantly in Maine. Northern hardwood–conifer forests in the New York, Vermont, and New Hampshire region were harvested at less than half of the frequency of the same forest type in Maine (Fig. 2A). Every forest type had a greater probability of harvest near improved roads (<100 feet) with one exception (Fig. 3). Bottomland forests were slightly more likely to be harvested at very large distances from roads (>1 mile) vs. small distances from roads (<100 feet). The annual probability of logging approximately tripled for the Maine region of northern hardwood–conifer forests as the distance to the nearest road decreased from 0.5 miles to <100 feet (ranging from 4% to 12% in Maine; Fig. 3).

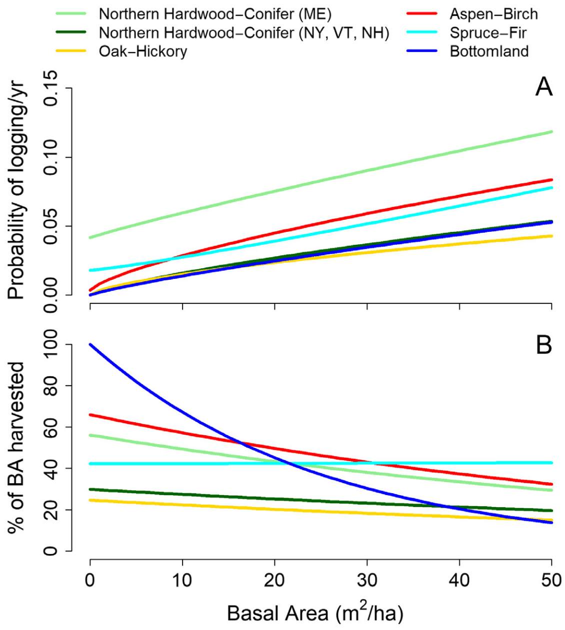

Fig. 2. (A) Estimated annual probability that a plot is harvested, and (B) estimated percentage of basal area removed as a function of total stand basal area for six forest type/regions, shown at 300–500 feet from the nearest road.

Partial harvesting predominated in all forest types/regions. When a stand was logged, the fraction of BAR (at a given distance from the nearest road) was predicted to be nearly constant across stands with a wide range of basal area (Fig. 2B). The observed distributions of harvest intensity showed oak–hickory forests and northern hardwood–conifer forests in New York, Vermont, and New Hampshire were primarily harvested at very low intensities, whereas the percent of BAR varied less in other forest types (Fig. 4).

Local population density, land protection (easement) status, and parcel size were omitted from the harvest regimes implemented in the simulations because they either did not improve model fit relative to model complexity (Appendix S2), or the data were insufficient for robust parameter estimates (as indicated by very large support intervals). There was a weak effect of increasing local population density in census tracts on reducing intensity of harvest in northern hardwood–conifer forests only, but no effect on frequency of harvest in any of the forest types (Appendix S2). There were sufficient numbers of plots to test for

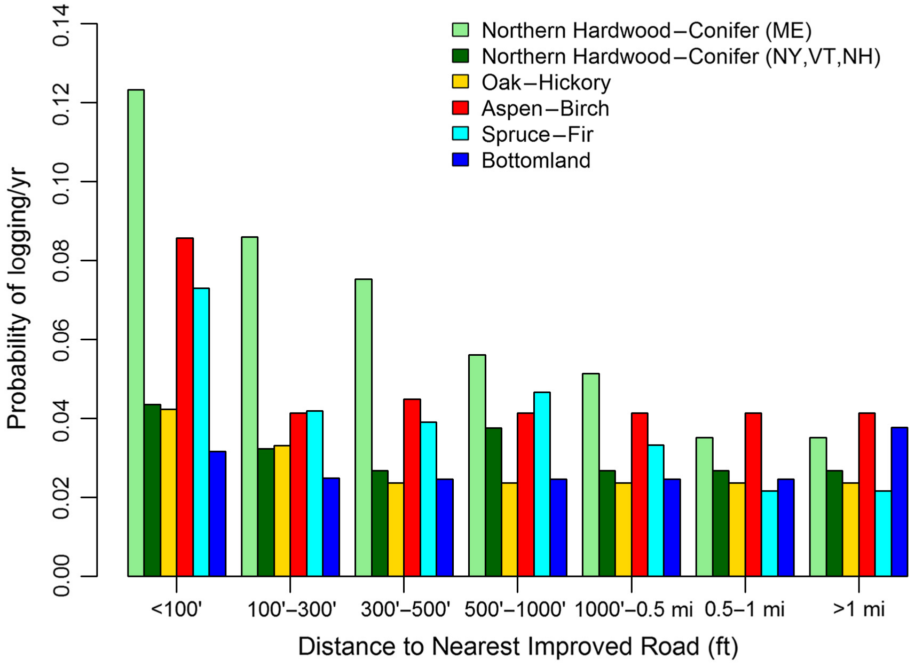

Fig. 3. Estimated annual probability of harvest as a function of distance to nearest improved road for six forest type/regions, shown for a stand with 20-m^2/ha basal area.

an effect of land protection status in only the spruce–fir and northern hardwood–conifer forest types. Twenty-five percent of the plots in spruce–fir forests were under some form of easement, but a model that estimated separate parameters for easement plots was not superior to the simpler model that ignored protection status (Akaike Information Criterion; AIC = 3410 vs. AIC = 3397 for the simpler model). Only 18% of plots in northern hardwood–conifer forests were under some form of easement. A model that estimated separate frequency and intensity of harvest for easement vs. non-easement lands was a very marginal improvement over the simpler model (ΔAIC = 1.07). Plots on easement lands were predicted to have slightly higher average fractions of BAR in a harvest, across the entire range of plot basal area, but the frequency of harvest was predicted to be slightly lower on easement lands, particularly for plots with high basal area (Appendix S2).

There was no effect of parcel size on frequency of harvest, but there was a very slight effect on harvest intensity (Appendix S2). Across all plots for which parcel size information was available (regardless of forest type), there was a predicted gradual increase in the average intensity of harvest with increasing parcel size up to an asymptote at approximately 1000 hectares (Appendix S2). The predicted responses by forest type varied widely, ranging from no effect of parcel size in oak–hickory forests to a step function in the intensity of harvest in spruce–fir forests when parcel size exceeded 2000 ha. However, the model that estimated separate parameters for the parcel size effect by forest type was not superior to the simpler model that lumped all forest types together (AIC = 12118 vs. AIC = 12097 for the simpler model). Parcel size data were only available for roughly two-thirds of the study region, and the gaps in coverage were not randomly distributed. Because of this, combined with the uncertainty in parameter estimates and lack of support for forest type-specific effects, parcel size effects were not included in the harvest regimes used in the simulations.

Predicted impacts of alternate harvest regime scenarios

All forest types/regions are predicted to show increases in live aboveground tree biomass in all scenarios, but they differed widely in the total amount of biomass accumulated (Fig. 5). Northern hardwood–conifer forests in Maine accumulated

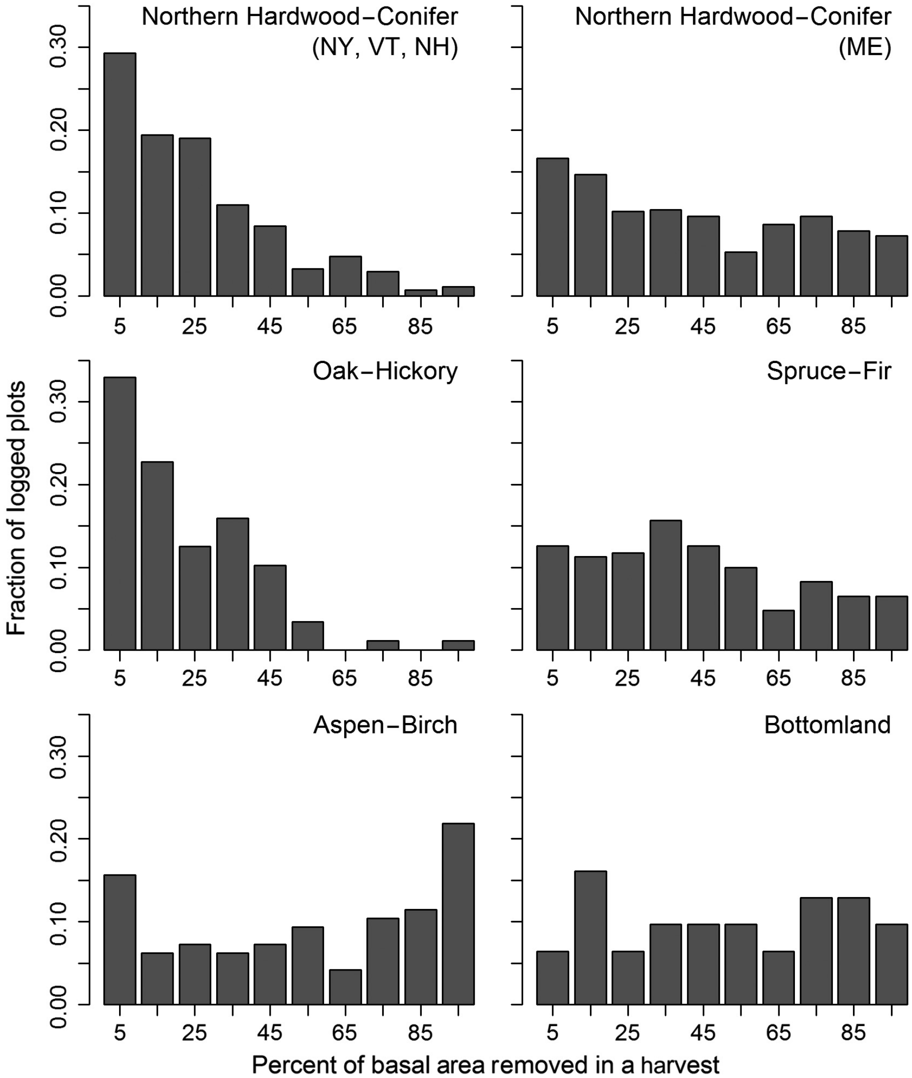

Fig. 4. Frequency distribution of the percentage of tree basal area harvested in a given plot, for plots that experienced some level of harvest, for six forest type/regions.

the least amount of biomass in every scenario that included harvest (ranging from 41% to 3% above current landscape averages in the current harvest scenario and most intensive harvest scenario, respectively). This pattern can largely be explained by high harvest rates (Fig. 2A). Aspen–birch or bottomland forest types resulted in the highest percent increase in biomass in every scenario (ranging from 120% to 78% above current landscape averages in the current harvest scenario [bottomland forests] and most intensive harvest scenario [aspen–birch forests], respectively). Land that is legally reserved from logging in the region currently has almost 50% higher live tree biomass (averaging 134 metric tons/ha vs. 90.4 metric tons/ha), but our simulations predict that even these reserved forests have significant additional carbon sequestration potential over the next 100 yr (Fig. 5). The sequestration potential would be even more dramatic on new reserves created on existing working forestland because current aboveground biomass on these lands is lower. Fig. 5 shows aboveground biomass (a carbon pool), increasing over time resulting in net sequestration (a carbon flux). The capacity to store additional carbon over time reflects stand biomass and biomass growth

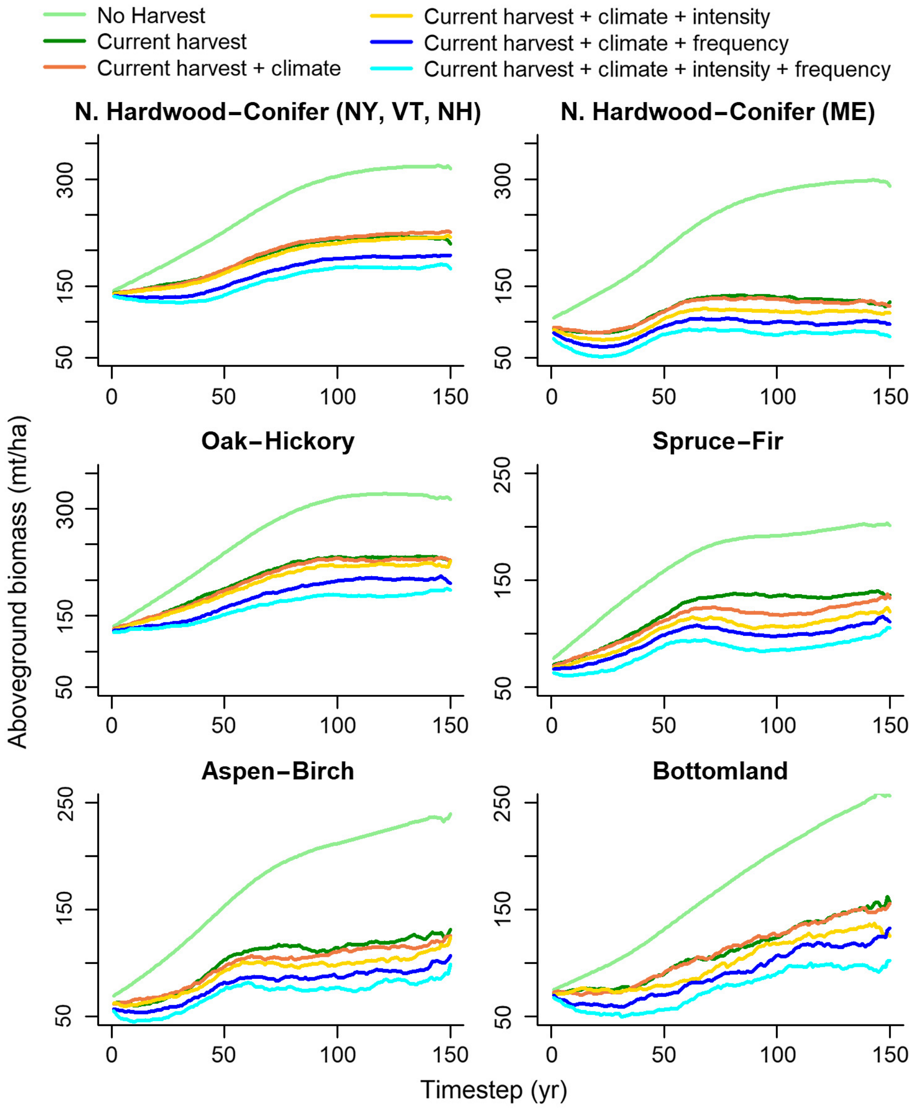

Fig. 5. Estimates of adult aboveground biomass (metric tons/ha) for six harvest scenarios and six forest type/regions over the next 150 yr. Timestep 1 corresponds to the year 2011.

rate, and the variation in regional stand biomass. The future biomass projections, which are directly proportional to carbon, incorporate growth and removals (harvest and natural mortality).

In all harvest intensification scenarios, the proportion of stands in young forest shifted toward more mature stands over time. Roughly 20% of the year 2012 landscape is comprised of forest stands with ≤40 mt/ha of live aboveground tree biomass. In the year 2120, the percent of the forested landscape in stands with ≤40 mt/ha biomass ranged from 5% in the current harvest scenario to 14% in the most intensive harvest scenario. Despite the steady biomass accumulation, however, only 8% or less of stands exhibited characteristics of old-growth forests (≥300 mt/ha) in the year 2120 under any of the regimes except the no harvest scenario. Thirty-seven percent of stands in the no harvest scenario had aboveground biomass ≥300 mt/ha by 2120, compared to <1% in 2012 (Fig. 6).

Northern hardwood–conifer forests in Maine are currently the most heavily harvested forest type in the study region (Fig. 7). These forests

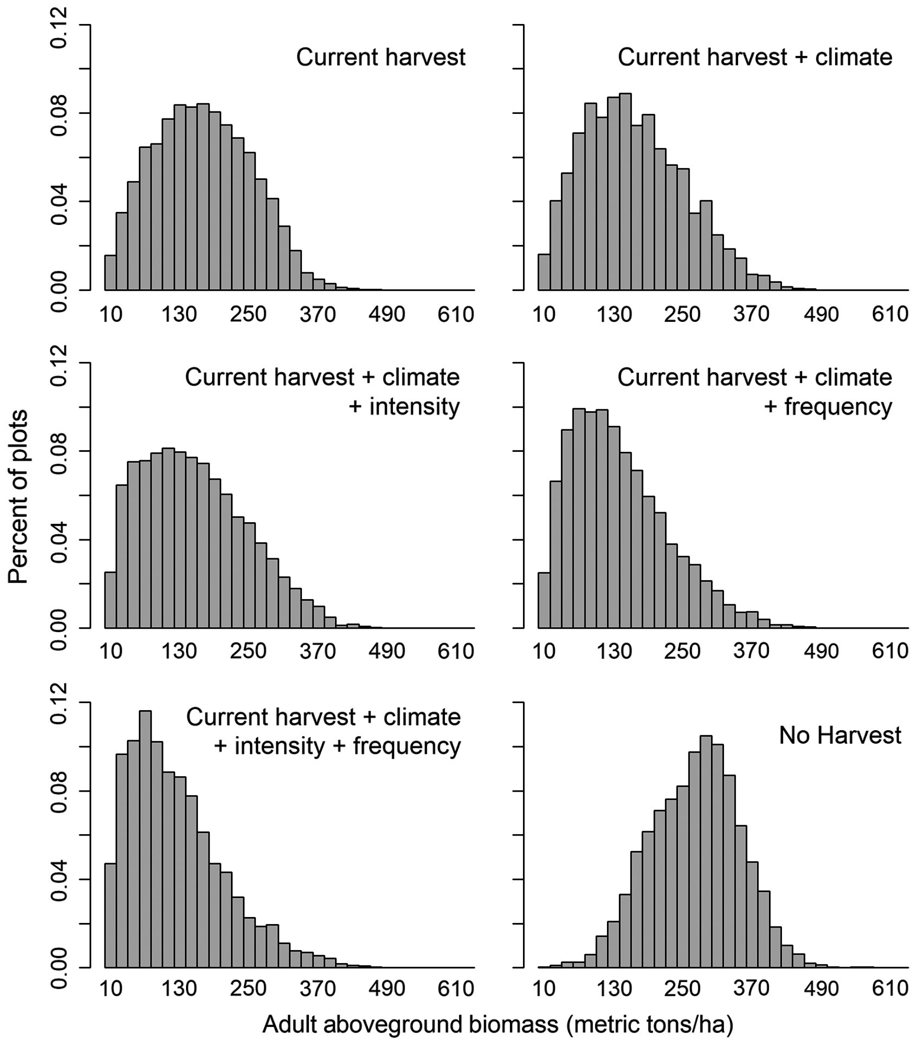

Fig. 6. Percentage of plots in aboveground biomass classes in the year 2120 for six harvest scenarios. The "No Harvest" scenario includes effects of climate change.

have the highest annual probability of being harvested and when they are harvested, the amount of biomass removed is relatively large (Fig. 2) resulting in the highest harvest yields of all forest types in every scenario. Harvest yields from aspen–birch forests also increased significantly under all of the harvest regimes (Fig. 7) because both the rate of harvest and the percentage of biomass harvested when logged are relatively high for these forests (Fig. 2). Several forest type and harvest scenario combinations showed a decline in harvest yield over the first several decades before rising dramatically and eventually somewhat stabilizing in the last 50 yr. This is due to changes in the frequency distribution of stand biomass (and therefore yield) across the forested landscape. Simply increasing the intensity of the harvest regimes did not have a large effect on the overall regional harvest yields because the rotation length increased in response.

While intensifying harvest had clear effects on both average stand biomass and the frequency distribution of stand biomass within a region or forest type, it had little effect on overall patterns of succession and stand development within a given forest type or region (Fig. 8; Appendix S3). A general pattern of stands progressing toward later successional forests emerged across all harvest scenarios, owing

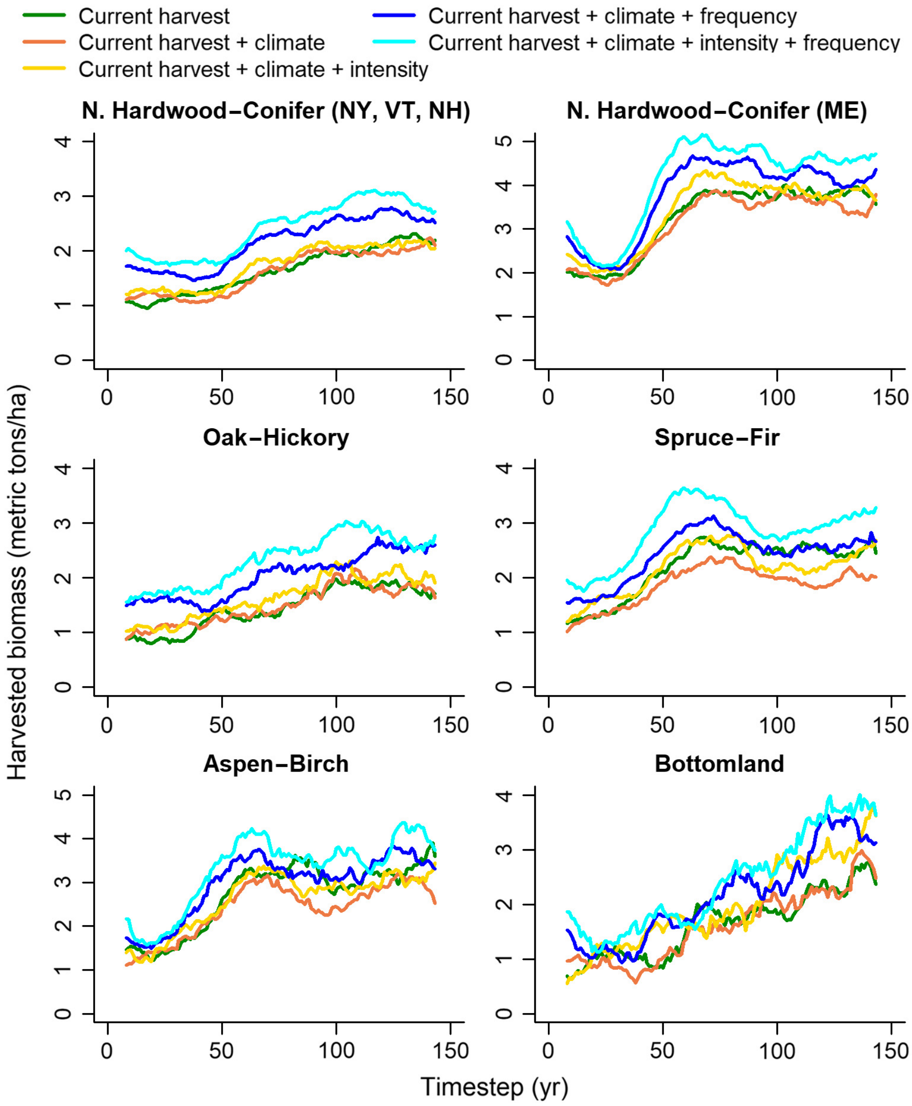

Fig. 7. Amount of harvested biomass (15-yr running averages) shown for five harvest scenarios and six forest type/regions. Timestep 1 corresponds to the year 2011.

to the high proportion of low biomass stands in the current landscape and the predominance of partial harvesting. Late-successional species like sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and eastern hemlock (*Tsuga canadensis*) consistently represented high proportions of biomass in future northern hardwood–conifer forests (Fig. 8), while balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) comprised a large portion of the biomass in spruce–fir forests. Biomass of eastern white pine (*Pinus strobus*) is predicted to increase substantially in all forest type/regions and scenarios over time (Fig. 8). Quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*), currently the two most common species in aspen–birch forests, decline steadily over time in that forest type and are replaced as the most common species (on average) by balsam fir and red maple within 20 yr (Appendix S3).

Comparing the current harvest regime with the current harvest + climate regime scenario isolates the effect of the projected climate change. Of the dominant species of these northern temperate forests, balsam fir was the most disproportionately

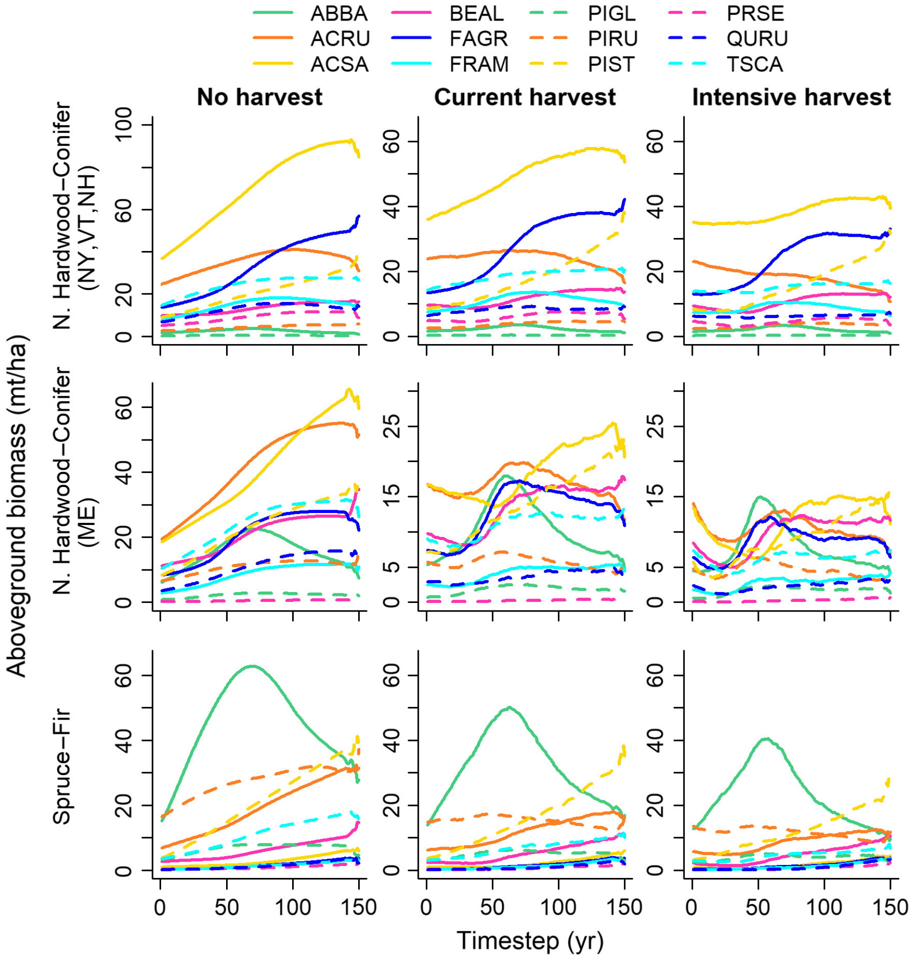

Fig. 8. Species development over 150 yr across three harvest regimes (columns): no harvest (with climate change), the current harvest regime but with climate change, and increased frequency and intensity of the current harvest regime with climate change; and three forest types/regions (rows): northern hardwood–conifer (New York, Vermont, New Hampshire), northern hardwood–conifer (Maine), and spruce–fir. Timestep 1 corresponds to the year 2011. Only 12 dominant species are shown: ABBA = *Abies balsamea*, ACRU = *Acer rubrum*, ACSA = *Acer saccharum*, BEAL = *Betula alleghaniensis*, FAGR = *Fagus grandifolia*, FRAM = *Fraxinus americana*, PIGL = *Picea glauca*, PIRU = *Picea rubens*, PIST = *Pinus strobus*, QURU = *Quercus rubra*, and TSCA = *Tsuga candensis.* Details for all of the forest types and all scenarios are given in Appendix S3.

affected by climate change (Appendix S3). Its abundance is predicted to begin to decline after 50 yr in all of the scenarios that include climate change. Eastern hemlock was also predicted to decline in the face of climate change, although to a smaller degree. While balsam fir is a frequently harvested species (Canham et al. 2013), in the absence of climate change it recovers biomass rapidly following harvest. The effect of the decline in balsam fir was so great in Maine that total biomass at the landscape scale declined given the climate change scenario under the current harvest regime. In contrast, the climate change scenario predicted a slight increase in landscape average aboveground biomass under the current harvest regime in the other three states. Other species responded differentially to the climate change scenario: Sugar maple, eastern white pine, and to a lesser extent American beech accumulated biomass at a greater rate under the climate change scenario (Appendix S3).

DISCUSSION

Harvest effects on landscape structure and composition

Our analyses indicate that in every harvest scenario, average forest biomass is expected to increase significantly over the next 150 yr (ranging from 3% to 120% above current landscape averages), even in the most intensive harvest scenario. In contrast to studies predicting that the strength of the carbon sink in eastern U.S. forests is already or will soon begin to decline (Hurtt et al. 2002, Zheng et al. 2011, USDA Forest Service 2012, Wear and Coulston 2015), our results suggest that at least in terms of live tree biomass, the amount of carbon stored in northeastern forests will continue to increase significantly over the next century (Rhemtulla et al. 2009, Keeton et al. 2011, Davis et al. 2012, Dangal et al. 2014, McGarvey et al. 2015). One of the primary reasons for the growth in carbon storage is the legacy of past land use, where land clearing and heavy harvest prevailed during the middle of last century (Thompson et al. 2011). The current forested landscape includes many stands with low biomass. These forests are predicted to accumulate significant additional biomass, although forest types/regions vary considerably in their contribution to the landscape-level increase in forest biomass (Fig. 5).

In terms of stand development, beyond the negative effects of climate change on balsam fir and eastern hemlock biomass, little difference was observed in successional dynamics under the different harvest scenarios (Fig. 8; Appendix S3). Several studies have predicted a delayed effect of climate change on tree species composition (Iverson et al. 2004, Murphy et al. 2010, Bertrand et al. 2011, Wang et al. 2015). It is plausible that our 150-yr simulations are too short to yield a more pronounced climate effect. In northern hardwood–conifer forests, our analyses predicted continued dominance by sugar maple and red maple (*Acer rubrum*), with eastern hemlock and American beech also showing increased relative and absolute abundance. The model parameterization for tree growth and mortality takes into account the fact that beech bark disease is endemic in the entire study region (Morin et al. 2007). Hemlock populations to the south of the study region are experiencing high mortality from the hemlock woolly adelgid (Morin et al. 2009), and climate change is expected to allow the insect to spread northward over time. Given uncertainty on that rate of spread, however, we did not attempt to account for this in the model. Albani et al. (2010) simulated the effects of the regional spread of the woolly adelgid in eastern U.S. forests and concluded that after several decades of reduced carbon sequestration due to hemlock mortality, uptake of carbon would subsequently be increased as hemlock was replaced by species with higher productivity. A host of subordinate species like black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), red oak (*Quercus rubra*), and red and white spruce (*Picea rubens* and *Picea glauca*) remained at consistently low proportions in northern hardwood–conifer forests over the next 150 yr. It is notable that the patterns of late-successional species response generally hold across all harvest regimes (albeit in different magnitudes). The early-successional nature of the current landscape and the pervasiveness of partial harvesting result in a steadily maturing landscape (Thompson et al. 2011) where the partial harvest gaps are not large enough to promote shade intolerant species even in the intensive harvest scenarios.

Eastern white pine did surprisingly well and accumulated large amounts of biomass across nearly all harvest scenarios in all forest types/regions. While it is often considered a pioneer and gap specialist that is replaced by more shade-tolerant species, our analyses predict white pine to thrive under highly variable partial harvest regimes and canopy conditions that otherwise favor shade-tolerant species. The success of white pine recruitment (in both amount and duration) has been linked to disturbance intensity (Abrams 2001, Black and Abrams 2005), but our results suggest white pine will increase in seedling and sapling density as well as adult biomass across a wide range of disturbance regimes.

Integrating timber harvest regimes into disturbance theory

Logging is clearly the current dominant source of disturbance in northeastern forests (Canham et al. 2013); therefore, understanding the effects of harvest and integrating harvest with natural disturbance is critical for assessing the future of these forests. We show that northeastern forest harvest regimes vary as a function of stand basal area, forest type/region, and distance to roads. Partial harvesting predominates in all forest types/regions.

At the scale of an individual stand, there is a tremendous amount of variation in how much biomass is removed during a harvest (Fig. 2B). Numerous stands near roads (<100 feet) are lightly harvested across several forest types, likely due to firewood cutting, and almost every forest type/region has a greater probability of harvest near improved roads (Figs. 3, 4).

At a landscape scale, the effects of harvest regimes are in many ways analogous to natural disturbance regimes (Gendreau-Berthiaume et al. 2012). Harvest regimes and natural disturbances are both predictable in terms of their frequency and intensity. The varying characteristics of individual harvests (i.e., frequency, severity, and scale) result in a spatially and temporally diverse landscape in a number of stand replacement stages, just as frequent, small-scale natural disturbances give rise to structurally heterogeneous small- and intermediate-scale canopy gaps (Payette et al. 1990, Frelich and Lorimer 1991, Seymour et al. 2002). Natural and anthropogenic disturbances are also both highly selective in mortality by species and size (Canham et al. 2001, 2013, Papaik and Canham 2006), which can result in widely diverging successional patterns depending on initial conditions at the time of a disturbance event and the severity of the disturbance (Uriarte et al. 2009).

The natural disturbance regime for much of the northeastern region is characterized by high-frequency, low-intensity partial disturbances and very low-frequency catastrophic disturbances (Seymour et al. 2002). Prior to European settlement, this pattern resulted in a landscape predominated by old-growth conditions (Barton et al. 2012, Thompson et al. 2013). In contrast, characteristics of older forests may be completely absent or diminished in working forest landscapes (McGee et al. 1999, Lindenmayer and Franklin 2002, Angers et al. 2005, Keeton 2006, Bauhus et al. 2009, Keeton et al. 2011, Morrissey et al. 2014). Our analyses predict only a small fraction of stands with biomass levels characteristic of old-growth conditions after 150 yr, despite an overall increase in aboveground biomass in all harvest scenarios (Fig. 6). The no harvest scenario corresponds closely to the growth and trajectory of biomass accumulation within a forested system driven by natural disturbance; stands with large amounts of live biomass (≥300 mt/ha) are five times greater in the no harvest scenario. A similar pattern is observed in the average annual input of dead and downed woody debris due to natural mortality: The average input is almost twice as large in the no harvest scenario as in any of the harvest scenarios. These differences in inputs of coarse woody debris have implications for carbon storage, sequestration, and biodiversity conservation and are exacerbated by increased harvest intensity (Lindenmayer and Franklin 2002, Nunery and Keeton 2010, Littlefield and Keeton 2012, Schwenk et al. 2012). In a landscape with limited protected lands (Table 1) and widespread partial harvesting, less intensive harvest regimes will result in more variability on working forest lands. As harvest regimes intensify, working forests will become less variable and the limited amount of protected lands will represent a greater proportion of the landscape in later successional stages and larger biomass classes.

Socioeconomic drivers of harvest disturbance regimes

The influence of human decision-making is a key difference between anthropogenic and natural disturbance regimes. A recent analysis illustrated that in addition to biophysical factors, regional harvest regimes are influenced by socioeconomic drivers like forest ownership type, household median income, and population density (Thompson et al. 2017). Landowners determine the fate of their individual lands and they decide whether to harvest based on a complex array of economic factors (e.g., timber price, alleviating debt), management influences (e.g., attitudes toward forest land, objectives for land ownership, family tenure), and policy issues (e.g., access to timber harvest programs; Silver et al. 2015, Butler et al. 2016). Landowner decision-making has significant reach as 80% of forest land in the northeastern United States is in private ownership (Thompson et al. 2017), and changes ownership frequently. National surveys indicate that nearly 20% of family forest owners are likely to sell their forest land in the next decade (Butler et al. 2016).

Socioeconomic factors pose challenges with respect to integrating logging with natural disturbance regimes and predicting the future condition of northern forests. Our analyses do not explicitly include future changes in macroeconomic and social factors as predictor variables. The harvest regimes we implemented in the model reflect current landowner decision-making regarding the local conditions in a given stand. For example, in our scenarios, changing the average intensity of harvests generally did not change overall biomass accumulation because harvest decisions were fundamentally still based on stand basal area. Changing the intensity of a particular harvest simply increased the average rotation length until the next harvest. As biomass increases in a stand, it becomes more likely the stand will be harvested. Under these conditions, the forest landscape eventually stabilizes when net growth equals net removals across the entire region, and the average biomass of forests in a region is inversely related to the average yield across the region.

From a climate perspective, the next two decades are the most important for sequestering and storing carbon to stabilize the climate (IPCC 2014). Thus, despite aboveground biomass being greater after a century of recovery and growth, any initial reduction in sequestration may be problematic. In several of our intensified harvest scenarios, there is a decrease in aboveground biomass for the first 25 yr before the trend reverses and eventually surpasses the initial biomass amounts. This is particularly evident in Maine northern hardwood–conifer forests and bottomland forests (Fig. 5). There is a clear tradeoff between higher intensity harvest regimes stabilizing at lower biomass but more productive forests. Currently, northeastern forests are an important offset for greenhouse gas emissions (Zheng et al. 2011). Our analyses predict there is enormous potential for continued carbon sequestration, even under intensified harvest regimes (Fig. 5). While this is consistent with several studies (Keeton et al. 2011, Davis et al. 2012, Dangal et al. 2014), there is serious debate as to the future direction and magnitude of the carbon sink in eastern U.S. forests (Hurtt et al. 2002, Zheng et al. 2011, USDA Forest Service 2012, Wear and Coulston 2015). Ultimately, the potential contribution of forest bioenergy to meeting state renewable energy goals and reducing fossil fuel dependencies will vary broadly by state, renewable energy objectives, feedstock supply, fossil fuel conversation technologies, forest landowner objectives, and other social and economic factors.

ACKNOWLEDGMENTS

This project was supported by the Northeastern States Research Cooperative through funding made available by the USDA Forest Service and funding from the USDA Animal and Plant Health Inspection Service (contracts 11-8130-0169, 12-8130-0169, 13-8130-0169 and 14-8130-0169, and 15-8130-0169) and the National Science Foundation under grant no. DEB-1257003. The conclusions and opinions in this paper are those of the authors and not the NSRC, the Forest Service, or the USDA. Use of trade names or products does not constitute endorsement by the U.S. Government. The Vermont Cooperative Fish and Wildlife Research Unit is jointly supported by the U.S. Geological Survey, University of Vermont, Vermont Department of Fish and Wildlife, and Wildlife Management Institute. This research is a contribution to the program of the Cary Institute of Ecosystem Studies.

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