

Regional variation in forest harvest regimes in the northeastern United States

CHARLES D. CANHAM,^{1,3} NICOLE ROGERS,^{1,4} AND THOMAS BUCHHOLZ²

¹*Cary Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545 USA*

²*Gund Institute for Ecological Economics, University of Vermont, 617 Main Street, Burlington, Vermont 05405 USA*

Abstract. Logging is a larger cause of adult tree mortality in northeastern U.S. forests than all other causes of mortality combined. We used Forest Inventory and Analysis (FIA) data to develop statistical models to quantify three different aspects of aggregate regional forest harvest regimes: (1) the annual probability that a plot is logged, as a function of total aboveground tree biomass, (2) the fraction of adult tree basal area removed if a plot was logged, and (3) the probability that an individual tree within a plot was removed, as a function of the fraction of basal area removed at the plot level, the species of tree, and its size. Results confirm that relatively frequent partial harvesting dominates the logging regimes, but with significant variation among different parts of the region and different forest types. The harvest regimes have similarities with natural disturbance regimes in imposing spatially and temporally dynamic mortality that varies predictably as a function of stand structure as well as tree species and size.

Key words: disturbance; harvest regimes; logging; northeastern United States; tree mortality; U.S. Forest Service Forest Inventory and Analysis.

INTRODUCTION

From a theoretical perspective, harvesting—particularly clear-cutting—has been viewed much as a catastrophic natural disturbance such as fire or windthrow that resets secondary succession (Odum 1969), with natural processes governing forest dynamics until the next harvest. This notion of “disturbance and recovery” has been an important framework for studies of forest ecosystems of the northeastern United States. For much of the past 50 years (Bormann and Likens 1979). Indeed, one of the most commonly used metrics of forest ecosystem condition is “forest age” (i.e., the time since either reforestation of abandoned agricultural land, or the time since the last clearcut). There has been a sea change, however, in management of northeastern forests over the past 50 years, and clear-cutting has become relatively rare outside of conifer-dominated ecosystems (Birdsey and Lewis 2003, Smith et al. 2009). Instead, a

wide variety of silvicultural systems using partial harvesting has become common, particularly in hardwood-dominated forests. Moreover, harvesting is not just an important source of adult-tree mortality, it is currently a larger source of tree mortality in northeastern forests than all other causes of mortality (natural and anthropogenic) combined (see results summarized in Appendix A).

From a systems perspective, harvesting has a number of important ecological features as a mortality agent. Partial harvesting is typically highly selective in terms of species and tree sizes. These regional harvest regimes may represent one of the most temporally dynamic and spatially variable anthropogenic impacts on northeastern forests. Timber markets are volatile, and there are economic forces and public policies that can create feedbacks (both stabilizing and destabilizing) on both overall harvest rates and species removed in a much more dynamic manner than most other agents of tree mortality.

Disturbance theory provides a useful framework for integrating the impacts of harvesting on forests at a landscape and regional scale. While individual harvests are almost infinitely variable, the aggregate harvest disturbance “regime” can be characterized statistically in

Manuscript received 1 February 2012; revised 16 November 2012; accepted 21 November 2012. Corresponding Editor: J. Franklin.

³ E-mail: canhamc@caryinstitute.org

⁴ Present address: Department of Forest Engineering, Resources and Management, Oregon State University, Corvallis, Oregon 97730 USA.

terms of overall disturbance frequency and intensity, and the selectivity of the mortality as a function of tree species and sizes. We have used data from the U.S. Forest Service Forest Inventory and Analysis (FIA) program to characterize the recent (ca. 2002–2008) harvest regimes for forests in different regions and forest types within the northeastern United States (Kentucky and Virginia north to Wisconsin and Maine). Our analyses quantify three different aspects of aggregate harvest regimes: (1) the annual probability that a plot is logged, as a function of total aboveground tree biomass, (2) the fraction of tree basal area removed, if a plot was logged, again as a function of total aboveground tree biomass, and (3) the probability that an individual tree within a plot was removed, if the plot was logged, as a function of the fraction of basal area removed at the plot level, the species of tree, and its size (dbh). The first two components are estimated simultaneously from a plot-level data set, while the third component is estimated separately from a much larger data set containing records for all trees (stems >12.7 cm dbh) in all plots that experienced any level of logging during the census interval.

METHODS

Plot and tree data were obtained from the website of the U.S. Forest Service Forest Inventory and Analysis (FIA) program (*available online*).⁵ We used data from plots for which there were two censuses conducted using the new national standard plot design (Woudenberg et al. 2010) to allow determination of plot and tree conditions at the time of the previous census, and the subsequent fate of the plot (whether there was logging, and what trees were removed). We omitted from the data set any plots for which logging was legally restricted. Our results are based on analyses using trees >12.7 cm dbh only. FIA methods distinguish between trees that die (from all other causes) and trees that were “removed,” i.e., “cut and removed by direct human activity related to harvesting, silviculture or land clearing” (Woudenberg et al. 2010:91). We refer to these removals generically as “harvested” trees.

In principle, there are many different ways the overall study region could be subdivided—both geographically and ecologically. For illustrative purposes we have parsed the data set into either (1) regions consisting of distinct states or sets of adjacent states or (2) broad forest types (using the forest type codes assigned by FIA). For the state-level analyses, separate models were fit for five states with >1000 usable plots: Kentucky (1359 plots), Maine (3092 plots), Michigan (6218 plots), Virginia (2262 plots), and Wisconsin (4501 plots). Pennsylvania had >1000 plots, but was lumped with Maryland (2176 plots combined). The Ohio Valley states of Illinois, Indiana, and Ohio were lumped (1925 plots

combined), and the New England States of Vermont, New Hampshire, Massachusetts, Connecticut, and Rhode Island were lumped with New York (1075 plots combined), rather than with Maine (3092 plots), primarily because previous analyses showed that Maine had a distinctively different harvest regime than the other New England states. There were no usable plots from three of the 19 states (New Jersey, Delaware, and West Virginia) because plot data from a second census under the new national standard methods had either not yet been done or had not yet been made available.

We then ran a second set of analyses for different broadly defined forest types, regardless of geographic region, based on the forest type classification used by FIA. Specifically, we ran separate analyses for (1) spruce–fir forests (forest type codes 121–129 in the FIA classification; 2243 plots), (2) oak–pine and oak–hickory forests combined (“oak” forests, type codes 401–520; 8149 plots), (3) maple–beech–birch and aspen–birch groups combined (i.e., “northern hardwood” forests, type codes 801–905; 8015 plots), and (4) aspen–birch forests separately (type codes 900–902; 2212 plots).

Plot-level analyses of regional variation in frequency and intensity of harvests

For each of these sets of states or forest types, our statistical model for the harvest regime estimates two components (probability of being logged, percentage of basal area removed if logged) simultaneously, using maximum-likelihood methods. We used a zero-inflated gamma distribution for the likelihood function, since the data set contains many zeros (unlogged plots), and the distribution of percentage of basal area (BA) removed (if logged) is skewed and better fit by a gamma distribution than a normal distribution. Zero-inflated likelihood functions typically estimate a constant zero inflation term, but in our case we also tested a model in which the zero term (probability of not being logged) varied as a function of the independent variable (adult tree biomass).

We tested several flexible function forms for the relationship between the independent variable and both the zero-inflation term and the percentage of basal area removed (if logged), including sigmoidal (logistic) functions. A negative exponential function was consistently the most parsimonious functional form for both relationships. Thus, the probability that a plot was not logged during census interval (P_z) was modeled as

$$P_z = [a \exp(-mX_i^b)]^{N_i} \quad (1)$$

where X_i is adult aboveground tree biomass at the beginning of the census interval in the i th plot, N_i was the census interval (in years) for that plot, and a , m , and b were estimated parameters. For purposes of parsimony, we also tested a simpler version of Eq. 1 in which the b parameter was fixed at a value of 1. As a result of raising the function to the power N_i , the parameters

⁵ <http://apps.fs.fed.us/fiadb-downloads/datamart.html>

specify the effective annual probability of not being logged.

The predicted percentage of basal area (BA) removed from plot i (BAR_i), given that the plot was logged during the census interval, was fit to the following equation:

$$BAR_i = \alpha \exp(-\mu X_i^\beta) \quad (2)$$

where X_i was adult aboveground tree biomass (in metric tons/ha) and α , β , and μ were estimated parameters. Again for the purposes of parsimony, we tested a simpler version of Eq. 2 in which the β parameter was fixed at a value of 1.

The likelihood function for the model was

$$\text{Prob}(y_i | \theta) = \begin{cases} P_z & \text{if } y_i = 0 \\ (1 - P_z)\text{Gamma}(y_i | \theta) & \text{if } y_i > 0 \end{cases} \quad (3)$$

where y_i was the observed percentage of BA harvested, θ is the vector of parameters in the model (including the shape parameter for the gamma distribution), and $\text{Gamma}(y_i | \theta)$ was the probability of observing y_i under a gamma distribution with parameters θ . We solved for the maximum-likelihood values of the parameters using a global optimization routine (simulated annealing) in the *likelihood* library for the R statistical software package (R Development Core Team 2011).

Tree-level analysis

The plot-level analyses characterize the overall level of basal area removed if a stand is logged, but do not address the question of which individual trees within a stand will be harvested. The marking of individual trees in any stand for a harvest involves a great many factors, including both the forest resource (species, size, and condition of all of the trees in the stand) and current market demand and pricing. Our current modeling does not incorporate those site-specific (and unknown) factors, but simply looks for consistent differences in the likelihood that a tree is selected for harvest, based on three factors: (1) the overall level of basal area removed in the plot, (2) species, and (3) tree size (dbh).

The tree-level data set takes all plots from the study region that experienced any level of logging during the most recent census interval, and compiles the records of all trees alive in those plots at the beginning of the census interval. The analysis then models the probability that an individual tree was harvested during the census interval, as a function of the three terms listed previously. The analysis is analogous to a logistic regression, but in a likelihood framework that allows much more flexible functional forms than traditional logistic regression.

In order to ensure sufficient sample sizes for the species-specific parameters, the analysis treats the 21 most common tree species in the sample as individual species, but lumped the remaining 29 species into one

category (“other” species). All of the commercially important tree species in the region fall into the former category, and were treated individually.

There are two components to the regression model. The first assumes that the probability that a tree is selected for harvest increases monotonically (from 0 to 1) as the fraction of total plot basal area removed increases, and that the shape of the function is species specific. We compared three different functional forms of increasing flexibility (and complexity), and the most parsimonious (lowest AIC) was a three-parameter exponential function of the following form:

$$F(R) = 1 - \gamma_s \exp(-\beta_s R^{\alpha_s}) \quad (4)$$

where R is the percentage of basal area removed in a given plot, and α_s , β_s , and γ_s are species-specific (estimated) parameters. We also tested simpler versions of Eq. 4 in which either α_s or γ_s or both were held constant at values of 1.

The second component of the model factors in the size of the tree. We assumed that there could be a preference for a particular size, and that this preference could be fit with a Gaussian function, largely because the Gaussian is flexible enough that it could range from effectively flat (no size preference) to a monotonic increase or decrease with size (if the estimate of the mean is very large or small, respectively), to a more traditional hump-shaped function. The function has to allow for the fact that as the percentage of total basal area removed increases, the selectivity necessarily decreases (i.e., the preference function becomes “flatter”), if only for the obvious reason that a clearcut takes all adult stems, regardless of size. We allowed for this by making the term for dispersion (σ) a power function of the plot-level removal R . This second component of the model takes the following form:

$$F(\text{dbh}) = \exp\left(-\frac{1}{2} \left[\frac{\text{dbh} - \mu_s}{\sigma}\right]^2\right) \quad (5)$$

where $\sigma = a + bR^c$ and where dbh is the dbh of the tree, R is the plot-level basal area removal rate, μ_s is a species-specific parameter, and a , b , and c are parameters common to all species and that control the change in degree of dispersion of the function as R varies. We also tested a model with $c = 1$ (in effect making the dispersion term a linear function of R).

Thus, the overall regression model is:

$$P(\text{logged}) = [1 - \gamma_s \exp(-\beta_s R^{\alpha_s})] \times \exp\left(-\frac{1}{2} \left[\frac{\text{dbh} - \mu_s}{\sigma}\right]^2\right) \quad (6)$$

where $\sigma = a + bR^c$.

Since the regression model is already probabilistic, the likelihood function is simply:

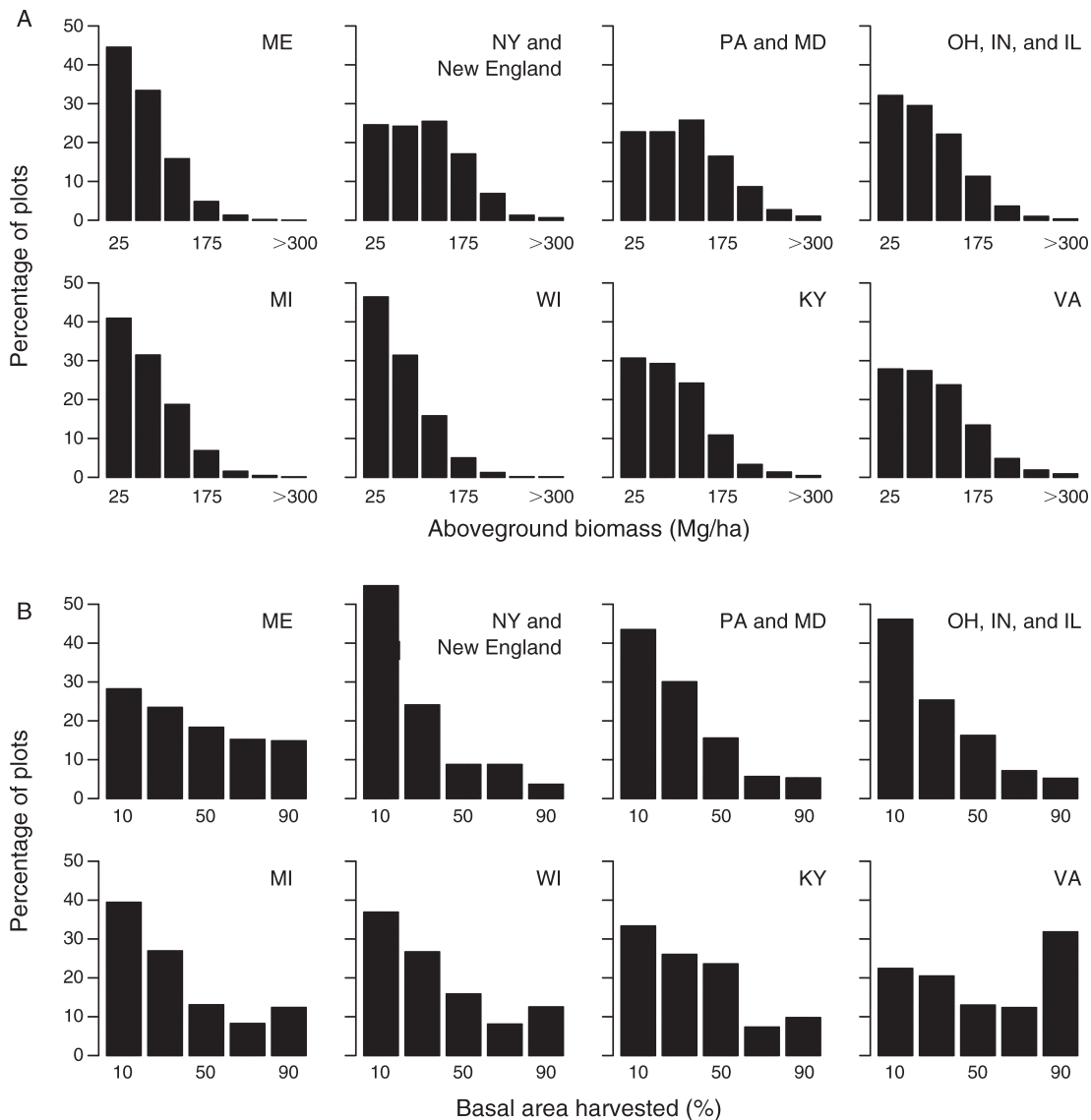


FIG. 1. (A) Frequency distribution of aboveground tree biomass in U.S. Forest Service Forest Inventory Analysis (FIA) plots from the eight regions (states or sets of adjacent states; state abbreviations are: ME, Maine; NY, New York; PA, Pennsylvania; MD, Maryland; OH, Ohio; IN, Indiana; IL, Illinois; MI, Michigan; WI, Wisconsin; KY, Kentucky; VA, Virginia). The histogram bins are in units of 50 metric tons/ha (metric ton = Mg), with the exception of the last bin, which includes all plots with >300 metric tons/ha. (B) Frequency distribution of the percentage of tree basal area removed in a given plot, for plots that experienced some level of removal during the census interval, for the same eight regions.

log likelihood

$$= \sum_{i=1}^n \begin{cases} \log[P(\text{logged})] & \text{if the stem was harvested} \\ \log(1 - P(\text{logged})) & \text{if the stem was not harvested} \end{cases}$$

for the $i = 1 \dots n$ trees. As in the plot-level analysis, maximum-likelihood estimates were obtained using simulated annealing using R statistical software. Metrics of goodness of fit of the models are presented in Appendix B.

RESULTS

Forests in the eight regions (individual states or sets of adjacent states) differ substantially in both mean

aboveground biomass and the frequency distribution of forest biomass across the landscape (Fig. 1A, Appendix A). The states of Maine, Wisconsin, and Michigan have distributions strongly skewed to lower biomass, and the lowest mean biomass overall (65, 64, and 72 metric tons/ha, respectively), while the U.S. Forest Service Forest Inventory and Analysis (FIA) plots from Pennsylvania northeast to New Hampshire had the highest mean aboveground biomass (112 metric tons/ha for Pennsylvania and Maryland, and 105 metric tons/ha for New York and the New England states other than Maine). In all of the regions, stands with >200

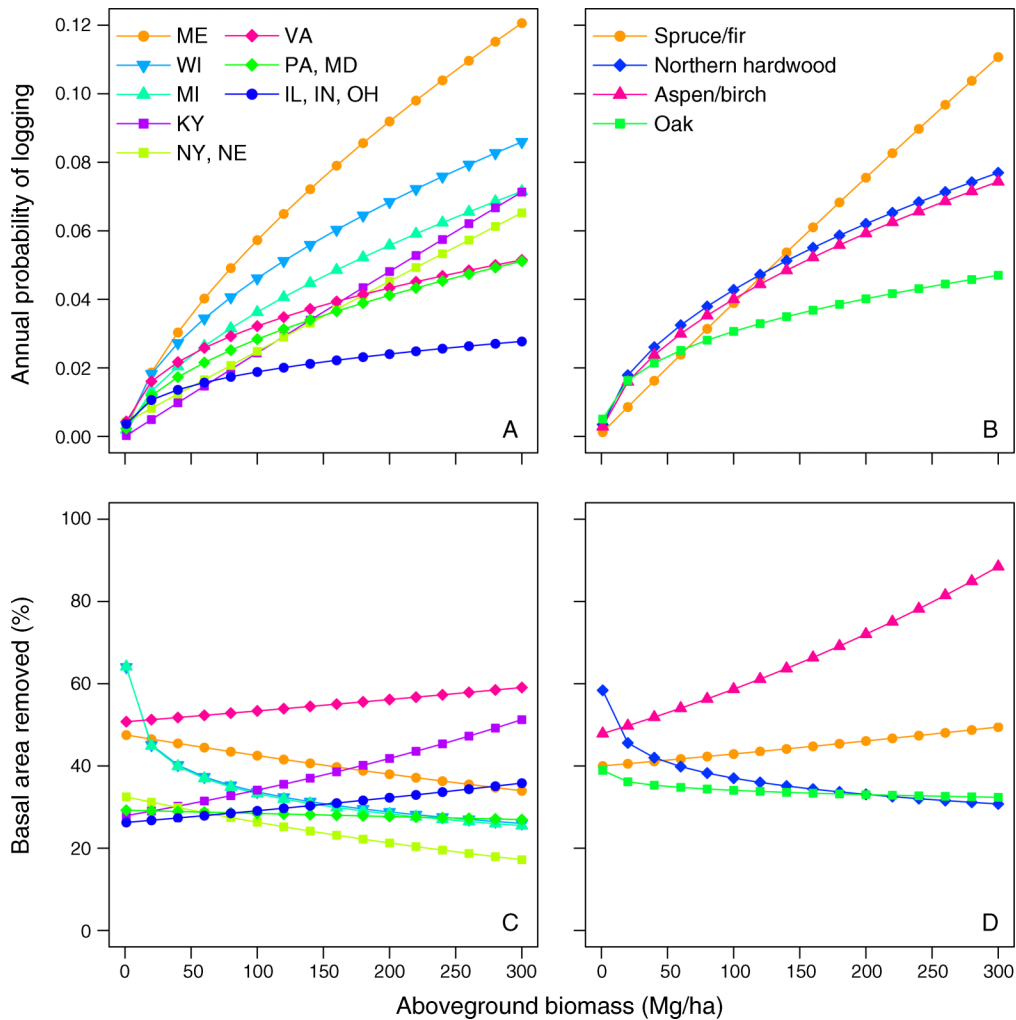


FIG. 2. (A, B) Estimated annual probability that a plot is logged: (A) as a function of the total aboveground tree biomass for the eight study regions (states or sets of adjacent states; state abbreviations are as Fig. 1) (NE stands for New England), and (B) for the four forest types. (C, D) Estimated percentage of basal area removed: (C) as a function of the total aboveground tree biomass for the eight study regions (states or sets of adjacent states) and (D) for the four forest types. Maximum-likelihood estimates and two-unit support intervals for all parameters, and measures of goodness of fit of the overall models, are reported in Appendix B.

metric tons/ha were rare. Partial harvesting is clearly much more common than clearcutting in all eight regions, but the regions show a range of patterns of variation in intensity of harvests (Fig. 1B).

Variation in frequency and intensity of harvests across regions and forest types

The eight regions show both overall similarities and some distinctive differences. In all cases, the probability of logging increases with increasing tree biomass (Fig. 2A), but logging is definitely not limited to only the highest-biomass stands. Maine had the highest annual probabilities of harvest across the entire range of total plot biomass, while the Ohio Valley states (IL, IN, and OH) had the lowest (Fig. 2A). The annual probability of a harvest in a stand with 100 metric tons/ha (≈100 Mg/

ha) aboveground biomass ranged from 1.9% in the Ohio Valley states to a high of 5.7% in Maine (average for the eight regions = 3.4% per year). For stands with 300 metric tons/ha, the probability of harvest had on average doubled (6.8% per year averaged across the eight subregions), with a range from 2.8% in the Ohio Valley to 12.1% in Maine (Fig. 2A).

The eight regions also show a wide range of variation in the fraction of basal area removed as a function of available tree biomass (Fig. 2B). In the northeastern states, the average fraction of basal area removed is actually lower in stands that had higher aboveground biomass (Fig. 2B). For the Ohio Valley and southernmost two states of Kentucky and Virginia, the average fraction of biomass removed increased with increasing biomass. There was very wide variation in the percent-

age removal on individual plots (gamma distributed with scale parameter ~ 25 ; Appendix B), reflecting the variety of even-aged and uneven-aged silvicultural systems used within the region.

Results for different forest types mirrored the general patterns broken down by state. While the probability of logging increased with plot biomass, there were still moderately high annual probabilities ($\sim 2\%$ per year) that even low-biomass stands would have some level of harvesting (Fig. 2C). The probability of logging increased almost linearly for spruce–fir and aspen–birch forests, but still did not conform to the expected sigmoidal function that would be a signature of classic even-aged silviculture with a long rotation length (i.e., very low probability of logging until stands reached a threshold biomass, after which probability of logging increased dramatically). In the spruce–fir forests, the mean harvest rate was only 40–50% of biomass removed in any given harvest, regardless of stand biomass, while in aspen–birch forests the average fraction of basal area removed was high even at low aboveground biomass, and increased almost linearly with increasing aboveground biomass (Fig. 2D). In both oak and northern hardwood forests, the mean harvest rate declined with increasing biomass, but even stands with relatively low biomass had a roughly 2% chance of being logged in a given year (Fig. 2C).

Variation in probability that an individual tree is harvested

There was a fairly wide range of preference for harvesting different species at any given overall level of harvest (Fig. 3A). The preference rankings also varied substantially as a function of harvest level, but this was true primarily for species with intermediate to low preference. For example, species with the lowest probability of harvest in very heavy cuts, such as sweetgum (*Liquidambar styraciflua*) and black cherry (*Prunus serotina*), tended to have intermediate probabilities of being harvested in lighter cuts. The preference rankings contained some surprises. In particular, both species of aspens (*Populus tremuloides* and *Populus grandidentata*), when present in a stand, consistently had higher-than-average probability of being harvested (Fig. 3A). Both of those species are harvested primarily for pulp, and this may reflect something distinctive about harvests (specifically, selectively removing low-grade species to encourage better growth of high-value timber species) in the upper Great Lakes where these species are particularly common.

Three commercially valuable conifers—loblolly pine (*Pinus taeda*), balsam fir (*Abies balsamea*), and red spruce (*Picea rubens*)—also had consistently higher-than-average probabilities of being selected for harvest (Fig. 3A). Note that the study region includes only a small portion of the range of loblolly pine in the south, and all three of these conifers can be found as components of hardwood-dominated stands. The results suggest that when present in these stands, they have a

higher probability of being selected for removal in a partial harvest than most of the hardwoods with which they are associated.

Species differed substantially in the size that had the highest probability of being logged (Fig. 3B). The two species most likely to be removed, loblolly pine (*Pinus taeda*) and trembling aspen (*Populus tremuloides*), were most likely to be removed as relatively small stems (mode = 33 and 36 cm, respectively). Black cherry (*Prunus serotina*) and sweetgum (*Liquidambar styraciflua*) were much more likely to be harvested (and at rates far above the average in typical partial harvests) when the stems were very large (mode = 54 cm for black cherry). There may be many explanations for the predicted low rates of removal for large stems. We suggest that one possibility is that trees that survive to very large sizes do so in part because of defects that reduce their economic value and likelihood of being selected for harvest.

DISCUSSION

Silvicultural systems using partial harvesting are far less visible to the public, but our analyses highlight the pervasive nature of logging in northeastern forests. There is ample evidence that patterns of variation in adult-tree mortality can be as important as adult-tree growth rates in their impact on forest structure and productivity (Das et al. 2008), and a long history of recognition of the importance of disturbance regimes in shaping forested landscapes (Radeloff et al. 2006). Failure to appreciate the regional impact of logging, however, would lead to misleading assumptions about the dynamics of forested landscapes. For example, current net rates of carbon sequestration in northeastern forests are expected to decline over time (Caspersen and Pacala 2001). There appears to be an assumption that such a decline will be a function of the maturing of a largely “even-aged” forest landscape that dates from clear-cutting or land abandonment more than a century ago (Siccama et al. 2007), but recent analyses suggest that harvesting has an enormous impact on the magnitude of the carbon sink in U.S. forests (Zheng et al. 2011). Thus, it would be erroneous to conclude that much of the forest landscape in the northeastern United States has reached a successional stage and level of aboveground biomass where the potential to sequester carbon has disappeared (Fig. 1A).

Our results have a more prosaic implication for the way that ecologists think about northeastern forests. Stand “age” is one of our most cherished metrics of forest ecosystem status. Our results suggest that, except for the small fraction of the landscape that has been reserved from harvest over the past century, stand age will be difficult to assign as a single, predictive metric of forest ecosystem status (*sensu* Odum 1969). The patterns of logging illustrated in Fig. 2 imply that stands will be partially harvested at least several times over the course

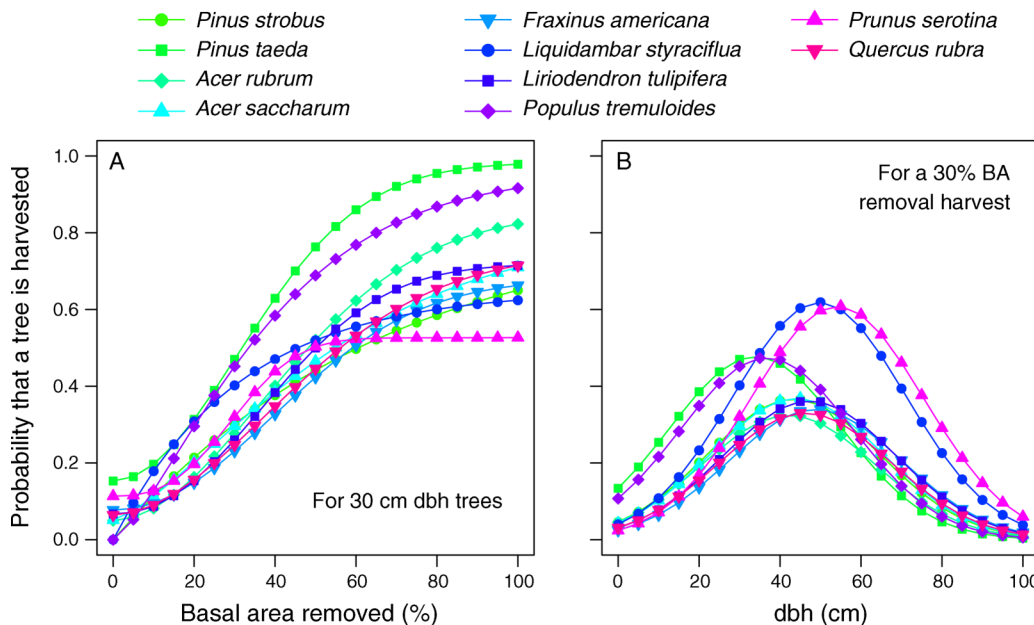


FIG. 3. (A) Probability that a tree is selected for harvest, as a function of the total percentage of basal area (BA) removed from the plot, by species. The curves are shown for a 30 cm dbh tree. (B) Probability that a tree was selected for removal in a 30% harvest, as a function of dbh (cm). Maximum-likelihood estimates and two-unit support intervals for parameters, and measures of goodness of fit, are reported in Appendix B. For illustrative purposes, only 10 species representing the range of observed patterns of variation are shown. Results for the remaining 14 species groups are given in Appendix B.

of a century, with a significant fraction of aboveground tree biomass removed in any given harvest.

Our analyses of the probability of logging include all plots on forest lands that are not recorded by the U.S. Forest Service Forest Inventory and Analysis (FIA) as legally reserved from logging. But there is clearly a subset of this “unreserved” forest land that is effectively unavailable for harvest because of a wide range of physical, social, and economic constraints (Ward et al. 2005, Butler et al. 2010, Buchholz et al. 2011). These constraints include physical factors such as steep slopes, economic factors such as distance from roads and parcelization, and social factors due to landowner interests. In effect, the annual probability of harvesting on truly “available” forest land is presumably higher than predicted by our models, while some fraction of the plots in the data set are effectively reserved. This issue has important implications for assessing the sustainability of the harvest regimes in the different regions, but there is still a great deal of uncertainty about the actual magnitude (and permanence) of these constraints on the availability of forest land for harvest.

Foresters traditionally study harvest regimes in terms of clearly defined alternative silvicultural systems, but our approach aggregates across the myriad decisions made when selecting trees for removal, and characterizes regional harvest regimes in statistical terms that are relevant to understanding the impact of harvesting on landscape-scale forest structure, composition, and productivity. While forest ecologists routinely consider the

impacts of natural disturbance regimes, and mortality from a wide range of anthropogenic causes including air pollution (e.g., Thomas et al. 2010) and introduced pests and pathogens (e.g., Busby et al. 2011), harvesting removes more adult-tree biomass from northeastern forests than all other causes of mortality combined (Appendix A). Our analyses provide statistical models that can be used to integrate forest harvest regimes within the context of both disturbance theory and an integrated assessment of human impacts on forested landscapes.

ACKNOWLEDGMENTS

We would like to acknowledge the remarkable resource provided by the Forest Inventory and Analysis program, and particularly Elizabeth LaPoint for her assistance and patience. Support for this research was provided under USDA-APHIS Cooperative Agreement No. 11-8130-1442. N. Rogers was partially supported on a REU fellowship under NSF grant DBI-0552871.

LITERATURE CITED

Birdsey, R. A., and G. M. Lewis. 2003. Current and historical trends in use, management, and disturbance of U.S. forestlands. Pages 15–33 in J. M. Kimble, L. S. Heath, R. A. Birdsey, and R. Lal, editors. The potential of U.S. forest soils to sequester carbon and mitigate the greenhouse effect. CRC Press, New York, New York, USA.

Bormann, F. H., and G. E. Likens. 1994. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, New York, USA.

Buchholz, T., C. D. Canham, and S. P. Hamburg. 2011. Forest biomass and bioenergy: opportunities and constraints in the Northeast United States. Cary Institute of Ecosystem Studies, Millbrook, New York, USA. http://www.caryinstitute.org/sites/default/files/public/downloads/news/report_biomass.pdf

- Busby, E. B., and C. D. Canham. 2011. An exotic insect and pathogen disease complex reduces aboveground tree biomass in temperate forests of eastern North America. *Canadian Journal of Forest Research* 41:401–411.
- Butler, B. J., Z. Ma, D. B. Kittredge, and P. Catanzaro. 2010. Social versus biophysical availability of wood in the northern United States. *Northern Journal of Applied Forestry* 27:151–159.
- Caspersen, J. P., and S. W. Pacala. 2001. Successional diversity and forest ecosystem function. *Ecological Research* 16:895–903.
- Das, A., J. Battles, P. J. van Mantgem, and N. L. Stephenson. 2008. Spatial elements of mortality risk in old-growth forests. *Ecology* 89:1744–1756.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* 164:262–270.
- R Development Core Team. 2011. R: a language and environment for statistical computing. Version 2.14.1. R Foundation for statistical computing, Vienna, Austria.
- Radeloff, V. C., D. J. Mladenoff, E. J. Gustafson, R. M. Scheller, P. A. Zollner, H. S. He, and H. R. Akçakaya. 2006. Modeling forest harvesting effects on landscape pattern in the northwest Wisconsin Pine Barrens. *Forest Ecology and Management* 236:113–126.
- Siccama, T. G., T. J. Fahey, C. E. Johnson, T. W. Sherry, E. G. Denny, E. B. Girdler, G. E. Likens, and P. A. Schwarz. 2007. Population and biomass dynamics of trees in a northern hardwood forest at Hubbard Brook. *Canadian Journal of Forest Research* 37:737–749.
- Smith, W. B., P. D. Miles, C. H. Perry, and S. A. Pugh. 2009. Forest resources of the United States, 2007. General Technical Report WO-78. U.S. Department of Agriculture, Forest Service, Washington, D.C., USA.
- Thomas, R. Q., C. D. Canham, K. C. Weathers, and C. L. Goodale. 2010. Increased tree carbon storage in response to nitrogen deposition in the US. *Nature Geoscience* 3:13–17.
- Ward, B. C., D. J. Mladenoff, and R. M. Scheller. 2005. Simulating landscape-level effects of constraints to public forest regeneration harvests due to adjacent residential development in northern Wisconsin. *Forest Science* 51:616–632.
- Woudenberg, S. W., B. L. Conkling, B. M. O'Connell, E. B. LaPoint, J. A. Turner, and K. L. Waddell. 2010. The forest inventory and analysis database: database description and users manual version 4.0 for Phase 2. General Technical Report RMRS-GTR-245. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Zheng, D. L., L. S. Heath, M. J. Ducey, and J. E. Smith. 2011. Carbon changes in conterminous US forests associated with growth and major disturbances: 1992–2001. *Environmental Research Letters* 6:014012.

SUPPLEMENTAL MATERIAL

Appendix A

Forest statistics reported by the U.S. Forest Service Forest Inventory and Analysis program for the 19 states from Virginia and Kentucky north to Wisconsin and Maine ([Ecological Archives A023-024-A1](#)).

Appendix B

Maximum-likelihood estimates and two-unit support intervals for parameters of the plot-level and tree-level analyses, and goodness-of-fit metrics for both sets of models ([Ecological Archives A023-024-A2](#)).