

# Shifting balance between natural mortality and harvesting in forests of the northeastern USA

Lucas B. Harris <sup>a</sup>, Melissa A. Pastore<sup>b</sup>, and Anthony W. D'Amato <sup>a</sup>

<sup>a</sup>Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT, USA; <sup>b</sup>USDA Forest Service, Research and Development, Forest Inventory and Analysis, St. Paul, MN, USA

Corresponding author: Lucas B. Harris (email: [lucas.harris@uvm.edu](mailto:lucas.harris@uvm.edu))

## Abstract

Natural disturbance is increasing in temperate forests worldwide as global change impacts intensify, potentially shifting the balance between forest harvesting and natural disturbance as drivers of biomass change and forest dynamics. Using national forest inventory data, we show that the balance between forest harvesting and natural mortality shifted considerably over the past two decades in the northeastern USA due to a rise in natural mortality, with harvesting accounting for 5% greater biomass loss than natural mortality in 2009 but natural mortality accounting for 39% greater biomass loss than harvesting in 2024. Occurrence of moderate–high-severity natural disturbance also increased. Our results challenge the paradigm of forest harvesting as the dominant cause of tree mortality and disturbance in the northeastern USA and support mitigation and recovery from natural disturbance as elements of forest policy and management strategies.

**Key words:** tree mortality, disturbance, forest harvesting, forest inventory, forest biomass, northern temperate and southern boreal forests

## Introduction

The balance between human-caused and natural disturbance has shifted over the past three decades in the USA as natural disturbances such as extreme weather, drought, insect outbreaks, disease, and fire have become more frequent and severe, while human-caused disturbance has declined (Qiu et al. 2025). Shifts in this balance may reshape priorities in forest management at state to regional scales. Within forests of the northeastern USA (Fig. 1), natural disturbances have historically tended to be uncommon or low in severity (Lorimer and White 2003). Meanwhile, forest harvesting accounted for the majority of adult tree mortality by volume as recently as 2002–2008, and is considered the dominant disturbance type in the region (Canham et al. 2013). Discourse around forest management in regard to biomass change, disturbance, and greenhouse gas mitigation has therefore tended to focus on harvesting more than natural mortality and disturbance in the northeastern USA, informing debates about the value of active versus passive management (Faison et al. 2023).

Although timber harvest patterns have been recently assessed (Russell et al. 2025), an up-to-date quantification of the relative balance of forest harvesting and mortality from other causes (hereafter “natural” mortality) is lacking in northeastern USA forests, despite evidence that natural mortality rates may have increased in recent decades. For example, non-indigenous pests and pathogens are causing substantial tree biomass loss (Fei et al. 2019). These shifting disturbance dy-

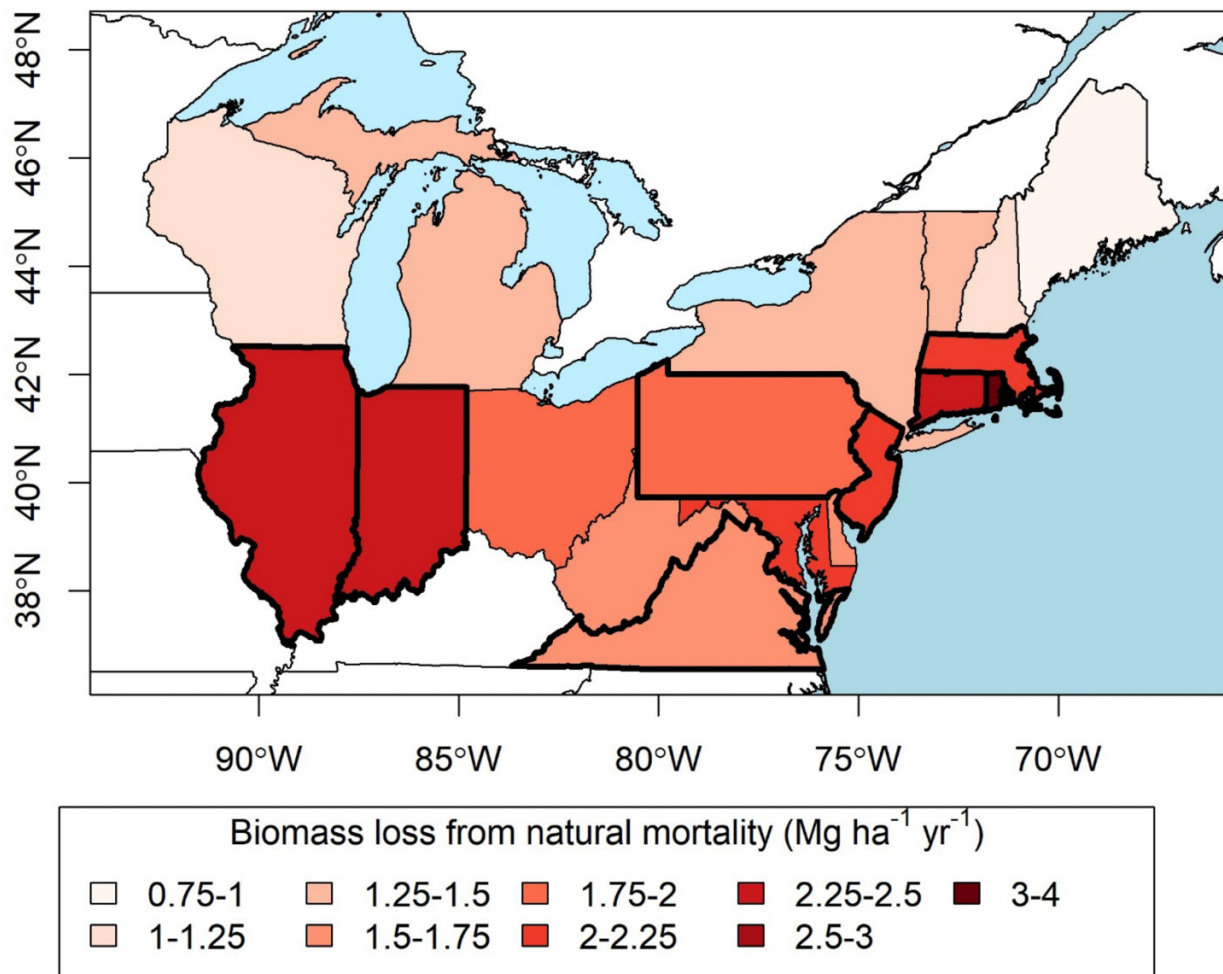
namics occur against a backdrop of widespread regeneration challenges in northeastern USA forests (Vickers et al. 2019; Miller et al. 2023) that may affect recovery and long-term biomass dynamics (Harris et al. 2024). Understanding the nature of recent natural disturbance patterns, particularly the occurrence of moderate to high-severity events, is critical to predicting the future diversity and abundance of tree regeneration across this region (Hanson and Lorimer 2007).

Our goals were to use national forest inventory data to (1) quantify annual aboveground live tree biomass loss due to harvesting and natural mortality since 2009 across forests of the northeastern USA, and (2) to assess the occurrence of moderate to high-severity disturbance. We expected biomass loss due to harvesting in the region to be relatively stable over time, and natural mortality rates to increase due to a combination of nonindigenous pests and pathogens, drought, extreme weather, and other disturbances.

## Methods

We quantified live aboveground tree biomass using field plots from the national forest inventory, the Forest Inventory and Analysis (FIA) program. The FIA plot design consists of four circular subplots of 168 m<sup>2</sup> spaced 36.6 m apart, with one subplot at the plot center and the others at 0°, 120°, and 240° azimuths (Bechtold and Patterson 2005). Adult trees ( $\geq 12.7$  cm diameter at breast height (DBH)) are measured within each subplot.

**Fig. 1.** Adult tree aboveground biomass loss from natural mortality in the most recent set of forest inventory plot measurements for each state in the northeastern USA (2018–2024). Bold outlines indicate states in which biomass loss from natural mortality increased significantly from 2004 to 2024 ( $p < 0.05$ , Mann–Kendall test with a Holm correction). See **Table A1** for state-level values and trend estimates. Note Kentucky was not included in the study area due to lack of inventory data after 2021. Figure was created using R version 4.5.1 and assembled using data from the national forest inventory (Gray et al. 2012), matched to boundaries from the US Census Bureau (<https://www.census.gov/geographies/mapping-files.html>) that form the base map.

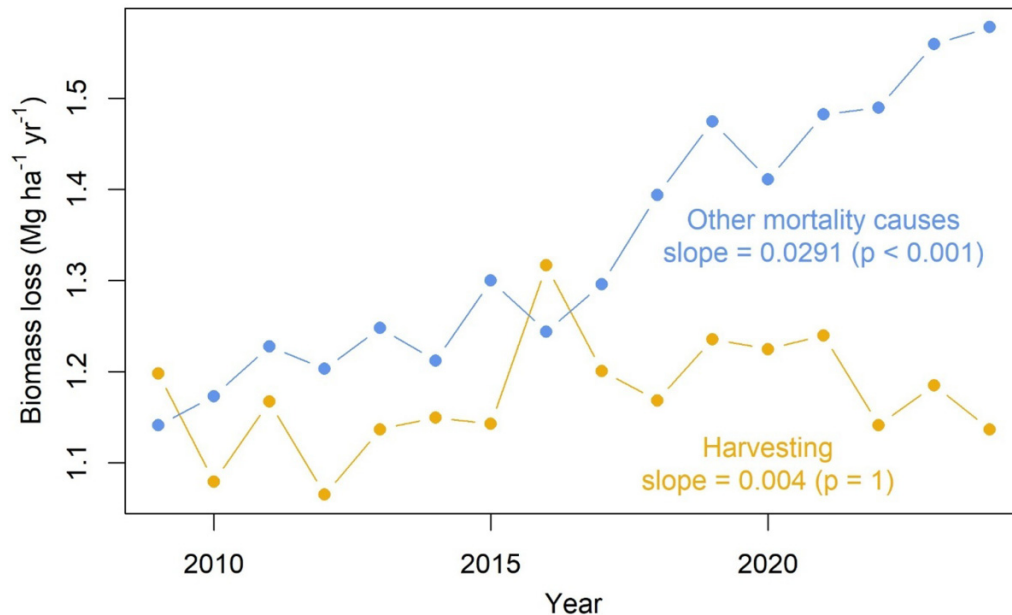


The northeastern USA was defined following Canham et al. (2013), except that Kentucky was omitted because data were only available through 2021 at the time of analysis. Note that tree biomass loss due to natural mortality exceeded harvesting in Kentucky for the most recent set of FIA measurements (1.52 and 1.20  $\text{Mg ha}^{-1} \text{ year}^{-1}$ , respectively, 2015–2021), suggesting that its inclusion would not substantially shift the balance between harvesting and natural mortality that we report here. Nationally standardized annual inventory protocols were initiated between 1999 and 2004 for northeastern USA states and are remeasured at 5–7-year intervals, meaning that annual remeasurements are available beginning from 2004 to 2009 depending on the state. At the time of analysis, data were available through 2024 for all states in the region after Kentucky was removed. Using the version of the FIA database (Gray et al. 2012) updated on 4 September 2025, we identified remeasured annual inventory subplots ( $n = 323\,892$

measurement pairs), representing approximately 62 million hectares of forest in the region, that lay fully on accessible forest land as defined by FIA (Bechtold and Patterson 2005) and which did not lie in reserves where harvesting is restricted. Subplots with reserved status (5.9% of all subplots) were withheld and analyzed separately to focus primarily on the balance between natural mortality and harvesting within forests where harvesting is allowed. We excluded partially forested subplots lying directly on the forest edge which have unique dynamics (Morreale et al. 2021) because using fully forested subplots provided a consistent and management-relevant spatial scale (168  $\text{m}^2$ ) for assessing disturbance severity.

Disturbance severity and type was assessed at the subplot level using tree-based biomass estimates and tree mortality agent codes. We used tree-level aboveground biomass estimates that the FIA program provides based on tree DBH,

**Fig. 2.** Mean annual live aboveground adult tree biomass loss due to harvesting (yellow) and all other causes of mortality (blue) from forest inventory subplot measurements across northeastern USA forests with annual trend estimates from Sen's slope tests and *p*-values from Mann–Kendall tests.



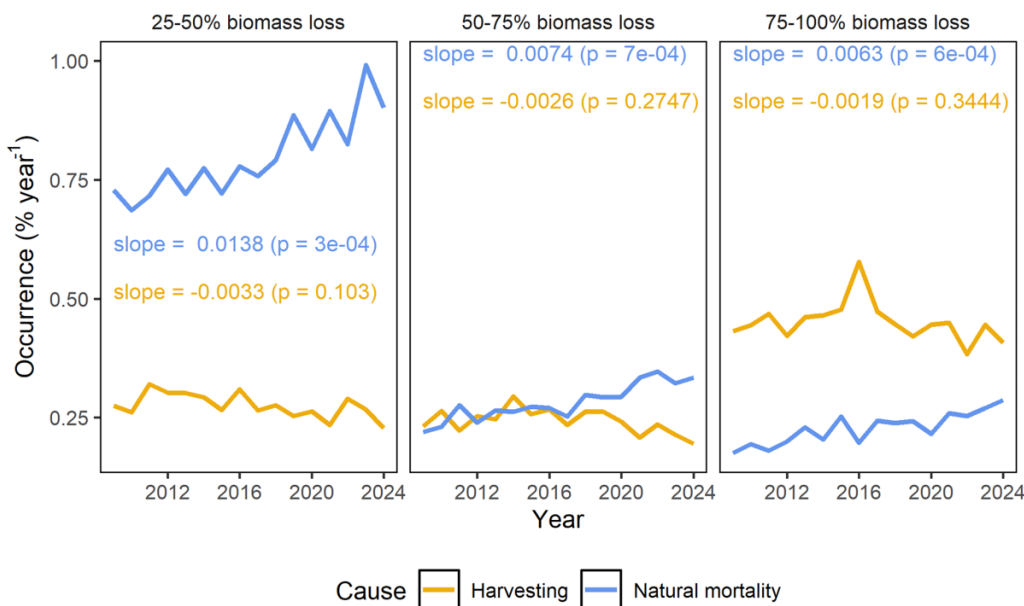
height and a suite of recently-updated allometric equations (Westfall et al. 2024). Loss in biomass was calculated at the subplot level by pairing biomass estimates from the midpoint between measurements with tree status (alive or dead) and mortality agent (insect, disease, fire, animal, weather, vegetation, unknown, or silvicultural activity) in the re-measurement, considering only adult trees  $\geq 12.7$  cm DBH. We considered all mortality agents except for silvicultural activity as natural mortality. Note that we refer to “year” throughout as the year of the re-measurement, with natural mortality or harvesting occurring at some point between measurements. Biomass loss per year was calculated using the re-measurement period given for each plot. To investigate the occurrence of moderate to high-severity disturbance, we also calculated the percentage of live aboveground tree biomass lost to natural mortality and harvesting for each subplot and tallied the annual occurrence of disturbances within three ordinal classes: 25%–50% and 50%–75% (both moderate severity), and  $\geq 75\%$  biomass loss (high severity). For both calculations of biomass loss and occurrence of disturbance, weighted averages were computed among subplots within the unit of interest (e.g., year or state and year) using population-level expansion factors and subplot adjustment factors developed for change estimates (i.e., growth, mortality, and removal, from FIA’s Population Stratum table) to account for differences in sampling intensity and completeness across the region. Note that the FIA program also provides assessments of disturbance and treatment types at the condition level, i.e., homogenous units within a plot, that are also useful for quantifying disturbance depending on study objectives (Fitts et al. 2022). Therefore, we also calculated annual disturbance and harvest occurrence based on condition-level estimates over the same set of FIA subplots to provide further context (see Appendix).

We investigated annual trends in tree biomass loss from each mortality agent as well as all natural mortality combined, along with trends in occurrence of moderate to high-severity natural disturbance and harvesting, using Sen’s slope tests (Sen 1968) via the “trend” R package (Pohlert 2020) and *p*-values from Mann–Kendall trend tests with a Holm correction for multiple comparisons. Regional trend analysis was limited to the common period of data availability among states (2009–2024,  $n = 269\,708$  subplot measurements). We also calculated state-level trends using the full time series available for each state, along with biomass loss from harvesting and natural mortality in the most recent full set of measurements (2018–2024, selected by FIA population evaluation identifier).

## Results

Loss of live aboveground adult tree biomass from natural mortality increased significantly from 2009 to 2024 across the northeastern USA (slope =  $0.029 \text{ Mg ha}^{-1} \text{ year}^{-1}$ ,  $p < 0.001$ ), while biomass loss from forest harvesting did not change significantly (Fig. 2). As a result, harvesting exceeded natural mortality by 5% as a cause of biomass loss in 2009, but natural mortality caused 39% more biomass loss than harvesting by 2024. In fact, natural mortality exceeded harvesting as a cause of tree biomass loss in all states except Maine and Virginia over the most recent set of subplot measurements, and insect-related mortality alone exceeded harvesting in four states (Connecticut, Massachusetts, New Jersey, and Rhode Island; Table A1). Natural mortality increased from 2009 to 2024 in eight states, whereas biomass loss due to harvesting did not change significantly in any state (Fig. 1, Table A1). Biomass loss from natural mortality and harvesting were negatively correlated at the state

**Fig. 3.** Occurrence of harvesting and natural disturbance (percentage of forest inventory subplot measurements per year) by levels of severity (percentage of live aboveground tree biomass loss, panels). Text indicates slope estimates from Sen's slope tests with Holm-corrected  $p$ -values from Mann-Kendall tests.



level ( $r = -0.64$ ,  $p = 0.004$ , Spearman rank correlation). Reserves, which were analyzed separately, had dramatically less harvesting than nonreserves and therefore lower combined biomass loss from natural causes and harvesting. However, reserves also had 48% greater biomass loss from natural mortality than nonreserves and experienced more frequent moderate–high-severity natural disturbance (Figs. A1 and A2).

In terms of tree biomass loss across the most recent set of subplot measurements, 49% of mortality was attributed to unknown causes, 22% to insects, 13% to weather, 9% to disease, 6% to vegetation, and <1% to fire and animals. Mortality from insects increased significantly ( $p < 0.01$ , Mann-Kendall test, Table A2) with no other significant trends in other causes of natural mortality. A supplementary condition-level analysis similarly showed significant increases in natural disturbances driven by both insects and disease, along with a concurrent decrease in harvesting (Table A3, Fig. A3).

Analyzing disturbances causing at least 25% loss in live aboveground tree biomass further suggested that the importance of natural disturbance has increased relative to harvesting due to significant increases in occurrence of natural disturbance and nonsignificant decreases in occurrence of harvesting (Fig. 3). Natural mortality made up the majority of disturbances causing 25%–50% and 50%–75% biomass loss, with the gap between natural disturbance and harvesting increasing over time. Harvesting comprised the majority of high-severity ( $\geq 75\%$  biomass loss) disturbance, but the gap between high-severity harvesting and natural disturbance narrowed over time.

## Discussion

Although northeastern USA forests have not experienced disturbance events at the scale and severity of wildfires,

droughts and insect outbreaks elsewhere in the country (Anderegg et al. 2022), we nonetheless found that occurrence of moderate–high-severity natural disturbance has increased over the past two decades in northeastern USA forests along with tree biomass loss from natural mortality. Meanwhile, occurrence of moderate to high-severity forest harvests declined even as rates of tree biomass harvested did not change, consistent with a multidecadal shift in eastern and northern USA forests away from high-severity harvests toward partial harvests in which a minority of biomass is removed (Canham et al. 2013; Russell et al. 2025). As a result, total biomass loss increased from  $2.34 \text{ Mg ha}^{-1} \text{ year}^{-1}$  in 2009 to  $2.71 \text{ Mg ha}^{-1} \text{ year}^{-1}$  in 2024 with the contribution of natural tree mortality rising from 49% to 58%, challenging the longtime paradigm of forest harvesting as the dominant disturbance in northeastern USA forests (Canham et al. 2013).

We observed a substantial increase in tree mortality attributed to insects that accounts for the majority of the overall increase in tree mortality from 2009 to 2024 in northeastern USA forests. An increase in insect-caused tree mortality is consistent with substantial biomass losses from insect invasions previously identified in the region (Fei et al. 2019), including from hemlock woolly adelgid (*Adelges tsugae*) and emerald ash borer (*Agrilus planipennis*). However, tree mortality is typically the result of multiple interacting stressors, and other factors may contribute to elevated tree mortality in the region including drought and extreme weather events, effects of forest fragmentation and growth of the wildland–urban interface (Sonti et al. 2023), competition from invasive plants (Golivets et al. 2019), and emerging threats such as beech leaf disease (Reed et al. 2022). We also found that natural tree mortality was 48% greater in reserves than nonreserves across the northeastern USA (Fig. A1), in apparent contrast to European temperate forests where reserves correspond with reduced natural disturbance and mortal-

ity (Idoate-Lacasia et al. 2025; Krüger et al. 2025). While the value of reserves extends well beyond biomass, our results highlight that the issue of increased natural mortality in the northeastern USA is not limited to managed forests.

Our results show that harvesting remains an important component of tree biomass loss and disturbance in northeastern USA forests. Indeed, applying silvicultural techniques through an ecological or adaptation lens provides an opportunity to reduce impacts of global change on important cultural and ecological values (D'Amato and Palik 2021), including in cases where natural disturbance and harvesting intersect such as salvage logging and proactive management in anticipation of pest and pathogen impacts (Higgins et al. 2025). However, our results support mitigation and recovery from natural disturbance as elements of forest policy and management strategies. Unfortunately, the areas where we identified high and increasing rates of tree biomass loss from natural mortality, largely in the Mid-Atlantic region and southern New England, also face acute tree regeneration challenges that threaten forest recovery (Miller and McGill 2019; Harris et al. 2024). Addressing these challenges may involve managing deer browse impacts (Harris et al. 2025), controlling competing vegetation including both native and nonnative species, and strategic tree planting. Given the strong ecological, cultural, and economic impacts of natural disturbance on temperate forests and the expectation that these impacts will worsen as global change impacts intensify, strategies targeted at resistance and recovery from natural disturbance are likely to become increasingly important in the northeastern USA (Anderegg et al. 2022; Mohr et al. 2025).

## Acknowledgements

We thank the field crews and employees of the USDA Forest Inventory and Analysis program, without whom this work would not be possible, and we thank Randall Morin and Scott Pugh for technical advice. This project was supported by the Northeastern States Research Cooperative through funding made available by the USDA Forest Service. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or US Government determination or policy.

## Article information

### History dates

Received: 7 November 2025

Accepted: 19 February 2026

Version of record online: 7 April 2026

### Copyright

© 2026 Authors Harris and D'Amato. Permission for reuse (free in most cases) can be obtained from [copyright.com](https://copyright.com).

### Data availability

This work utilizes public data from the national forest inventory, which is available from the USDA Forest Service FIA DataMart (<https://apps.fs.usda.gov/fia/datamart/datamart.html>). Code is available upon request.

## Author information

### Author ORCIDs

Lucas B. Harris <https://orcid.org/0000-0002-1416-5645>

Anthony W. D'Amato <https://orcid.org/0000-0002-2570-4376>

### Author contributions

Conceptualization: LBH, AWD

Formal analysis: LBH

Methodology: LBH, MAP, AWD

Writing – original draft: LBH

Writing – review & editing: MAP, AWD

### Competing interests

The authors declare there are no competing interests.

### Funding information

This work was supported by the Northeastern States Research Cooperative (grant number 23DG11242311-020).

## References

- Anderegg, W.R.L., Chegwidden, O.S., Badgley, G., Trugman, A.T., Cullenward, D., Abatzoglou, J.T., et al. 2022. Future climate risks from stress, insects and fire across US forests. *Ecol. Lett.* **25**(6): 1510–1520. doi:10.1111/ele.14018. PMID: 35546256.
- Bechtold, W.A., and Patterson, P.L. (Editors). 2005. The enhanced forest inventory and analysis program—national sampling design and estimation procedures. USDA Forest Service Southern Research Station General Technical Report. SRS-80, Asheville, NC, USA.
- Canham, C.D., Rogers, N., and Buchholz, T. 2013. Regional variation in forest harvest regimes in the northeastern United States. *Ecol. Appl.* **23**(3): 515–522. doi:10.1890/12-0180.1. PMID: 23734482.
- D'Amato, A.W., and Palik, B.J. 2021. Building on the last “new” thing: exploring the compatibility of ecological and adaptation silviculture. *Can. J. For. Res.* **51**(2): 172–180. doi:10.1139/cjfr-2020-0306.
- Faison, E.K., Masino, S.A., and Moomaw, W.R. 2023. The importance of natural forest stewardship in adaptation planning in the United States. *Conserv. Sci. Pract.* **5**(6). doi:10.1111/csp2.12935.
- Fei, S., Morin, R.S., Oswalt, C.M., and Liebhold, A.M. 2019. Biomass losses resulting from insect and disease invasions in US forests. *Proc. Natl. Acad. Sci. U.S.A.* **116**(35): 17371–17376. doi:10.1073/pnas.1820601116. PMID: 31405977.
- Fitts, L.A., Domke, G.M., and Russell, M.B. 2022. Comparing methods that quantify forest disturbances in the United States' national forest inventory. *Environ. Monit. Assess.* **194**(4): 304. doi:10.1007/s10661-022-09948-z. PMID: 35348883.
- Golivets, M., Woodall, C.W., and Wallin, K.F. 2019. Functional form and interactions of the drivers of understory non-native plant invasions in northern US forests. *J. Appl. Ecol.* **56**(12): 2596–2608. doi:10.1111/1365-2664.13504.
- Gray, A., Brandeis, T., Shaw, J., McWilliams, W., and Miles, P. 2012. Forest inventory and analysis database of the United States of America (FIA). *Biodivers. Ecol.* **4**(Jovan): 225–231. doi:10.7809/b-e.00079.
- Hanson, J.J., and Lorimer, C.G. 2007. Forest structure and light regimes following moderate wind storms: implications for multi-cohort management. *Ecol. Appl.* **17**(5): 1325–1340. doi:10.1890/06-1067.1. PMID: 17708211.
- Harris, L.B., Pastore, M.A., and D'Amato, A.W. 2025. Effects of browsing by white-tailed deer on tree regeneration vary by ontogeny and palatability in forests of the northeastern USA. *Forest Ecol. Manag.* **593**: 122906. doi:10.1016/j.foreco.2025.122906.
- Harris, L.B., Woodall, C.W., and D'Amato, A.W. 2024. Sapling recruitment as an indicator of carbon resiliency in forests of the northern USA. *Ecol. Evol.* **14**: e70077. doi:10.1002/ece3.70077. PMID: 39114162.
- Higgins, H., D'Amato, A.W., and Siegert, N.W. 2025. Effects of harvest treatments anticipating emerald ash borer invasion on northern

hardwood forests in New England, USA. *Forest Ecol. Manag.* **588**. doi:10.1016/j.foreco.2025.122748.

Idoate-Lacasia, J., Stillhard, J., Portier, J., Bigler, C., Bugmann, H., Nagel, T.A., et al. 2025. Trends in background mortality in unmanaged forests across Europe over the last century. *J. Ecol.* **113**: 2905–2920. doi:10.1111/1365-2745.70135.

Krüger, K., Senf, C., Hagge, J., and Seidl, R. 2025. Setting aside areas for conservation does not increase disturbances in temperate forests. *J. Appl. Ecol.* **62**(5): 1271–1281. doi:10.1111/1365-2664.70036.

Lorimer, C.G., and 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**(1–2): 41–64. doi:10.1016/S0378-1127(03)00245-7.

Miller, K.M., and McGill, B.J. 2019. Compounding human stressors cause major regeneration debt in over half of eastern US forests. *J. Appl. Ecol.* **56**(6): 1355–1366. doi:10.1111/1365-2664.13375.

Miller, K.M., Perles, S.J., Schmit, J.P., Matthews, E.R., Weed, A.S., Comiskey, J.A., et al. 2023. Overabundant deer and invasive plants drive widespread regeneration debt in eastern United States national parks. *Ecol. Appl.* (January): e2837. doi:10.1002/eap.2837.

Mohr, J.S., Bastit, F., Grünig, M., Knoke, T., Rammer, W., Senf, C., et al. 2025. Rising cost of disturbances for forestry in Europe under climate change. *Nat. Clim. Chang. Nat. Res.* doi:10.1038/s41558-025-02408-9.

Morreale, L.L., Thompson, J.R., Tang, X., Reinmann, A.B., and Hutrya, L.R. 2021. Elevated growth and biomass along temperate forest edges. *Nat. Commun.* **12**(1). doi:10.1038/s41467-021-27373-7. PMID: 34893596.

Pohlert, T. 2020. Trend: non-parametric trend tests and change-point detection. R package version 1. 1. (4). Available from <https://cran.r-project.org/package=trend>.

Qiu, S., Zhu, Z., Yang, X., Woodcock, C.E., Fahey, R.T., Stehman, S., et al. 2025. A shift from human-directed to undirected wild land disturbances in the USA. *Nat. Geosci. Nat. Res.* doi:10.1038/s41561-025-01792-3.

Reed, S.E., Volk, D., Martin, D.K.H., Hausman, C.E., Macy, T., Tomon, T., and Cousins, S. 2022. The distribution of beech leaf disease and the causal agents of beech bark disease (*Cryptococcus fagisuga*, *Neonectria faginata*, *N. ditissima*) in forests surrounding Lake Erie and future implications. *Forest Ecol. Manag.* **503**. doi:10.1016/j.foreco.2021.119753.

Russell, M.B., Chamberlain, C.J., Riley, L., Mushegian, N.A., Gunn, J.S., Belair, E.P., and Busby, S.U. 2025. Characterizing timber harvest occurrence and intensity to inform forest carbon management across the eastern United States. *Front. For. Glob. Change*, **8**. doi:10.3389/ffgc.2025.1594324.

Sen, P.K. 1968. Estimates of the regression coefficient based on Kendall's tau. *J. Am. Stat. Assoc.* **63**(324): 1379–1389. doi:10.1080/01621459.1968.10480934.

Sonti, N.F., Riemann, R., Mockrin, M.H., and Domke, G.M. 2023. Expanding wildland-urban interface alters forest structure and landscape context in the northern United States. *Environ. Res. Lett.* **18**(1). doi:10.1088/1748-9326/aca77b.

Vickers, L.A., McWilliams, W.H., Knapp, B.O., D'Amato, A.W., Dey, D.C., Dickinson, Y.L., et al. 2019. Are current seedling demographics poised to regenerate northern US forests? *J. For.* **117**(6): 592–612. doi:10.1093/jofore/fvz046.

Westfall, J.A., Coulston, J.W., Gray, A.N., Shaw, J.D., Radtke, P.J., Walker, D.M., et al. 2024. A national-scale tree volume, biomass, and carbon modeling system for the United States. USDA Forest Service General Technical Report WO-104. Washington, D.C., U.S.A. doi:10.2737/WO-GTR-104.

## Appendix A

**Table A1.** Annual aboveground biomass loss (Mg ha<sup>-1</sup>) from adult trees due to total natural mortality, insects and unknown causes, and harvesting over the most recent panel of measurements in states of the northeastern USA (2018–2024), with trends in annual natural mortality (Sen's slope and Holm-corrected *p*-values from Mann–Kendall tests) evaluated using the full time series of annual inventory plot remeasurements available for each state (2004–2024).

| State         | Mortality trends ( <i>p</i> -value) | Natural (all) | Insects | Unknown | Harvesting* |
|---------------|-------------------------------------|---------------|---------|---------|-------------|
| Connecticut   | 0.135 (0.018)                       | 2.297         | 1.257   | 0.335   | 0.500       |
| Delaware      | 0.044 (0.929)                       | 1.749         | 0.077   | 0.998   | 0.846       |
| Illinois      | 0.058 (0.048)                       | 2.341         | 0.39    | 1.400   | 0.681       |
| Indiana       | 0.078 (0.001)                       | 2.489         | 0.824   | 1.094   | 0.945       |
| Maine         | 0.006 (0.929)                       | 0.889         | 0.001   | 0.839   | 1.177       |
| Maryland      | 0.055 (0.423)                       | 2.157         | 0.163   | 1.554   | 0.781       |
| Massachusetts | 0.084 (0.008)                       | 2.025         | 0.858   | 0.430   | 0.573       |
| Michigan      | 0.019 (0.423)                       | 1.278         | 0.342   | 0.614   | 1.184       |
| New Hampshire | 0.003 (0.929)                       | 1.191         | 0.068   | 0.724   | 1.084       |
| New Jersey    | 0.085 (0.021)                       | 2.124         | 0.836   | 1.047   | 0.228       |
| New York      | 0.023 (0.87)                        | 1.399         | 0.294   | 0.802   | 0.966       |
| Ohio          | 0.041 (0.153)                       | 1.843         | 0.681   | 0.949   | 0.864       |
| Pennsylvania  | 0.065 (<0.001)                      | 1.932         | 0.517   | 1.034   | 1.234       |
| Rhode Island  | 0.235 (0.028)                       | 3.578         | 2.377   | 0.493   | 0.706       |
| Vermont       | 0.007 (0.929)                       | 1.333         | 0.062   | 0.516   | 0.803       |
| Virginia      | 0.023 (0.041)                       | 1.609         | 0.258   | 0.081   | 2.326       |
| West Virginia | 0.021 (0.153)                       | 1.615         | 0.368   | 1.016   | 0.784       |
| Wisconsin     | 0.012 (0.056)                       | 1.165         | 0.138   | 0.547   | 1.116       |

\*Note that no significant (*p* < 0.05) trends in biomass loss from harvesting were observed at the state level.

**Table A2.** Estimated trends ( $\text{Mg ha}^{-1} \text{ year}^{-1}$ ) in adult aboveground tree biomass loss due to harvesting, natural mortality and its components across northeastern USA forests from Sen's slope tests with Holm-corrected  $p$ -values from Mann-Kendall tests.

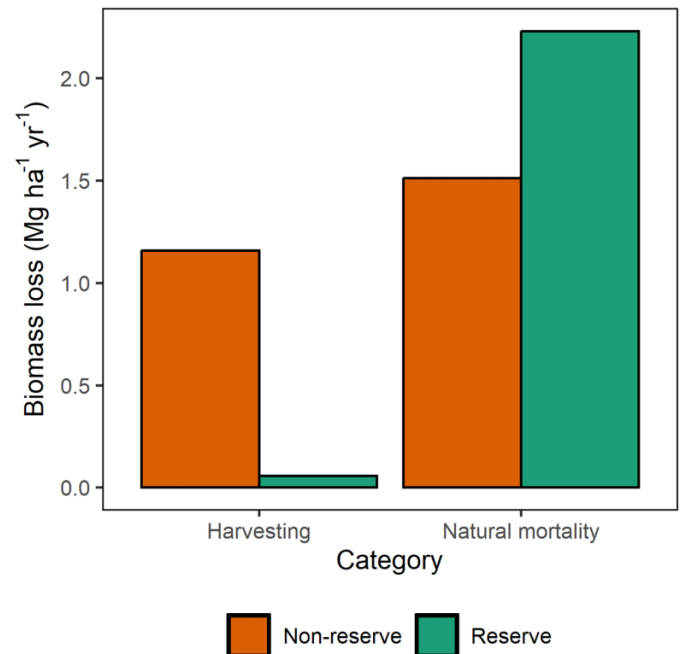
| Category                  | Nonreserves |            | Reserves* |            |
|---------------------------|-------------|------------|-----------|------------|
|                           | Estimate    | $p$ -value | Estimate  | $p$ -value |
| Insects                   | 0.022       | <0.0001    | 0.024     | 0.0034     |
| Disease                   | 0           | 1          | -0.005    | 1          |
| Fire                      | 0           | 1          | 0         | 1          |
| Animals                   | 0           | 1          | 0         | 1          |
| Weather                   | -0.003      | 0.6867     | -0.013    | 1          |
| Vegetation                | 0.002       | 0.2566     | 0.001     | 1          |
| Unknown                   | 0.007       | 0.1517     | 0.024     | 1          |
| Natural mortality (total) | 0.029       | <0.0001    | 0.033     | 0.5192     |
| Harvesting                | 0.004       | 1          | 0         | 1          |

\*Subplots in reserves where harvesting is restricted made up 5.9% of measurements and were analyzed separately.

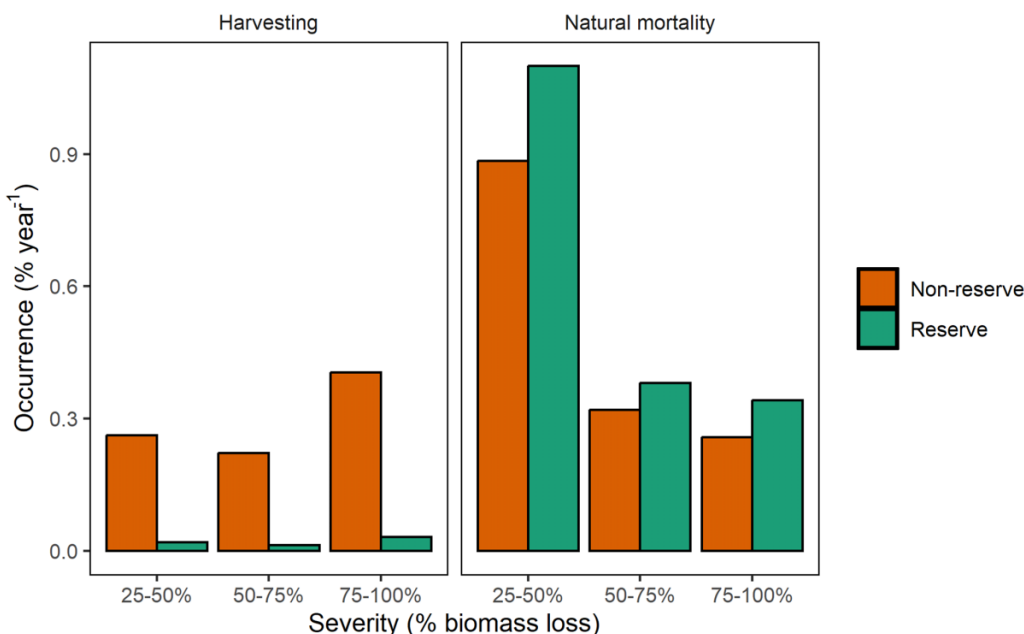
**Table A3.** Estimated trends in natural disturbance and harvesting occurrence ( $\% \text{ year}^{-1}$ ) from Sen's slope tests with Holm-corrected  $p$ -values from Mann-Kendall tests, based on condition-level primary disturbance and treatment codes.

| Category                    | Estimate | $p$ -value |
|-----------------------------|----------|------------|
| Animals                     | -0.007   | 0.3833     |
| Disease                     | 0.069    | <0.0001    |
| Fire                        | -0.001   | 0.3833     |
| Geologic                    | -0.006   | 0.1283     |
| Insects                     | 0.214    | <0.0001    |
| Vegetation                  | -0.006   | 0.0681     |
| Weather                     | -0.029   | 0.0023     |
| Natural disturbance (total) | 0.221    | <0.0001    |
| Harvesting                  | -0.016   | 0.0395     |

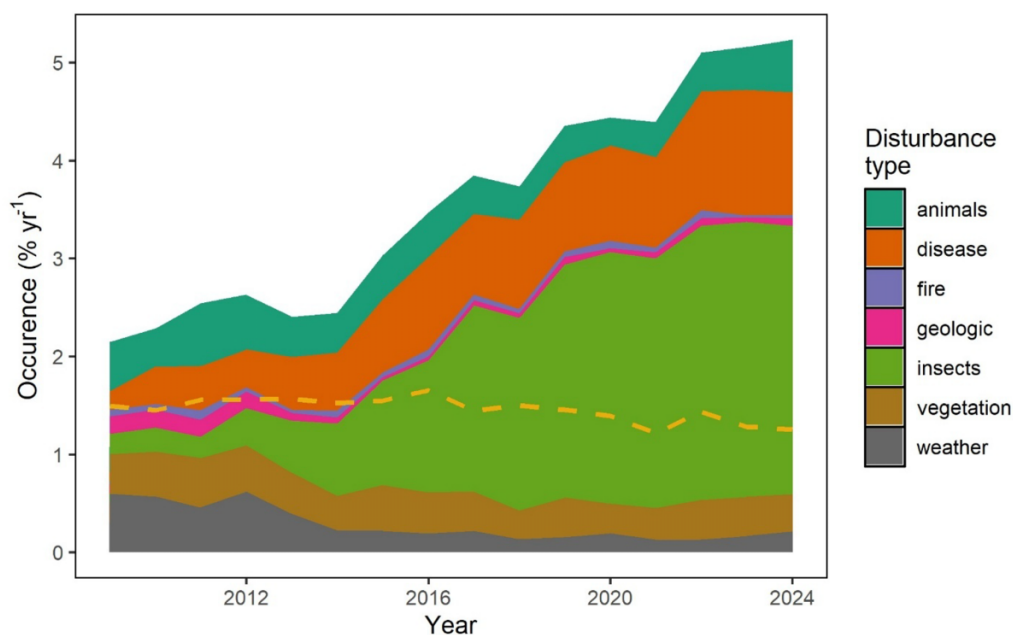
**Fig. A1.** Aboveground adult tree biomass loss from forest harvesting and natural mortality by reserve status from the most recent set of subplot measurements (2018–2024) across northeastern USA forests.



**Fig. A2.** Occurrence of moderate to high-severity disturbance by reserve status from the most recent set of subplot measurements (2018–2024) across northeastern USA forests. Severity categories are defined by percentage of adult aboveground live tree biomass loss.



**Fig. A3.** Annual occurrence of different types of natural disturbance as well as forest harvesting (dashed yellow line) quantified from condition-level primary disturbance and treatment codes. See Table A3 for estimated annual trends and *p*-values. The Forest Inventory and Analysis program defines condition-based disturbances as  $\geq 0.4$  ha in size and impacting  $\geq 25\%$  of trees (mortality and damage), and cutting (i.e., harvesting) as harvests affecting  $\geq 0.4$  ha.



Can. J. For. Res. Downloaded from cdnservicepub.com by UNIVERSITY OF VERMONT on 04/08/26 For personal use only.