ARTICLE

Contemporary status, distribution, and trends of mixedwoods in the northern United States[1]

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Abstract: As interest in managing and maintaining mixedwood forests in the northern United States (US) grows, so does the importance of understanding their abundance and distribution. We analyzed Forest Inventory and Analysis data for insights into mixedwood forests spanning 24 northern US states from Maine south to Maryland and westward to Kansas and North Dakota. Mixedwoods, i.e., forests with both hardwoods and softwoods present but neither exceeding 75%–80% of composition, comprise more than 19 million hectares and more than one-quarter of the northern US forest. They are most common in the Adirondack – New England, Laurentian, and Northeast ecological provinces but also occur elsewhere in hardwood-dominated ecological provinces. These mixtures are common even within forest types nominally categorized as either hardwood or softwood. The most common hardwoods within those mixtures were species of *Quercus* and *Acer*, and the most common softwoods were species of *Pinus*, *Tsuga*, and *Juniperus*. Although mixedwoods exhibited stability in total area during our analysis period, hardwood saplings were prominent, suggesting widespread potential for eventual shifts to hardwood dominance in the absence of disturbances that favor regeneration of the softwood component. Our analyses suggest that while most mixedwood plots remained mixedwoods, harvesting commonly shifts mixedwoods to either hardwood- or softwood-dominated cover types, but more specific information is needed to understand the causes of these shifts.

Key words: hardwood, softwood, deciduous, coniferous, Forest Inventory and Analysis (FIA).

Résumé : Au fur et à mesure qu'augmente l'intérêt pour l'aménagement et le maintien des forêts mixtes dans le nord des États-Unis, la compréhension de leur abondance et de leur répartition devient de plus en plus importante. Dans le but d'obtenir de l'information, nous avons analysé les données du programme d'inventaire forestier et d'analyse portant sur les forêts mixtes de 24 États du nord des États-Unis, à partir du Maine vers le sud jusqu'au Maryland et vers l'ouest jusqu'au Kansas et au Dakota du Nord. Les forêts mixtes, c'est-à-dire les forêts composées à la fois de feuillus et de résineux, dont la proportion n'excède pas 75 à 80 % dans un cas comme dans l'autre, représentent plus de 19 millions d'hectares, ce qui correspond à plus du quart des forêts du nord des États-Unis. Elles sont plus fréquentes dans les provinces écologiques des Adirondacks en Nouvelle-Angleterre, Laurentienne et du Nord-Est, mais elles sont aussi présentes ailleurs dans les provinces écologiques dominées par les feuillus. Les forêts mixtes sont courantes même dans les types forestiers catégorisés nominalement comme étant feuillus ou résineux. Les feuillus les plus courants dans ces forêts sont des espèces des genres *Quercus* et *Acer* alors que les résineux les plus courants sont des espèces des genres *Pinus*, *Tsuga* et *Juniperus*. Bien que la superficie totale des forêts mixtes soit demeurée stable au cours de notre période d'analyse, les gaules de feuillus étaient prédominantes, ce qui indique que la composition d'une forte proportion de ces forêts pourrait tendre vers une dominance des feuillus s'il n'y a pas de perturbations favorisant la régénération de la composante résineuse. Nos analyses indiquent que même si la plupart des parcelles de forêts mixtes sont demeurées des forêts mixtes, la récolte de bois modifie généralement la composition des forêts mixtes vers des types de couvert dominés par des feuillus ou des résineux, mais la compréhension des causes de ces changements nécessite de l'information plus spécifique. [Traduit par la Rédaction]

Mots-clés : feuillus, résineux, espèces décidues, conifères, programme d'inventaire forestier et d'analyse (FIA).

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Introduction

Forests with both hardwoods and softwoods (i.e., generally broadleaf, deciduous, and needle-leaf, evergreen trees, respectively) present but neither exceeding 75%–80% of basal area, crown cover, or other metric are known as "mixedwoods" (Helms 1998). There is a growing recognition of the value of mixed species forests, and more specifically those with mixedwood composition, throughout the northern hemisphere due to their potential for increased productivity and carbon storage, climate change adaptation, resistance to forest insects and diseases, and market flexibility relative to pure stands (Kabrick et al. 2017; Pretzsch and Zenner 2017; A.W. D'Amato and D.C. Dey, unpublished). This has led to increasing interest in their ecology (Kelty et al. 1992; Kern et al. 2021), health (MacLean and Clark 2021), and silviculture (Bauhus et al. 2017; Kabrick et al. 2017; Guldin 2019*a*; Kenefic et al. 2021), particularly in the northern United States (US) and Canada, where it has been estimated that 17%–19% of forest is a mixedwood cover type (North American Forest Commission 2017; Smith et al. 2018).

Growing recognition and interest in mixedwoods have highlighted the many gaps in our understanding of temperate mixedwood stand dynamics, including their successional trends and the influences of forest management and other disturbances. Furthermore, the prevalence and composition of mixedwoods are thought to be changing, with increases in some forest types and regions and decreases in others (e.g., Irland 1999; Foster and D'Amato 2015). Changes such as these may not be apparent in existing summaries of regional inventory data, because mixedwoods are not always identified as distinct forest types. It is thus important to determine their abundance and distribution, as the first step toward sustainable, efficacious mixedwood management. This information, along with temporal trends and demographics, provides managers and policymakers with insight into the potential scope of management opportunities for mixedwood forests in the northern US.

In the northern US, the US Department of Agriculture (USDA) Forest Service, Forest Inventory and Analysis program (FIA) quantifies several tree and forest attributes such as the area of forestland by forest type (https://www.fia.fs.fed.us). FIA inventories generate unique and powerful datasets that are well suited for broad-scale analyses to make forest resource estimates and address myriad research questions; however, estimates of the abundance and distribution of mixedwoods are neither provided in standard FIA reports nor readily attainable from summary data. The FIA delineates several established forest types (and broader forest type groups) adapted from Eyre (1980) using a classification algorithm (Arner et al. 2003; Ruefenacht et al. 2008). Some of the forest types inherently reflect softwood–hardwood mixtures, e.g., "shortleaf pine – oak" (*Pinus echinata* – *Quercus*), but a more general "mixedwood" forest type or forest type group is not recognized. Furthermore, the underlying composition of many recognized forest types often meets a mixedwood threshold due to common associates not explicitly in the type name (Kabrick et al. 2020). For example, about one-third of northern US forest identified as "maple–beech–birch" (*Acer*–*Fagus*–*Betula*), the second most abundant forest type group in the northern US, has a sufficient softwood component to qualify as mixedwood (Kabrick et al. 2020).

Despite mixedwoods lacking recognition as a formal forest type, the northern US mixedwood resource can be summarized with tailored analyses of publicly available FIA inventory data. In this paper, our objectives were to (1) summarize the contemporary northern US mixedwood resource and delineate its distribution, including subregional trends and mixedwood types (based on primary softwood species), (2) examine demographics and size distributions of hardwood and softwood components by broad cover types (i.e., hardwood, softwood, mixedwood) and mixedwood types more specifically, and (3) explore recent trends of remeasured inventory plots to gain insights into the short-term stability of broad cover types with and without harvesting and whether the short-term stability of the mixedwood cover type varied by mixedwood type along with harvesting.

Materials and methods

Study region

We define the northern US study region as the 24 states where the national forest inventory is administered by the USDA Forest Service Northern Research Station (Fig. 1). This region encompasses over 240 million (M) hectares of land area (US Census Bureau 2018). This broad area spans a range of climatic conditions with mean minimum temperatures in January that range from −1 to 0 °C north to south, respectively, and mean maximum temperatures in July that range from 22° to 38 °C north to south, respectively (NOAA 2018). Mean annual precipitation generally increases from 250 mm to 1800 mm west to east, respectively (NOAA 2018). Elevation ranges from sea level to over 2200 m (US Geological Survey 2001). The majority of the region is located within the Humid Temperate Domain with prominent ecosystem divisions including Hot Continental and Mountains, Warm Continental and Mountains, Subtropical, and Prairie (Bailey 1994; Cleland et al. 2007; McNab et al. 2007). The western part of the region falls within the Temperate Steppe and Mountains division of the Dry Domain (Bailey 1994; Cleland et al. 2007; McNab et al. 2007). Almost two-thirds of the 74 million forested hectares in this region are oak–hickory (*Quercus*–*Carya*; 26.5 M ha) or maple–beech–birch (18.3 M ha) forest type groups (USDA Forest Service 2019*a*). Those two forest type groups, along with spruce–fir (*Picea*–*Abies*; 6.6 M ha), aspen–birch (*Populus*–*Betula*; 6.3 M ha), elm–ash–cottonwood (*Ulmus*–*Fraxinus*–*Populus*; 5.8 M ha), white–red–jack pines (*Pinus strobus* – *Pinus resinosa* – *Pinus banksiana*; 3.8 M ha), oak–pine (*Quercus*–*Pinus*; 2.4 M ha), and loblolly–shortleaf pines (*Pinus taeda* – *Pinus echinata*; 0.7 M ha) type groups describe about 95% of the region's forests (USDA Forest Service 2019*a*).

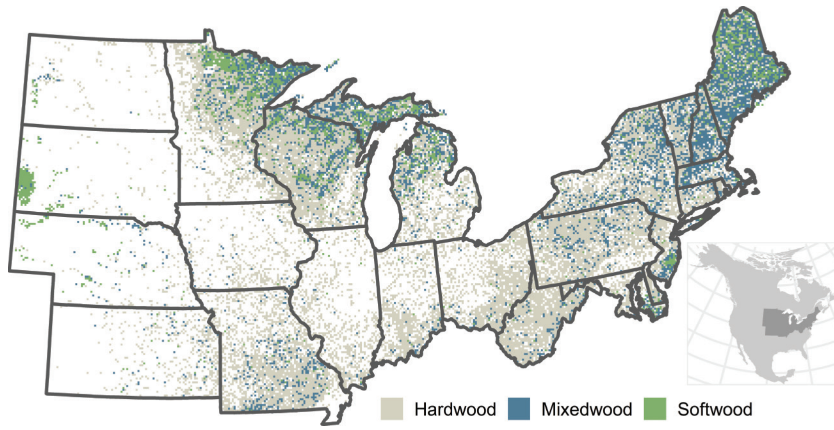
Data source

All inventory data used herein were collected by FIA on northern US forestland and are publicly available (USDA Forest Service 2019*b*). Forestland is defined as areas that are at least 10% stocked by trees of any size, including land that formerly had such tree cover and that will be naturally or artificially regenerated (see Bechtold and Patterson 2005). The FIA national inventory is a uniform grid of sample locations, each representing approximately 2400 ha, though some states and ownerships have been sampled at higher intensities. Field data are collected using a 0.4 ha plot cluster design composed of four circular subplots (7.31 m radius), each containing a circular microplot (2.07 m radius). Several tree attributes, including species, status (live or dead), cause of death (e.g., harvesting), and diameter at breast height (dbh, 1.37 m), are collected on these subplots and microplots. Attributes of trees with a dbh ≥ 12.7 cm are measured on subplots, whereas saplings (2.5–12.6 cm dbh) are measured on microplots. Seedlings (dbh < 2.5 cm), which include hardwoods ≥ 30 cm in height and softwoods ≥ 15 cm in height, are tallied on the same microplots.

Field crews also record a condition class at each location based on several site attributes such as ownership group, forest type, and stand size and (or) maturity. If distinct or contrasting conditions are present at a plot location because of variation in certain attributes, multiple condition classes are delineated and recorded (USDA Forest Service 2019*c*). For each subplot and microplot, the area of all distinct recognized condition classes is recorded, and one of the condition classes is associated with each tree, sapling, and seedling inventoried.

The annualized forest inventory sampling scheme currently used by FIA was adopted across the region from 1999–2004, varying by state (Burrill et al. 2018). Under the annualized inventory, a

Fig. 1. Distribution of forestland by cover type, northern US, 2017. Shading indicates the cover type with the most area within a 50 km^2 cell. Inset: map of study region within North America. Maps created with R statistical software (R Core Team 2019). US state boundaries from US Census Bureau data (www.census.gov) via the maps package (Becker et al. 2018) for R statistical software.



subset of FIA plots is measured every year so that all plots in a state are measured over a 5- to 7-year period, and each plot is remeasured after another 5–7 years (Bechtold and Patterson 2005). Under this sampling scheme, FIA identifies evaluation datasets (EVALID codes) for each state that can be used to select the most recent complete set of statewide measurements relevant to various attributes of interest in a given year (Bechtold and Patterson 2005; Pugh et al. 2018). In Missouri, for example, a current area evaluation dataset for 2017 included all plots measured from 2011–2017, whereas the 2018 current area evaluation dataset included 2012–2018 measurements. At the time of data acquisition (April 2019), current area evaluation datasets were publicly available for 2005–2017 across all 24 states in the study region (USDA Forest Service 2019*b*).

Defining mixedwood and mixedwood types

In our analyses, a given plot condition (objectives 1 and 2) or plot (objective 3) was designated a mixedwood cover type when both hardwood and softwood species were present as stems ≥ 12.7 cm dbh and each comprised ≥20% of the basal area or tree density (number of trees) among stems ≥ 12.7 cm dbh. Alternative cover types included "hardwood" or "softwood" depending on which component exceeded 80% composition. The same method was used to categorize saplings in analyses that compared cover type and composition among sapling stems (2.5–12.6 cm dbh).

We delineated 10 mixedwood types according to the primary softwood species (or species group) per basal area (dbh ≥ 12.7 cm). This was consistent with recent syntheses of mixedwood silviculture reporting that the regeneration ecology and silvics of the primary softwood species should often be prioritized during management activities to perpetuate mixedwood compsition (Kabrick et al. 2017; Kenefic et al. 2021). Four mixedwood types were identified using common single softwood species: *Pinus strobus* (white pine), *Tsuga canadensis* (hemlock), *Pinus resinosa* (red pine), and *Pinus banksiana* (jack pine). Three types were identified using all members of common genera: *Abies* (fir, almost exclusively *A. balsamea*, rarely *A. concolor* or *A. fraseri*), *Picea* (spruce, usually *P. rubens*, *P. glauca*, or *P. mariana*, sometimes *P. pungens*), and *Juniperus* (juniper, usually *J. virginiana*, sometimes *J. scopulorum*). The yellow pine type included mixedwoods where the primary softwood component was usually *Pinus echinata*, *P. virginiana*, or *P. rigida*, but sometimes *P. taeda*, *P. pungens*, or *P. serotina*. The white-cedar group included mixedwoods where the primary softwood component was usually *Thuja occidentalis*, but sometimes *Chamaecyparis thyoides*. The final group, "Misc.", included all remaining mixedwoods where the primary softwood species was relatively infrequent across the northern US (*Larix laricina*, *Pinus ponderosa*, *Pseudotsuga menziesii*, *Taxodium distichum*) or exotic (other *Larix* spp., *Picea abies*, *Pinus nigra*, *Pinus sylvestris*). Given the disparate nature of the "Misc." type, we omit its mention throughout the Results and Discussion sections but include its results in all relevant tables and figures. We stress that the 10 mixedwood types delineated in our analysis are not recognized "forest types" sensu Eyre (1980) and note that the species naming convention used for the types was utilitarian for simplicity in this broad-scale analysis. Other publications more strictly focused on certain assemblages may use different nomenclature.

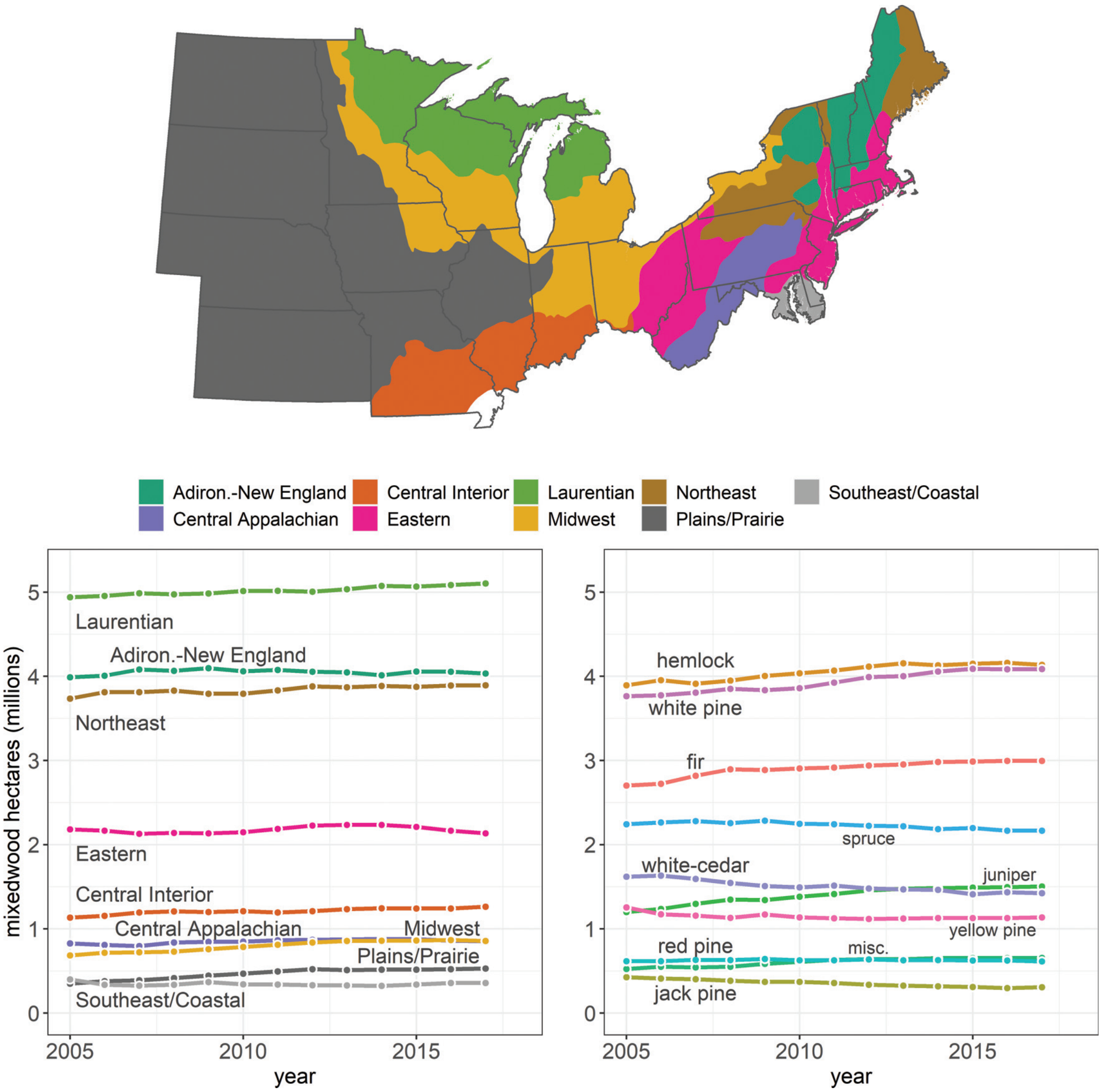
Analysis

We used the 2017 "current area, current volume" evaluation datasets for all 24 states (n = 40 684 FIA plots) to estimate the current northern US forest area for the various cover types (objective 1). Similarly, our analysis of recent temporal trends in northern US mixedwood area used "current area, current volume" evaluation datasets for each corresponding year from 2005–2017 ($n \approx$ 11 262 mixedwood FIA plots, varying by year). Area estimates were calculated at the plot-condition level when multiple conditions were present on a given plot.

To explore the current spatial distribution of mixedwoods across the study region, we created a systematic grid and summarized the representative area of mixedwood conditions present on all FIA inventory plots within each cell. Cell sizes were 50 km^2 for cover type analysis and 500 km^2 for analysis of mixedwood types. We also obtained estimates of the current mixedwood area for nine prominent ecological provinces (Cleland et al. 2007; McNab et al. 2007); which included seven individual provinces and two aggregate provinces that we formed from geographically adjacent provinces with low sample size (see Fig. 2). The seven individual provinces were the Northeastern Mixed Forest (code 211), Laurentian Mixed Forest (212), Eastern Broadleaf Forest (221), Midwest Broadleaf Forest (222), Central Interior Broadleaf Forest (223), Adirondack – New England Mixed Forest – Coniferous Forest – Alpine Meadow (M211), and Central Appalachian Broadleaf Forest – Coniferous Forest – Meadow (M221). The two aggregate provinces were Southeastern – Coastal Plain Mixed Forest (231, 232) and Prairie–Plains (251, 255, 331, 332, M334).

To examine the demographics and size distributions of hardwood and softwood components by cover types (objective 2), we used the same 2017 "current area, current volume" evaluation dataset from objective 1 for the analysis related to sapling layers and diameter distributions. Our analysis of ingrowth, mortality, and harvest removals used the 2017 "area change, growth,

Fig. 2. Temporal trends in mixedwood area by ecological province (bottom left) and mixedwood type (bottom right), northern US forestland, 2005–2017. Ecological provinces (top) adapted from Cleland et al. 2007; "misc." includes all remaining mixedwoods where the primary softwood species was relatively infrequent across the northern US or an exotic species. Map created with R statistical software (R Core Team 2019). Ecological province boundaries from USDA Forest Service data (https://data.fs.usda.gov/geodata/edw). US state boundaries from US Census Bureau data (www.census.gov) via the maps package (Becker et al. 2018) for R statistical software.



removals, and mortality" evaluation dataset, which included plots that were measured twice over 6–8 years. Ingrowth was defined as a stem less than 12.7 cm dbh that grows into or beyond 12.7 cm dbh at a successive measurement while remaining alive; mortality was defined as a stem with dbh ≥ 12.7 cm that died (non-harvest) between successive measurement periods; harvest was defined as a live stem with a dbh ≥ 12.7 cm that was cut between successive measurements (Bechtold and Patterson 2005).

Our analysis of recent temporal plot-level cover type trends (objective 3) included individual inventory plot locations that had been remeasured at least twice (i.e., ≥three visits) since the national plot design was adopted for a given state (1999–2004 in the study area). For the 32 489 FIA plots that met that criterion, about 38% had been remeasured three times, with the rest remeasured twice. The time from initial to final measurement averaged 12 years across all remeasured plots used. We explored the short-term relative stability of cover types (objective 3) by computing the proportion of plots that experienced a shift in cover type (i.e., hardwood, mixedwood, softwood) with and without harvesting during the analysis period.

We tested whether the probability that a sampled plot classified as mixedwood at the end of the analysis period was statistically influenced by initial cover type (hardwood, mixedwood, or softwood), harvesting (harvested or not), and their interaction through analysis of deviance for a binomial logit generalized linear model (i.e., logistic regression; McCullagh and Nelder 1989) in R statistical software. Analysis of deviance tables are provided as Supplemental material.[2] In this analysis, we first ascertained the potential utility of the overall model by comparing it with a null model (intercept-only) using a likelihood ratio test. If the overall model was superior, we next assessed the statistical significance of the cover type – harvesting interaction term with a type-III

[2]Supplemental material is available with the article at https://doi.org/10.1139/cjfr-2020-0467.

likelihood ratio test via the car package for R statistical software (Fox and Weisberg 2019). We planned pairwise contrasts for harvesting occurrence within each cover type using the emmeans package for R statistical software (Lenth 2020) on occasion of a statistically significant cover type – harvesting interaction to ascertain the harvesting influence within each cover type individually.

Additionally, we investigated whether the proportion of plots that were initially categorized as mixedwoods and maintained a mixedwood composition at the end of the analysis period statistically varied as a function of initial mixedwood type, harvesting (harvested or not), and their interaction. We followed the same procedure outlined in the preceding paragraph, using analysis of deviance for a binomial logit generalized linear model (McCullagh and Nelder 1989). Analysis of deviance tables are provided as Supplemental material.[2] In this analysis, we again ascertained the potential utility of the overall model first by comparing it with a null model (intercept-only) using a likelihood ratio test. If the overall model was superior, we next assessed the statistical significance of the mixedwood type – harvesting interaction term with a type-III likelihood ratio test via the car package (Fox and Weisberg 2019). We planned pairwise contrasts for harvesting occurrence within each mixedwood type using the emmeans package (Lenth 2020) on occasion of a statistically significant mixedwood type – harvesting interaction to ascertain the harvesting influence within each mixedwood type individually.

All data processing and statistical analyses were conducted in R statistical software version 3.6.1 (R Core Team 2019). Our analyses for objective 2, which included stand structure and ingrowth, mortality, and harvest removals, were conducted with the rFIA package for R statistical software (Stanke et al. 2020; Stanke and Finley 2020).

Results

Objective 1: distribution of northern US mixedwood forests

Mixedwoods made up nearly 26% of the northern US forest in 2017 (over 19 M ha; Table 1) and were present in all 24 states that we analyzed (Fig. 1). Hardwood cover types were ubiquitous across the northern US (60% of forests), and softwood forests made up only about 11% of northern US forests (~3% of forests without trees ≥12.7 cm dbh went uncategorized). Three ecological provinces, the Northeast, Laurentian, and Adirondack – New England, together contained over 13 M ha of mixedwood, which was over two-thirds of all northern US mixedwoods (Fig. 2). Mixedwoods were most prevalent in the northeastern and upper Great Lakes states (Fig. 3), where softwood forests also were most common (Fig. 4).

Almost one-third of the northern US mixedwood area was categorized as maple–beech–birch forest type groups (Appendix A, Table A1). Another 16% of northern US mixedwoods were in the oak–hickory forest type group, and other forest type groups with prominent mixedwoods included aspen–birch (12%), oak–pine (12%), white–red–jack pine (10%), and spruce–fir (9%). Mixedwoods with hemlock or white pine as the primary softwood components (per basal area) were the two most common types in the northern US and each encompassed over 4 M ha (Table 1).

Quercus or *Acer* were the most common primary hardwood components for all mixedwood types. *Acer* was the primary hardwood component on 34% of northern mixedwoods (Table 2) This was largely due to *Acer rubrum*, which was the primary hardwood at least twice as often as *Acer saccharum*. *Quercus* was the next most common primary hardwood genus with subgenus *Lobatae* (red oaks) being about twice as common as subgenus *Quercus* (white oaks), which only outranked *Lobatae* in the juniper and yellow pine mixedwoods.

The total area of mixedwood and its proportion of northern US forests appeared stable over the short term (2005–2017) based on annualized inventory data for the entire region (Fig. 2); however, some mixedwood types exhibited varying increasing trends in area, while others exhibited decreasing trends. The area of hemlock mixedwoods increased by nearly 0.24 M ha from 2005–2017, and mixedwoods with white pine, fir, or juniper as the primary softwood components each increased by over 0.28 M ha. Juniper mixedwoods surpassed both yellow pine and white-cedar mixedwoods in area after 2005 and had a relative increase of 25% compared with 6%–11% for the other two. Jack pine mixedwoods exhibited the greatest relative decrease since 2005 (28%), followed by white-cedar mixedwoods (12%) and yellow pine mixedwoods (9%).

Table 1. Mixedwood cover type area by primary softwood component for the northern US, 2017.

Mixedwood type	No. of hectares	Mixedwood area (%)	Forestland area (%)
Hemlock	4134298	21.7	5.6
White pine	4086515	21.6	5.6
Fir	2994019	15.7	4.1
Spruce	2164470	11.4	2.9
Juniper	1502944	7.9	2.0
White-cedar	1424680	7.5	1.9
Yellow pine	1135670	6.0	1.6
Red pine	613848	3.2	0.8
Jack pine	305694	1.6	0.4
Misc.	653887	3.4	0.9
Total	19016024	100.0	25.8

Note: Types were defined according to the species that was the majority softwood component (per basal area, dbh ≥ 12.7 cm). "Misc." includes all remaining mixedwoods where the primary softwood species was relatively infrequent across the northern US or an exotic species.

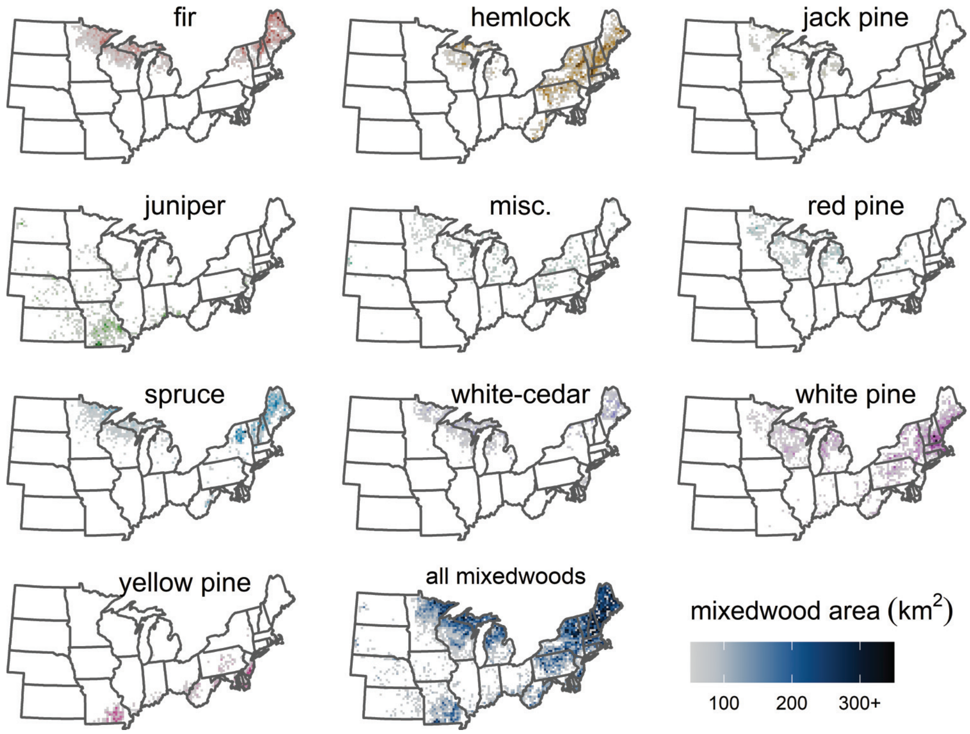
Objective 2: demographics and size distributions

Across the northern US, diameter distributions showed hardwoods to be prominent components of small size classes under all three cover types (Fig. 4). Small diameter hardwoods were common under softwood canopies, but the inverse — small diameter softwoods under hardwood canopies — was relatively rare. However, the diameter distribution of softwoods, especially those classes < 30 cm dbh, showed notably fewer stems under mixedwood canopies than under softwood canopies. We found similar demographic trends in the seedling layer. Under mixedwood canopies, there were almost twice as many seedlings of hardwood versus softwood, despite the FIA threshold height for sampling hardwood seedlings being twice as stringent as softwood (30 cm versus 15 cm height).

Across mixedwood types, disparities among hardwood and softwood components usually occurred in smaller size classes where hardwoods were considerably more abundant than softwoods in 7 of 10 types (Fig. 5). The abundance of softwoods < 10 cm dbh equaled or exceeded that of hardwoods only in mixedwoods with fir, spruce, or white-cedar as primary softwood components. Those three types also had the least disparity in seedling abundances between hardwood and softwood components, but hardwood seedlings were more abundant than softwood seedlings across all types. For the other types, the ratio of hardwood to softwood for seedlings ranged from ≈2:1 for hemlock or white pine mixedwoods to ≥4:1 for jack pine, juniper, red pine, or yellow pine mixedwoods.

The hardwood cover type usually (76%) had a hardwood-dominated sapling layer (Table 3). In the softwood cover type, the sapling composition was more diverse, but the majority (52%) was softwood dominated. In contrast, only about one-third of mixedwoods also had a mixedwood sapling layer. Within mixedwoods, sapling layers

Fig. 3. Distribution of mixedwood forestland by primary softwood component, northern US, 2017. For a given mixedwood type, darker shading depicts a higher magnitude of mixedwood area within a 500 km^2 cell; "misc." includes all remaining mixedwoods where the primary softwood species was relatively infrequent across the northern US or an exotic species. Maps created with R statistical software (R Core Team 2019). US state boundaries from US Census Bureau data (www.census.gov) via the maps package (Becker et al. 2018) for R statistical software.



dominated by hardwood were about twice the area of softwood sapling layers.

Mixedwood sapling layers under mixedwood forests were more prevalent in the Adirondack – New England and Laurentian provinces (Fig. 6). Fir mixedwoods were the only type with a majority of its area (52.3%) comprised of a mixedwood sapling layer (Table 4). Mixedwood sapling layers occupied the most relative forest area for the white-cedar (47.7%), spruce (44.4%), juniper (34.8%), and hemlock (34.3%) mixedwood types. For all other types, more of their area had hardwood-dominated sapling layers, some exceedingly so (yellow pine, 69.8%). Hardwood-dominated sapling layers were at least twice as prevalent in area as softwood sapling layers for 7 of the 10 mixedwood types. Only fir, white-cedar, spruce, or yellow pine mixedwoods had saplings of all kinds absent from <10% of their area.

Analysis of ingrowth, mortality, and harvest on plots remeasured over 5–7 years showed little net population change among large stems, with any density increases from ingrowth (small trees growing beyond a 12.7 cm dbh threshold) nearly offset by density losses from mortality and harvest (Fig. 7). An exception may be the softwood component in softwood cover types, where ingrowth appeared to outpace mortality and harvest. Ingrowth of softwood outpaced mortality and harvest in fir mixedwoods and to a lesser degree in juniper and spruce mixedwoods (Fig. 8). Ingrowth of hardwood appeared to outpace mortality and harvest in the fir, jack pine, and red pine mixedwood types.

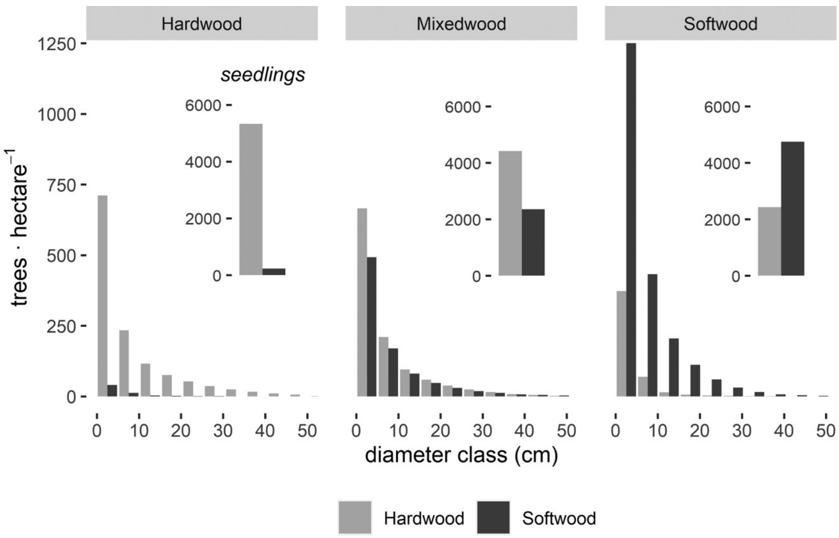
Objective 3: cover type trends of remeasured inventory plots

The cover type of individual plots that were remeasured during the analysis period usually did not shift (Table 5). The probability of a sampled plot being classified as mixedwood at the end of the analysis period modeled as a function of initial cover type (hardwood, mixedwood, or softwood), harvesting (harvested or not), and their interaction was found superior to a null model (intercept only) according to a liklihood ratio test ($\chi^2_{[5]}$, $p < 0.001$). The covertype·harvesting interaction was statistically significant ($\chi^2_{[2]}$, n = 32 489, $p < 0.001$). Harvesting increased the probability that a hardwood or softwood plot would become a mixedwood, but it decreased the probability that a mixedwood plot would stay a mixedwood (Fig. 9). Softwood and mixedwood plots shifted cover type more frequently than hardwoods (Table 5). Nearly all hardwood and softwood plots that shifted became a mixedwood, whereas mixedwoods shifted to either hardwood or softwood at similar rates.

The probability of a mixedwood plot remaining a mixedwood throughout the analysis period modeled as a function of mixedwood type, harvesting (harvested or not), and their interaction was found superior to a null model (intercept only) according to a liklihood ratio test ($\chi^2_{[19]}$, $p < 0.001$). The mixedwood type·harvesting interaction was statistically significantly ($\chi^2_{[9]}$, n = 8793, p = 0.002). Mixedwood plots that shifted cover types did so to hardwood at least twice the rate of softwood for mixedwoods dominated by fir, hemlock, juniper, or yellow pine (Appendix B, Table B1). White-cedar mixedwoods usually shifted to a softwood cover type, while mixedwoods dominated by red pine, spruce, or white pine shifted to hardwood or softwood at similar rates.

Harvested mixedwood plots were less likely to remain a mixedwood than plots that were not harvested. The difference was statistically significant for fir, hemlock, jack pine, spruce, and white pine mixedwood types (Fig. 10). The decrease in likelihood of mixedwood composition after harvesting was most severe for plots that were originally jack pine (80.2% to 52.3%) or spruce (85.4% to 63.0%) mixedwoods. Non-harvested plots that shifted cover types did so to hardwood at a rate at least twice that of softwood for mixedwoods dominated by fir, hemlock, jack pine, juniper, or yellow pine (Appendix B, Table B1). Non-harvested white-cedar

Fig. 4. Average stem diameter distribution for trees and saplings in hardwood, mixedwood, and softwood cover types by component, northern US forestland, 2017. Insets within each panel indicate the number of seedlings (dbh < 2.5 cm) of hardwoods ≥ 30 cm height and softwoods ≥ 15 cm height.



mixedwoods shifted to softwood more often than hardwood, while red pine, spruce, and white pine mixedwoods shifted to hardwood or softwood at similar rates. For mixedwoods dominated by juniper or white-cedar, harvesting magnified the trends in cover type shifts found in non-harvested plots. For jack pine mixedwoods, harvesting largely muted the trends in cover type shifts between hardwood and softwood that were observed in non-harvested plots. While non-harvested red pine mixedwoods shifted to hardwood or softwood at similar rates, harvested red pine mixedwoods shifted to softwood about four times as often as hardwood.

Discussion

Mixedwoods are a major part of the northern US forested landscape. We estimate their regional proportion (26%) to be somewhat greater than the broader North America average of 17%–19% but comparable with the 25% that has been estimated across eastern North American Temperate Continental (26%) and Subtropical Humid (24%) forests (North American Forest Commission 2017; Smith et al. 2018). Mixedwoods of varying assemblages were found throughout the northern US, but for most types analyzed (except juniper or yellow pine mixedwoods), the greatest area and highest concentrations tended to be within the three northernmost ecological provinces (Laurentian, Adirondack – New England, and Northeast). This can be explained by the overlap in the distribution of temperate and boreal species in the northern portion of northeastern North America.

Our analysis indicated short-term regional-scale stability of mixedwood area in the study region from 2005–2017; however, even in the short term, some trends emerged, including a 25% increase in area of juniper-dominated mixedwoods since 2005, a type most prominent in the Central Interior and Plains–Prairie provinces. Juniper encroachment and densification is an ongoing concern in much of the central, western, and southwestern US (Miller et al. 2008; Hanberry et al. 2012; Poulos et al. 2013; Meneguzzo and Liknes 2015). Mixedwoods dominated by juniper or fir were the only two types where ingrowth of softwoods far outpaced their combined mortality and harvest. The fir observation seems to follow the silvics of the species (*Abies balsamea*), which can lead to prolific advance reproduction: frequent, large seeds (Hart 1959) that germinate well on a wide range of substrates (Weaver et al. 2009); relatively low browsing pressure in the southern part of its range in the US (Bergeron et al. 2011; White 2012); and rapid early growth relative to its shade-tolerant associates (Westveld 1928; Moores et al. 2007). Fir has a wide ecological amplitude but is highly susceptible to fire, insects, and disease (Frank 1990) and has increased in fire-dependent pine communities in the Lake States due to fire suppression (D'Amato et al. 2011; Sturtevant et al. 2012). Fire suppression may also have a role in harvested red pine mixedwoods shifting to softwood about four times as often as hardwood by enabling the accumulation of understory fir (D'Amato et al. 2011).

In contrast to the unsurprising increase in juniper and fir mixedwoods, the increased area of hemlock mixedwoods is less easily explained. Extensive mortality of eastern hemlock caused by hemlock wooly adelgid (*Adelges tsugae*), an exotic invasive insect, may be a factor in some parts of the region; model projections and empirical evidence suggest increases in hardwood relative abundance following the invasion of eastern hemlock forests (e.g., Spaulding and Rieske 2010; Mulroy et al. 2019). However, this does not explain the increasing area of hemlock mixedwoods in regions not yet strongly affected by this pest (e.g., the Great Lakes region). The high number of hardwood stems in the small size classes of hemlock mixedwoods could be an indicator of hardwood recruitment into hemlock stands as a mechanism for the increase in hemlock mixedwoods. On the other hand, a greater proportion of late-seral species such has hemlock is probably to be expected with natural dynamics as the forest ages. Further investigation of this, including harvesting trends of hemlock-dominated softwood cover types, is warranted.

There are gaps in our understanding of mixedwood stand dynamics. An open question is whether a mixedwood can be maintained perpetually or if, instead, long-term successional trends eventually favor the more shade-tolerant species of the mixture, with mixedwoods occurring during early or middle stages of secondary succession. Some research indicates that forests with late-successional, shade-tolerant species that can self-replace in absence of major disturbance can be stable for hundreds of years (Frelich and Reich 1999). Kenefic et al. (2021) report that the softwood component of mixedwoods is often the most challenging to regenerate, suggesting that silviculture may need to prioritize treatments based on the regeneration ecology and silvics of the primary softwood to perpetuate the mixedwood (Kabrick et al.

Table 2. Frequency of major hardwood species components by mixedwood types (% of area by mixedwood type) in the northern US, 2017.

	Mixedwood area by type (%)															
						Spruce					Yellow pine					
Dominant hardwood	Fir	Hemlock	Jack pine	Juniper	Red pine	Total[a]	*P. glauca*	*P. rubens*	White-cedar	White pine	Total[b]	*P. echinata*	*P. rigida*	*P. virginiana*	Misc.[c]	All
Acer[d]	37	50	9	4	21	36	7	27	30	39	12	<1	4	4	25	34
A. rubrum	29	34	9	1	16	31	6	23	26	34	11	<1	4	4	19	27
A. saccharum	8	16	0	2	4	5	1	4	4	5	1	<1	0	<1	4	7
Betula[e]	27	16	9	0	8	32	5	24	24	6	1	0	1	0	9	15
B. lenta	16	2	9	<1	7	14	3	7	12	3	<1	0	<1	0	8	7
B. alleghaniensis	10	9	0	0	0	17	1	16	12	1	0	0	0	0	<1	7
Fagus grandifolia	1	7	0	0	0	5	<1	5	1	2	<1	<1	0	<1	0	3
Fraxinus	4	4	1	10	3	3	2	1	22	4	2	<1	<1	1	14	6
Juglandaceae[f]	0	1	0	11	1	0	<1	0	<1	2	4	3	<1	1	1	2
Carya spp.	0	1	0	5	<1	0	0	0	<1	1	4	3	<1	1	0	1
Juglans spp.	0	<1	0	7	<1	<1	<1	0	<1	1	1	0	0	<1	1	1
Populus[g]	26	2	36	2	28	18	11	3	18	10	<1	0	1	<1	19	12
Aspen[h]	24	2	35	0	27	17	10	3	13	10	<1	0	1	<1	17	11
Prunus serotina	2	2	1	2	6	2	1	1	1	4	3	1	1	1	11	3
Quercus[i]	2	15	43	48	30	2	1	1	1	31	62	29	16	11	12	20
Lobatae	2	12	37	18	26	1	1	1	1	23	26	10	9	5	6	13
Quercus	0	3	7	30	4	<1	<1	0	0	8	36	19	7	7	6	7
Ulmus	<1	<1	<1	6	1	<1	<1	0	<1	<1	1	<1	0	<1	4	1
Other	1	3	0	16	2	1	<1	<1	2	2	15	1	4	5	6	4
Total	100	100	100	100	100	100	27	62	100	100	100	34	26	25	100	100

Note: For a given mixedwood type (column), percentages reflect the area where a given hardwood species (row) is the majority hardwood component (per basal area; dbh ≥ 12.7 cm).

[a]Total for listed spruce species and non-specified spruce cases.

[b]Total for listed yellow pine species and non-specified yellow pine cases.

[c]Misc. includes all remaining mixedwoods where the primary softwood species was relatively infrequent across the northern US or an exotic species.

[d]Total across all *Acer* spp., including those listed below.

[e]Total across all *Betula* spp., including those listed below.

[f]Total across all *Juglandaceae* genera, including those listed below.

[g]Total across all *Populus* spp., including those listed below.

[h]*Populus grandidentata* or *P. tremuloides*.

[i]Total across all *Quercus* spp., including the subgenera listed below.

2017). About one-third of the area currently occupied by mixedwoods could conceivably maintain a mixedwood status into the future in the event of an immediate releasing disturbance, based on our analysis of the sapling layers underneath current mixedwoods. Although our assessment is short term and a comprehensive treatment was beyond our scope, findings suggest that some mixedwood types in the study area are more persistent than others. Mixedwoods with fir, spruce, or white-cedar as primary softwood components had more of their area occupied by mixedwood sapling layers and were the only types where softwood saplings were equally or even more abundant than hardwoods. These shade-tolerant, later successional primary softwood species are generally considered more persistent in mixture than those reflecting a land-use legacy (e.g., forest expansion onto retired farm land) or transitional period in stand development (Kenefic et al. 2021). We would expect hemlock to be included in that group as well, but ungulates in the Lake States may dampen the abundance of hemlock saplings and further exacerbate the aforementioned potential for hardwood proliferation in the sapling layer of hemlock mixedwoods (McWilliams et al. 2018).

However, more than half of the current mixedwood area shows potential to transition away from a mixedwood cover type based on the sapling layer analysis, and hardwood-dominated understories were most prominent. Much of this area was juniper or pine mixedwoods, each of which has generally shade-intolerant primary softwood species. These mixedwood types are likely transitional or dependent on disturbances for perpetuation (Kenefic et al. 2021). Mixedwood cover types with ubiquitous hardwood saplings are likely at greater risk of becoming hardwood stands if silvicultural interventions are lacking or disturbances that differentially reduce the hardwood component (e.g., as with outbreaks of emerald ash borer (*Agrilus planipennis*) or gypsy moth (*Lymantria dispar*)) are uncommon.

Future increases in mixedwood area are more likely to come from softwood cover types with partial canopy disturbance that releases naturally established and accumulated hardwood reproduction than from hardwood cover with encroaching softwoods. We observed that softwood and mixedwood plots shifted cover type more frequently than hardwoods. In our analysis, softwood cover types were predominantly located in the Laurentian province and Maine, areas that also exhibited the greatest concentrations of mixedwood sapling layers. Mixedwoods of this sort would fit a transitional development model. Schweitzer et al. (2016) describe the intentional transition from softwood plantation to hardwood forest via this mechanism by favoring the establishment and recruitment of *Quercus* species in *Pinus taeda* plantations with the eventual goal of restoring mixed hardwood stands. Other studies have suggested that at least some mixedwood types may be naturally transitional. For example, in New Brunswick, Amos-Binks et al. (2010) suggested that *Abies balsamea* – tolerant hardwood mixtures may be transitional due to disturbance regime, species, and stand conditions, which complicates objectives to maintain specific proportions of mixedwood and softwood stands.

The potential for hardwood understories to result in shifting cover types also depends on disturbance patterns and the composition and silvical characteristics of the hardwood understory.

Fig. 5. Average stem diameter distribution for trees and saplings in mixedwoods by mixedwood type, northern US forestland, 2017. Insets within each panel indicate the number of seedlings (dbh < 2.5 cm) of hardwoods ≥ 30 cm height and softwoods ≥ 15 height; "misc." includes all remaining mixedwoods where the primary softwood species was relatively infrequent across the northern US or an exotic species.

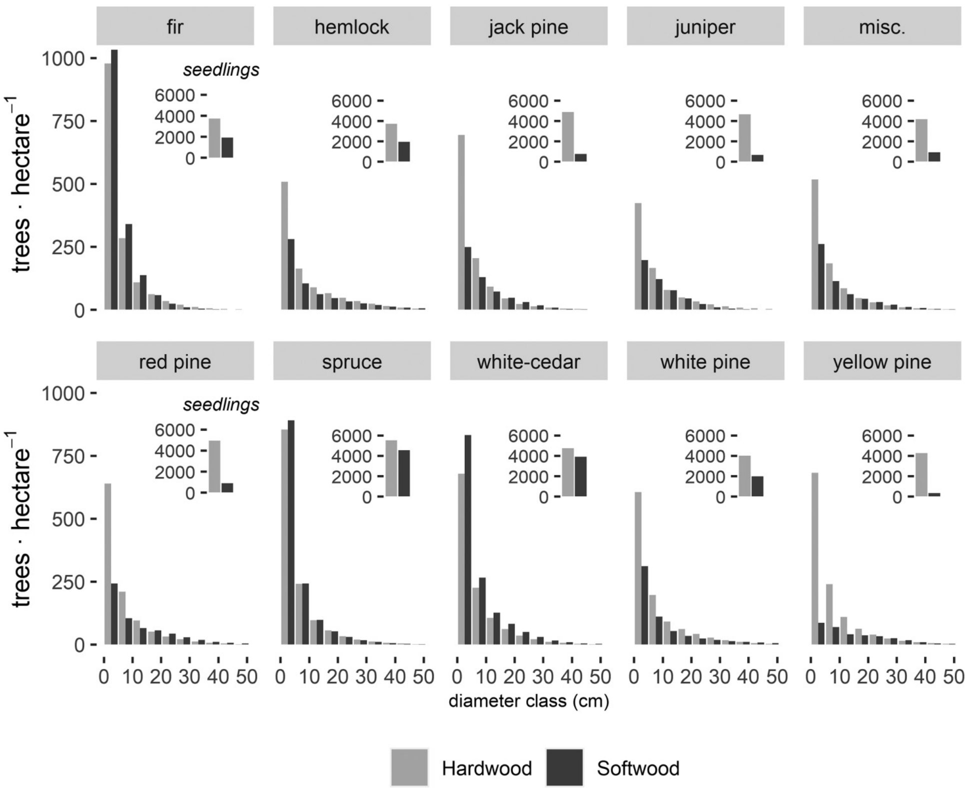


Table 3. Cover type sapling composition contingency table for the northern US, 2017.

	Saplings (% of forestland)			
Cover type	Hardwood	Mixedwood	Softwood	None
Hardwood	76.1	6.4	1.2	16.3
Mixedwood	36.2	35.9	16.9	11.0
Softwood	10.8	21.7	51.6	15.9

Note: For a given cover type (row), percentages reflect the proportion of forestland by sapling composition category (column). Cover type refers to all live trees with a dbh ≥ 12.7 cm; saplings refer to all live trees with a dbh ranging from 2.5 to 12.6 cm.

For example, *Acer rubrum*, which was the most common prominent hardwood associate in later successional mixedwoods, is a species notorious for its understory proliferation and potential to ascend into the canopy of many forest types, especially when historical disturbance regimes are altered (Fei and Steiner 2007; Nowacki and Abrams 2008). Conversely, *Betula alleghaniensis*, another common associate of the later successional mixedwood types, takes more effort to regenerate, especially in mixture with conifers. Success is more likely after treatments that cause moderate disturbance of both forest cover and forest floor (e.g., Prévost and Charette 2015; Raymond and Bédard 2017; Raymond et al. 2018), while severe disturbances (e.g., patch clearcuts) result in intense interspecific competition that limits softwood associates (Prévost et al. 2010). In *Pinus*-dominated softwood or mixedwood cover types, established *Quercus* reproduction, a frequent associate, often outcompetes *Pinus* reproduction without timely, and often multiple, disturbances — typically prescribed fire (Fan et al. 2012; Kabrick et al. 2015; Guldin 2019*b*; Stambaugh et al. 2019).

The demographics and structural trends observed in contemporary mixedwoods support the view that some mixedwoods are likely more dependent on disturbance-driven perpetuation than others (Kabrick et al. 2017; Kenefic et al. 2021). Even in assemblages where relatively light and infrequent disturbances are possible, choosing appropriate silvicultural regimes that can diversify ecological niches both spatially and temporally will be an important determinant of sustainability (Grubb 1977; Coates and Burton 1997; Kneeshaw and Prévost 2007). However, site productivity and land-use legacies complicate shade-tolerance – successional-based notions of stability. Spruce and fir mixedwoods on poor quality sites are transitional even though late-successional softwoods predominate because these "spruce flats" (Westveld 1930) were historically converted to mixedwoods by repeated, heavy partial harvesting that disrupted the small-scale natural disturbance regimes that favor the softwood species (Boucher et al. 2009; Danneyrolles et al. 2019).

Mixedwoods, especially in the northeastern US, are widely thought to be changing due to the legacies of preferential harvesting of softwoods, which removed seed sources. In many cases, these harvests could set back the natural successional process and decrease softwood proportions, because harvesting regimes had a greater frequency and intensity than natural disturbance regimes (e.g., Seymour et al. 2002). We found harvesting statistically increased the probability that a hardwood or softwood plot would become a mixedwood, but it statistically decreased the probability that a mixedwood plot would stay a mixedwood, suggesting room for improvement in current mixedwood management practices, specifically for those where fir, hemlock, jack pine, spruce, and white pine are the prominent softwood component. Those types collectively encompass 72% of

Fig. 6. The proportion of mixedwood cover type with mixedwood sapling layer in 50 km^2 cells, northern US, 2017. Map created with R statistical software (R Core Team 2019). US state boundaries from US Census Bureau data (www.census.gov) via the maps package (Becker et al. 2018) for R statistical software.

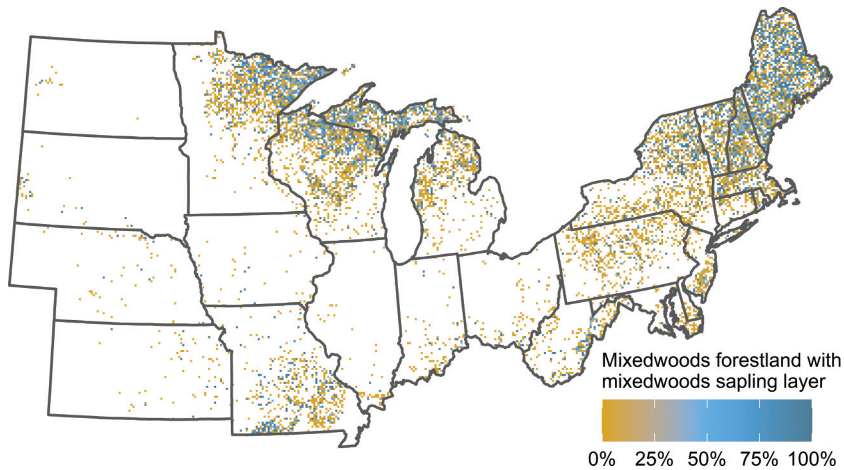
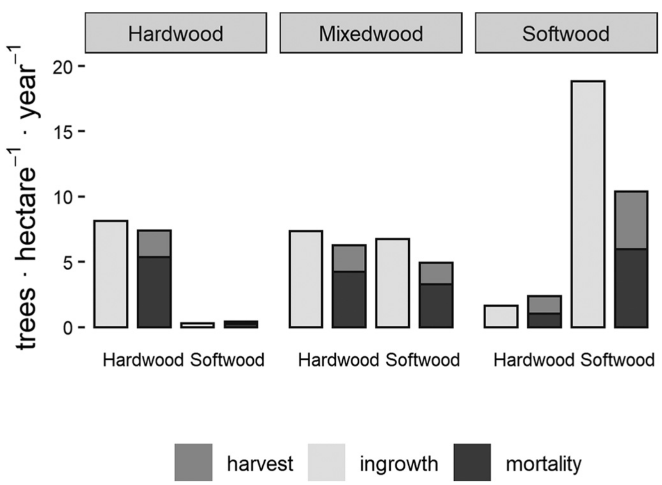


Table 4. Proportion of mixedwood forestland by sapling cover type and mixedwood type for the northern US, 2017.

Mixedwood type	Saplings (% of forestland)			
	Hardwood	Mixedwood	Softwood	None
Fir	19.6	52.3	23.5	4.6
Hemlock	35.1	34.3	15.3	15.2
Jack pine	46.7	27.5	10.7	15.0
Juniper	33.8	34.8	16.1	15.4
Red pine	47.3	23.5	12.0	17.2
Spruce	26.9	44.4	23.7	5.0
White-cedar	23.7	47.7	22.4	6.3
White pine	46.2	27.7	13.5	12.6
Yellow pine	69.8	17.6	3.5	9.0
Misc.	46.6	17.9	16.8	18.7
All	36.2	35.9	16.9	11.0

Note: For a given mixedwood type (row), percentages reflect the proportion of forestland by sapling composition category (column). Mixedwood type refers to all live trees with a dbh ≥ 12.7 cm; saplings refer to all live trees with a dbh ranging from 2.5 to 12.6 cm. "Misc." includes all remaining mixedwoods where the primary softwood species was relatively infrequent across the northern US or an exotic species.

Fig. 7. Average annual population density changes for hardwood and softwood components by cover type for the most recent remeasurement period, northern US forestland, 2010–2017 (approx.). Elements of change include ingrowth, mortality, and harvest. Ingrowth refers to live stems less than 12.7 cm dbh at time 1 that grew to or beyond 12.7 cm dbh by time 2; mortality refers to live stems (dbh ≥ 12.7 cm) that died (non-harvest) between successive measurement periods; harvest refers to live stems (dbh ≥ 12.7 cm) that were cut and removed between successive measurements (Bechtold and Patterson 2005). Cover type refers to all live trees with a dbh ≥ 12.7 cm.



northern US mixedwoods. Species compositions and rates of cover type transitions can be expected to differ along a spectrum of harvest intensity (Kern et al. 2014; Olson et al. 2017; Raymond and Bédard 2017; Rogers et al. 2018). It was not obvious that harvesting had a consistent influence on the direction of the shift, i.e., more toward hardwood versus softwood dominance, when compared with plots that shifted without harvesting. This may be a byproduct of a cursory harvesting analysis and the relatively small number of harvested plots for some mixedwood types. It is also likely that some harvests were part of a silvicultural system not aiming to perpetuate mixedwoods. For much of the region investigated, there is a long history of harvesting driven by the desire to merchandize certain species or sizes of trees (Nyland 1992; Kelty and D'Amato 2006). All of these nuances would affect the directional shift resulting from harvesting in mixedwoods in addition to the relative abundance, structure, and silvical properties of the component species. Harvesting, like other disturbances, is not a uniform treatment; the effects on forest characteristics can be multifaceted and driven by complex and interrelated dynamics all acting on various scales (Lafon and Kutac 2003; Webster and Lorimer 2005; Bataineh et al. 2013).

While most plots that we examined did not experience cover type shifts in the short term, the trends in understories, diameter distributions, and ingrowth, mortality, and harvesting show patterns suggestive of future shifts away from mixedwood. Etheridge et al. (2006) found that most mixedwood stands in northern New Brunswick, which include mixtures of *Picea* spp., *Abies balsamea*, *Thuja occidentalis*, *Fagus grandifolia*, *Betula* spp., and *Acer* spp., eventually shift away from mixedwoods with or without harvest, but harvesting and other disturbances strongly influenced whether the shift was towards softwood or hardwood dominance over 57 years.

Fig. 8. Average annual population changes for hardwood and softwood components (shades) by mixedwood type for the most recent remeasurement period, northern US forestland, 2010–2017 (approx.). Elements of change include ingrowth, mortality, and harvest. Ingrowth refers to live stems less than 12.7 cm dbh at time 1 that grew to or beyond 12.7 cm dbh by time 2; mortality refers to live stems (dbh ≥ 12.7 cm) that died (non-harvest) between successive measurement periods; harvest refers to live stems (dbh ≥ 12.7 cm) that were cut between successive measurements (Bechtold and Patterson 2005); mixedwood type refers to all live trees with a dbh ≥ 12.7 cm; "misc." includes all remaining mixedwoods where the primary softwood species was relatively infrequent across the northern US or an exotic species.

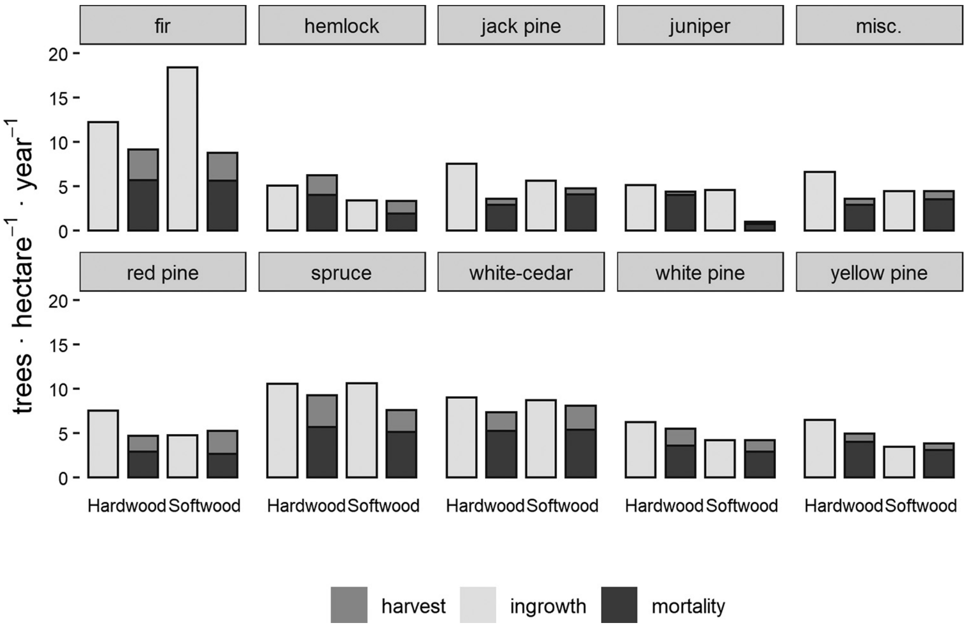


Table 5. Proportion of plots by initial cover type, final cover type, and harvest occurrence for the northern US, 1999–2017 (approx.).

Initial cover type	Harvesting	Final cover type (% of plots) Hardwood	Mixedwood	Softwood
Hardwood	No harvest	94.1	5.7	0.2
	Harvest	90.3	8.7	1.0
Mixedwood	No harvest	7.7	86.8	5.5
	Harvest	13.4	74.8	11.8
Softwood	No harvest	1.0	14.3	84.7
	Harvest	2.2	20.6	77.2

Note: For a given initial cover type (row), percentages reflect the proportion of plots by final cover type (column) after 8–18 years.

The ingrowth potential of a shade-tolerant subcanopy probably has not manifested in the time frame examined, whereas loss of canopy softwoods from harvest can have a bigger impact on mixedwoods staying mixedwoods. We suggest continued investigation and more detailed analysis to better understand mixedwood stand dynamics.

Disturbances from both native and non native forest pests, e.g., eastern spruce budworm (*Choristoneura fumiferana*), gypsy moth, or hemlock woolly adelgid, are another example of especially important drivers of mixedwood composition for many assemblages and regions (Maclean and Clark 2021). In New Brunswick, for example, several studies have shown shifts in species composition under both harvesting and insect disturbances from the 1940s to the 2000s. Colford-Gilks et al. (2012) looked at the effects of spruce budworm outbreaks in shifting mixedwoods to hardwood dominance by killing the balsam fir component. Amos-Binks and MacLean (2016) found *Picea rubens* to be less vulnerable to budworm and suffered less mortality in mixedwoods than in pure stands. Birch dieback reduced the hardwood component of mixedwoods in some regions, causing an eventual shift to softwood dominance in some stands (Etheridge et al. 2006). Some of the notable decrease in area for jack pine mixedwoods, which exhibited the greatest decrease during the time period examined (28%), is likely attributable to jack pine budworm (*Choristoneura pinus*) outbreaks and several large fires in the study region (Radeloff et al. 2000; D'Amato et al. 2011). Southern pine beetle (*Dendroctonus frontalis*), a major pest of yellow pines in the

Fig. 9. Probability of final mixedwood cover type by initial cover type and harvest occurrence over two or more remeasurement periods, northern US forestland, 1999–2017 (approx.). The time elapsed averaged 12 years. Error bars depict 95% confidence intervals. Asterisks (*) denote initial cover types where harvesting occurrence had a statistically significant influence on the probability of being classified as mixedwoods at the end of the analysis period.

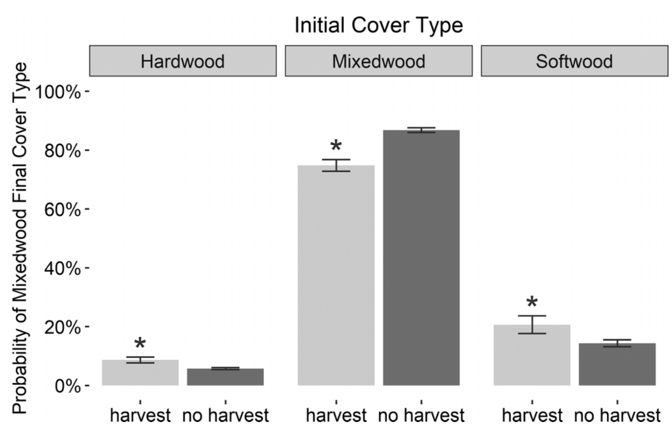
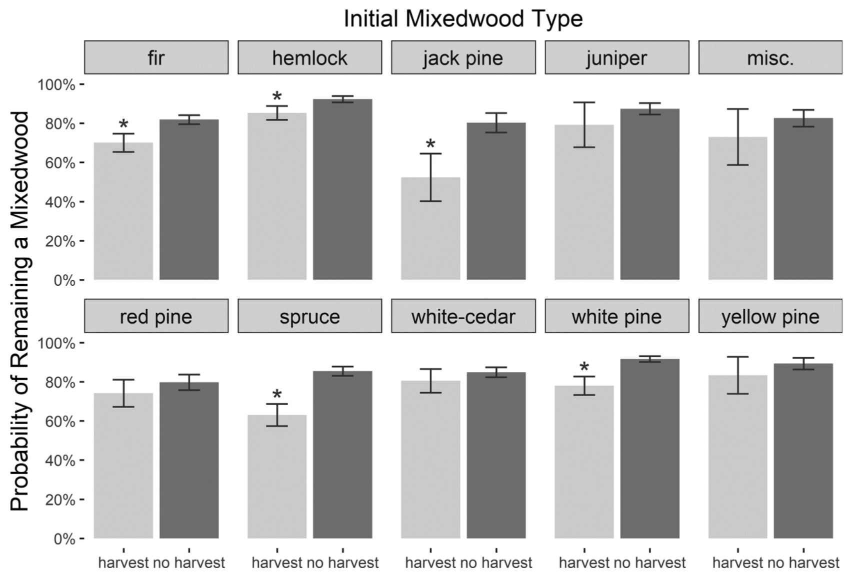


Fig. 10. Probability of an initial mixedwood plot remaining a mixedwood by mixedwood type and harvest occurrence over two or more remeasurement periods, northern US forestland, 1999–2017 (approx.). The time elapsed averaged 12 years. Error bars depict 95% confidence intervals. Asterisks (*) denote mixedwood types where harvesting occurrence had a statistically significant influence on the probability of being classified as mixedwoods at the end of the analysis period; "misc." includes all remaining mixedwood stands where the primary softwood species was relatively infrequent across the northern US or an exotic species.



southern US, is increasingly threatening or expanding into the northeastern US (Brandt et al. 2014; Lesk et al. 2017). Depending on the yellow pine density and severity of the infestation, yellow pine mortality can promote mixedwood development by increasing the proportion of hardwoods (Harrington et al. 2000; Lafon and Kutac 2003) or thwart mixedwood development in areas where the yellow pine component may be underrepresented (Lafon and Kutac 2003; Elliot et al. 2012).

Conclusion

Mixedwoods, i.e., forests with both hardwoods and softwoods present but neither exceeding 75%–80% of composition, are common throughout the northern US, comprising more than 19 M ha and more than one-quarter of the forestland in the region. They are most common in the Adirondack – New England, Laurentian, and Northeast ecological provinces in the northeastern US, but they also occur elsewhere in hardwood-dominated provinces. Mixtures of hardwoods and softwoods are common even within forest types nominally categorized as hardwood or softwood. The most common hardwoods of mixedwoods were species of *Quercus* and *Acer*, and the most common softwoods were species of *Pinus*, *Tsuga*, and *Juniperus*. Although mixedwoods exhibited stability in total area during the 12-year analysis period (2005 to 2017), our analysis also showed that hardwood saplings were prominent in most mixedwood types, suggesting an eventual shift to hardwood dominance in the absence of disturbances, either natural or silvicultural, which favor the regeneration and recruitment of the softwood component. The only exception appears to be with mixedwoods dominated by *Juniperus* or *Abies* due to their rapid ingrowth and low mortality and harvest removal. Kabrick et al. (2017) noted that difficulty ensuring regeneration and canopy recruitment of softwood in the presence of hardwood competitors is a common and persistent research theme in mixedwood management across eastern North America. Our results support their observation and suggest that softwood recruitment could indeed be a looming bottleneck to sustaining current mixedwoods, and for some types, it may be more difficult than others (Kenefic et al. 2021). We found that the softwood–hardwood recruitment disparity was more pronounced in mixedwoods with relatively shade-intolerant primary softwood components, particularly *Pinus* (i.e., jack, red, white, and yellow pines). Our analyses suggest that harvesting is shifting mixedwoods to either hardwood- or softwood-dominated stands in the near term, although more specific information is needed to understand the underlying reasons for the direction of these shifts. Finally, we suggest continued research into site, disturbance history and land-use legacy and other factors likely to influence the development, dynamics, and management of northern mixedwoods.

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Appendix Table A1 and Table B1 appear on the following pages.

Appendix A

Table A1. Distribution of mixedwood cover type area by FIA forest type groups and mixedwood type, northern US forestland, 2017.

	Distribution (% mixedwood type area (columnwise))										
FIA forest type group	Fir	Hemlock	Jack pine	Juniper	Red pine	Spruce	White-cedar	White pine	Yellow pine	Misc.[a]	All
Aspen–birch[b]	36	2	17	<1	12	22	16	6	1	14	12
Douglas-fir[c]	0	0	0	0	0	0	0	0	0	<1	<1
Elm–ash–cottonwood[d]	5	2	1	6	1	4	20	2	1	11	4
Exotic hardwoods	0	0	0	<1	<1	0	0	0	0	0	<1
Exotic softwoods	0	0	0	0	1	0	0	1	0	13	1
Loblolly–shortleaf pine[e]	0	0	0	<1	0	0	0	<1	31	0	2
Maple–beech–birch[f]	37	66	3	2	5	48	24	15	1	19	32
Non-stocked	<1	0	0	1	1	<1	<1	<1	0	1	<1
Oak–gum–cypress[g]	0	<1	0	1	1	<1	1	0	<1	1	<1
Oak–hickory[h]	2	13	19	52	14	2	3	23	27	18	16
Oak–pine[i]	<1	<1	27	27	29	<1	<1	26	39	1	12
Other eastern softwoods	0	0	0	10	0	0	0	0	0	0	1
Other hardwoods	1	2	1	<1	0	1	1	1	<1	2	1
Other softwoods	0	0	0	0	0	<1	0	0	0	0	<1
Pinyon–juniper[j]	0	0	0	1	0	0	0	0	0	0	<1
Ponderosa pine[k]	0	0	0	<1	0	<1	0	0	0	4	<1
Spruce–fir[l]	19	1	1	0	1	23	35	2	0	14	9
White–red–jack pine[m]	<1	14	31	<1	35	<1	<1	24	0	2	10
Total	100	100	100	100	100	100	100	100	100	100	—

Note: For a given mixedwood type (columns), percentages approximate the proportion of mixedwood cover type within each FIA forest type group (row).

[a]Misc. includes all remaining mixedwood stands where the primary softwood species was native but relatively infrequent across the northern US or an exotic species.

[b]*Populus–Betula*.

[c]*Pseudotsuga menziesii*.

[d]*Ulmus–Fraxinus–Populus*.

[e]*Pinus taeda – Pinus echinata*.

[f]*Acer–Fagus–Betula*.

[g]*Quercus–Nyssa–Taxodium*.

[h]*Quercus–Carya*.

[i]*Quercus–Pinus*.

[j]*Pinus edulis – Juniperus*.

[k]*Pinus ponderosa*.

[l]*Picea–Abies*.

[m]*Pinus strobus – Pinus resinosa – Pinus banksiana*.

Appendix B

Table B1. Proportion of plots by initial mixedwood type, final cover type, and harvest occurrence, northern US forestland, 1999–2017 (approx.). For a given mixedwood type (row), percentages reflect the proportion of plots by final cover type (column) after 8–18 years.

		Final cover type (% initial mixedwood plots)		
Initial mixedwood type	Harvesting	Hardwood	Mixedwood	Softwood
Fir	No harvest	12.8	81.8	5.4
	Harvest	19.8	70.0	10.2
Hemlock	No harvest	6.5	92.2	1.3
	Harvest	10.9	85.3	3.8
Jack pine	No harvest	12.8	80.2	7.0
	Harvest	20.0	52.3	27.7
Juniper	No harvest	8.3	87.4	4.3
	Harvest	16.7	79.2	4.1
Red pine	No harvest	10.3	79.7	10.0
	Harvest	5.3	74.2	20.5
Spruce	No harvest	6.3	85.4	8.3
	Harvest	20.3	63.0	16.7
White pine	No harvest	5.1	91.6	3.3
	Harvest	10.5	78.0	11.5
White-cedar	No harvest	4.0	84.8	11.2
	Harvest	2.4	80.5	17.1
Yellow pine	No harvest	8.8	89.3	1.9
	Harvest	13.3	83.3	3.4
Misc.[a]	No harvest	9.8	82.7	7.5
	Harvest	13.5	73.0	13.5

[a]Misc. includes all remaining mixedwood stands where the primary softwood species was relatively infrequent across the northern US or an exotic species.