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Are Current Seedling Demographics Poised to Regenerate Northern US Forests?

Lance A. Vickers, William H. McWilliams, Benjamin O. Knapp, Anthony W. D'Amato, Daniel C. Dey, Yvette L. Dickinson, John M. Kabrick, Laura S. Kenefic, Christel C. Kern, David R. Larsen, Alejandro A. Royo, Michael R. Saunders, Stephen R. Shifley, and James A. Westfall

Lance A. Vickers (lance.vickers@mizzou.edu), Benjamin O. Knapp (knappb@missouri.edu), David R. Larsen (larsendr@missouri.edu), School of Natural Resources, University of Missouri, 203 ABNR Building, Columbia, MO 65211. William H. McWilliams (will.mcwilliams@usda.gov), James A. Westfall (james.westfall@usda.gov), USDA Forest Service, Northern Research Station, Forest Inventory and Analysis, 11 Campus Blvd, Suite 200, Newtown Square, PA 19073. Anthony W. D'Amato (awdamato@uvm.edu), Rubenstein School of Environmental and Natural Resources, University of Vermont, 204E Aiken Center, Burlington, VT 05405. Daniel C. Dey (daniel.c.dey@usda.gov), John M. Kabrick (john.kabrick@usda.gov), Stephen R. Shifley (stephen.shifley@usda.gov), USDA Forest Service, Northern Research Station, 202 ABNR Building, Columbia, MO 65211. Yvette L. Dickinson (yldickin@mtu.edu), School of Forest Resources and Environmental Science, Michigan Technological University, 170 UJ Noblet Forestry Building, 1400 Townsend Dr., Houghton, MI, 49931-1295. Laura S. Kenefic (laura.kenefic@usda.gov), USDA Forest Service, Northern Research Station, 5755 Nutting Hall, University of Maine, Orono, ME 04469-5755. Christel C. Kern (christel.c.kern@usda.gov), USDA Forest Service, Northern Research Station, 5985 Highway K, Rhinelander, WI 54501-9128. Alejandro A. Royo (alejandro.royodesedas@usda.gov), USDA Forest Service, Northern Research Station, 335 National Forge Road, P.O. Box 267, Irvine, PA 16329. Michael R. Saunders (msaunder@purdue.edu), Department of Forestry and Natural Resources, Purdue University, 715 W. State St., West Lafayette, IN 47907.

Abstract

Securing desirable regeneration is essential to sustainable forest management, yet failures are common. Detailed seedling measurements from a forest inventory across 24 northern US states were examined for plausible regeneration outcomes following overstory removal. The examination included two fundamental regeneration objectives: 1) stand replacement- securing future forest and 2) species maintenance- securing upper canopy species. Almost half the plots lacked adequate seedlings to regenerate a stand after canopy removal and over half risked compositional shifts. Based on those advance reproduction demographics, regeneration difficulties could occur on two-thirds of the plots examined. The remaining one-third were regeneration-ready. However, compared to historical norms, increased small-tree mortality rates reduces that proportion. Not all forest types rely on advance reproduction and results varied among the forest types examined. Some variability was associated with browsing intensity, as areas of high deer browsing had a lower proportion of regeneration-ready plots.

Keywords: Advance reproduction, sustainability, regeneration, recruitment, oak/hickory forests, maple/beech/birch forests, northern hardwoods, spruce-fir, Forest Inventory and Analysis (FIA)

Management and Policy Implications

It appears that millions of acres of northern forest will be difficult to regenerate successfully, based on criteria outlined in this analysis. The information provided here can be used to focus regeneration harvests to areas with a higher likelihood of success while ensuring that silviculture to increase regeneration potential is targeted toward forest types and locations where correctable regeneration shortfalls are anticipated, rather than those with a higher likelihood of success from natural regeneration processes. With expanding emphasis on ecosystem services and resilience to changing conditions, the impetus for regenerating forests is strongly influenced by management goals intended to sustain wildlife, water quality, diversity, forest health, and rural communities. Consequently, broad-scale policy decisions about when and where to invest in forest regeneration activities such as site preparation, precommercial treatments, or supplemental planting must take those factors into account. This research illustrates the magnitude of the problem and helps policy makers discern where and when to focus regeneration investments based on ecological information that can be coupled with social and economic criteria.

Nearly half the forestland across the northern US (defined in Figure 1) is at least 75 years old (Miles 2018) resulting from repeated, widespread forest disturbances that occurred in many portions of this region in the 19th and early 20th centuries (Foster 1992, Rhemtulla et al. 2009). For many forest types, the youngest stands in this condition are approaching the lower bounds of suggested rotation ages (Roach and Gingrich 1968, Barrett 1994, Leak et al. 2014), though multi-aged stands have been common in many areas historically (Frelich 1995, Seymour et al. 2002, Lorimer and White 2003). Regardless of ownership or management goals, a capacity for regeneration success becomes critical as trees and stands mature. Hence, information on plausible regeneration outcomes is increasingly pertinent to the sustainability of over 80 million acres of forestland.

Sources of natural forest regeneration include advance reproduction[1] that established before a disturbance as well as seedlings and vegetative sprouts that establish after a disturbance. The relative importance of these sources varies within and across tree genera and species, ecological sections, forest types, and silvicultural systems. Some forest types and management strategies rely almost exclusively on a single source. For example, aspen (*Populus tremuloides*) management typically uses coppice silviculture to promote sprouting. More commonly, multiple sources contribute to a new cohort after disturbance. Seedlings and sprouts can establish in abundance following disturbance, but projecting those contributions beforehand often depends on prior experience or empirical models of historical trends (Clark et al. 1999, Knapp et al. 2017, Vickers et al. 2017). Advance reproduction likely has the greatest potential to influence management decisions because it can be inventoried prior to a prospective disturbance, and silviculturally manipulated to promote a desired outcome. A variety of economically and ecologically important tree species, such as sugar maple *(Acer saccharum)*, red spruce (*Picea rubens*), and most oaks (*Quercus* spp.), rely largely on advance reproduction for success (Egler 1954, Horn 1974, Brose et al. 2008).

Advance reproduction inventories have been used to project regeneration outcomes in several species- or locale-specific applications, particularly for oak/hickory, maple/beech/birch, and spruce/fir forests (Westveld 1931, Marquis et al. 1994, Dey et al. 1996). The application of such techniques at various scales can successfully inform management and policy (McWilliams et al. 1995) and there has been increasing interest in examining advance reproduction demographics at the landscape scale (e.g., Rooney et al. 2000, Matonis et al. 2011, McEwan et al. 2011, Miller and McGill 2019). In 2012, opportunities to examine understory demographics at the landscape scale were improved when the USDA Forest Service, Northern Research Station, Forest Inventory and Analysis program (NRS-FIA) adopted a new *Regeneration Indicator* inventory protocol across 24 northern states. The *Regeneration Indicator* measures all established seedlings ≥0.17 ft tall according to species and several height classes (McWilliams et al. 1995, 2015).

This study examined the capacity of current understory tree demographics to attain desirable regeneration outcomes on more than 3000 forest sites across the northern US. The region includes a diverse set of physiographic, edaphic, and climatic conditions, and includes multiple ecological provinces (Table 1, Cleland et al. 2007). The study used FIA source data from nine FIA forest-type groups (FTG[s]) which collectively encompass 96% of the forestland within the region (Table 2, Miles 2018). The most prevalent are

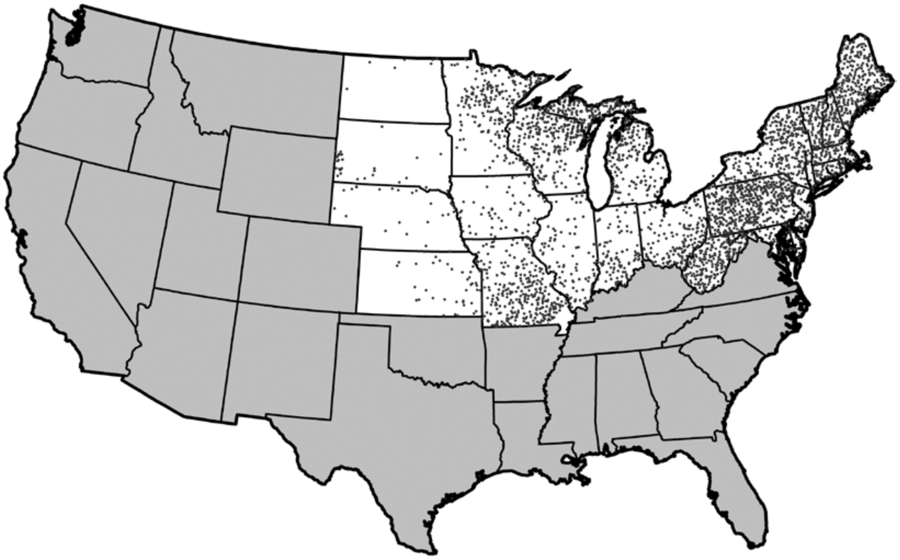


Figure 1. The 24-state northern US study region (white) and approximate locations (points) of the 3215 regeneration-eligible NRS-FIA *Regeneration Indicator* plots used to examine regeneration.

Table 1. Prominent ecological provinces with number of regeneration-eligible NRS-FIA *Regeneration Indicator* plots by select forest-type groups, northern US, 2018. Note: the 'Southeastern/Coastal Plain' and 'Prairie/Plains' provinces are aggregates of multiple geographically adjacent provinces with low representation.

Ecological Province[1]		Forest-type group		
Name	Code(s)	Oak/hickory	Maple/beech/ birch	Spruce/fir
		------------------number of plots -----------		
Northeastern Mixed Forest	211	75[a]	236	43
Laurentian Mixed Forest	212	93	201	69
Eastern Broadleaf Forest	221	295	118	1[c]
Midwest Broadleaf Forest	222	174	54[b]	2[c]
Central Interior Broadleaf Forest	223	281	12[b]	-
Adirondack-New England Mixed/Coniferous Forest	M211	11[a]	219	57
Central Appalachian Broadleaf/Coniferous Forest	M221	230	73	-
'Southeastern/Coastal Plain'	231,232	25	-	-
'Prairie/Plains'	251,255,331,332,M334	157	2[c]	-
Sample size (n)		1341	915	172

[1]Cleland et al. 2007, [a]Provinces merged for oak/hickory analyses, [b] Provinces merged for maple/beech/birch analyses, [c]Provinces not statistically analyzed due to low sample size.

oak/hickory, maple/beech/birch, and spruce/fir, which account for 7 out of every 10 acres of forestland in the region and rely heavily on advance reproduction. The other FTGs often rely more strongly on other reproduction sources or planting.

In this study, two regeneration objectives benchmark success following overstory removal. The first (stand replacement) stipulates that existing advance reproduction must have the capacity to produce a fully stocked stand (as defined later) upon loss or removal of overstory trees, without regard for future species composition. The second (species maintenance) stipulates that existing advance reproduction must have the capacity to maintain a component of upper canopy species for an FTG upon loss of overstory trees. The analytical methods used were developed to estimate plausible regeneration outcomes using the *Regeneration Indicator* data (Vickers et al. 2019). The methods were based on estimating mortality budgets for inventoried reproduction and provide flexibility to examine regeneration

Table 2. Percent of total forestland area, sample size, and upper canopy proportion for nine prominent forest-type groups (Miles 2018) based on forestland area, northern US, 2018. Sample size refers to regeneration-eligible NRS-FIA *Regeneration Indicator* plots used to examine regeneration. Upper canopy proportion refers to the proportion of all trees (dbh ≥ 1 inch) that typically occupy the upper canopy (dominant and codominant crown classes) on plots at least 75 years old with at least 50% of live stocking in trees with dbh ≥ 5 inches. Namesake species refers to the proportion of the upper canopy comprised of species named by a forest-type group (see Table 5).

Forest-type group	Forestland Area (%)	Sample Size (n)	Upper Canopy (%)	Namesake Species (%)
oak/hickory (*Quercus/Carya*)	36	1341	33	61
maple/beech/birch (*Acer/Fagus/Betula*)	25	915	33	60
aspen/birch (*Populus/Betula*)	9	249	31	63
spruce/fir (*Picea/Abies*)	9	172	38	38
elm/ash/cottonwood (*Ulmus/Fraxinus/Populus*)	8	245	39	49
white/red/jack pine (*Pinus strobus/P. resinosa/P. banksiana*)	5	132	36	46
oak/pine (*Quercus/Pinus*)	3	113	31	62
loblolly/shortleaf pine (*Pinus taeda/P. echinata*)	1	23	37	75
ponderosa pine (*Pinus ponderosa*)	<1	25	59	91
Total	96	3215	-	-

trends for multiple species, site conditions, and user-defined regeneration objectives. Criteria specific to forest types and well-established silvicultural tenets can be utilized with the *Regeneration Indicator* to obtain provisional insight into this aspect of sustainable forest management across the northern US. Further analyses explore the impact of browsing on regeneration dynamics, primarily by white-tailed deer (*Odocoileus virginianus*).

Methods

Study Region

The study region consists of 24 states in the northern US. The region spans about 36–49°N latitude and 67–104°W longitude, encompassing 607 million acres of land area with over 182 million acres of forestland (https://www.census.gov/geo/reference/state-area.html, Miles 2018). Elevations range from sea level to 7242 ft (https://pubs.usgs.gov/gip/Elevations-Distances/elvadist.html). Average annual temperatures range from 40–55°F north to south, and average annual precipitation totals range from 18–50 in, increasing generally from west to east (https://www.ncdc.noaa.gov/data-access).

Regeneration Examination Procedures and Assumptions

The inventory data were collected by NRS-FIA on sample plots located randomly within a systematic national grid of cells where each plot in the base sample represents roughly 6000 ac (Bechtold and Patterson 2005). The sampling methodology includes an inventory of trees across a plot-cluster of four, fixed-radius subplots. Intensive plots are a randomly selected subsample of base plots inventoried for ecological health indicators, e.g., vegetative structure, soils, dead and down woody material, regeneration, and others. The sampling intensity of these plots varies by indicator; *Regeneration Indicator* variables are collected on 12.5% of the base plot network using 6.8 ft (2.07 m) radius microplots nested within each subplot (McWilliams et al. 2015). Established reproduction ≥0.17 ft tall is inventoried by species in six height classes (Table 3), except for oak, hickory, and walnut (*Juglans* spp.) which are not tallied until their root-collar diameter is ≥0.25 inches. Advance reproduction data were extracted from these intensively sampled plots. For these analyses, small saplings (dbh: 1–2 inches) sampled as part of the base protocols located within the same microplots were included with the *Regeneration Indicator* tally in size class 6 (Table 3). Additionally, categorical assessments of browsing

Table 3. Weighting factors for all species of reproduction by size-class code.

	Reproduction Size		
Size Class Code	Height (ft)	DBH (in)	Weighting Factor
1	0.17–0.49	-	0.033
2	0.5–0.9	-	0.075
3	1.0–2.9	-	0.195
4	3.0–4.9	-	0.395
5	5.0–9.9	-	0.745
6	≥10	1.0–2.0	1.00

intensity (very low, low, moderate, high, very high) at the plot-cluster level are recorded for the area surrounding the sample plot (McWilliams et al. 2015). The *Regeneration Indicator* includes an apparent source (seedling or stump sprout) for all inventoried reproduction, but this variable was not used.

The role of advance reproduction in the future stand depends on survival rates (Beckage et al. 2005). Accordingly, a mortality budget was used to examine plausible regeneration outcomes for inventoried reproduction following three steps outlined by Vickers et al. (2019): 1) define regeneration objectives, 2) estimate an *Allowable Mortality* to meet the regeneration objectives, and 3) compare the *Allowable Mortality* rate to an *Expected Mortality* rate. The two regeneration objectives examined were quantitatively defined by *Targets* and *Endpoints*, which vary by FTG (descriptions follow). Targets approximate minimum abundance thresholds for desired stand conditions at a specified future point in stand development. Endpoints approximate the length of time required for a young, even-aged stand to reach the future point in stand development associated with the Target for each FTG. Available stocking charts, normal yield tables, growth models, management guides, and other relevant literature were consulted to establish Targets and Endpoints consistent with the stated regeneration objectives for young, even-aged stands (Table 4).

Regeneration Objective 1—Stand Replacement

The goal of stand replacement is that regeneration events eventually result in fully stocked stands, regardless of tree species composition. A fully stocked stand is defined as the minimum number of trees necessary to occupy available growing space, which is analogous to crown closure and the onset of intertree competition for even-aged stands (Gingrich 1967, Johnson et al. 2009). The Targets used for stand replacement represent 'C-level' stocking on a Gingrich-style stocking guide (Gingrich 1967) at or near the smallest applicable quadratic mean stand diameter (QMD), which tended to be 3 or 4 inches. C-level stocking is the density expected to develop into a fully stocked condition (B-level) within 10 years under normal conditions (Gingrich 1967). The Target for ponderosa pine is an exception, representing the lower boundary of a management zone identified on a stocking guide by Shepperd and Battaglia (2002). FTG specific stocking guides were not available for white/red/jack pine or oak/pine. In the case of white/red/jack pine, C-level values were found only for white pine (Lancaster and Leak 1978). Thus, a composite C-level value was assumed by applying the white pine C-level stocking percent to an average A-line value for the three species (citations in Table 4) at a 4 inch QMD (extrapolated from 5 inches for red pine). For oak/pine, which are often described as mixedwood forests and include varying combinations of oak/hickory, white/red/jack pine, and loblolly/shortleaf pine elements, mixedwood C-level values from Leak et al. (2014) were averaged with those used for oak/hickory, white/red/jack pine, and loblolly/shortleaf pine.

Regeneration Objective 2—Species Maintenance

The goal of species maintenance is that regenerated stands maintain an adequate component of upper canopy (dominant and codominant crown class) species defined by the initial FTG. Acceptable species generally included those in the named genera of an FTG (i.e., namesake) that occurred in the upper canopy on mature NRS-FIA base plots (Table 5). Species that met these criteria but commonly inhabit early seral or understory communities were excluded (striped maple [*Acer pennsylvanicum*], gray birch [*Betula populifolia*], bear oak [*Quercus ilicifolia*], and winged elm [*Ulmus alata*]). Exotic invasive species were also excluded (Swearingen and Bargeron 2016). American beech (*Fagus grandifolia*) reproduction was not an acceptable species for the maple/beech/birch FTG due to its proclivity to form dense understory thickets of low-quality stems that are unlikely to become mature trees in areas affected by beech bark disease (*Neonectria* spp., Mize and Lea 1979, Houston and O'Brien 1983, Ostrofsky and McCormack 1986). Ash (*Fraxinus* spp.) is also a named genus (elm/ash/cottonwood) afflicted by an invasive exotic (emerald ash borer [*Agrilus planipennis*]), but ash reproduction was not excluded because it retains the potential for overstory recruitment following overstory mortality caused by the initial emerald ash borer attack (Kashian 2016).

Table 4. Targets, Endpoints, and annual *Expected Mortality* rates for stand replacement (Obj. 1) and species maintenance (Obj. 2) regeneration objectives by forest-type group. QMD is quadratic mean diameter.

	Target		Endpoint		
Forest-type group	Obj. 1	Obj. 2	Years	QMD	*Expected Mortality*
	...trees·ac^{-1}...		...yrs...	...in...	...%...
oak/hickory	429[a]	86	20[a]	3.0	1.5[j]
maple/beech/birch	400[b]	79	35[b]	4.0	2.0[k]
aspen/birch	517[c]	102	23[c]	3.0	5.0[l]
spruce/fir	695[d]	101	38[d]	4.0	3.0[m]
elm/ash/cottonwood	380[e]	74	16[e]	3.0	3.5[n]
white/red/jack pine	432[f]	72	25[f]	4.0	4.3[o]
oak/pine	428[afgh]	83	26[afgh]	4.0	3.2[jopr]
loblolly/shortleaf pine	521[h]	145	20[h]	3.0	1.5[q]
ponderosa pine	150[i]	81	25[i]	3.0	2.5[r]

[a] Gingrich 1967, Sander et al. 1976, Dey et al. 1998.
[b] Spaeth 1920, Solomon and Leak 1969, Leak et al. 2014
[c] Solomon and Leak 1969, Plonski 1974, Perala 1977, Safford 1983
[d] Meyer 1929, Solomon et al. 1987
[e] Shifley and Smith 1982, Smith and Shifley 1984, Larsen et al. 2010, Rives and Knapp *unpublished*
[f] Frothingham 1914, Woolsey and Chapman 1914, Gevorkiantz and Zon 1930, Eyre and Zehngraff 1948, Marty 1965, Bella 1968, Plonski 1974, Benzie 1977a, b, Lancaster and Leak 1978, Lundgren 1981
[g] Payandeh and Field 1986, Leak et al. 2014
[h] Rogers 1983, Mattoon 1915, Smalley and Bailey 1974, Shifley and Smith 1982, Smith and Shifley 1984
[i] Meyer 1938, Shepperd and Battaglia 2002
[j] Sander et al. 1976, Shifley and Smith 1982, Smith and Shifley 1984, Fan et al. 2006
[k] Spaeth 1920
[l] Solomon and Leak 1969, Plonski 1974, Perala 1977, Buchman 1983
[m] Meyer 1929, Plonski 1974, Buchman 1983
[n] Shifley and Smith 1982, Bowling and Kellison 1983, Smith and Shifley 1984, Aust et al. 1985
[o] Frothingham 1914, Eyre and Zehngraff 1948, Bella 1968, Plonski 1974, Buchman 1983
[p] Payandeh and Field 1986
[q] Smalley and Bailey 1974, Shifley and Smith 1982, Smith and Shifley 1984, Fan et al. 2006
[r] Meyer 1938

Species maintenance targets were determined for each forest type using proportions of the tree density defined for the fully stocked stand replacement Targets. Based on empirical analysis of 10,764 NRS-FIA base sample plots from across the northern US, the proportion of tree density (dbh ≥ 1 inch) in the upper canopy of mature stands (age ≥ 75 yrs for this analysis) averaged about 37%, with some differences among FTGs (Table 2). Within the upper canopy, namesake species comprised about 61% of trees on average, thus, the proportion of namesake upper canopy trees averaged only about 23% (37% × 61%) of tree density in mature stands, but this varied considerably for some FTGs (Table 5). For example, in mature oak/hickory forests, 33% of all trees are in the upper canopy, with namesake species comprising about 61% of those on average (Tables 2, 5). Accordingly, an oak/hickory tree density Target for species maintenance based on an equivalent namesake proportion (33% × 61% = 20%) of the stand replacement Target (429 trees·ac^{-1}) requires about 86 trees·ac^{-1} (Table 4).

Analyses

Annual *Allowable Mortality* estimates were derived from an algebraic re-arrangement of the classic future value formula (Fisher 1930) as shown in Equations 1 and 2.

$$\text{Survival rate} = (\text{Target}/\text{Inventory})^{(1/\text{Endpoint})} \qquad (1)$$

$$\mathit{Allowable\ Mortality} = 1 - \text{Survival rate} \qquad (2)$$

where:

Survival rate is the minimum annual survival rate required for the inventory to meet the Target condition by the Endpoint; Target is a pre-defined number of desired future trees (future value); Inventory is the tally of advance reproduction (present value); Endpoint is a pre-defined number of years (or n compounding periods) for the Target to be met; and *Allowable Mortality* is the maximum annual mortality rate that can be afforded for the inventory to meet the Target by the Endpoint. If inventoried reproduction is less than the Target, *Allowable Mortality* is set to zero to reflect imminent failure to meet the regeneration objective.

An inventory-weighting scheme was adopted from Fei et al.'s (2006) aggregate height hypothesis to approximate the general trend of large reproduction surviving more than smaller reproduction (Sander 1972, Marquis 1994, Brose et al. 2008). Fei et al. (2006) postulated an equivalence across structural permutations yielding the same aggregate (summed) height, e.g., 10 stems, each 1 ft tall is approximately equivalent to a single 10 ft tall stem. Following this, stems were standardized across each size class based on class midpoints with a single stem in the largest size class weighted as one to derive the weighting factor for each size class (Table 3). For the species maintenance objective, the inventory component of Equation 1 was filtered to include only reproduction from namesake species for a given FTG.

Calculated *Allowable Mortality* rates were compared to *Expected Mortality* (i.e, ambient, background, random) rates that were obtained for each FTG from relevant research articles, management guides, normal yield tables, and growth models with a preference for rates applicable to small trees in young regenerating stands when available (citations in Table 4). *Allowable Mortality* was compared to *Expected Mortality* for a qualitative assessment of regeneration success or security using three categories: "Imminent Failure",

Table 5. Namesake upper canopy (dominant and codominant crown classes) species and their average proportion of upper canopy tree density (parentheses) in mature forests for nine prominent forest-type groups in the northern US. Based on analysis of 10,764 NRS-FIA base plots across the northern US at least 75 yrs old with at least 50.0% of the live stocking in trees with dbh ≥ 5 inches.

	Namesake Upper Canopy Species		
Forest-type group	Genus	Species (upper canopy tree density composition)	Total (%)
oak/hickory	*Quercus*	*alba* (14.4), *bicolor* (0.1), *coccinea* (1.8), *ellipsoidalis* (1.5), *falcata* (0.3), *pagoda* (0), *imbricaria* (0.2), *macrocarpa* (4.9), *marilandica* (0.1), *michauxii* (0), *muehlenbergii* (0.6), *nigra* (0), *palustris* (0.2), *phellos* (0), *prinus* (4.9), *rubra* (13.7), *shumardii* (0.1), *stellata* (2.6), *velutina* (7.2)	61.2
	Carya	*cordiformis* (1.3), *glabra* (2.4), *illinoinensis* (0), *laciniosa* (0), *ovata* (3.4), *texana* (0.5), *tomentosa* (1.0), *pallida* (0)	
maple/beech/birch	*Acer*	*nigrum* (0.1), *rubrum* (17.8), *saccharinum* (0), *saccharum* (31.5)	59.7
	Betula	*alleghaniensis* (7.1), *lenta* (1.2), *nigra* (0), *papyrifera* (2.0)	
aspen/birch	*Populus*	*balsamifera* (1.9), *grandidentata* (9.3), *tremuloides* (28.5)	62.7
	Betula	*alleghaniensis* (1.4), *lenta* (0.1), *nigra* (0), *papyrifera* (21.5)	
spruce/fir	*Picea*	*glauca* (2.4), *mariana* (12.6), *rubens* (10.3)	38.0
	Abies	*balsamea* (12.8)	
elm/ash/cottonwood	*Ulmus*	*americana* (2.7), *rubra* (0.2), *thomasii* (0)	49.1
	Fraxinus	*americana* (1.2), *nigra* (32.6), *pennsylvanica* (9.0), *quadrangulata* (0)	
	Populus	*balsamifera* (0.6), *deltoides* (2.8)	
white/red/jack pine	*Pinus*	*banksiana* (4.9), *resinosa* (12.5), *strobus* (28.9)	46.3
oak/pine	*Quercus*	*alba* (5.3), *bicolor* (0), *coccinea* (2.5), *ellipsoidalis* (2.3), *falcata* (0.3), *pagoda* (0), *imbricaria* (0.2), *macrocarpa* (0.7), *marilandica* (0.1), *michauxii* (0), *muehlenbergii* (0.5), *nigra* (0.1), *palustris* (0.2), *phellos* (0), *prinus* (0.9), *rubra* (9.0), *shumardii* (0.4), *stellata* (1.2), *velutina* (2.8)	61.8
	Pinus	*banksiana* (2.0), *echinata* (4.1), *pungens* (0.4), *resinosa* (3.4), *rigida* (0.5), *strobus* (21.6), *taeda* (1.5), *virginiana* (1.8)	
loblolly/shortleaf pine	*Pinus*	*echinata* (26.8), *pungens* (0.4), *rigida* (17.3), *strobus* (3.0), *taeda* (15.4), *virginiana* (11.9)	74.8
ponderosa pine	*Pinus*	*ponderosa* (91.4)	91.4

"Insecure", and "Secure". The categories represent potential outcomes because the study was unable to factor in active or passive management, costs, or environmental factors. Imminent Failure was assigned if the weighted reproduction inventory was less than the Target for a regeneration objective. Insecure was defined as cases where *Allowable Mortality* was less than the *Expected Mortality*, indicating that advance reproduction will likely fall short of the objective Target under normal conditions. The Secure category was designated when *Allowable Mortality* was at least as great as the *Expected Mortality*, indicating the plot was regeneration-ready by having enough advance reproduction to meet the regeneration objective Target. Regeneration objectives were analyzed separately for each plot, and a designation of Imminent Failure for one objective does not necessarily limit the possibility of being rated as Secure for the other.

All sample data were acquired from FIA's online database portal (https://apps.fs.usda.gov/fia/datamart/) and included all inventory years publicly available since 2012 at the time of download (August 17, 2018). For simplicity, analyses assumed that tallied advance reproduction was the only regeneration source available and was immediately released from the overstory. Analyses were limited to "regeneration-eligible" microplots within the nine FTGs examined. Regeneration-eligible microplots were defined as free from physical site restrictions (excessive rock cover or water inundation) and land use/management (recently regenerated/planted) that would limit the establishment of advance reproduction. Approximately 10% of the intensively sampled microplots had physical site restrictions recorded, 17% had a tree (dbh ≥ 8 inches) completely occupying the 6.8 ft microplot area sensu Gingrich's (1967) minimum tree area equation, 13% were immature/recently regenerated, and 2% were already planted. This left 57% of the intensively sampled microplots, which were spread across 3215 NRS-FIA plot-clusters (individual inventory sites), as regeneration-eligible (Figure 1). About 75% of the regeneration-eligible plots were on private or tribal forest land, 17% were on state (74%) or local (26%) government land, 7% were on USDA Forest Service land, and 1% were on other US Federal land (National Park Service: 30%, Departments of Defense or Energy: 46%, Fish and Wildlife Service: 17%, other: 7%).

Allowable Mortality calculations were computed at the plot-cluster level using the averaged advance reproduction inventory of all regeneration-eligible microplots on a given plot-cluster (up to four per plot-cluster) expanded to a per-acre basis. For a given FTG,

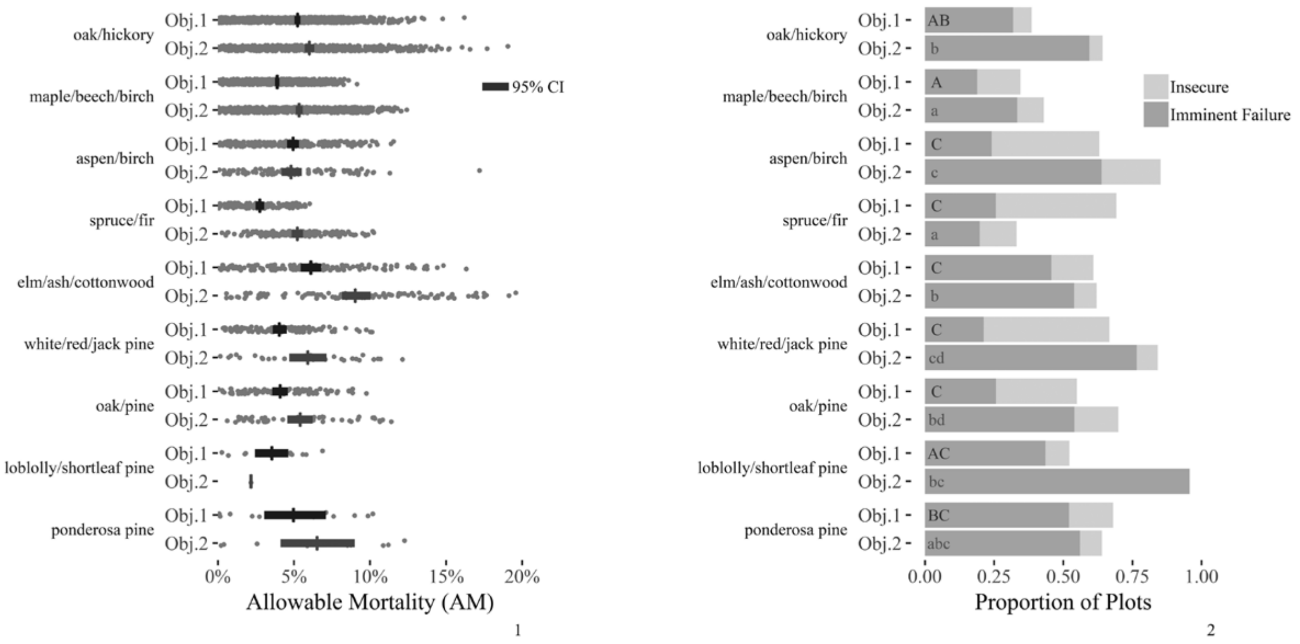
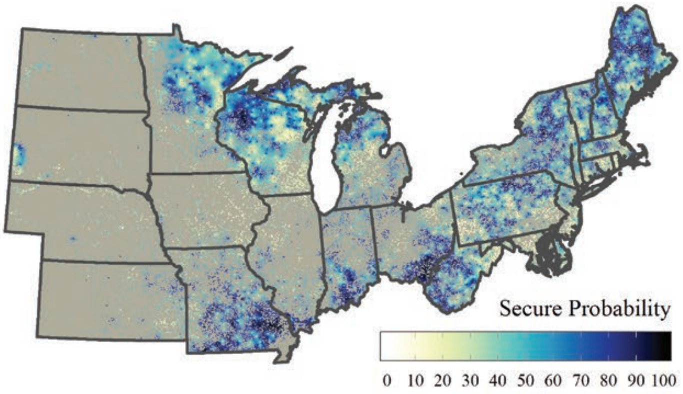


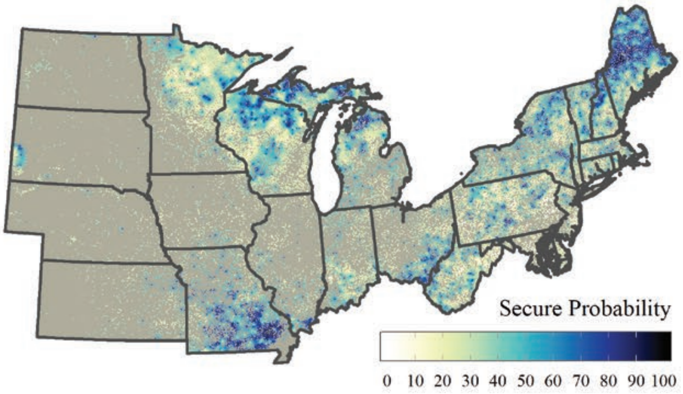
Figure 2. *Allowable Mortality* (2a) and categorical regeneration examination (2b) by forest-type group (left axis) for stand replacement (Obj. 1) and species maintenance (Obj. 2) regeneration objectives in the northern US study region. Points depict *Allowable Mortality* for each NRS-FIA *Regeneration Indicator* plot. Bands (dark shading) depict a 95% confidence interval for the mean (vertical lines) *Allowable Mortality* estimates. Barplots depict the proportion of NRS-FIA *Regeneration Indicator* plots for a given forest-type group and regeneration objective rated Imminent Failure (dark gray), Insecure (light gray) or Secure (remaining barplot area).

Stand Replacement



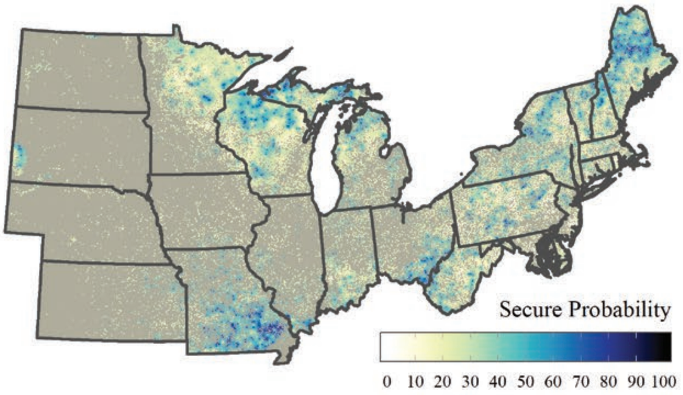
1

Species Maintenance



2

Stand Replacement & Species Maintenance



3

Figure 3. Spatially interpolated probability (shading) that existing advance reproduction will be rated Secure for stand replacement (3a) and species maintenance (3b) regeneration objectives, as well as both simultaneously (3c) based on 3215 regeneration-eligible NRS-FIA *Regeneration Indicator* plots across the northern US. Brown denotes non-forest areas. Spatial interpolation performed by ordinary indicator kriging.

the same Endpoints and Expected Mortality rates were used for both regeneration objectives.

Analyses were conducted with R statistical software (R Core Team 2018, version 3.4.4). One-way ANOVA was used to test for differences in *Allowable Mortality* among FTGs for each regeneration objective. Logistic regression was used to test for differences in the proportion of plots rated as Secure among FTGs, ecological provinces, and browsing intensity levels for each regeneration objective. Ecological provinces with low numbers of plots for a given FTG were aggregated with geographically adjacent provinces in some cases, including provinces 211 and M211 for oak/hickory and 222 and 223 for maple/beech/birch. Browsing intensity categories were simplified in this analysis by grouping 'very low' with 'low' and 'very high' with 'high' because low sample sizes preclude inference. Tukey's honest significant difference tests were used for multiple comparisons. Logistic regression was also used to investigate the effect of alternative mortality rates on the proportion of plots rated Secure for each regeneration objective and FTG. Statistical significance was indicated by $p < 0.05$. The 'rgdal' (Bivand et al. 2017) and 'sp' packages (Pebesma and Bivand 2005, Bivand et al. 2013) were used for processing geospatial data. The 'gstat' package (Pebesma 2004, Gräler et al. 2016) was used to fit and evaluate variograms and perform kriging analyses. Ordinary indicator kriging was used to obtain a geospatial interpolation of the probability for a given locale being rated Secure for each regeneration objective. Interpolated probabilities are a function only of distances from other intensively sampled plots and their respective categorization as Secure (1) or otherwise (0). The interpolated probabilities were kriged from a 3281 ft (1 km) grid within forested areas of the study region. Variograms used in all kriging analyses were fit with an exponential class model.

Results

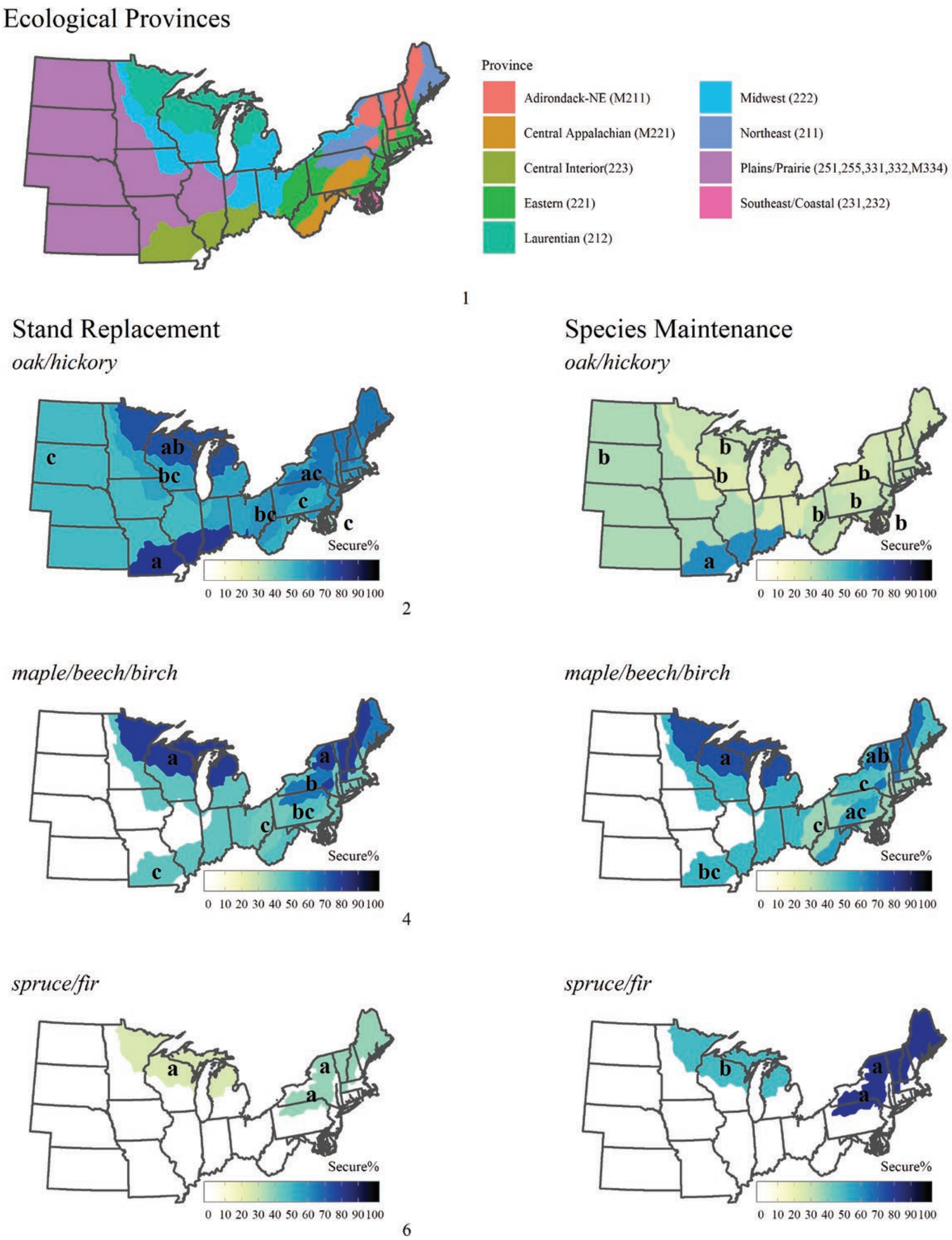
Stand Replacement

Across all FTGs and ecological provinces examined in the northern US, about 28% of regeneration-eligible plots were rated as Imminent Failures (Table 6). Another 17% of regeneration-eligible plots were rated Insecure, leaving 55% as Secure. On plots where inventoried reproduction met or exceeded the stand replacement Target, an annual maximum mortality rate near 5% (standard error [SE]: 0.1%) was affordable in the advance reproduction layer while meeting the stand replacement objective.

On Insecure and Secure plots, *Allowable Mortality* for stand replacement varied significantly among FTGs ($F_{8,2310} = 29.4$, $p < 0.001$, Figure 2a). Similarly, the proportion of plots rated Secure for stand replacement varied among FTGs ($\chi^2_{8,n:3215} = 197.8$, $p < 0.001$). Maple/beech/birch (65%) and oak/hickory (61%) were the only FTGs with more than half of their plots rated Secure (Figure 2b). In contrast, about 45% of oak/pine and loblolly/shortleaf pine plots, and about one-third of the plots for all other FTGs were rated Secure for stand replacement.

The probability of rating a plot as Secure for stand replacement varied across the study region (Figure 3a) as confirmed for two of the three FTGs most reliant on advance reproduction (Figure 4). The proportion of oak/hickory plots rated Secure varied by ecological province ($\chi^2_{7,n:1341} = 82.2$, $p < 0.001$, Figure 4b). The Central Interior province had the greatest proportion of oak/hickory plots rated Secure (80%), although the Laurentian (73%) and the combined Northeast/Adirondack-New England (65%) provinces were statistically similar. The combined Southeast/Coastal Plain province had the lowest proportion of plots rated Secure (36%), and all remaining provinces were statistically similar, ranging from 49 to 59%. The proportion of maple/beech/birch plots rated Secure for stand replacement also varied by ecological province ($\chi^2_{5,n:913} = 82.6$, $p < 0.001$, Figure 4d). The Adirondack-New England (79%) and Laurentian (79%) provinces were statistically similar and had the greatest proportions of Secure plots while the Northeast province was the only other province with over half (65%). The Eastern, combined Midwest/Central Interior, and Central Appalachian provinces had statistically similar proportions of Secure plots, ranging from 42 to 47%. The proportion of Secure spruce/fir plots for stand replacement ranged from 25 to 37% and did not vary by ecological province ($\chi^2_{2,n:169} = 2.3$, $P = 0.318$, Figure 4f).

The proportion of northern US plots rated Secure for stand replacement also varied by browsing intensity ($\chi^2_{2,n:3215} = 45.9$, $p < 0.001$). The proportion for low and moderate browsing intensities were both 57–58%, which was significantly different from the 40% for high browse plots (Table 7); however, browsing intensity was only statistically significant for the oak/hickory ($\chi^2_{2,n:1341} = 66.5$, $p < 0.001$), maple/beech/birch ($\chi^2_{2,n:915} = 17.6$, $p < 0.001$), and loblolly/shortleaf pine FTGs ($\chi^2_{2,n:23} = 6.2$, $P = 0.044$). The proportion of Secure oak/hickory plots was reduced from 72% to 39% when browsing intensity increased from low to high. The decline was considerable for maple/



Ecological Provinces

Stand Replacement

Species Maintenance

oak/hickory

maple/beech/birch

spruce/fir

Figure 4. Boundaries of prominent ecological provinces within northern US (4a) and proportion of regeneration-eligible NRS-FIA *Regeneration Indicator* plots rated Secure for stand replacement (left column) and species maintenance (right column) regeneration objectives for the three prominent forest-type groups most reliant on advance reproduction for regeneration success (rows). Within a panel, provinces with differing letters indicate statistically different proportions of plots rated Secure.

beech/birch (71-47%) and also for loblolly/shortleaf (86-33%).

Species Maintenance

The prospects of maintaining upper canopy species were less likely than successfully achieving the stand replacement objective. On 50% of the plots across the northern US, inventoried reproduction was less than the species maintenance Target resulting in imminent failure ratings (Table 6). On the 50% of plots rated as Insecure (9%) or Secure (41%) for the species maintenance objective, the average annual Allowable Mortality rate was nearly 6% (SE: 0.1%).

On Insecure and Secure plots, *Allowable Mortality* for species maintenance varied significantly among FTGs ($F_{8,1581} = 22.4, p < 0.001$, Figure 2a). The proportion of plots rated Secure for species maintenance also varied among FTGs ($\chi^2_{8,n:3215} = 299.9, p < 0.001$). The spruce/fir (67%) and maple/beech/birch (57%) FTGs were statistically similar, and the only types with more than half of their plots rated Secure (Figure 2b).

The probability of a Secure rating for species maintenance varied across the study region with expected difficulties in regeneration being more widespread than for the stand replacement objective (Figure 3). Regional variability was confirmed for the three FTGs most reliant on advance reproduction (Figure 4). The proportion of Secure plots for species maintenance varied by ecological province within the oak/hickory FTG ($\chi^2_{7,n:1341} = 102.5, p < 0.001$, Figure 4c). The Central Interior province had the greatest proportion of Secure oak/hickory plots (61%), which was roughly twice or more than the 20 to 34% observed in all other provinces that did not differ among themselves. The proportion of Secure maple/beech/birch plots also varied by ecological province ($\chi^2_{5,n:913} = 61.3, p < 0.001$, Figure 4e). The Laurentian (74%), Adirondack-New England (66%), and Central Appalachian (56%) provinces were statistically similar with over half their plots rated Secure. The Northeastern (48%) and Eastern (36%) provinces nominally had the lowest proportions of Secure plots and were statistically lower than the Laurentian and Adirondack-New England provinces. The proportion of Secure plots also varied by ecological province under the species maintenance objective in the spruce/fir FTG ($\chi^2_{2,n:169} = 17.6, p < 0.001$, Figure 4g). The proportion of Secure plots in the Laurentian province (42%) was statistically lower than those in the Adirondack-New England (81%) or Northeast (79%) provinces.

Browsing intensity was associated with the proportion of northern US plots rated Secure for species maintenance ($\chi^2_{2,n:3215} = 70.26, p < 0.001$). The proportion of Secure plots under low (47%) and moderate (40%) browsing intensities were nominally closer compared to high browsing plots (24%), but all were statistically different (Table 7). Browsing intensity was only associated with the proportion of Secure plots for species maintenance for oak/hickory ($\chi^2_{2,n:1,341} = 56.7$, $p < 0.001$) and maple/beech/birch ($\chi^2_{2,n:915} = 24.0$, $p < 0.001$) FTGs. Within those FTGs the proportion of Secure plots for species maintenance were statistically lower with each categorical increase in browse intensity.

On plots where the current FTG was not Secure under the species maintenance objective, over half (55%) lacked the potential to regenerate any of the alternative FTGs examined. In many cases, multiple FTGs were plausible on a single plot meaning that current understory demographics allowed Secure ratings for more than one FTG outcome. For the three FTGs most reliant on advance reproduction, the most Secure (by *Allowable Mortality*) transitional FTG is shown in Table 8. Imminent Failure and Insecure oak/hickory plots were equally plausible to transition to maple/beech/birch (25%) or elm/ash/cottonwood (25%), but transition to any other FTGs was unlikely. Nineteen percent of Imminent Failure and Insecure maple/beech/birch plots showed a potential to transition to the elm/ash/cottonwood FTG and 9% to the spruce/fir FTG.

Table 6. Contingency table of categorical regeneration examination outcomes for all NRS-FIA *Regeneration Indicator* plots in the northern US study region and each regeneration objective.

	Species Maintenance			
Stand Replacement	Imminent Failure	Insecure	Secure	Total
Imminent Failure	764	68	64	896
Insecure	270	75	196	541
Secure	591	134	1053	1778
Total	1625	277	1313	3215

Table 7. Sample size and percent of regeneration-eligible NRS-FIA *Regeneration Indicator* plots rated secure for each regeneration objective by browsing intensity class for the nine forest-type groups examined in this study. For a given regeneration objective, browsing intensities with differing letters for a forest type indicate statistically different proportions of plots rated secure.

	Sample Size (n)			Stand Replacement			Species Maintenance		
	Browsing Intensity[1]			Browsing Intensity			Browsing Intensity		
Forest-type group	Low	Mod.	High	Low	Mod.	High	Low	Mod.	High
	… # plots…			…Secure plots (%)…					
oak/hickory	418	703	220	^{a}72	^{b}62	^{c}39	^{a}46	^{b}35	^{c}17
maple/beech/birch	310	512	93	^{a}71	^{a}65	^{b}47	^{a}66	^{b}54	^{c}40
aspen/birch	132	92	25	38	38	28	18	12	8
spruce/fir	110	53	9	35	25	22	66	68	67
elm/ash/cottonwood	103	119	23	38	43	26	40	39	22
white/red/jack pine	70	55	7	31	36	29	14	18	14
oak/pine	46	48	19	43	42	58	37	25	26
loblolly/shortleaf pine	7	13	3	86	31	33	0	0	33
ponderosa pine	14	8	3	21	50	33	29	50	33
northern US	1210	1603	402	^{a}58	^{a}57	^{b}40	^{a}47	^{b}40	^{c}24

[1] Browsing Intensity definitions (combined browse impact codes). **Very Low/Low:** Plot is inside a well-maintained exclosure *OR* minimal browsing observed or vigorous seedlings present and of varied height (no well-maintained exclosure present). Herbaceous plants are present and they are able to flower and fruit. **Moderate:** Browsing evidence observed but not common. Seedlings are common, but with limited variability in height. Stump sprouts are heavily browsed or not evident. Herbaceous plants show a lack of or inhibited flowering and fruiting. There is little or evidence of browsing on non-preferred plants. **High/ Very High**: Browsing evidence common on preferred vegetation. Preferred seedlings and herbaceous plants are rare or absent. Non-preferred plants show some evidence of herbivory and browse-resistant vegetation is limited in height growth. A browse line is beginning to be visible; *OR* browsing evidence is omnipresent. Non-preferred and browse-resistant plants show signs of heavy repeated browsing. A browse line is obvious.

Table 8. Plausible species composition transitions for plots where difficulty was assessed (rated imminent failure or insecure) for species maintenance of their current forest-type group. On each such plot, the alternative secure rated forest-type group with the greatest calculated *Allowable Mortality* rate was deemed the most secure and plausible transition.

	Current forest-type group		
Future forest-type group (most Secure)	oak/hickory	maple/beech/birch	spruce/fir
	(…% Current Imminent Failure and Insecure plots...)		
oak/hickory	-	1%	0%
maple/beech/birch	25%	-	25%
aspen/birch	1%	1%	3%
spruce/fir	<1%	9%	-
elm/ash/cottonwood	25%	19%	2%
white/red/jack pine	<1%	0%	0%
oak/pine	1%	1%	0%
loblolly/shortleaf pine	0%	0%	0%
ponderosa pine	0%	0%	0%
none	47%	69%	70%

Conversely, maple/beech/birch was the most common plausible transition for spruce/fir plots.

Table 9. Regeneration examination outcomes by forest-type group for all NRS-FIA *Regeneration Indicator* plots in the northern US study region. Successful plots were Secure for both the stand replacement and species maintenance regeneration objectives together. Unsuccessful plots had an Imminent Failure for at least one of the two regeneration objectives. Because Insecure outcomes are not included row-wise totals may not sum to 100%.

Forest-type group	Unsuccessful	Successful
	(… % plots…)	
oak/hickory	63%	32%
maple/beech/birch	37%	49%
aspen/birch	68%	9%
spruce/fir	31%	26%
elm/ash/cottonwood	61%	26%
white/red/jack pine	77%	8%
oak/pine	60%	22%
loblolly/shortleaf pine	96%	4%
ponderosa pine	60%	32%

Potential difficulties meeting at least one of the regeneration objectives (Insecure or Imminent Failure) were found on 67% of the plots examined (Table 6). The probability of having inventoried advance reproduction sufficient for both stand replacement and maintenance of upper canopy species was 33% across the northern US. However, the probability varied considerably across the study region (Figure 3c). Maple/beech/birch had the highest proportion of plots rated Secure for both regeneration objectives together (49%), whereas five other FTGs had 22–32% of plots rated Secure for both regeneration objectives together (Table 9).

Expected Mortality Rates and Regeneration Security

The proportion of plots rated Secure decreased as mortality rates increased for both regeneration objectives (Figure 5). There were differing rates of decrease for both regeneration objectives across FTGs and thus differing potential for mortality rates to influence results. Under the stand replacement objective, spruce/fir, maple/beech/birch, and loblolly/shortleaf pine

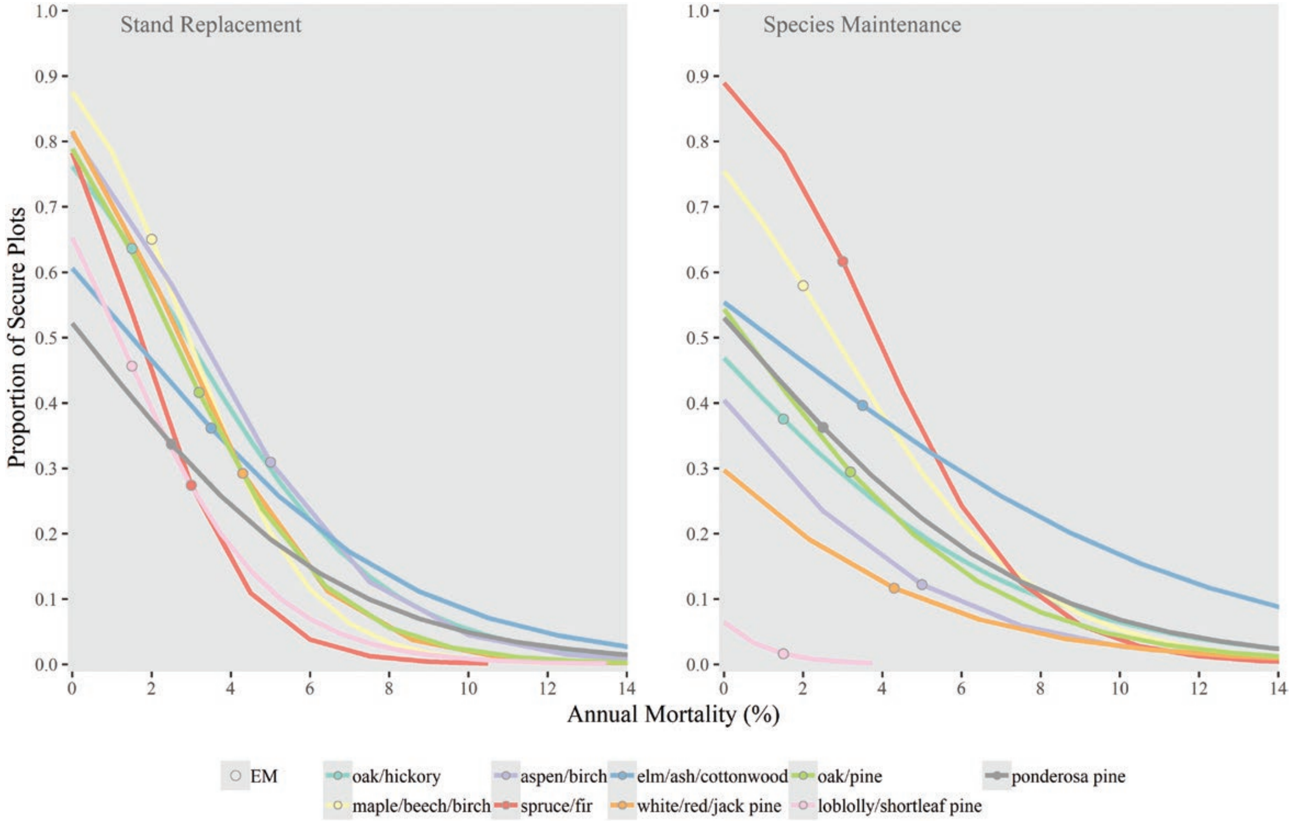


Figure 5. Proportion of NRS-FIA *Regeneration Indicator* plots rated Secure for stand replacement (5a) and species maintenance (5b) regeneration objectives by forest-type group (colors) under alternative annual mortality rates. *Expected Mortality* (EM) rates for each forest-type group (points) were obtained via a literature review.

FTGs exhibited the sharpest nominal declines with increasing seedling mortality rate (Figure 5a). The decline was nominally lowest for the elm/ash/cottonwood FTG, though ponderosa pine was similar. The decrease in proportion of plots rated Secure with increasing mortality rates was slower under the species maintenance objective than the stand replacement objective in general, but with greater variation across FTGs (Figure 5b). The spruce/fir FTG had the greatest nominal decline with increasing mortality rates, whereas elm/ash/cottonwood had the lowest. If mortality rates were less than *Expected Mortality*, security ratings under the stand replacement objective would increase for all FTGs. Aspen/birch, spruce/fir and white/red/jack pine FTGs had the highest potential to increase the proportion of plots rated Secure for stand replacement when mortality rates were below *Expected Mortality* levels. The oak/hickory FTG showed the least potential to increase in security with reduced mortality rates. Security rating could increase for all FTGs with reduced mortality under the species maintenance objective as well, albeit slightly less than under the stand replacement objective. For stand replacement, aspen/birch, spruce/fir, and oak/pine FTGs had the highest potential for increase in the proportion of Secure plots wheares oak/hickory and loblolly/shortleaf pine had the lowest potential.

Discussion

Many forest stands in the northern US are reaching the developmental stage when regeneration treatments are likely to be applied, i.e., understory reinitiation/demographic transition (Oliver and Larson 1996, Frelich 2002). In the event of overstory removal, the results of this study suggest that existing understory demographics are insufficient to meet regeneration objectives on over two-thirds of the plots examined, with failure for one or more objectives imminent on over half (55%). Regeneration success was plausible on nearly one-third of the plots. Other broad studies of reproduction demographics have reported similar findings of widespread regeneration concern (McEwan et al. 2011, Miller and McGill 2019).

There was much variation in regeneration security across the northern US and the ability to sustain current overstory species will be more challenging in certain regions and FTGs than others. Among FTGs reliant on advance reproduction, which were the majority of plots in this study, failure for one or more objective was more likely (51% of plots) than success for both objectives together (38%). This seemingly low probability of success based on advance reproduction alone is particularly concerning in those FTGs that rely strongly on advance reproduction to maintain a significant component of desirable canopy tree species, notably sugar maple, red spruce, and oaks.

Regeneration difficulties varied geospatially within FTGs. For example, oak regeneration difficulties have been well-documented across the eastern US (Loftis and McGee 1993, Johnson et al. 2009, McEwan et al. 2011), but those difficulties are often related to differences in site quality, competition from associated species, and browsing pressure (McWilliams et al. 1995, Johnson et al. 2009). This analysis corroborates the reports of McWilliams et al. (1995) and Johnson et al. (2009) that regenerating oak would be less difficult in the Central Interior province than in the Central Appalachian province. However, regeneration difficulties were not limited to oaks in the Central Appalachian or other provinces within the mid-Atlantic region, where the proportion of plots rated Secure for any FTG was generally low (Figures 3, 4). Miller and McGill (2019) similarly found that the central mid-Atlantic region was particularly problematic for regeneration of several species.

Many of the locales in this study that had high regeneration difficulties were found in areas such as the mid-Atlantic region and portions of the Great Lakes region with high intensity browsing by white-tailed deer (McWilliams et al. 2018). Increases in browse intensity resulted in decreased probability for regeneration success, primarily in the oak/hickory and maple/beech/birch FTGs. The effects of browsing on reproduction have long been acknowledged (Leopold et al. 1947, Marquis 1981), and continued over-browsing has negative long-term consequences on regeneration (Côté et al. 2004, Nuttle et al. 2014, Bernes et al. 2018). For example, Russell et al. (2017) found that NRS-FIA plots with very high browsing levels had 50% fewer ingrowth saplings than non-browsed plots. Browsing is one of multiple, interacting factors that may influence reproduction abundance and patterns at various spatial scales (Rooney et al. 2000, Didier and Porter 2003, Matonis et al. 2011, Patton et al. 2018). The presence of invasive pests, pathogens, and plants may exacerbate regeneration struggles resulting in wholesale changes in species composition and corresponding changes in ecological function (Nowacki and Abrams 2015, D'Amato et al. 2018, Miller and McGill 2019).

The FTGs showing fewer regeneration difficulties were often composed of upper canopy species that are tolerant to mid-tolerant of shade and able to establish in the understory with little canopy disturbance. For example, the maple/beech/birch FTG demonstrated fewer regeneration difficulties, particularly in the Laurentian ecological province. Red and sugar maples, along with other mesophytic species, are known to accumulate in the understory, particularly when managed using selection silviculture or harvested by diameter limits (Webster and Jensen 2007, Nowacki and Abrams 2008, McEwan et al. 2011, Bose et al. 2017). Therefore, it was little surprise that a transition to maple/beech/birch FTG was plausible on 25% of the oak/hickory and spruce/fir plots where species maintenance was not assured. Balsam fir can also establish in the understory of areas treated with harvesting methods that leave a residual overstory (Brown et al. 2018) which have become increasingly common in areas of spruce-fir dominance, such as northern Maine (Legaard et al. 2015).

Recruitment into the canopy is often strongly limited at two stages of stand development: seedling establishment/initiation, and stem exclusion. On plots with assessed difficulties, most (81%) were rated as Imminent Failure for at least one objective because advance reproduction insufficiencies were apparent early rather than in subsequent stages of development. This finding supports other research where lack of seedling establishment can hinder canopy recruitment of desirable species (Dey 2014). On these plots, amelioration will first require efforts to increase the density and competitive status of advance reproduction before regeneration events. On plots rated Insecure, competition control may increase the likelihood of regeneration success and improve early survival of targeted stems when the shortfall is minor (Brose et al. 2008). Assessed shortfalls may increase over time as yet unaccounted for competition begins to influence canopy recruitment in the latter stages of the regeneration period and into the stem exclusion stage of development (Oliver and Larson 1996, Dey 2014). Approximating complex competition dynamics within the current analytical framework would likely require a suite of inventory weighting factors more expansive than the current generalized weights, which may be optimistic for some species and management scenarios but pessimistic for others. Such attempts may be best served by the development of comprehensive regeneration simulators for existing vegetation models.

Some caution in applying these findings is warranted because regeneration objectives were assessed using Targets that approximate minimum numbers of desirable stems in young forests rather than more stringent thresholds that have been used in other studies (Solomon and Leak 1969, Steiner et al. 2008). Another caveat is that efforts to maintain current species composition are only worthwhile if the current composition is desirable. Degraded stands are commonplace and challenge both the development and execution of management objectives (Nyland 1992, Foley et al. 2005, Chazdon 2008). Moreover, the analyses did not adjudicate the desirability of compositional shifts among taxa within an FTG. In some cases, compositional shifts among namesake species within an FTG could be an important consideration, such as spruce versus fir in the spruce/fir FTG. Conversely, some FTG shifts may be less drastic than others given overlapping common associates, e.g., if a plausible transition from maple/beech/birch to elm/ash/cottonwood was largely driven by ash reproduction, a common maple/beech/birch associate.

The focus of these analyses has been on advance reproduction, but common species within the FTGs examined often establish following disturbances via windblown seeds, seed banking, or sprouting. For this reason, silvics of species under management must be taken into consideration when evaluating the relevance of advance reproduction assessments in a given FTG. The plots rated Insecure for one or more objectives can likely expect contributions from seeds and sprouts potentially alleviating some concern, especially those plots where species maintenance was assessed to be less difficult than stand replacement. Assessed regeneration difficulties may be less concerning than shown for those specific FTGs and the locales where other regeneration sources are prevalent. This includes aspen/birch forests, which are often regenerated using coppice management, and the pine FTGs where artificial regeneration or post-disturbance seed germination are common. Red maple, a prolific sprouter and namesake species of the maple/beech/birch FTG, is another example where the absence of advance reproduction may be less indicative of likely regeneration failure. Areas with high prevalence of these FTGs (aspen/birch and white/red/jack pine in the Northeast and Lake States) tended to have lower Secure probabilities for species maintenance based on advance reproduction but light-seeded species such as birches or sprouting species such as aspens may still dominate those sites post disturbance. For shortleaf pine, the predominant species of the loblolly/shortleaf pine FTG in the northern states, empirical evidence suggests higher success with greater reliance on advance reproduction (Guldin 2007). Initial establishment difficulties are common for shortleaf pine (Kabrick et al. 2007, 2015) and appear widespread with the Imminent Failure of almost all loblolly/shortleaf pine plots for species maintenance.

Although the analyses suggest that the majority of mature northern US forestlands have low potential for regeneration success from advance reproduction alone, it is not clear what proportion of a landscape *should* be regeneration-ready at a given time. Stands need desirable advance reproduction in place only before a releasing natural disturbance or when overstory removal is imminent in managed stands. It is desirable for every regeneration-eligible acre to eventually become regeneration-ready, but it is somewhat premature to discern the acceptability of a 33% regeneration-ready rate across the northern US without science-based guidance for what constitutes a sustainable age class distribution at the regional scale. A key element of that determination is the relative mix of planned harvest and unplanned natural disturbance, which influences the cost of management required. Varied ownerships, fragmented holdings, and diverse management objectives present further complications to that determination.

Increased forest management activity has been suggested to combat compositional shifts in the northeastern US that exacerbate regeneration concerns (Bose et al. 2017). The current aggregate ratio of forest volume growth to removals across the northern US averages about 2.6 for the FTGs examined in this study (Miles 2018), suggesting the potential for increased forest management in the region (Shifley et al. 2014). Given the results of this study, widespread overstory removal harvesting before landowners have the ability to practice silviculture to increase regeneration security could hasten compositional shifts or regeneration failures in many areas. Although the data used here are too coarse to justify specific treatments, the results can help foresters and policymakers identify regions and FTGs where regeneration harvests will have a higher likelihood of success, and those locales where forests are in greater need of silvicultural intervention to improve understory demographics for increased regeneration success. Focusing overstory removal on stands that are currently 'regeneration-ready', while prioritizing available resources towards silviculture in stands to improve desired regeneration potential could increase the efficacy of forest management activity (Iverson et al. 2018). Investments may include treatments aimed at establishing and promoting regeneration prior to overstory removal (shelterwood methods), post-harvest release of desired stems, or site preparation to remove competition and prepare the seedbed for new establishment.

The broad geographic scope and coarse spatial resolution of these analyses provides information that can be integrated with efforts at different spatial scales and compatible silvicultural research to advance forest research and management. The analytical methods used here can also be applied to stand-level inventories and there are opportunities for additional research at finer scales to identify and assess the role of other sources of regeneration, the local influences of drivers of regeneration success, and adaptive silvicultural prescriptions and practices to promote desired regeneration and increase certainty of successful outcomes. Such work would increase the specificity with which regeneration difficulties can be identified and refine the scope and scale of options available through silviculture to foster regeneration success. Future work could examine the adequacy of advance reproduction at sustaining multi-aged conditions, particularly for the shade-tolerant species for which multi-aged approaches are commonly applied.

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Endnote

1. Terminology follows Johnson et al. (2009, pg. 58) where *regeneration* refers to '…the ecological processes involving the establishment, growth, and population changes of juvenile trees…' and *reproduction* refers to '…individual or populations of juvenile trees…'

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