



Complex regeneration responses of eight tree species to partial harvest in mixedwood forests of northeastern North America

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ABSTRACT

Ecosystem-based forest management associated with partial harvesting (PH) is intended to balance ecological and economic values of sustainable forest management. The potential for delayed growth response and elevated mortality of advance regeneration following PH remains a critical concern, and may present a barrier to more widespread implementation of this approach. We used 835 permanent continuous forest inventory plots to examine the rate and time course of species-specific regeneration growth and mortality of eight tree species in the first fifteen years following operational partial harvests in the mixed-species forests of Maine, United States. We aimed to provide a quantitative understanding on how regeneration of different species responded to PH in terms of growth and mortality. In addition, we evaluated how the patterns and magnitudes of growth and mortality responses developed over time, if these responses occur gradually or suddenly, and if the patterns of the responses were persistent. We found that the response magnitude, temporal trajectories of responses, and the length of initial lag-period largely varied across species, PH treatments, and the variables examined. For sapling diameter growth, paper birch (*Betula papyrifera* Marshall) and red maple (*Acer rubrum* L.) showed immediate responses to high-intensity PH, while a five-year lag-period was observed in balsam fir (*Abies balsamea* (L.) Mill.), American beech (*Fagus grandifolia* Ehrh.), red spruce (*Picea rubens* Sarg.) and eastern hemlock (*Tsuga canadensis* (L.) Carrière) and a 10-year lag period in northern white-cedar (*Thuja occidentalis* L.). The initial increase in sapling mortality was observed in balsam fir, American beech, red maple and northern white-cedar, but not in other species. Sapling survival reached a stable state irrespective of species after the initial five-years following harvests. In partially harvested stands, identifying preharvest conditions related to postharvest density, growth, and mortality was complex and interacted with time since harvest. Our results suggest that broad application of PH only results in species-specific gains, losses, and delays in regeneration responses within mixed-species stands. Future research should consider PH in combination with other treatments to initiate immediate responses to a wider range of species.

1. Introduction

Recent decades have witnessed a shift in forest management approaches from purely commercial wood production objectives to greater consideration of the natural dynamics and provision of multiple ecosystem services (Puettmann et al., 2015). This recognition has

generated interest in ecosystem-based forest management approaches that aim to maintain ecosystem functions (Brais et al., 2004; Gauthier et al., 2009; Nolet et al., 2018). The central goal of this approach in North America and elsewhere is to maintain the natural variability of non-harvested stands for biodiversity and other ecosystem services in managed stands (Ameray et al., 2021; Brang et al., 2014; Seymour et al.,

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2002). Ecosystem-based management and the need to adapt forests to climate change stressors (Achim et al., 2022) frequently involve diversifying silvicultural treatments at the landscape level (Harvey et al., 2002; Royer-Tardif et al., 2021), including the implementation of stand-scale partial harvests (PH) (e.g., Kenefic et al., 2021; Nolet et al., 2014). PH encompasses a range of silvicultural treatments (e.g., commercial thinning, regular shelterwood, irregular shelterwood, selection cutting, retention forestry) that remove a portion of trees but retain others (Bose et al., 2014b; Montoro Girona et al., 2016; Thorpe and Thomas, 2007). When PH is used in conventional shelterwood or selection systems, tree removal is aimed to retain healthy trees to provide seed, moderate understory regeneration environments, and provide future harvest opportunities (Nyland, 2016). From an ecosystem-based management perspective, these silvicultural systems intersect with aspects of low- to moderate-severity natural disturbances (Seymour et al., 2002). When PH is used in recently-established retention forestry, the retained trees are selected primarily for biodiversity objectives and to emulate post-disturbance stand conditions and provide continuity across the landscape (Gustafsson et al., 2012). PH is argued to be key to reversing decades of homogenizing forest practices and land use and restoring forest heterogeneity and diversity (Kohm and Franklin, 1997). A long-standing question about PH whether used in conventional or recently-developed silviculture is the impact of the retained trees on tree regeneration and recruitment for long-term sustainable forest management.

While applying PH treatments with a range of harvesting intensities and spatial configurations provides flexibility for achieving desirable growing conditions for natural regeneration, actual responses of natural regeneration to PH are not clear. For instance, logging operations during PH can physically damage advance regeneration and thus the quality of the future growing stock (Montoro Girona et al., 2018; Thorpe et al., 2008). In addition, delayed growth response and competition from non-desirable species after harvesting may affect the recruitment of advance regeneration into the overstory (Bourgeois et al., 2004; Kern et al., 2017). Moreover, mortality of advance regeneration has also been reported for a number of species after PH because of combined effects of logging damage, competition from woody shrubs and shock from sudden changes in environmental conditions (Bose et al., 2014b). For these reasons, practitioners have critical concerns about when and where to apply PH treatments.

Although several studies have examined the growth and mortality of advance regeneration following PH under experimental conditions, in which harvesting treatments were carefully applied (Bataineh et al., 2013; Bédard et al., 2022; Mohammed et al., 2021), few have documented treatment effects on regeneration at the operational scale (e.g., Bose et al., 2020; Danyagri et al., 2017; Guay-Picard et al., 2015). Those that have examined regeneration responses did not provide a quantitative comparison regarding how responses to PH treatments vary across species that commonly occur in northeastern North America. This knowledge gap is important as the operational-scale PH has increased over the past years and is expected increase further in times to come.

Mixedwood stands in northeastern United States are characterized by a mixed composition of boreal conifer and temperate deciduous tree species (Seymour, 1995). Management of these stands can be challenging because the co-occurring species are associated with different traits and functions (Greene et al., 1999; Messier et al., 1999; Vickers et al., 2019) and thus display different growth and survival strategies for coping with changes in stand-level micro-environmental conditions after harvests (Table 1). A recent review by Kenefic et al. (2021) highlighted how past management has shifted mixedwood forests into hardwood dominance and how PH is critical to recovery of softwoods and restoration of mixedwood composition.

The life history traits of mixedwood species in northeastern United States usually determine the responses to PH treatments. Dominance of American beech (*Fagus grandifolia* Ehrh.) after PH is common, because it is very shade-tolerant and can regenerate from root suckers (Nyland et al., 2006). Beech suckers can grow and establish faster after PH than

Table 1

Ecological traits of tree species considered in the analyses.

Scientific Name	Common Name	Leaf Habit	Tolerance to Shade	Sprouting Ability
<i>Acer rubrum</i> L.	Red maple	Deciduous, Broadleaf	Mid-tolerant	Adult, Branch Layering
<i>Acer saccharum</i> Marsh	Sugar maple	Deciduous, Broadleaf	Tolerant	Adult
<i>Betula papyrifera</i> Marsh.	Paper birch	Deciduous, Broadleaf	Intolerant	Sapling
<i>Fagus grandifolia</i> Ehrh.	American beech	Deciduous, Broadleaf	Tolerant	Sapling, Branch Layers, Root Sprouting
<i>Abies balsamea</i> (L.) Mill.	Balsam fir	Evergreen, Needle	Tolerant	Seedling, Branch Layering
<i>Picea rubens</i> Sarg.	Red spruce	Evergreen, Needle	Tolerant	Seedling, Branch Layering
<i>Thuja occidentalis</i> L.	Northern white-cedar	Evergreen, Needle	Tolerant	Seedling, Branch Layering
<i>Tsuga canadensis</i> (L.) Carrière	Eastern hemlock	Evergreen, Needle	Tolerant	Seedling, Branch Layering

Source: Del Tredici (2001); Niinemets and Valladares (2006).

seed originated competitors (Beaudet and Messier, 2008; Bose et al., 2017). In addition, herbivore preference for sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britton) over beech promotes dominance of the latter in the understory areas with heavy browse pressure (Bose et al., 2018). After low-severity disturbances, faster-growing sugar maple can better exploit the canopy gaps than slower-growing beech (St-Jean et al., 2021). Paper birch (*Betula papyrifera* Marsh.) is relatively understudied regarding its responses to PH treatments, but grows faster than most species after harvesting, especially in well-lit, open conditions (Prévost et al., 2016). Between balsam fir (*Abies balsamea* (L.) Mill.) and red spruce (*Picea rubens* Sarg.), the two most frequently occurring softwood species in northeastern United States, balsam fir is better able to capture and utilize light and growing space than red spruce (Pothier and Prévost, 2008). Indeed, red spruce displays a greater sensitivity to full sunlight conditions compared to balsam fir and benefits from exposed mineral soils during logging operations (Dumais and Prévost, 2007). Responses of natural regeneration of eastern hemlock (*Tsuga canadensis* (L.) Carrière), northern white-cedar (*Thuja occidentalis* L.), and red maple (*Acer rubrum* L.) to PH or clear-cutting treatments are not well studied in northeastern North America (but see Larouche et al., 2010). Northern white-cedar is an extremely shade tolerant and long-lived species; it is often found in old-growth forest stands (Fraver et al., 2020). Eastern hemlock and red maple can be found in a wide range of stand conditions and site types (Weaver et al., 2009).

In this study, we aimed to unravel species-specific responses to PH to improve sustainability and stability of mixedwood forests for ecosystem-based management. To do this, we viewed PH as a gradient of intensity such that greater intensity will result in more overstory removal and more light resources available to the understory tree seedlings and saplings. Based on past studies and known plant traits, we anticipated that species with less shade tolerance will respond more immediately after PH with higher growth rates and less mortality than more shade tolerant species. Moreover, we viewed PH as a potential gradient of residual stand damage from large heavy equipment and merchantable tree removal, where greater PH intensity is related to greater understory tree seedling and sapling damage. Therefore, our anticipated species responses to PH based on shade tolerance would be modified by vegetative reproduction traits; species with high capability for sprouting would respond more immediately after PH and would be less likely

succumb to mortality.

To address our hypotheses, we aimed to: (1) examine how the effect of low-intensity (5–40 % of overstory basal area removal) and high-intensity (41–80 % of basal area removal) PH on growth and mortality of natural regeneration vary across eight tree species commonly found in northeastern North America over a 15-year post-treatment period, (2) quantify how responses to PH, including the direction (positive or negative), magnitude, immediacy, and persistency vary across species, and (3) assess interactive effects of preharvest understory regeneration density (an indicator of crowding) and preharvest overstory stand basal area (an indicator of suppression history) in explaining densities of seedlings (<2.5 cm DBH) and diameter growth and mortality of saplings (2.5–12.7 cm DBH).

2. Methods

2.1. Study sites

From northeastern United States, we selected the mixedwood forested landscape of Maine as study sites considering the predominance of partial harvesting based silvicultural practices and the availability of long-term (i.e., 20 years) database. The study sites are located across a latitudinal gradient from 43°08'N to 47°43'N and longitudinal gradient from 66°99'W to 71°07'W (Bose et al., 2020). The study sites have a cool humid continental climate with a mean annual precipitation of 901–1501 mm and mean annual temperature of 1.2–8.4 °C. Soil types are generally characterized as podzols, and species composition largely determines the fertility status in soils. Maine has an approximately 6-month growing season from April to September, however the length of the growing season varies from north to south (Bose et al., 2016; Seymour, 1995).

The forested landscape in Maine has a natural disturbance regime characterized by low- to moderate-severity disturbances caused by host-specific agents and windstorms (Fraver et al., 2007; Fraver et al., 2009). As a result, this region's forest composition is dominated by shade-tolerant tree species primarily due to the disturbance regime and long fire-return intervals and absence of clearcutting-based forest management (Seymour, 1995).

2.2. Data

For this study, we used the Forest Inventory and Analysis (FIA) data of United States Department of Agriculture Forest Service. FIA is a nationwide forest inventory program with a long history that uses a consistent sampling protocol across the country (<http://www.fia.fs.fed.us>). The FIA sampling protocol consists of four points arranged in a cluster (i.e., plot), where point 1 is the center, and points 2 to 4 are located 36.58 m from point 1 at azimuths of 0, 120, and 240°, respectively. Each point in the cluster is surrounded by a 7.3 m fixed-radius subplot where all trees with a diameter at breast height (DBH; 1.37 m) $\geq$ 12.7 cm are measured for DBH by species and characterized as “live” or “dead” (Bechtold and Patterson, 2005). Each subplot comprises one 2.07 m fixed radius microplot where all live saplings (2.5–12.7 cm DBH) are measured for DBH, living status, and species. Within each microplot, all live tree seedlings (i.e., <2.5 cm DBH with minimum heights of 15.2 cm for conifers and 30.4 cm for hardwoods) are counted and identified to species (Bechtold and Patterson, 2005).

In this study, we characterized PH as any harvest that removed 5 to 80 % of overstory (trees $\geq$ 12.7 cm at DBH) basal area in a forest stand (Bose et al., 2020). Harvest intensity was quantified from the ratio of preharvest to the postharvest overstory basal area. We then selected all plots that received PH since 1999 and had a preharvest measurement, at least three postharvest measurements, and were not harvested again between 1999 and 2016. We assumed that the PH treatments are intended to establish or release regeneration. A total of 424 plots met these criteria within the area of interest. We then randomly selected an

equal number plots ($n = 424$) that were not harvested from 1999 to 2016 and considered as “unharvested control stands”. We excluded 13 of the 424 unharvested plots due to very low overstory basal area (<1 m² ha⁻¹). As we were assessing the postharvest diameter growth and mortality responses to PH treatment, it was important to consider only those unharvested plots whose stand structure and composition did not differ from the preharvest stand conditions of partially harvested stands (Bose et al., 2020). We characterized 5–40 % and 41–80 % basal area removal as low-intensity and high-intensity PH, respectively, based on the median of harvesting intensity distribution to which the sample plots were submitted and for consistency with previous studies (see details in Bose et al., 2020; Bose et al., 2021). From the 424 original partially harvested plots, we had 171 and 253 low-intensity and high-intensity PH plots available for study, respectively.

2.3. Data analysis

We quantified the effects of low-intensity (5–40 % of overstory basal area removal) and high-intensity (41–80 % of basal area removal) PH on seedling density (stems ha⁻¹) sapling diameter (DBH) growth and mortality for eight commonly occurring tree species in Maine. These include paper birch, balsam fir, red spruce, eastern hemlock, northern white-cedar, American beech, sugar maple, and red maple. We considered preharvest and three postharvest measurement periods, 1–5 years, 6–10 years, and 11–15 years since the harvest. The postharvest periods represented practical timeframes that managers would assess regeneration harvest success to plan the next harvest. The DBH of seedlings and dead saplings were not available, therefore, the quantification of DBH growth was limited to live saplings. In addition, we only analysed the mortality of saplings due to unavailability of seedling mortality data. Sapling diameter growth was calculated as the growth between successive measurement periods, and was quantified following:

$$1) \text{ Growth} = \text{Sapling diameter at measurement period}_j - \text{Sapling diameter at measurement period}_i$$

Where $i = \text{measurement } 1 \dots \dots \dots n-1$, and $j = \text{measurement } i + 1 \dots \dots \dots n$.

Sapling mortality was quantified by the change in the tree status i.e., live in previous measurement but dead in the current measurement.

2.4. Statistical analysis

The statistical analyses were performed using the R programming language version 3.2.5 (R Development Core Team, 2018). For quantifying the pattern and magnitude of responses to two types of PH treatments, we analysed diameter growth of saplings using the linear mixed-effect models and probability of sapling mortality (i.e., live or dead) and seedling density (number of stems) using the generalized linear-mixed effect model (Zuur et al., 2009), where PH treatments were considered as fixed-effect variables and subplots nested within plots, plots nested within counties, and counties nested within management units as random effects variables. The linear mixed-effect model was performed using the *lme* functions of the *nlme* package (Pinheiro et al., 2014) while the *glmer* function of the *lme4* package was used for the generalized linear-mixed effect models (Bates et al., 2017). We used binomial family for probability of sapling mortality and Poisson family for seedling density (i.e., count data).

Modelling was performed separately for each time since harvesting period to understand the effect size of the two PH treatments in each year; a single model with year as a predictor variable would not provide the difference between a PH treatment and unharvested control treatment for every year. Therefore, we would not be able to know exactly when the statistically significant response (i.e., initial lag period) occurred and if that response was transient or persisting (Bose et al., 2021). Species-specific models were performed for all response

variables. Preliminary analyses showed that an additional error structure to account for temporal autocorrelation due to repeated measurements of sample plots and plot spatial autocorrelation did not improve the performance of the growth or mortality models; it was thus not incorporated in the final model. We visually verified normality and variance homogeneity of the residuals and used square-root transformation for sapling diameter growth data.

We used partially harvested stands for understanding the interactive effects between time since harvesting and other predictor variables (i.e., PH intensity, preharvest density of seedlings and saplings and total overstory basal area) on species-specific number of seedlings, sapling diameter growth, and probability of sapling mortality. For species-specific seedling density, we also included preharvest conspecific basal area in addition to other variables mentioned earlier. Like the previous analysis we used linear mixed-effect models for sapling diameter growth and generalized linear mixed-effect models for seedling density and sapling mortality. For understanding which factors affect sapling

mortality in partially harvested stands, we only considered the first five-year period as the mortality between unharvested and partially harvested stands were not significant in later periods.

3. Results

3.1. Species abundance preharvest

In preharvest stands, balsam fir was the most frequently found tree species across unharvested and partially harvested stands, for both the seedling and sapling layers (Fig. 1). Seedling density of American beech was higher in partially harvested stands, while seedling density of balsam fir and northern white-cedar were lower in partially harvested stands compared to unharvested stands. In addition, sapling density of American beech was higher in partially harvested stands, while sapling density of balsam fir was lower in partially harvested stands compared to unharvested stands. Seedling and sapling densities of other tree

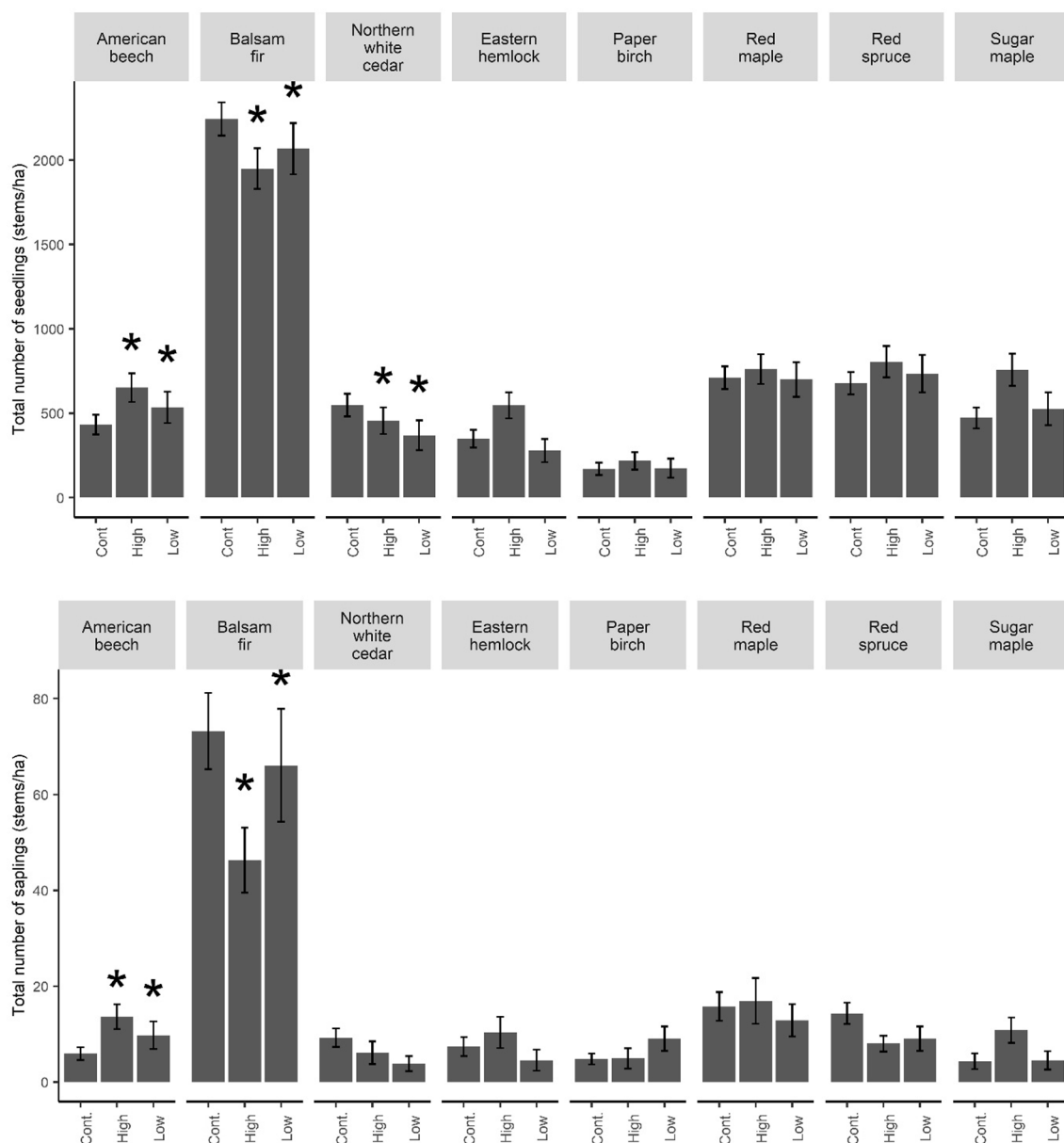


Fig. 1. Preharvest density of tree seedlings (<2.5 cm DBH) and saplings (2.5–12.7 cm DBH) of eight major tree species found in unharvested control and two partial harvesting (PH) treatments (i.e., low intensity and high intensity) in forested landscapes of Maine, United States. The error bars represent the mean $\pm$ standard error. * indicates significant differences ($p < 0.05$) between high intensity PH or low intensity PH against unharvested controls.

species were similar across partially harvested and unharvested stands (Fig. 1).

3.2. Magnitude and immediacy of seedling density responses to PH

PH treatments increased the density of tree seedlings for red spruce,

red maple, and paper birch, but decreased for northern white-cedar. Seedling density of eastern hemlock was not affected by either PH treatments (Fig. 2). However, the response patterns of balsam fir and American beech to PH treatments were relatively complex; seedling density decreased in high-intensity PH stands compared to control stands during the initial post-treatment periods (1–5 and 6–10 years) but

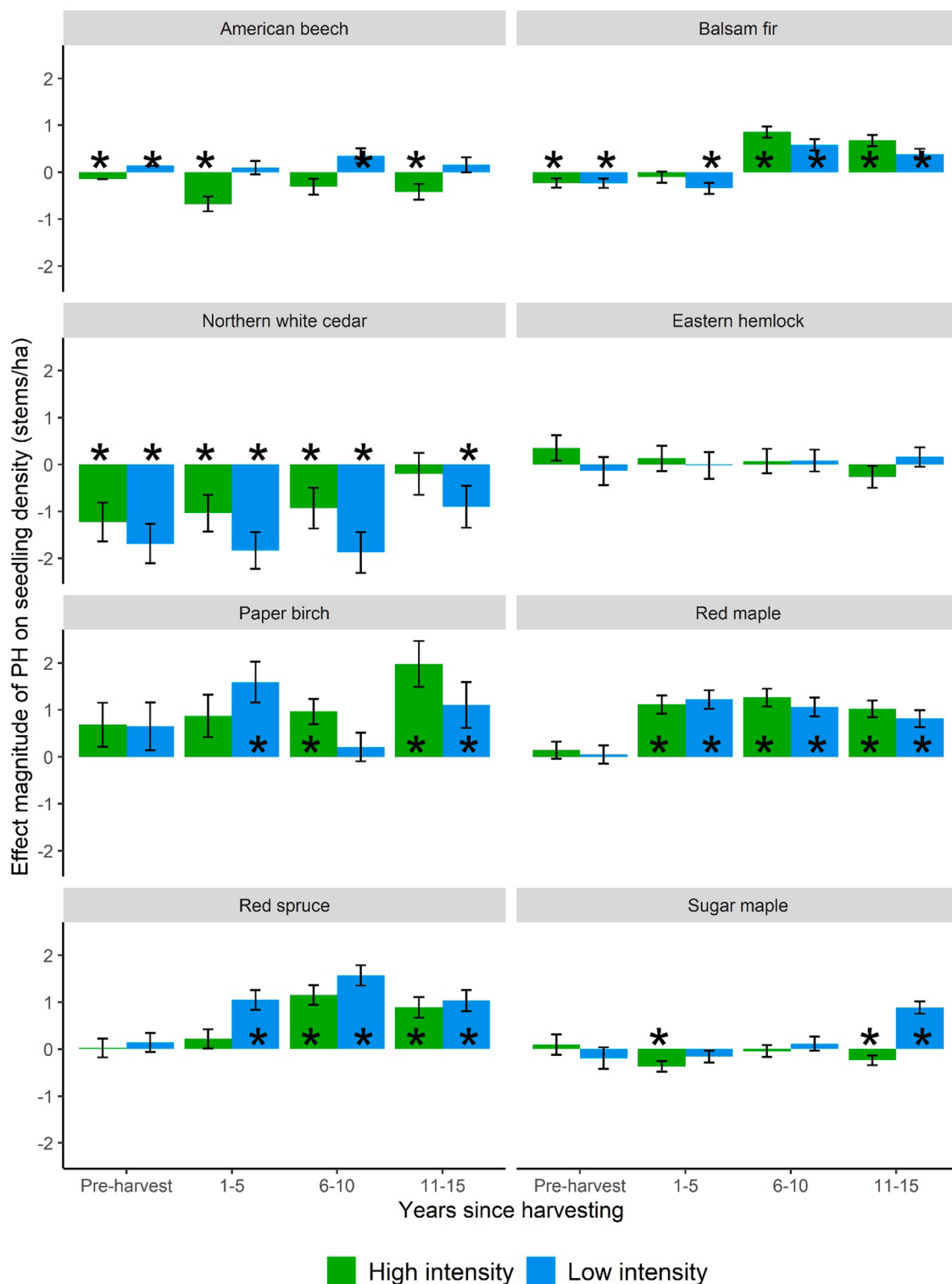


Fig. 2. Effect magnitudes of two partial harvesting (PH) intensity on seedling density from preharvest conditions to 15-year postharvest period in forested landscapes of Maine, United States. The effect sizes represent the slope of the mixed-effect models. The error bars represent the mean $\pm$ standard error and * indicates a significant ($p < 0.05$) difference between high intensity PH or low intensity PH against unharvested controls.

increased in the later period (11–15 years) (Fig. 2). Seedling density of American beech responded positively to low-intensity PH, but negatively to high-intensity PH (Fig. 2). We detected different lag periods prior to significant responses across species. For example, density responses from American beech and balsam fir were immediate, but

densities of red spruce, red maple, sugar maple and paper birch showed a 5-year lag period prior to showing significant responses to treatments (Fig. 2).

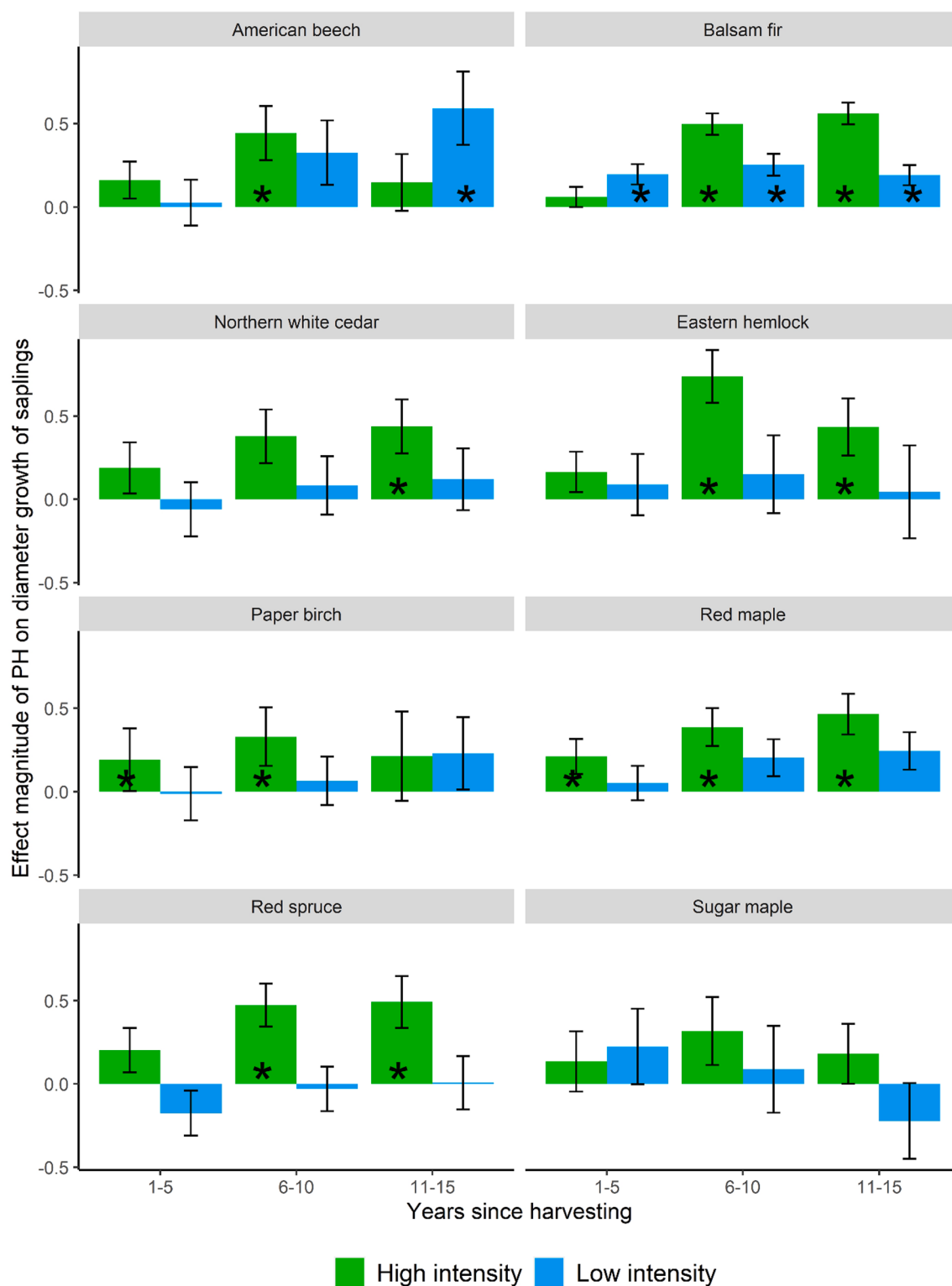


Fig. 3. Effect magnitudes of two partial harvesting (PH) treatments on sapling-level diameter growth over a 15-year post-treatment period in forested landscapes of Maine, United States. The effect sizes represent the slope of the mixed-effect models where growth was modelled as a function of unharvested vs low intensity PH and unharvested vs high intensity PH. The error bars represent the mean $\pm$ standard error and * indicates a significant ($p < 0.05$) difference between high intensity PH or low intensity PH against unharvested controls.

3.3. Magnitude and immediacy of sapling diameter growth responses to PH

High-intensity PH improved diameter growth of all studied species, except for sugar maple. Balsam fir and American beech were the only species that showed a significant growth response to low-intensity PH.

Diameter growth responses to high-intensity PH was rapid for paper birch and red maple, while the other species took more than five years to express a statistically significant response. The response of balsam fir and red spruce to high-intensity PH was significant from 6 to 10 to 11–15 years after treatment, however, statistically significant growth response was only visible during the 11–15 years period for northern

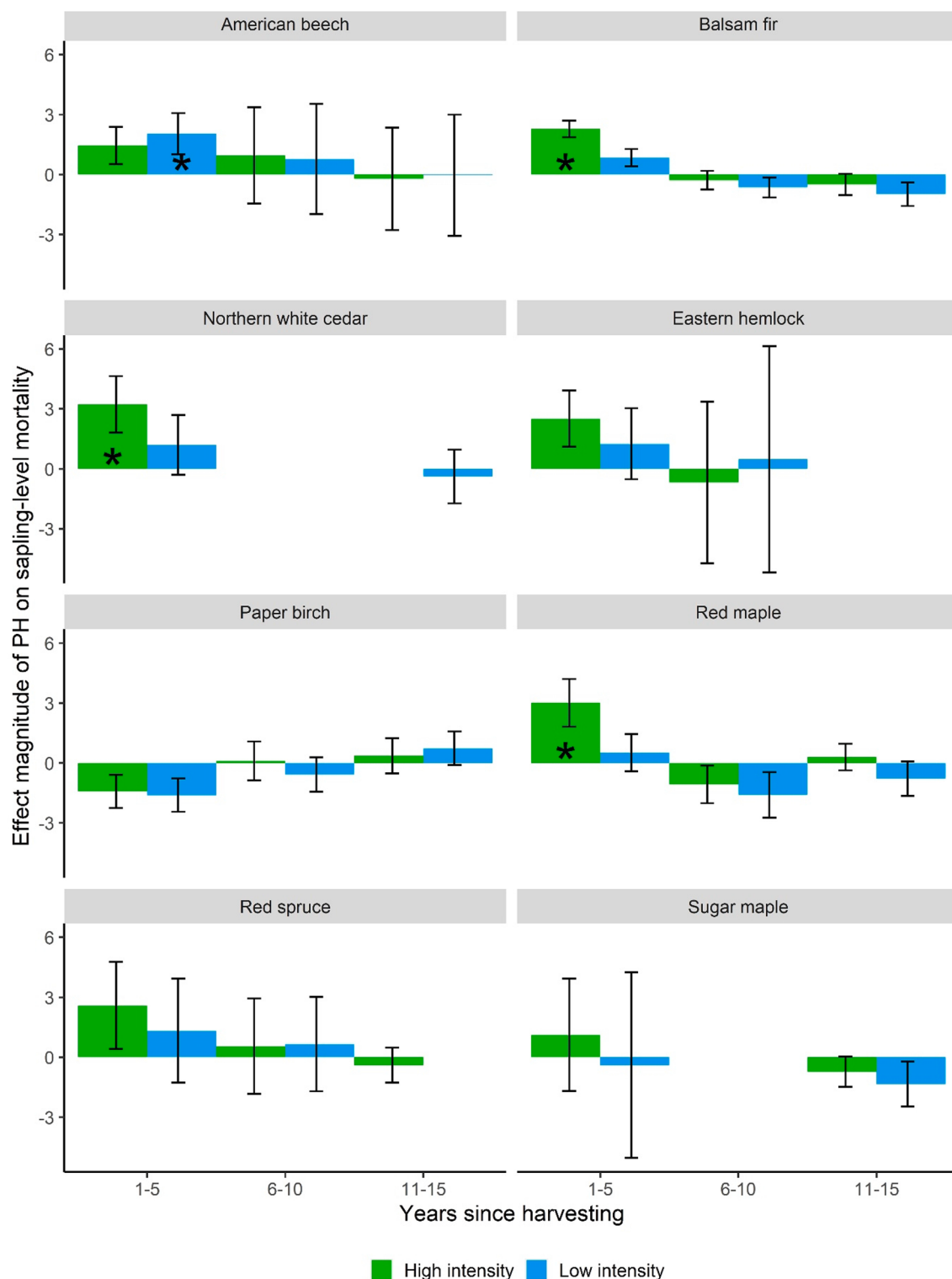


Fig. 4. Effect magnitudes (i.e., slope of the generalized linear mixed-effect models) of two partial harvesting (PH) treatments on probability of sapling mortality over a 15-year post-treatment period in forested landscapes of Maine, United States. The error bars represent the mean $\pm$ standard error and the * sign indicates a significant ($p < 0.05$) difference between high intensity PH or low intensity PH against unharvested controls. Missing data indicates that those analyses were not performed because of inadequate data (i.e., overly zero inflated).

white-cedar (Fig. 3). The response of American beech and eastern hemlock diameter growth to high-intensity PH was only significant at 6–10 years after treatment (Fig. 3).

3.4. Sapling mortality

High-intensity PH increased sapling mortality of balsam fir, northern white-cedar and red maple compared to unharvested control stands, but only during the initial five years since treatment (Fig. 4). Low-intensity PH increased sapling mortality only for American beech at the initial five-years since treatment. Sapling mortality of sugar maple, paper birch, eastern hemlock and red spruce were not higher in PH stands (low-intensity or high-intensity) compared to unharvested control stands (Fig. 4). Our analysis detected no significant difference in mortality between the two intensities of PH and unharvested control stands during 6–10 to 11–15 years since treatment (Fig. 4).

3.5. Factors affecting seedling density in partially harvesting stands

Conspecific seedling density in partially harvested stands were driven by the density of preharvest seedlings and saplings, total basal area of overstory trees, conspecific basal area of overstory trees and harvesting intensity. However, the influences of these variables on seedling density were dependent on time since harvest (i.e. significant interaction effects) (Table 2). For example, the interactive effects between harvesting intensity and time since harvest was significant for American beech, balsam fir, northern white-cedar, red maple and red spruce seedling densities but varied over time after harvest periods (Table 2). This indicate that the effect size of PH intensity varied over time after harvest periods (i.e., 1–5 vs 6–10 as well as 1–5 vs 11–15 years after PH) as well as across species. For example, the effect of conspecific basal area changes from 1 to 5 years to 6–10 years after harvest for balsam fir, northern white-cedar and sugar maple seedling densities but not for other species (Table 2). The interactive effects between preharvest sapling density and time since harvest was significant for seedling densities of balsam fir, eastern hemlock, northern white-cedar, paper birch, red spruce and sugar maple, whereas the interactive effects between preharvest seedling density and time since harvest were significant for all species except paper birch (Table 2).

Table 2

Factors affecting seedling (<2.5 cm DBH) density in partially harvested stands: how the effects of partial harvesting (PH) intensity, preharvest overstory basal area (m^2/ha), preharvest density of saplings (2.5–12.7 cm DBH) (stems ha^{-1}), preharvest density of seedlings (stems ha^{-1}) and conspecific basal area (m^2/ha) interacted with time since harvest (TSH) in determining postharvest seedling density of eight tree species in forested landscapes of Maine, United States. Three levels of TSH periods were considered 1–5, 6–10, and 11–15 years. Coefficients (mean $\pm$ SEM) of the generalized linear mixed-effects models are presented and the values in bold indicate a significant effect ($p < 0.05$).

Species	PH intensity		Basal area of adult trees		Conspecific basal area of adult trees		Density of saplings		Density of seedlings	
	1–5	1–5	1–5	1–5	1–5	1–5	1–5	1–5	1–5	1–5
	vs	vs	vs	vs	vs	vs	vs	vs	vs	vs
	6–10	11–15	6–10	11–15	6–10	11–15	6–10	11–15	6–10	11–15
American beech	–0.005 $\pm$ 0.003	–0.007 $\pm$ 0.003	0.0005 $\pm$ 0.006	0.017 $\pm$ 0.007	–0.014 $\pm$ 0.010	–0.035 $\pm$ 0.011	0.042 $\pm$ 0.028	0.058 $\pm$ 0.031	–0.017 $\pm$ 0.007	–0.024 $\pm$ 0.007
Balsam fir	0.003 $\pm$ 0.001	0.005 $\pm$ 0.002	0.007 $\pm$ 0.003	0.003 $\pm$ 0.003	0.046 $\pm$ 0.008	0.053 $\pm$ 0.008	–0.001 $\pm$ 0.009	0.022 $\pm$ 0.009	–0.019 $\pm$ 0.003	–0.028 $\pm$ 0.003
Eastern hemlock	0.0001 $\pm$ 0.005	–0.007 $\pm$ 0.005	0.019 $\pm$ 0.010	0.031 $\pm$ 0.010	–0.016 $\pm$ 0.011	–0.022 $\pm$ 0.011	–0.069 $\pm$ 0.027	–0.055 $\pm$ 0.028	–0.027 $\pm$ 0.008	–0.030 $\pm$ 0.008
Northern white cedar	0.009 $\pm$ 0.004	0.008 $\pm$ 0.004	–0.00003 $\pm$ 0.007	–0.003 $\pm$ 0.007	0.019 $\pm$ 0.007	0.019 $\pm$ 0.006	–0.072 $\pm$ 0.019	–0.015 $\pm$ 0.021	–0.019 $\pm$ 0.008	–0.041 $\pm$ 0.008
Paper birch	0.003 $\pm$ 0.004	–0.002 $\pm$ 0.004	0.006 $\pm$ 0.008	–0.00005 $\pm$ 0.008	0.034 $\pm$ 0.035	0.094 $\pm$ 0.039	0.061 $\pm$ 0.030	–0.013 $\pm$ 0.036	–0.015 $\pm$ 0.009	–0.005 $\pm$ 0.009
Red maple	0.005 $\pm$ 0.002	0.006 $\pm$ 0.002	0.007 $\pm$ 0.004	0.011 $\pm$ 0.005	0.009 $\pm$ 0.011	0.010 $\pm$ 0.011	–0.006 $\pm$ 0.019	–0.027 $\pm$ 0.020	–0.026 $\pm$ 0.005	–0.043 $\pm$ 0.005
Red spruce	0.007 $\pm$ 0.003	0.006 $\pm$ 0.003	0.017 $\pm$ 0.006	0.013 $\pm$ 0.006	0.007 $\pm$ 0.005	0.012 $\pm$ 0.005	–0.002 $\pm$ 0.020	0.050 $\pm$ 0.021	–0.025 $\pm$ 0.006	–0.028 $\pm$ 0.007
Sugar maple	0.007 $\pm$ 0.003	0.003 $\pm$ 0.003	0.007 $\pm$ 0.007	0.007 $\pm$ 0.006	–0.032 $\pm$ 0.008	0.004 $\pm$ 0.007	–0.046 $\pm$ 0.023	–0.059 $\pm$ 0.023	–0.008 $\pm$ 0.007	–0.024 $\pm$ 0.007

3.6. Factors affecting sapling diameter growth in partially harvesting stands

In partially harvested stands, harvesting intensity, preharvest overstory basal area, sapling density and seedling density interacted with time since harvest to affect sapling diameter growth (Table 3). However, the interactive effects of predictor variables on sapling diameter growth varied across species. For example, the interactive effects between harvesting intensity and time since harvest was significant for sapling diameter growth of American beech, balsam fir, eastern hemlock and sugar maple, but not for the other species (Table 3). The interactive effects between preharvest overstory basal area and time since harvest on sapling diameter growth was significant for American beech and eastern hemlock only, whereas the interactive effects between preharvest sapling density and time since harvest was significant for American beech and balsam fir only (Table 3). Understory seedling density interacted with time since harvest to influence diameter growth of balsam fir, eastern hemlock and red maple, but not for the other species (Table 3).

3.7. Factors affecting sapling mortality in partially harvesting stands

In partially harvested stands, harvesting intensity positively influenced sapling mortality of balsam fir but had no relationship with sapling mortality of other tree species (Table 4). Balsam fir sapling mortality was positively related to preharvest overstory basal area but not with preharvest sapling density and seedling density. However, preharvest overstory basal area was not related to sapling mortality of the other tree species considered in this study (Table 4). Sapling mortality of American beech was negatively associated with sapling densities, but not with the other predictor variables (Table 4). In partially harvested stands, sapling mortality of sugar maple, red maple, red spruce, paper birch, eastern hemlock and northern white-cedar was not impacted by harvesting intensity, preharvest overstory basal area, sapling density and seedling density (Table 4).

4. Discussion

Adequate natural regeneration and establishment of commercially desired species are major silvicultural challenges for PH-based forest management approaches (Bose et al., 2020; Kern et al., 2017; Messier

Table 3

Factors affecting sapling (2.5–12.7 cm DBH) diameter growth in partially harvested stands: how the effects of partial-harvesting (PH) intensity, preharvest overstory basal area (m^2/ha), preharvest density of saplings (stems ha^{-1}), and preharvest density of seedlings (stems ha^{-1}) interacted with time since harvest (TSH) in determining postharvest sapling diameter growth of eight tree species in forested landscapes of Maine, United States. Three levels of TSH periods were considered 1–5, 6–10, and 11–15 years. Coefficients (mean $\pm$ SEM) of the linear mixed-effects models are presented and the values in bold indicate a significant effect ($p < 0.05$). $\uparrow$ indicates that the effect of that variable was positive and not dependent upon TSH periods.

Species	PH intensity		Basal area of adult trees		Density of saplings		Density of seedlings	
	1–5	1–5	1–5	1–5	1–5	1–5	1–5	1–5
	vs	vs	vs	vs	vs	vs	vs	vs
	6–10	11–15	6–10	11–15	6–10	11–15	6–10	11–15
American beech	0.001 $\pm$ 0.001	−0.003 $\pm$ 0.001	−0.0002 $\pm$ 0.001	−0.006 $\pm$ 0.001	−0.004 $\pm$ 0.009	0.023 $\pm$ 0.012	−0.001 $\pm$ 0.003	−0.003 $\pm$ 0.003
Balsam fir	0.005 $\pm$ 0.001	0.005 $\pm$ 0.001	−0.0007 $\pm$ 0.002	0.003 $\pm$ 0.002	0.0002 $\pm$ 0.002	0.008 $\pm$ 0.002	−0.006 $\pm$ 0.002	−0.008 $\pm$ 0.002
Eastern hemlock	0.003 $\pm$ 0.001	0.002 $\pm$ 0.001	0.004 $\pm$ 0.001	−0.0005 $\pm$ 0.001	−0.003 $\pm$ 0.004	−0.0005 $\pm$ 0.004	−0.011 $\pm$ 0.003	−0.017 $\pm$ 0.003
Northern white cedar	0.0001 $\pm$ 0.002	0.0001 $\pm$ 0.002	0.008 $\pm$ 0.005	0.007 $\pm$ 0.005	−0.001 $\pm$ 0.016	−0.003 $\pm$ 0.016	0.013 $\pm$ 0.011	0.007 $\pm$ 0.011
Paper birch	0.0003 $\pm$ 0.002 $\uparrow$	−0.001 $\pm$ 0.002 $\uparrow$	−0.002 $\pm$ 0.005	−0.002 $\pm$ 0.007	−0.008 $\pm$ 0.011	0.0002 $\pm$ 0.013	−0.003 $\pm$ 0.006 $\uparrow$	−0.009 $\pm$ 0.007 $\uparrow$
Red maple	0.0009 $\pm$ 0.001	0.0003 $\pm$ 0.002	−0.002 $\pm$ 0.004	0.002 $\pm$ 0.005	−0.004 $\pm$ 0.006	−0.003 $\pm$ 0.006	−0.005 $\pm$ 0.003	−0.007 $\pm$ 0.003
Red spruce	−0.0002 $\pm$ 0.002 $\uparrow$	−0.003 $\pm$ 0.002 $\uparrow$	0.0002 $\pm$ 0.004	−0.004 $\pm$ 0.004	−0.007 $\pm$ 0.007	−0.010 $\pm$ 0.007	−0.008 $\pm$ 0.005	−0.007 $\pm$ 0.005
Sugar maple	0.005 $\pm$ 0.002	0.005 $\pm$ 0.002	0.0004 $\pm$ 0.005	0.004 $\pm$ 0.005	0.002 $\pm$ 0.013	0.008 $\pm$ 0.015	0.007 $\pm$ 0.006	0.002 $\pm$ 0.006

Table 4

Factors affecting sapling (2.5–12.7 cm DBH) mortality in partially harvested stands: Effects of partial harvesting (PH) intensity, time since harvest (TSH), preharvest overstory basal area (m^2/ha), preharvest density of saplings (stems ha^{-1}), preharvest density of seedlings (<2.5 cm DBH (stems ha^{-1})) on post-harvest sapling mortality of eight tree species in forested landscapes of Maine, United States. Coefficients (mean $\pm$ SEM) of the generalized linear mixed-effects models are presented and the values in bold indicate a significant effect ($p < 0.05$).

Species	PH intensity	Basal area of adult trees	Density of saplings	Density of seedlings
American beech	0.022 $\pm$ 0.026	0.046 $\pm$ 0.039	−0.540 $\pm$ 0.269	0.013 $\pm$ 0.049
Balsam fir	0.038 $\pm$ 0.010	0.044 $\pm$ 0.022	−0.024 $\pm$ 0.043	−0.011 $\pm$ 0.026
Eastern hemlock	0.005 $\pm$ 0.027	0.016 $\pm$ 0.044	−0.188 $\pm$ 0.143	0.059 $\pm$ 0.091
Northern white-cedar	0.111 $\pm$ 0.235	−0.272 $\pm$ 0.490	−1.332 $\pm$ 1.945	−0.040 $\pm$ 0.424
Paper birch	0.003 $\pm$ 0.165	−0.080 $\pm$ 0.476	−0.458 $\pm$ 1.282	0.044 $\pm$ 0.429
Red maple	0.046 $\pm$ 0.024	0.058 $\pm$ 0.039	−0.046 $\pm$ 0.094	0.006 $\pm$ 0.055
Red spruce	0.022 $\pm$ 0.022	0.061 $\pm$ 0.041	0.0004 $\pm$ 0.095	0.044 $\pm$ 0.047
Sugar maple	0.055 $\pm$ 0.096	0.122 $\pm$ 0.187	−0.076 $\pm$ 0.539	0.048 $\pm$ 0.216

et al., 1999; Vickers et al., 2019). In this study, we examined regeneration (i.e. seedling and sapling) responses as a function of two intensities of PH treatments over large latitudinal and longitudinal gradients in northeastern mixed-species forests of the United States. Our results showed that responses varied greatly across species in terms of initial lag-period prior to observing a significant response, response magnitude, direction of responses (positive or negative) and temporal trajectories of responses. We expected that PH would increase sapling mortality because of potential postharvest shock and damages from logging activities (Beckage et al., 2000; Fraser et al., 2004). Indeed, high-intensity PH had a stronger impact than low-intensity PH on postharvest sapling mortality for balsam fir, northern white-cedar, and red maple, but we did not detect greater mortality in stands submitted to high-intensity harvest for other species. Moreover, when detected, this effect was limited to the initial 1–5 years since harvest operations

(Fig. 3). Sapling mortality of American beech, balsam fir, red maple, and northern white-cedar were higher in partially harvested stands compared to unharvested stands, indicating the sensitivity of these species to either logging damages or postharvest shock. Sapling mortality immediately after partial harvests has also been reported before, primarily for shade-tolerant species such as balsam fir (Power et al., 2022; Raymond et al., 2016), red spruce, and northern white-cedar (Larouche et al., 2010). These shade-tolerant species might have suffered from long-time suppression prior to harvest (Danyagri et al., 2017) and postharvest competition with shade-intolerant species who can grow faster when exposed to full lights (Beckage et al., 2000; Brais et al., 2013; Man et al., 2008). Moreover, shade-tolerant species such as red spruce can be sensitive to the environmental conditions created by canopy removal, such as full sunlight, high temperatures, and frost (Dumais and Prévost, 2007).

Following release from competition, trees generally display an increased growth rate (Wagner et al., 2005), however, magnitude of their responses may depend on species-specific resource acquisition- and resource use-efficiency (Messier et al., 1999). We expected that by increasing overall light availability, partial harvesting would increase seedling density and sapling diameter growth, irrespective of species (Bannon et al., 2015). However, we detected delays in the response patterns. The magnitude of responses and the length of lag-periods also varied strongly across species (Figs. 1 and 2). Our analyses showed that sapling diameter growth of shade-intolerant paper birch and mid-tolerant red maple increased immediately after high-intensity partial harvest, whereas shade-tolerant American beech, balsam fir, eastern hemlock, and red spruce took more than five years to display significant diameter growth responses to treatments (Fig. 2). Unlike sapling diameter growth, seedling density of paper birch and red maple did not increase immediately, but with a 1–5 years lag-period. The delayed seedling-level responses were probably due to their short stature compared to tall saplings that had a height advantage to usurp available light (Bose et al., 2020; Power et al., 2022). Indeed, shaded and suppressed understory trees may not benefit from partial overstory removal and may, therefore, display a longer time lag compared to their taller neighbours (Messier et al., 1999). While harvest intensity was linearly associated with diameter growth of shade-intolerant paper birch and mid-tolerant red maple saplings, it did not significantly impact shade-tolerant species growth except balsam fir and American beech.

The lack of response or extremely delayed response in sugar maple, northern white-cedar, and other shade-tolerant species might have been

caused by suppressed growth prior to harvesting (Canham, 1990). Moreover, Jones and Thomas (2004) showed that sugar maple saplings displayed lack of response to selection harvests when they were located in the southern side of the gaps. Low preharvest growth rates have often been associated with modest growth increases (e.g., Danyagri et al., 2017). Delays in growth response to release have been reported previously for a number of tree species, including balsam fir (Bourgeois et al., 2004; Man et al., 2008), lodgepole pine (*Pinus contorta* Douglas) (Kneeshaw et al., 2002), black spruce (Montoro Girona et al., 2016) and red maple (Raymond et al., 2018). This delay may reflect physiological and morphological adjustments of saplings to overstory removal (Kneeshaw et al., 2002) and depend on the degree of preharvest suppression (Bose et al., 2020). Regeneration growth following release can also be affected by the density of other non-woody vegetation (Bose et al., 2014a; Gasser et al., 2010; Raymond et al., 2018) and ungulate browsing (Bose et al., 2018; Kern et al., 2012).

Low-intensity partial harvesting (which we defined as 5–40 % of overstory basal area removal, representing a range of silvicultural systems and cutting practices) was not related to an increased diameter growth of tree saplings, except for balsam fir and American beech. In addition, the effect size of low-intensity compared to high-intensity harvest was smaller for increasing seedling density or sapling diameter growth, irrespective of species. This suggests that the increase in light availability and lower postharvest competition resulting from high-intensity harvest may be crucial for seedling density and sapling diameter growth. The positive role of partial harvest intensity on sapling diameter growth has been reported (Bose et al., 2015; Brais et al., 2018; Dumais and Prévost, 2008; Montoro Girona et al., 2018). However, our analyses identified negative effects of partial harvest on seedling density for several species, including northern white-cedar, balsam fir, American beech and sugar maple. Although adult trees of these species responded positively to partial harvest (Bose et al., 2021), it appears that understory trees, especially seedlings (<2.5 cm at DBH), were not related to the PH categories we studied. The significant effect of PH on sapling diameter growth for paper birch and American beech became insignificant during the 11–15 year after treatments. These results may indicate that residual tree crowns and root systems expanded after harvest as well and, over time, which diminished understory growing conditions and interfered the long-term effect of PH treatments (Pothier et al., 2003).

Several studies have indicated that the understory light availability can decrease significantly within the 5–10 years after partial harvest (e.g., Beaudet et al., 2011; Prévost and Pothier, 2003). Therefore, it is crucial to understand how the influence of partial harvesting changes over time since harvest and if the other factors such as competition from understory, midstory, and overstory vegetations become more important in determining regeneration responses (Messier et al., 1999; Wagner et al., 2011). In partially harvested stands, seedling density and sapling diameter growth responses to time since harvest were dependent not only on PH intensity but also on stocking at different vegetation layers (overstory, midstory, and understory) (Table 2 and 3). These results indicate that both resource availability and competition for resources were important for determining postharvest regeneration responses (Kern et al., 2017; Wright et al., 1998). The responses of seedlings growing in dense patches below canopy generally depend on their potentials of light acquisition and light use-efficiency (Messier et al., 1998). Indeed, we detected strong differences across species. The response patterns across eight different tree species were dependent on how they have responded to interactive effects between time since harvest and harvesting intensities and the interactive effects between time since harvest and stocking across different vegetation layers (Table 2 and 3). In partially harvested stands, seedling density responses to harvesting intensity were mostly significant but dependent upon time since harvesting and vegetation stocking across understory-overstory vegetation layers (Table 2).

The intensity of PH was not important for increasing sapling

diameter growth of red maple, rather the interactive effects between time since harvesting and understory seedling density (Table 3). Sapling diameter growth of red maple declined in a later time period after harvest when seedling density increased. Similarly, the increase of seedling densities in later periods after harvest also had a negative influence on sapling diameter growth of balsam fir (Table 3). Faster height development of woody shrubs after harvest can reduce the light availability to understory vegetations and can reduce the response magnitudes to partial harvests (Bourgeois et al., 2004; Kern et al., 2017; Man et al., 2008). Our study suggests that the use of partial harvestings to promote abundance and growth of advance regeneration can be challenged by a number of factors including the size of advance regeneration, species, basal area of conspecific overstory trees and crowding effect at the understory and midstory vegetation layers, and crown expansion of overstory trees after harvests. Therefore, a strategy for combined manipulation of both overstory and understory may be required to achieve desired regeneration outcomes. This can be executed by identifying constraints for regeneration establishment of the target species prior to silvicultural interventions such as overstory removal can increase light availability while overstory retention can maintain the propagule sources. Meanwhile, targeted understory removal can reduce competition among understory vegetations (Wagner and Colombo, 2001).

Implications for forest management

Our 15-year postharvest results of PH impacts on tree regeneration represent a practical timeframe that managers use to assess treatment success and followup treatments. In some cases, such as lands managed under the National Forest Management Act, the assessments occur immediately in the first 5 years postharvest. Among the eight study species, mortality impacts were only detected in the initial 1–5 years, indicating managers can immediately assess the need for additional reforestation activities. However, mortality was not clearly linked to preharvest structural variables; additional research is needed to identify indicators of preharvest mortality, during the tree marking stage. The ability to assess seedling density targets is immediate for most of the study species, except hemlock which showed no significant response in density. Immediate sapling growth was only detected for red maple, paper birch, and balsam fir. The results suggest some ability to quickly address loss of advance regeneration for some species, but management goals associated with the evaluation of growth responses will need longer timeframes than the initial 5 years postharvest for most species. Careful logging operations could reduce mortality (Fraser et al., 2004). Seedling densities and sapling growth were related to PH intensity; high-intensity PH that removed 41–80 % of the initial basal area produced the highest abundance of seedlings and growth responses of saplings. If the species that respond to high PH are a management goal in regeneration, then high intensity PH could be favoured in silvicultural systems and alternatives to clear-cutting for achieving objectives of ecosystem-based forest-management.

Overall, improving growth and abundances of mixed species forests are challenging through the sole manipulation of partial harvesting intensity. A combined overstory and understory manipulation strategy might require promoting a desirable and stable composition of mixed-woods (Kern et al., 2021; Royo et al., 2019). Future research should consider PH in combination with other treatments to initiate immediate growth responses of advance regeneration while minimizing the growth lag period and logging induced mortality of a wide range of species.

CRedit authorship contribution statement

Arun K. Bose: Conceptualization, Writing – original draft. **Martín Alcalá-Pajares:** Writing – review & editing. **Christel C. Kern:** Conceptualization, Writing – review & editing. **Miguel Montoro-Girona:** Writing – review & editing. **Nelson Thiffault:** Writing – review

& editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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