

Increasing the utility of tree regeneration inventories: Linking seedling abundance to sapling recruitment

Lucas B. Harris^{a,*}, Christopher W. Woodall^b, Anthony W. D'Amato^a

^a Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT, USA

^b USDA Forest Service, Research and Development, Forest Inventory & Analysis, Durham, New Hampshire, USA

ARTICLE INFO

Keywords:

Tree regeneration
Tree seedling surveys
Sapling recruitment
Forest inventory
Northeastern USA
Northern temperate and boreal forest

ABSTRACT

Tree regeneration surveys provide insight into potential forest change and trajectories of stand development, which can guide management in an era of global change. However, most tree regeneration surveys tend to be coarse and/or rapid assessments which can introduce considerable uncertainty into translating estimates of seedling abundance into models of sapling recruitment and subsequent overstory tree abundance and composition. Observations of seedling abundance changes across size classes may be essential to accurately predicting recruitment from seedling sized trees to advanced size classes, which is fundamental to informing our understanding of future forest composition and dynamics. Using the USDA Forest Service's Forest Inventory and Analysis (FIA) program's Regeneration Indicator (RI) dataset, in which seedlings are monitored by six height classes, we developed Boosted Regression Tree models to predict presence of sapling recruitment for five common, north temperate and boreal tree species as a function of seedling abundance by height class and site/stand factors. Models using the six RI seedling height classes were compared to models using the single seedling size class as commonly surveyed by programs such as FIA. Use of seedling height classes improved models for all species. Seedlings > 1.5 m tall were the most influential predictors of recruitment for each species while seedlings in classes < 1.5 m tall were either removed entirely from models or had low relative influence (<8%). Seedlings < 0.3 m tall had both positive and negative relationships with sapling recruitment depending on species, suggesting that abundances of small seedlings should be interpreted cautiously. This approach demonstrates the importance of collecting relatively coarse seedling height data during regeneration surveys with potential application to other regions and scenarios to expand the utility of tree regeneration surveys to predict future forest dynamics.

1. Introduction

As threats to forest health and resilience from climate change, disturbance and other stressors intensify (Forzieri et al., 2022; Trumbore et al., 2015), it is increasingly important to interpret early indicators of forest change as accurately as possible. Monitoring tree seedling abundance and composition is crucial to assess how the distribution and composition of forests are likely to change in the future. For example, comparisons of seedling and adult tree distributions can indicate range shifts in response to climate change (Zhu et al., 2015; Dobrowski et al. 2015). Post-disturbance tree regeneration surveys are vital to assessing forest recovery, and contemporary concern over regeneration failure or compositional shifts following high-severity disturbance lends urgency to such post-disturbance assessments (Coop et al., 2020; Martínez-

Vilalta and Lloret, 2016).

Once trees grow to sapling and subsequent tree sizes within canopy openings, forest composition and structure can become increasingly resistant to management efforts to alter stand development trajectories (Seidl and Turner, 2022). Understanding how tree seedling abundances relate to sapling recruitment can inform management strategies at this critical early phase in stand development, when stand trajectories can still be altered through tree planting, vegetation management, or other interventions. Yet, traditional tree regeneration inventories have been conducted with relatively sparse sample intensities across space and time with their primary focus in service of merchantable timber assessment (i.e., focus species stocking assessment during management activities) with little emphasis on predicting stand trajectories (Brand et al., 1991; Gillis et al., 2005; Gschwanter et al., 2022; Lawrence et al.,

* Corresponding author at: Aiken Center, 81 Carrigan Drive, Burlington, VT 05405, USA.

E-mail address: lucas.harris@uvm.edu (L.B. Harris).

<https://doi.org/10.1016/j.ecolind.2022.109654>

Received 21 August 2022; Received in revised form 2 November 2022; Accepted 7 November 2022

Available online 12 November 2022

1470-160X/© 2022 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

2010). These coarse survey methods (e.g., single seedling size class stocking assessments that are not geo-referenced nor repeated) may be insufficient to predict whether observed regeneration patterns will lead to desirable forest composition and structure in the future (McWilliams et al., 2015). As forest management goals have become more holistic, forest inventory protocols have broadened and interest in more complete and accurate tree regeneration surveys is growing (Gschwantner et al., 2022; McWilliams et al., 2015; Vidal et al., 2016).

Similarly, ecological surveys of post-disturbance tree regeneration have proliferated over the past decade, particularly as concern mounts that some forests in the western US may be unable to recover following disturbances such as drought and wildfire in the context of climate change (Davis et al., 2019; Minott and Kolb, 2020; Stevens-Rumann et al., 2018). However, seedling surveys in these post-disturbance landscapes have tended to be rudimentary as the primary focus is often identifying areas of regeneration failure (Stevens-Rumann et al., 2022) rather than more comprehensive assessments of forest compositional and structural trajectories that are increasingly needed to effectively manage forests in the face of global change (Seidl and Turner, 2022).

One particular concern in tree regeneration surveys is the common use of a single size class to represent seedlings, which is efficient but not necessarily effective as it cannot account for the consideration that larger seedlings are typically more likely to attain sapling size than smaller seedlings (McWilliams et al., 2015). To account for these differences in the probability of recruitment, seedlings can be subdivided into multiple height classes which allow seedling abundance to be

adjusted according to anticipated mortality rates within each class (McWilliams et al., 1995; Vickers et al., 2019b). Yet as seedlings establish and grow, they are subject to strong environmental filtering due to factors such as understory vegetation, browsing, and canopy tree cover that may generate highly variable seedling mortality and growth rates according to local or stand-level conditions (George and Bazzaz, 1999; Henry et al., 2021; Matonis et al., 2011; Walters et al., 2016). Substrate characteristics such as litter depth and coarse woody material may also have strong effects on seedling establishment, growth and survival (Bolton and D'Amato, 2011; Collins, 1990; McGee and Birmingham, 1997). Finally, climatic influences on seedling growth and survival are likely to change over the course of seedling development (Muffler et al., 2021). Such filtering processes imply that inferences about sapling recruitment and stand development trends made from abundance of small-size seedlings (<1.5 m tall and especially < 0.9 m tall), or abundance of small and large seedlings lumped together, may be inaccurate unless these drivers of seedling mortality and growth are taken into account (Walters et al., 2020).

The USDA Forest Service (USFS) Forest Inventory and Analysis (FIA) program has monitored tree seedlings for decades in permanent field plots throughout US forests, using a single size class for seedlings defined as < 2.5 cm diameter at breast height (DBH) but ≥ 15.2 cm tall for softwood species and ≥ 30.4 cm tall for hardwood species (Bechtold and Patterson, 2005; Burrill et al., 2021). More detailed protocols were introduced to a subset of FIA plots across all 24 states of the northern US beginning in 2012, to enable the adequacy of tree regeneration to be assessed particularly in the context of harvesting and disturbance

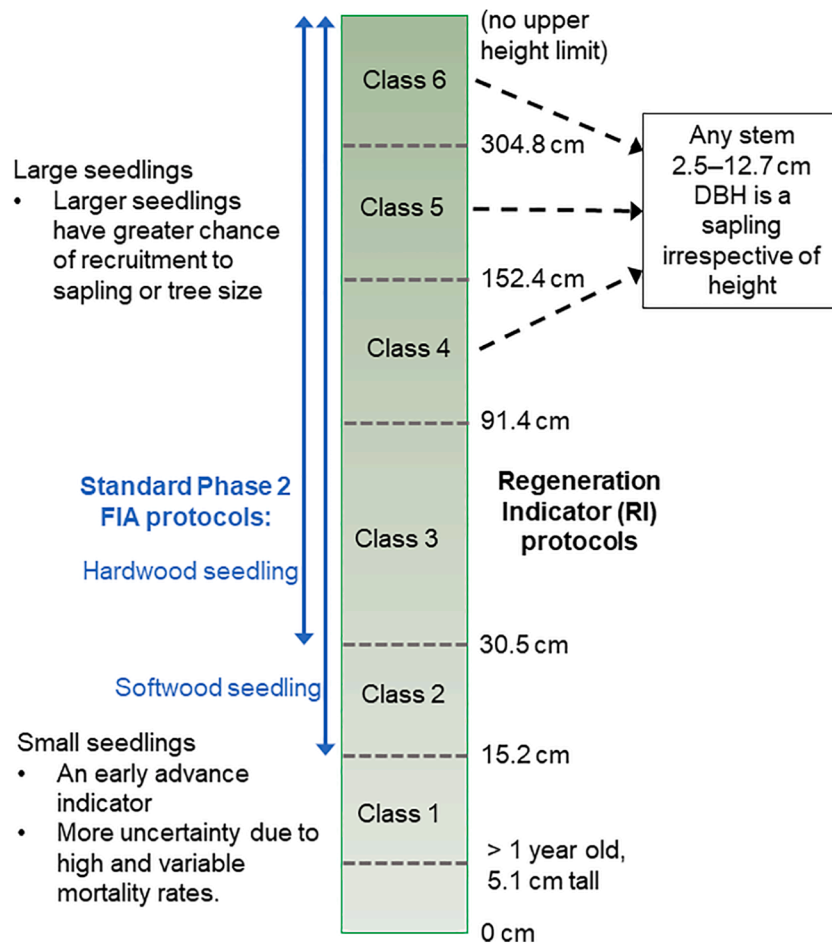


Fig. 1. Comparison of measuring seedlings in six height classes following Regeneration Indicator protocols with the more standard use of a single seedling size class. Dashed lines indicate that Class 4–6 seedlings can all recruit directly to the sapling class if and when their diameter at breast height (DBH, measured at 1.37 m in height) exceeds 2.5 cm.

(McWilliams et al., 2015, McWilliams et al., 1995). This “Regeneration Indicator” (RI) dataset divides tree seedlings into six height classes (Fig. 1). RI data have been used to predict stocking and future species composition by weighting seedling height classes according to estimated mortality rates (McWilliams et al., 1995; Vickers et al., 2019b, Vickers et al., 2019a). Estimating expected mortality rates for seedlings is challenging, though, because quantitative data on seedling survival in different height classes over periods of > 1–3 years are scarce due to the work required to track individual seedlings over time (Beckage et al., 2005). FIA plots are remeasured at 5–7-year intervals in the eastern US, meaning that repeated RI plot measurements have recently become available. These plot remeasurements allow seedling abundances to be empirically linked to subsequent sapling recruitment without the need to estimate mortality rates. Therefore, the RI surveys afford an opportunity to determine the utility of more detailed tree seedling surveys in predicting near-term stand development, and to identify potential strengths and pitfalls associated with interpreting such surveys.

The goals of this study were to leverage the longitudinal RI plot data to (1) quantify how well tree seedling abundances translate into the presence of sapling recruitment 5–7 years later for common tree species, and (2) to evaluate the implications of using six versus a single seedling height class for abundance surveys. These goals were accomplished using statistical models of sapling recruitment presence that considered seedling abundance as well as vegetation and ground cover characteristics, terrain, and climate. We hypothesized that the tallest seedling height classes would be the strongest predictors of sapling recruitment, and that a greater abundance of shorter seedlings would be needed to translate into successful recruitment as compared to taller seedlings. In addition, we expected sapling recruitment to be moderated by other processes such as competition, tolerance to shade and climate, ground cover characteristics, and response to disturbance and harvesting.

2. Materials and methods

2.1. Field data

The FIA program conducts systematic annual inventories of permanent field plots (Bechtold and Patterson, 2005). Each FIA plot consists of four circular subplots of 168 m² in which one subplot is in the plot center and the other three are 36.6 m away at azimuths of 0°, 120° and 240° (Bechtold and Patterson, 2005). Adult trees > 12.7 cm DBH are surveyed in these subplots, and each subplot contains a circular 13.5 m² microplot in which seedlings, saplings and trees < 12.7 cm diameter at breast height (DBH) are surveyed (Bechtold and Patterson, 2005). In 2012 the USFS Northern Research Station began collecting data following RI protocols in a subset of 12.5 % of all FIA field plots, or a density of one plot per ~ 194 km², across the 24 states of the northeastern US (McWilliams et al., 2015) with remeasurement occurring at a 5–7 year interval. Under the RI protocols, a seedling is defined as > 1 year old and ≥ 5.1 cm tall but < 2.5 cm DBH, and stems meeting these criteria are subdivided into six height classes (Fig. 1). Note that because saplings are defined by DBH (which is measured at a height of 137.2 cm), seedlings may grow directly from Class 5 (152.4–304.7 cm tall) or even Class 4 (91.4–152.3 cm tall) to sapling stage without growing tall enough to be tallied in Class 5 or Class 6 (≥ 304.8 cm tall).

We identified all FIA subplots using the RI seedling height protocols that had been surveyed twice (i.e., remeasured for change analysis) and in which microplots were located on accessible forest land (<https://apps.fs.usda.gov/fia/datamart/datamart.html>, download date July 25, 2022). Microplots in areas noted as having artificial regeneration were also excluded, to focus on natural regeneration. Analysis was conducted at the subplot level as opposed to the plot level as this scale is relevant for evaluating vegetation and ground cover influences on tree seedlings (e.g., Woodall et al., 2018). The resulting dataset contained 5229 subplots derived from 1524 plots with intervals of 4.7–8.1 years between remeasurements (mean = 5.8 years).

Our response variable was the presence of sapling recruitment within each microplot at Time 2, i.e., saplings (2.5–12.7 cm DBH) noted as ingrowth when the microplot was remeasured. For predictor variables, seedling densities by species and height class were extracted along with an array of microplot and subplot-level variables (Table 1), all relative to the time of first measurement (i.e., Time 1). Seedling and sapling densities of other tree species within each microplot were considered as indicators of interspecific competition. Tree basal area (BA) was calculated from DBH for trees > 12.7 cm DBH. Tree-level mortality agent codes (AGENTCD) were used to quantify the percentage of total tree BA that experienced mortality due to harvesting or to all other causes

Table 1

Variables used in models of sapling recruitment including source (Forest Inventory and Analysis Database table name or reference) and the scale at which the variable was derived.

Variable	Source (scale)	Description
Sapling recruitment (response)	TREE (microplot)	Presence/absence of new saplings in remeasurement not present in prior measurement, by species
Seedling abundance	SEEDLING_REGEN (microplot)	Either one seedling density variable for each of six size classes, or a single variable following standard FIA Phase-2 protocols
Seedling abundance of other species	SEEDLING_REGEN (microplot)	Seedling density for all other tree species combined, by size class
Conspecific sapling abundance	TREE (microplot)	
Sapling abundance of other species	TREE (microplot)	Sapling density of all other species combined
Elevation	SUBPLOT (subplot)	
Aspect	SUBPLOT (subplot)	
Mean litter depth	COND_DWM_CALC (condition)	
Mean duff depth	COND_CWM_CALC (condition)	
Volume of Coarse Woody Material	COND_DWM_CALC (condition)	
Remeasurement interval	PLOT (plot)	Period between measurements in years and fractions of year
Conspecific live tree basal area (BA)	TREE (subplot)	BA of conspecific trees > 12.7 cm DBH in prior measurement
Total live tree BA	TREE (subplot)	BA of all live trees > 12.7 cm DBH in prior measurement
Conspecific live tree density	TREE (subplot)	
Total live tree density	TREE (subplot)	
Forb cover	P2VEG_SUBP_STRUCTURE (subplot)	
Grass cover	P2VEG_SUBP_STRUCTURE (subplot)	
Shrub cover	P2VEG_SUBP_STRUCTURE (subplot)	
Percentage of trees harvested	TREE (subplot)	Percentage of total tree basal area (BA) harvested (AGENTCD = 80)
Percentage tree mortality	TREE (subplot)	Percentage of total tree BA dead but not harvested (AGENTCD < 80)
Precipitation (1991–2020)	Daly et al. 2008 (~4 km grid cell)	Means from (a) November–April and (b) May–October
Mean temperature (1991–2020)	Daly et al. 2008 (~4 km grid cell)	Means from (a) November–April and (b) May–October
Maximum vapor pressure deficit (1991–2020)	Daly et al. 2015 (~4 km grid cell)	Means from (a) November–April and (b) May–October

combined (Table 1). In addition, mean depths of litter and duff and volume of coarse woody material (>7.6 cm in diameter) were extracted at the condition level and matched to the condition of each microplot. Conditions represent discrete areas of each plot that vary by forest type, land use or ownership, or other factors (Bechtold and Patterson, 2005).

2.2. Climate data

In addition to field measurements, we characterized plot-level climate using 1991–2020 mean temperature, precipitation, and maximum vapor pressure deficit averaged over May–October (growing season) and November–April (six climate variables in total). Climate variables were derived from the 4-km gridded PRISM dataset (Daly et al., 2015; Daly et al., 2008) and extracted to plot locations using Google Earth Engine (Gorelick et al., 2017). The coarse 4-km grain size is appropriate because FIA plot coordinates have been perturbed by up to 1.6 km and sometimes swapped with coordinates of similar nearby plots per federal privacy laws and agency guidelines (Burrill et al., 2021).

2.3. Tree species selection

To ensure a sufficiently large sample size for analysis, we selected species in which sapling recruitment was present at Time 2 in ≥ 50 subplots (~1% of all subplots analyzed). Five species met this threshold: balsam fir (*Abies balsamea* L.), red spruce (*Picea rubens* Sarg.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.) and beech (*Fagus grandifolia* Ehrh.) (Table 2). Due to our specific interest in linking seedling abundance to sapling recruitment, only subplots containing at least one seedling of a given species at Time 1 (in any height class) were analyzed.

The five species analyzed have distinct distributions within the study area (Fig. 2), as well as associated silvics and management concerns. Red maple has been termed a “super-generalist” given its ability to occur across a wide range of site conditions with its occurrence promoted by fire exclusion and disturbances such as partial harvesting and insect outbreaks (Abrams, 1998). Sugar maple is the most commercially valuable of the five species, but low regeneration and recruitment have been the subject of recent concern due to a number of factors including browsing by deer, competition with other tree species or shrubs, site quality and effects of harvesting or disturbance on stand structure (Henry et al., 2021; Leak, 2005; Matonis et al., 2011). Beech recruitment is commonly seen as undesirable due to its susceptibility to beech bark disease and ability to outcompete more economically desirable species (Nyland et al., 2006). Nevertheless, beech saplings have been increasing in abundance for decades in the northeastern US due in part due to its tolerance of shade, browsing, and associated interactions with harvesting disturbance (Bormann et al., 1970; Bose et al., 2017). Red spruce is a shade-tolerant, slow-growing species often abundant at the transition between hardwood and spruce-fir forest, whereas balsam fir, a shade-

tolerant red spruce associate, is prevalent at higher elevations/ latitudes with more abundant and faster-growing seedlings and saplings (Battles and Fahey, 2000; Cogbill and White, 1991). Much of the suitable habitat for balsam fir and red spruce in the northeastern US may be lost over the next 40 years due to climate change (Andrews et al., 2022).

2.4. Analyzing recruitment

First, violin plots were used to visually compare seedling abundance in Time 1 for plots in which new sapling recruitment of a given species was absent vs present in Time 2, and significant differences within each seedling size class were assessed using Wilcoxon signed rank tests with a Holm correction for multiple comparisons.

To determine whether these relationships between seedlings and sapling recruitment occurred in stands with recently-created canopy gaps, we repeated this first analysis using only subplots that had been recently disturbed. For purposes of this analysis, a subplot was considered disturbed if $\geq 25\%$ of total tree BA was comprised of trees that had a cause of death recorded at Time 1 (i.e., had died since the previous subplot measurement), including both harvesting and all other causes of mortality. Disturbances can be identified in different ways using FIA data depending on research objectives (Fitts et al., 2022), and we chose the tree mortality threshold to identify subplots that were likely to have newly-created canopy gaps with increased opportunities for sapling recruitment.

2.5. Sapling recruitment modeling

Next, we developed statistical models to predict sapling recruitment presence in remeasured plots for each species as a function of seedling densities and the other environmental factors shown in Table 1. This approach enabled the accounting of major factors that might mediate seedling survival and growth. A boosted regression trees (BRT) framework was used as BRT can account for non-linear relationships and interacting influences (Elith et al., 2008).

For each species, a BRT model of the presence of sapling recruitment was built with the “dismo” R package (Hijmans et al., 2021) using the default logistic regression approach with a Bernoulli error distribution. The learning rate was set at 0.001, resulting in ≥ 2500 trees built for each model. Tree complexity was set at four after testing different values while other parameters were left at their default settings. To create parsimonious models that identified key influences on recruitment, the “gbm.simplify” function was used with default settings to perform variable selection by backward elimination. After variable selection all remaining pair of variables had a Spearman rank correlation coefficient $|r_s| < 0.7$ except for live tree basal area and density, which were both retained for red maple and sugar maple and had $r_s = 0.77$ and 0.71 , respectively. We concluded that multicollinearity was not a substantial issue (Dormann et al., 2013).

Model accuracy was evaluated from the cross-validation folds using the area under the receiver operating characteristic curve (AUC), a robust and commonly-used measure with values ranging from a low of 0.5 (no better than chance) to a high of 1.0 (Fielding and Bell, 1997). Variable importance was quantified using relative influence, or the square of model improvement at each split in a tree, multiplied by the number of times a variable was selected then scaled to sum to 100 within each model (Elith et al., 2008; Friedman and Meulman, 2003). Partial dependence plots, implemented using the “pdp” R package (Greenwell, 2017), were used to assess the relationships between individual predictor variables and recruitment for the top three variables in each model, and to check for signs of model overfitting. In addition, the strongest interaction between variables within each model was determined using the “gbm.interactions” function (Elith et al., 2008) with these interactions shown using bivariate partial dependence plots.

Once recruitment models were created for each species, we compared model performance using the RI seedling height class data

Table 2

Number of subplots (plots) with seedlings and sapling recruitment, and mean and standard deviation of sapling recruitment abundance for subplots in which recruitment was present for the species analyzed.

Species	Seedlings	Sapling recruitment	Recruitment abundance (stems ha ⁻¹)
<i>Abies balsamea</i>	1298 (498)	180 (137)	1165 ± 747
<i>Picea rubens</i>	452 (221)	74 (56)	1121 ± 728
<i>Acer rubrum</i>	2002 (851)	116 (105)	1412 ± 1266
<i>Acer saccharum</i>	1091 (460)	53 (43)	1021 ± 654
<i>Fagus grandifolia</i>	683 (314)	97 (73)	1092 ± 643

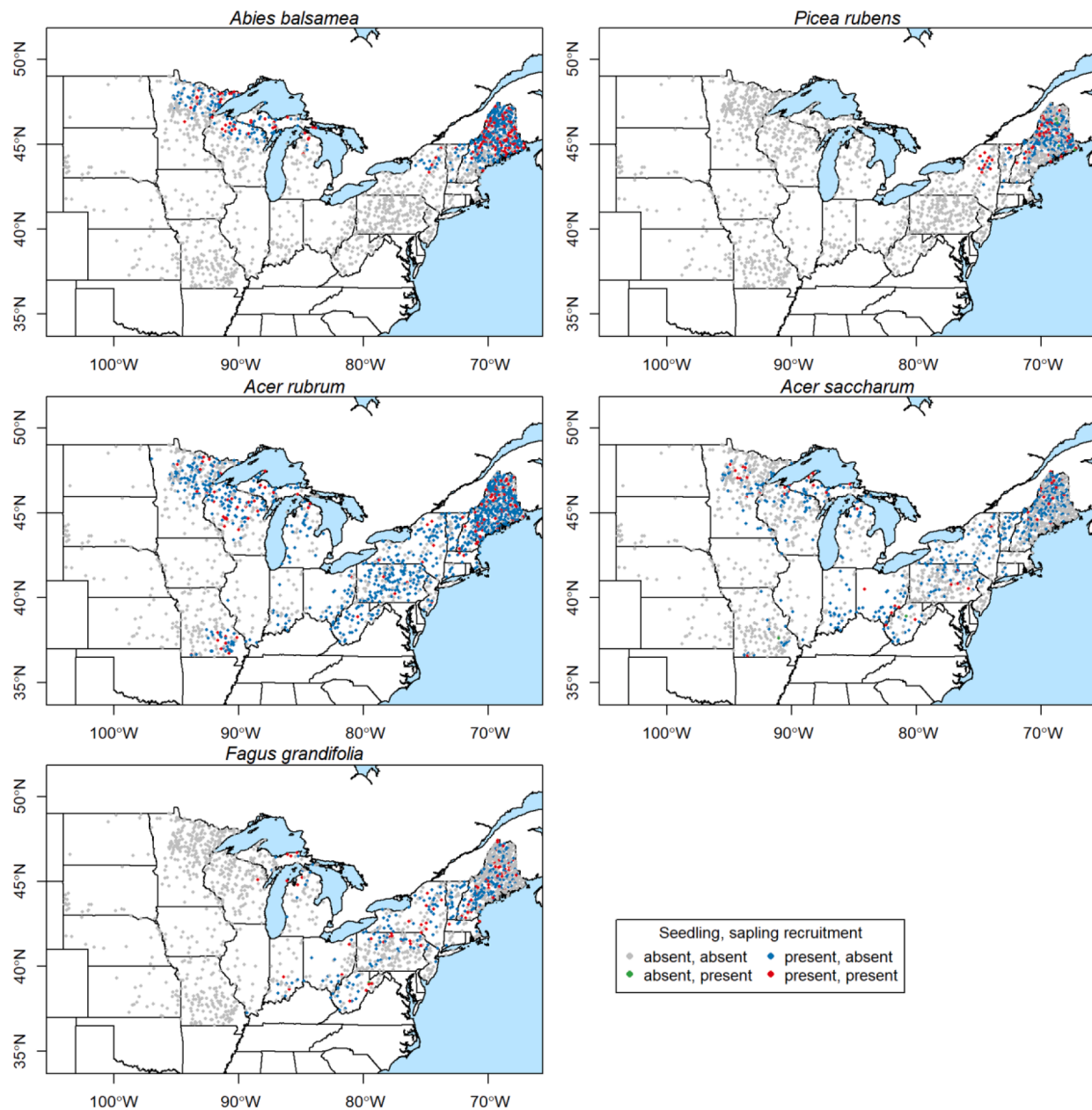


Fig. 2. Plot-level presence of seedlings (Time 1) and sapling recruitment (Time 2) for the four tree species analyzed among all remeasured plots for which seedlings were tallied by height class. Plots in which seedlings were present (blue and red points) contain at least one subplot used for analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

against the same models run with just one seedling size class (i.e., standard Phase 2 FIA protocols, Fig. 1), hereafter the “six-class” and “one-class” models after the number of seedling height classes.

3. Results

Subplots with sapling recruitment of a given species in Time 2 tended to have more seedlings of Class 3 (30.5–91.3 cm) or taller in Time 1, and plots with recruitment had significantly more Class 4 and 5 seedlings (91–305 cm) across all five tree species analyzed (Fig. 3, A1–A4). By contrast, greater abundance of Class 1 seedlings (5.1–15.1 cm tall) was negatively related to recruitment for red maple and red spruce, and Class 2 seedlings (15.2–30.4 cm tall) were positively related to recruitment only for balsam fir and sugar maple (Fig. 3, A3). These results were similar when considering just subplots that had been disturbed: disturbed subplots with sapling recruitment tended to have more Class

4–6 seedlings whereas Class 1 and 2 seedlings were either less abundant in subplots with recruitment (Fig. 4) or not significantly different (Figures A5–A8).

Although some differences among species were evident, models of sapling recruitment were notably similar in terms of accuracy and which variables exerted the strongest influence (Tables 3 and 4). Using six seedling height classes instead of one class improved model AUC for all species, which indicates improved ability to correctly classify recruitment presence and absence across a range of probability thresholds when using six classes (Table 3, Figure A7). Class 5 or 6 seedlings were the most important variable for each species whereas Classes 1–4 were only retained in two cases: Class 4 for balsam fir and Class 2 for sugar maple (Table 4). Seedling abundance made up 37–65 % of relative influence on sapling recruitment. In total, between two (red spruce) and 15 variables (sugar maple) were retained. Other notable variables were total live tree BA (four species) and density (three species); shrub, grass

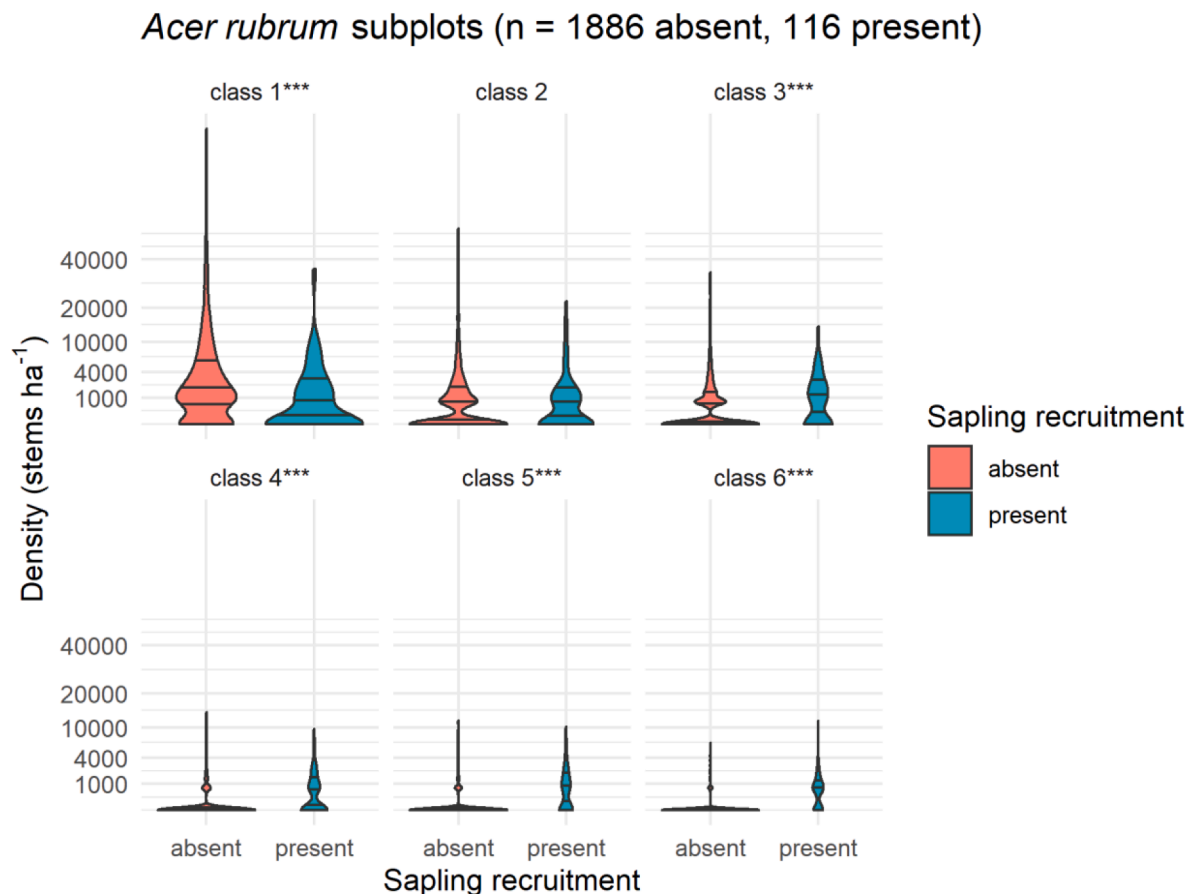


Fig. 3. Violin plots comparing red maple seedling abundance in different size classes at Time 1 for subplots with and without sapling recruitment at Time 2. Seedling height classes range from < 15.2 cm tall (Class 1) to > 304.8 cm tall (Class 6) (see Fig. 1 for full height class definitions). Black lines represent 25th, 50th and 75th-percentile values. Asterisks indicate significant differences based on a Wilcoxon signed rank test with a Holm correction: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Note that y-axis values are square root transformed for visibility. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

or forb cover (four species); sapling abundance of other species (three species); and harvesting intensity (two species) (Table 4).

Partial dependence plots suggested that across species, the probability of sapling recruitment increased sharply over low abundances of Class 5 and 6 seedlings but leveled off at higher abundances of 1000–10000 stems ha^{-1} depending on the species (Fig. 5). Recruitment also tended to respond nonlinearly to total live tree BA and density, with more recruitment in subplots with low BA or density (Fig. 5, A10–13). Beech and sugar maple recruitment had positive threshold responses to harvesting intensity (Figs. 5 and 6). Overall, relationships within the five recruitment models were ecologically plausible and did not suggest substantial overfitting (Fig. 5, A10–A13).

The strongest interaction within each model involved Class 5 or 6 seedlings for four of five species (Fig. 6). These interactions suggested that recruitment was more likely when Class 5 or 6 seedlings were present and growing season precipitation was low (balsam fir), total live tree BA was low (red spruce), red maple saplings were abundant at Time 1 (red maple), and close to 100 % of tree BA was harvested (sugar maple). Beech recruitment was more likely in subplots with > 60 % of BA harvested and < 10 % grass cover (Fig. 6).

4. Discussion

4.1. Significance and applications of approach

Carefully structuring field surveys of tree regeneration and subsequent analyses is important to accurately predict future forest

composition and development. These near-term predictions are becoming increasingly important in an era of global change, in which forest dynamics are being altered by interactions among warming, precipitation extremes and disturbances such as fire and insect outbreaks (McDowell et al., 2020; Millar and Stephenson, 2015; Seidl et al., 2017). The increasing quantity and availability of longitudinal data, both from national forest inventories like FIA and smaller-scale tree regeneration surveys (e.g., states or industrial ownerships), allows tree regeneration patterns to be empirically linked to subsequent recruitment. Additionally, such empirically derived indicators offer a path toward more robust assessments of the ecological and management implications of observed tree regeneration patterns. As interest in tree planting to mitigate climate change impacts and promote forest resilience surges worldwide (Domke et al., 2020; Holl and Brancalion, 2020; Messier et al., 2022), the approach described here could be used to assess where tree planting might be necessary to meet management objectives, and potentially the density at which seedlings of different sizes and species would need to be planted to achieve successful recruitment. Our results highlight how such quantitative assessments can help maximize utility and insight from tree regeneration surveys, while avoiding pitfalls that could lead to inaccurate or misleading conclusions about forest development.

An additional advantage of constructing empirical models of recruitment is that factors mediating seedling growth and survival can be taken into account. For example, Zhu et al. (2015) used empirical modeling to quantify the effects of density dependent-mortality on seedling-to-sapling recruitment rates using standard (one seedling size

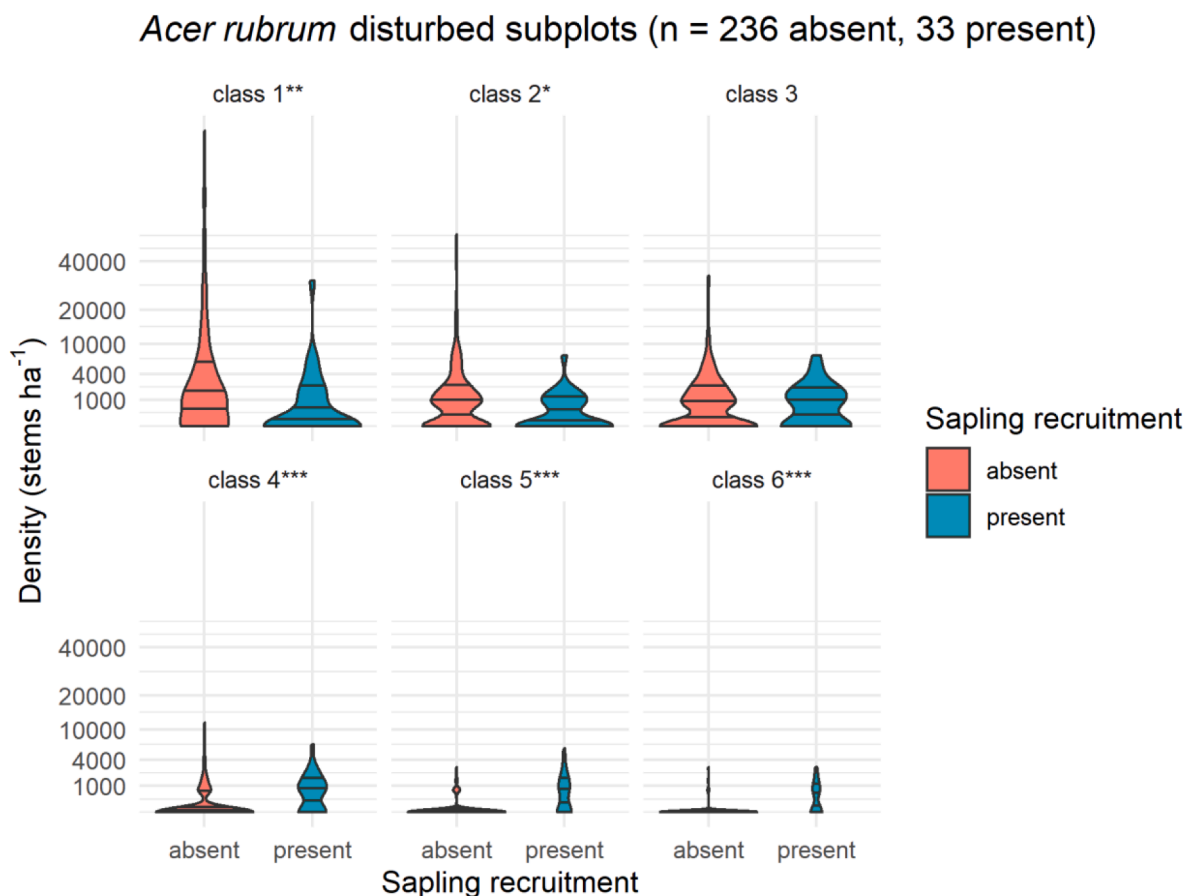


Fig. 4. Violin plots comparing *Acer rubrum* seedling abundance in different size classes at Time 1 for subplots with and without sapling recruitment at Time 2 for disturbed subplots only. Seedling height classes range from < 15.2 cm tall (Class 1) to > 304.8 cm tall (Class 6) (see Fig. 1 for full height class definitions). Black lines represent 25th, 50th and 75th-percentile values. Asterisks indicate significant differences based on a Wilcoxon signed rank test with a Holm correction: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Note that y-axis values are square root transformed for visibility.

Table 3

Accuracy of sapling recruitment models using one vs six seedling size classes, shown by mean (standard error) of the area under the curve (AUC).

Species	AUC one	AUC six
<i>Abies balsamea</i>	0.788 (0.009)	0.879 (0.009)
<i>Picea rubens</i>	0.720 (0.036)	0.850 (0.038)
<i>Acer rubrum</i>	0.845 (0.008)	0.910 (0.013)
<i>Acer saccharum</i>	0.776 (0.028)	0.871 (0.028)
<i>Fagus grandifolia</i>	0.766 (0.024)	0.871 (0.020)

class) FIA data. However, multiple seedling height classes are useful for examining influences on sapling recruitment because factors such as browsing and competition with understory vegetation may affect seedlings differently depending on their size (Henry et al., 2021; Walters et al., 2020). Four of five species that we analyzed were influenced by shrub, forb, or grass cover, indicating that understory vegetation does influence sapling recruitment. The influence of duff depth on red maple recruitment and coarse woody material on balsam fir recruitment in our analysis suggests that substrate characteristics can shape sapling recruitment patterns as well. The present study's approach could be used to characterize and account for influences on seedling survival such as competition and climate variability. Examining seedling-recruitment relationships across gradients of harvesting intensity and disturbance severity is a particularly important topic for future research because predicting stand development is most critical when canopy gaps open and provide opportunities for recruitment.

4.2. Effects of seedling height classes

We found that the abundance of seedlings in the two tallest size classes (>1.5 m tall) were the best predictors of subsequent sapling recruitment. This result was expected because larger seedlings are already closer to sapling size and more likely to be competitively dominant relative to other seedlings, which are ideas implicit across prior studies that weight seedlings by size class (e.g., Bohn and Nyland, 2003; McWilliams et al., 1995; Vickers et al., 2019a,b). Surveying dominant seedlings and saplings may be the best way to predict tree recruitment at multi-decadal time scales (Leak, 2007). Our study was also conducted over a relatively short 5–7-year window that likely favored sapling recruitment from already-tall seedlings. Separating Class 5 from Class 6 seedlings was useful in predicting sapling recruitment, as demonstrated by the fact that a greater abundance of Class 5 than Class 6 seedlings was needed to maximize the probability of sapling recruitment for the three hardwood species. The probable reason why Class 5 rather than Class 6 seedlings were the strongest predictor of sapling recruitment for balsam fir and red spruce is that stems of these species commonly attain a DBH of ≥ 2.5 cm before growing > 3 m tall and therefore Class 6 seedlings of these species rarely exist. For example, in our analysis Class 5 seedlings were 23-fold and 14-fold more abundant than Class 6 seedlings for balsam fir and red spruce, respectively, whereas Class 5 was only two to threefold more abundant for the other three species.

In contrast to the strong influence of the tallest seedlings on sapling recruitment was the surprisingly minimal effect of Class 3 and 4 (0.3–1.5-m tall) seedlings, as shown by low influence of these seedling

Table 4

Relative influence of variables retained in the six-class version of each species model, scaled to sum to 100% within each model. Refer to Table 1 for details on variables, and for the directionality and shape of each relationship refer to Figs. 5, 6 and A10–13.

Variable	<i>Abies balsamea</i>	<i>Picea rubens</i>	<i>Acer rubrum</i>	<i>Acer saccharum</i>	<i>Fagus grandifolia</i>
Class 2 seedlings				4.8 %	
Class 4 seedlings	7.2 %				
Class 5 seedlings	44.0 %	64.5 %	10.4 %	10.8 %	18.6 %
Class 6 seedlings			38.8 %	21.3 %	23.9 %
Conspecific saplings			5.1 %		
Other saplings	7.7 %		6.6 %	3.1 %	
Conspecific tree BA				5.0 %	
Total tree density	10.5 %		7.4 %	7.4 %	
Total tree BA		35.5 %	5.9 %	4.1 %	6.3 %
Elevation					7.0 %
Aspect				2.7 %	5.6 %
Coarse woody material	7.9 %			6.0 %	
Litter depth				5.2 %	
Duff depth			8.1 %		
Forb cover			5.9 %	7.0 %	
Grass cover	7.3 %				5.8 %
Shrub cover			6.3 %		7.8 %
Nov.-Apr. precipitation				7.1 %	6.4 %
Nov.-Apr. temperature	7.6 %		5.5 %		
May-Oct. precipitation	7.8 %				
Nov.-Apr. max. VPD				5.7 %	8.9 %
BA harvested				5.8 %	9.9 %
BA mortality				4.1 %	

cohorts in the recruitment models. Our results suggest that the common practice of lumping smaller seedlings together with larger ones, as is done in standard FIA Phase 2 protocols, may in fact hinder our ability to forecast near-term sapling recruitment by treating smaller, less competitive seedlings identically to larger, more competitive seedlings. This may be particularly problematic for slower-growing, shade-tolerant species, such as those included in this work, that may require extended time periods to recruit to the sapling stage including periods of suppressed growth under closed canopies and growth releases when canopy gaps open (Canham, 1990, 1985).

Perhaps the most novel result was that the abundance of Class 1 and 2 seedlings (<0.3 m tall) were in some cases negatively related to sapling recruitment. One potential explanation is that high abundance of short seedlings may be associated with closed-canopy forest in which opportunities for sapling recruitment are limited. Yet, these relationships were notably similar in subplots that had been recently disturbed (>25 % tree mortality), and therefore were likely to have canopy gaps and abundant opportunity for sapling recruitment. One explanation is that the regeneration strategy of having abundant small-sized seedlings able to respond rapidly to disturbance, (e.g., red maple, Walters and Yawney, 1990) can fail if small seedlings of a particular species are so abundant that they are weakened by density-dependent interactions such as competition, disease or herbivory (Yamazaki et al., 2009). Although an analysis covering longer than 5–7 years would be necessary to firmly establish the relationship between small seedlings and sapling recruitment (see *Limitations and future work*), our results suggest that counts of small seedlings must be interpreted cautiously. It is tempting to interpret patterns of these smallest seedlings as early indicators of forest change,

but small seedling counts alone may paint a misleading picture of stand development unless their relationship with subsequent recruitment and forest change can be established.

We also note that our analysis was focused on identifying key indicators of near-term sapling recruitment at strategic scales. Factors such as tree BA, browsing and competition with shrubs may limit seedling survival and growth preferentially within intermediate-large size classes such that abundance of small-sized seedlings may be an unreliable predictor of sapling recruitment (Elenitsky et al., 2020; Henry et al., 2021; Matonis et al., 2011; Walters et al., 2020). While the methodological framework that we used can account for some interacting influences, detailed analyses of seedling survival over successive height classes or process-based models may be needed to accurately represent such complexities when estimating seedling growth and survival. Therefore, the full set of six seedling height classes may be useful at the scale of intensive site monitoring aimed at understanding ecological processes, whereas separating Class 5 and Class 6 from other seedling sizes may be a more efficient way to monitor potential recruitment at strategic scales given limited resources.

4.3. Limitations and future work

Our analysis has several key limitations that could be addressed in future work. First, the 5–7-year remeasurement window in our study may not be long enough to capture the influence of the smallest seedlings on sapling recruitment, particularly for shade-tolerant species. Average annual height growth rates may be < 5 cm year⁻¹ for balsam fir and red spruce seedlings (Battles and Fahey, 2000; Dumais and Prévost, 2016; Walters et al., 2016) suggest that sapling recruitment from seedlings < 0.3 m tall is highly unlikely over 5–7 years. Prior work on seedling height growth suggests that it is possible for hardwood species within the study area, including red maple and sugar maple, to grow from < 0.3 m tall to sapling size within 5–7 years, but only under the most favorable conditions such as abundant light availability, minimal browsing and little competition with understory vegetation (Beaudet and Messier, 1998; Walters et al., 2016). Indeed, canopy gaps were important for sapling recruitment of all species in our analysis as shown by negative relationships with tree density or BA and/or positive relationships with harvesting intensity. We did not separate vegetative sprouts from reproduction by seed in this analysis, but sapling recruitment especially from smaller seedling size classes was likely to be skewed toward sprouts because they tend to have rapid growth rates (Forrester et al., 2014; Solomon and Blum, 1967). Vigorous stump-sprouting is a noted trait of red maple in particular that may explain why recruitment was more likely in subplots which already had a high abundance of red maple saplings (Solomon and Blum, 1967). Sprouting may also account for the positive relationship between harvesting intensity and recruitment that we observed for beech. Use of a longer remeasurement period and/or successive inventories might reveal varying relationships between seedling height classes and sapling or tree recruitment.

Second, we did not consider some factors likely to influence seedling survival and growth such as browsing pressure or microsite characteristics (Gray and Spies, 1997; McGee and Birmingham, 1997; Walters et al., 2020). To some extent, several of the climate and possibly ground cover variables in our models could be serving as indicators of regions or stands in which some of these factors that were not considered in our analysis influenced sapling recruitment.

Third, initial results suggest that if field inventory resources are very limited that perhaps only the tallest seedlings are inventoried when recruitment monitoring is a key resource concern. However, in the case of FIA's inventory and undoubtedly other inventories the measurement of a somewhat coarse but inclusive definition of seedlings over recurring inventory cycles has resulted in a critical baseline of tree regeneration abundance across numerous decades which could serve to augment future analyses especially if tall seedling measurement protocols are

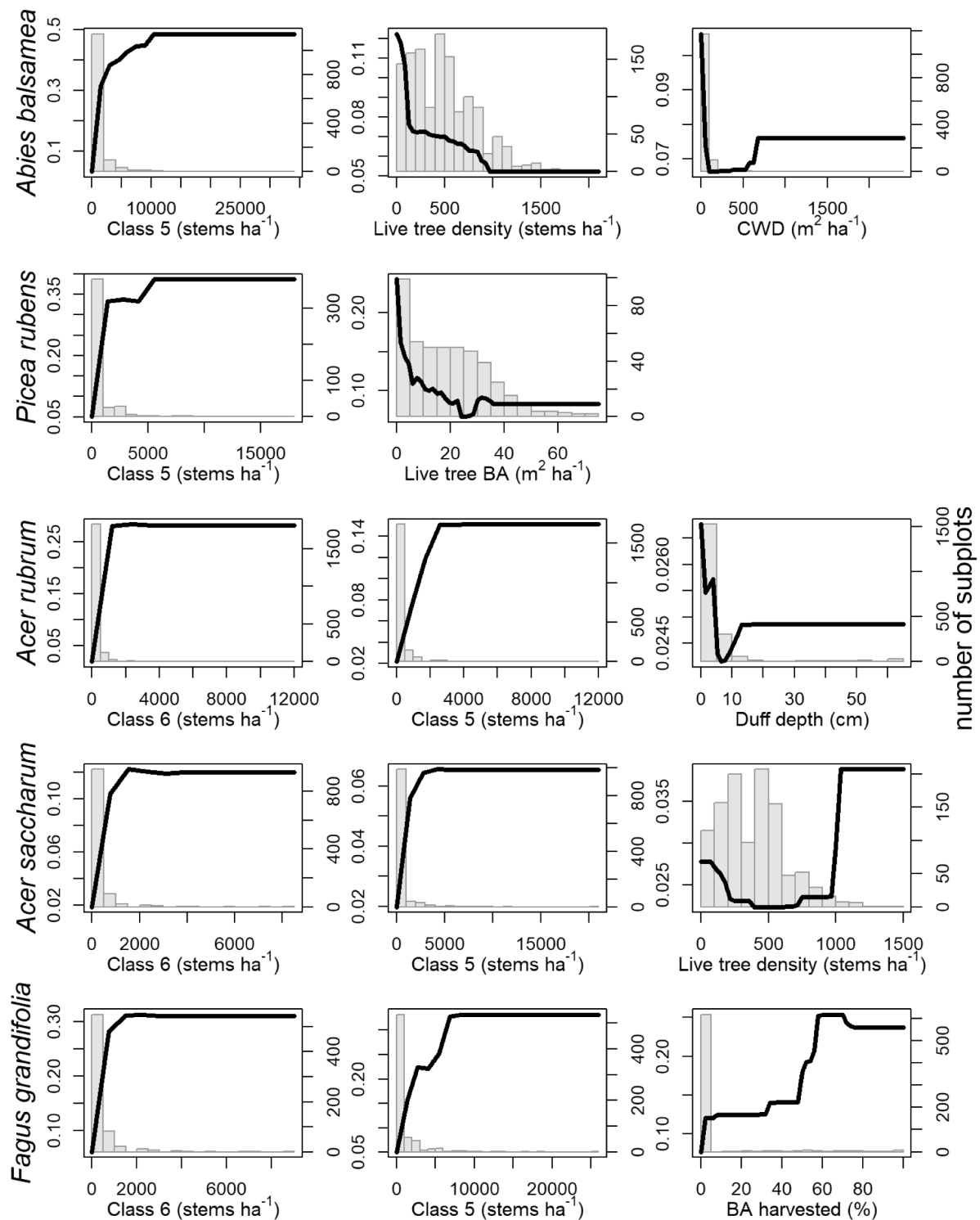


Fig. 5. Partial dependence plots (lines) showing the marginal effect of the top three most important variables in each model on the marginal probability that sapling recruitment is present for each species. Scale of y-axes differ to highlight the shape of each relationship. Histograms with axes at right show the distribution of each variable. Details on variables are shown in Table 1. Note that the red spruce (*Picea rubens*) model only contains two variables. CWD is coarse woody debris and BA is basal area.

widely adopted. Furthermore, the optimal seedling size classes for predicting sapling recruitment are likely to vary by region and biome according to rates of seedling growth and survival.

Finally, we limited our analysis to five species due to sample size limitations. In particular, the five species analyzed are shade-tolerant and can establish and grow relatively well under a closed canopy but may respond more slowly to the opening of canopy gaps than could be

expected for less tolerant species (Canham, 1988; Wu et al., 1999). Therefore, future work could examine the seedling-recruitment relationship among tree species representing a broader spectrum of functional traits and/or silvics. As more plots are remeasured following RI protocols a wider array of analytical opportunities should present themselves such as a greater array of study species, evaluation of disturbance/harvest events, and incorporation of refined recruitment

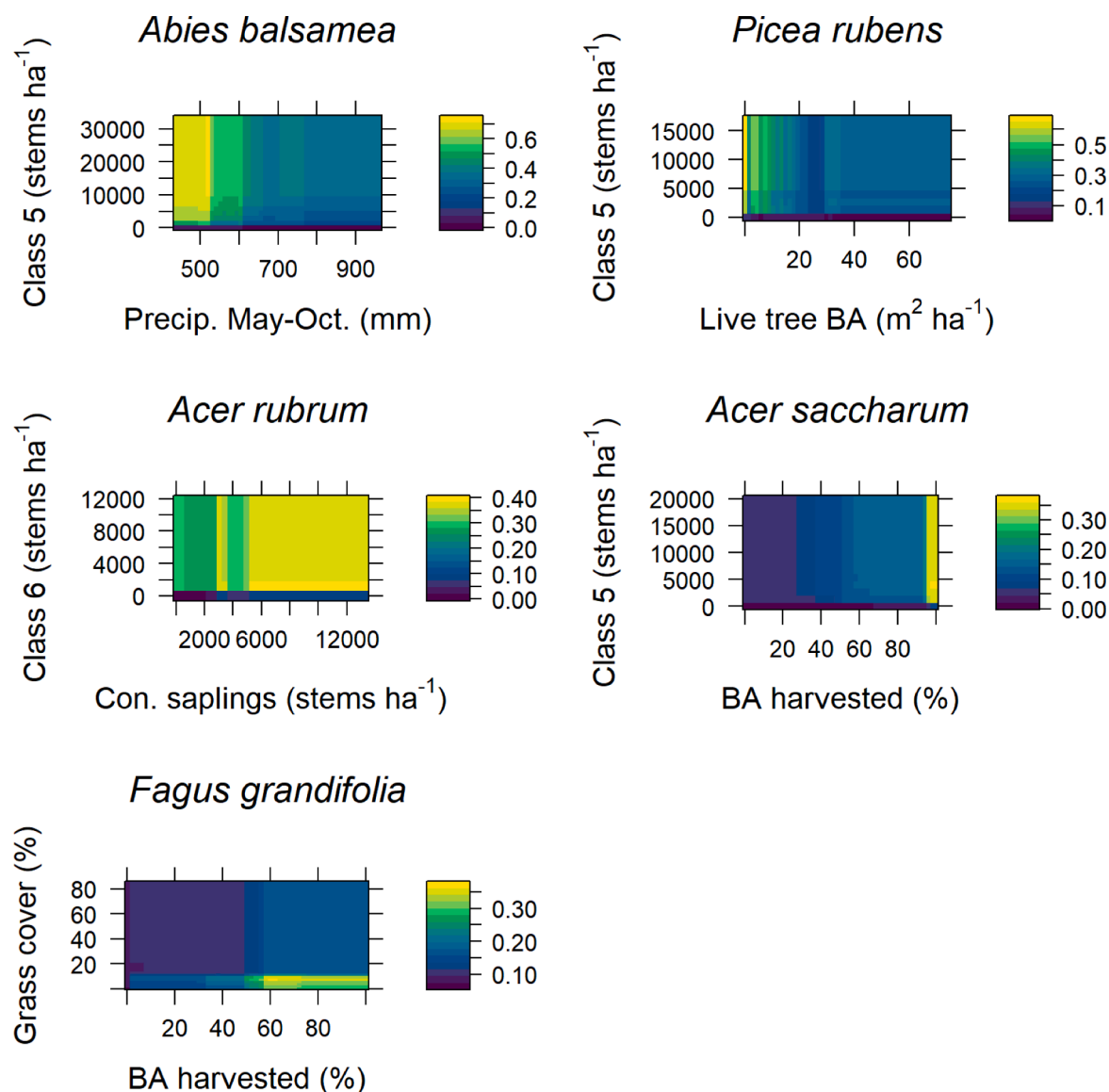


Fig. 6. Partial dependence plots of the strongest pair of interacting variables within each sapling recruitment models. Colors indicate the marginal probability that sapling recruitment is present. See Table 1 for further information on each variable. BA is basal area.

dynamics beyond basic presence metrics.

5. Conclusions

Tree regeneration inventories may become increasingly important over the coming decades as a means to document and forecast how forests are responding to climate change, altered disturbance regimes, invasive species, and other stressors. To ensure that the conclusions drawn from tree regeneration data are accurate and relevant to land managers and policy makers (e.g., 1 [t.org](#)), it is crucial to link seedling abundances with likely outcomes in terms of recruitment and expected forest change. Our analysis demonstrates the utility of combining longitudinal field data with empirical modeling to characterize the relationship between seedling and sapling recruitment and therefore development of more robust forest change inferences. In terms of field protocols, our results suggest that distinguishing and subdividing the tallest seedlings (>1.5 m tall) is highly useful for predicting recruitment whereas small seedling counts (<0.3 m tall) may have less utility beyond long-term baseline assessments unless future work can establish their relationship to stand development. Although our specific results apply to five tree species in the northeastern USA, our methodology could be

applied to other tree species and ecoregions worldwide wherever longitudinal field data that include seedling size classes are available.

Funding

Department of Interior Northeast and Midwest Climate Adaptation Science Centers.

CRediT authorship contribution statement

Lucas B. Harris: Conceptualization, Methodology, Formal analysis, Writing – original draft. **Christopher W. Woodall:** Conceptualization, Methodology, Writing – review & editing. **Anthony W. D’Amato:** Conceptualization, Methodology, 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.

Acknowledgements

We would like to acknowledge the leadership and dedication of Will McWilliams and numerous state partners which gave rise to the RI project over a decade ago in addition to hundreds of field crews who have diligently surveyed tree seedlings following this vision. Finally, we would like to acknowledge the guidance of Thomas Albright in summarizing and interpreting RI field data.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109654>.

References

- Abrams, M.D., 1998. The Red Maple Paradox. *Bioscience* 48, 355–364. <https://doi.org/10.2307/1313374>.
- Andrews, C., Foster, J.R., Weiskittel, A., D'Amato, A.W., Simons-legaard, E., 2022. Integrating historical observations alters projections of eastern North American spruce – fir habitat under climate change. *Ecosphere* 1–14. <https://doi.org/10.1002/ecs2.4016>.
- Battles, J.J., Fahey, T.J., 2000. Gap dynamics following forest decline: A case study of red spruce forests. *Ecol. Appl.* 10, 760–774. [https://doi.org/10.1890/1051-0761\(2000\)010\[0760:GDFDA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0760:GDFDA]2.0.CO;2).
- Beaudet, M., Messier, C., 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. *Can. J. For. Res.* 28, 1007–1015. <https://doi.org/10.1139/x98-077>.
- Bechtold, W.A., Patterson, P.L. (Eds.), 2005. The Enhanced Forest Inventory and Analysis Program — National Sampling Design and Estimation Procedures. USDA Forest Service Southern Research Station General Technical Report SRS-80, Asheville, NC, USA.
- Beckage, B., Lavine, M., Clark, J.S., 2005. Survival of tree seedlings across space and time: Estimates from long-term count data. *J. Ecol.* 93, 1177–1184. <https://doi.org/10.1111/j.1365-2745.2005.01053.x>.
- Bohn, K.K., Nyland, R.D., 2003. Forecasting development of understory American beech after partial cutting in uneven-aged northern hardwood stands. *For. Ecol. Manage.* 180, 453–461. [https://doi.org/10.1016/S0378-1127\(02\)00614-X](https://doi.org/10.1016/S0378-1127(02)00614-X).
- Bolton, N.W., D'Amato, A.W., 2011. Regeneration responses to gap size and coarse woody debris within natural disturbance-based silvicultural systems in northeastern Minnesota, USA. *Forest Ecol. Manage.* 262, 1215–1222. <https://doi.org/10.1016/j.foreco.2011.06.019>.
- Bormann, F.H., Siccama, T.G., Likens, G.E., Whittaker, R.H., 1970. The Hubbard Brook Ecosystem Study: Composition and Dynamics of the Tree Stratum. *Ecol. Monogr.* 40, 373–388. <https://doi.org/10.2307/1942336>.
- Bose, A.K., Weiskittel, A., Wagner, R.G., 2017. A three decade assessment of climate-associated changes in forest composition across the north-eastern USA. *J. Appl. Ecol.* 54, 1592–1604. <https://doi.org/10.1111/1365-2664.12917>.
- Brand, D.G., Leckie, D.G., Cloney, E.E., 1991. Forest regeneration surveys: design, data collection, and analysis. *For. Chron.* 67, 649–657. <https://doi.org/10.5558/tfc67649-6>.
- Burrill, E.A., DiTommaso, A.M., Turner, J.A., Pugh, S.A., Christensen, G., Perry, C.J., L., C.B., 2021. The Forest Inventory and Analysis Database: Database Description and User Guide for Phase 2 (version 9.0.1). USDA Forest Service, Forest Inventory and Analysis Program.
- Canham, C.D., 1985. Suppression and release during canopy recruitment in *Acer saccharum*. *Bull. Torrey Bot. Club* 112, 134–145.
- Canham, C.D., 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69, 786–795.
- Canham, C.D., 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bull. Torrey Bot. Club* 117, 1–7.
- Cogbill, C.V., White, P.S., 1991. The latitude-elevation relationship for spruce-fir forest and treeline along the Appalachian mountain chain. *Vegetatio* 94, 153–175. <https://doi.org/10.1007/BF00032629>.
- Collins, S.L., 1990. Habitat relationships and survivorship of tree seedlings in hemlock-hardwood forest. *Can. J. Bot.* 68, 790–797. <https://doi.org/10.1139/b90-105>.
- Coop, J.D., Parks, S.A., Stevens-Rumann, C.S., Crausbay, S.D., Higuera, P.E., Hurteau, M.D., Tepley, A., Whitman, E., Assal, T., Collins, B.M., Davis, K.T., Dobrowski, S.Z., Falk, D.A., Fornwalt, P.J., Fulé, P.Z., Harvey, B.J., Kane, V.R., Littlefield, C.E., Margolis, E.Q., North, M., Parisien, M.A., Prichard, S., Rodman, K.C., 2020. Wildfire-Driven Forest Conversion in Western North American Landscapes. *Bioscience* 70, 659–673. <https://doi.org/10.1093/biosci/biaa061>.
- Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., Pasteris, P.P., 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *Int. J. Climatol.* 28, 2031–2064. <https://doi.org/10.1002/joc>.
- Daly, C., Smith, J.I., Olson, K.V., 2015. Mapping atmospheric moisture climatologies across the conterminous United States. *PLoS ONE* 10, e0141140.
- Davis, K.T., Dobrowski, S.Z., Higuera, P.E., Holden, Z.A., Veblen, T.T., Rother, M.T., Parks, S.A., Sala, A., Maneta, M., 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proc. Natl. Acad. Sci.* 1–6. <https://doi.org/10.1073/pnas.1815107116>.
- Domke, G.M., Oswald, S.N., Walters, B.F., Morin, R.S., 2020. Tree planting has the potential to increase carbon sequestration capacity of forests in the United States. *Proc. Natl. Acad. Sci.* 1–3. <https://doi.org/10.1073/pnas.2010840117>.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>.
- Dumais, D., Prévost, M., 2016. Germination and establishment of natural red spruce (*Picea rubens*) seedlings in silvicultural gaps of different sizes. *For. Chron.* 92, 90–100. <https://doi.org/10.5558/tfc2016-021>.
- Elenitsky, L.M., Walters, M.B., Farinosi, E.J., 2020. Tree regeneration structure following beech bark disease-motivated harvests: Factors associated with patterns and management implications. *Forests* 11, 1–26. <https://doi.org/10.3390/f11020180>.
- Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>.
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence / absence models. *Environ. Conserv.* 24, 38–49. <https://doi.org/10.1017/S0376892997000088>.
- Fitts, L.A., Domke, G.M., Russell, M.B., 2022. Comparing methods that quantify forest disturbances in the United States' national forest inventory. *Environ. Monit. Assess.* 194. <https://doi.org/10.1007/s10661-022-09948-z>.
- Forrester, J.A., Lorimer, C.G., Dyer, J.H., Gower, S.T., Mladenoff, D.J., 2014. Response of tree regeneration to experimental gap creation and deer herbivory in north temperate forests. *For. Ecol. Manage.* 329, 137–147. <https://doi.org/10.1016/j.foreco.2014.06.025>.
- Forzieri, G., Dakos, V., McDowell, N.G., Ramdane, A., Cescatti, A., 2022. Emerging signals of declining forest resilience under climate change. *Nature*. <https://doi.org/10.1038/s41586-022-04959-9>.
- Friedman, J.H., Meulman, J.J., 2003. Multiple additive regression trees with application in epidemiology. *Stat. Med.* 22, 1365–1381. <https://doi.org/10.1002/sim.1501>.
- George, L.O., Bazzaz, F.A., 1999. The fern understory as an ecological filter: Growth and survival of canopy-tree seedlings. *Ecology* 80, 846–856. [https://doi.org/10.1890/0012-9658\(1999\)080\[0846:TFAAE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[0846:TFAAE]2.0.CO;2).
- Gillis, M.D., Omule, A.Y., Brierley, T., 2005. Monitoring Canada's forests: The national forest inventory. *For. Chron.* 81, 214–221. <https://doi.org/10.5558/tfc81214-2>.
- Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., Moore, R., 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sens. Environ.* 202, 18–27. <https://doi.org/10.1016/j.rse.2017.06.031>.
- Gray, A.N., Spies, T.A., 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. *Ecology* 78, 2458–2473. [https://doi.org/10.1890/0012-9658\(1997\)078\[2458:MCOTSE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[2458:MCOTSE]2.0.CO;2).
- Greenwell, B.M., 2017. *pdp: An R Package for Constructing Partial Dependence Plots*. *R J.* XX 1–16.
- Gschwantner, T., Alberdi, I., Bauwens, S., Bender, S., Borota, D., Bosela, M., Bouriaud, O., Breidenbach, J., Donis, J., Fischer, C., Gasparini, P., Heffernan, L., Hervé, J.C., Kolozs, L., Korhonen, K.T., Koutsias, N., Kovácsévics, P., Kučera, M., Kulbokas, G., Kuliešis, A., Lanz, A., Lejeune, P., Lind, T., Marin, G., Morneau, F., Nord-Larsen, T., Nunes, L., Pantić, D., Redmond, J., Rego, F.C., Riedel, T., Sebeň, V., Sims, A., Skudnik, M., Tomter, S.M., 2022. Growing stock monitoring by European National Forest Inventories: Historical origins, current methods and harmonisation. *For. Ecol. Manage.* 505, 119868. <https://doi.org/10.1016/j.foreco.2021.119868>.
- Henry, C.R., Walters, M.B., Finley, A.O., Roloff, G.J., Farinosi, E.J., 2021. Complex drivers of sugar maple (*Acer saccharum*) regeneration reveal challenges to long-term sustainability of managed northern hardwood forests. *For. Ecol. Manage.* 479, 118541. <https://doi.org/10.1016/j.foreco.2020.118541>.
- Hijmans, R.J., Phillips, S., R. Leathwick, J., Elith, J., 2021. *dismo: Species Distribution Modeling*. <https://cran.r-project.org/web/packages/dismo/index.html>.
- Holl, K.D., Brancalion, P.H.S., 2020. Tree planting is not a simple solution. *Science* 368, 580–582.
- Lawrence, M., McRoberts, R.E., Tomppo, E., Gschwantner, T., Graber, K., 2010. Comparisons of National Forest Inventories. In: *National Forest Inventories: Pathways for Common Reporting*, pp. 19–32. <https://doi.org/10.1007/978-90-481-3233-1>.
- Leak, W.B., 2005. Effects of small patch cutting on sugar maple regeneration in new hampshire northern hardwoods. *North. J. Appl. For.* 22, 68–70. <https://doi.org/10.1093/njaf/22.1.68>.
- Leak, W.B., 2007. Accuracy of regeneration surveys in New England northern hardwoods. *North. J. Appl. For.* 24, 227–229. <https://doi.org/10.1093/njaf/24.3.227>.
- Martínez-Vilalta, J., Lloret, F., 2016. Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics. *Global Planet. Change* 144, 94–108. <https://doi.org/10.1016/j.gloplacha.2016.07.009>.
- Matonis, M.S., Walters, M.B., Millington, J.D.A., 2011. Gap-, stand-, and landscape-scale factors contribute to poor sugar maple regeneration after timber harvest. *For. Ecol. Manage.* 262, 286–298. <https://doi.org/10.1016/j.foreco.2011.03.034>.
- McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G.C., Jackson, R.B., Johnson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B.,

- Pugh, T.A.M., Seidl, R., Turner, M.G., Uriarte, M., Walker, A.P., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. *Science* 368. <https://doi.org/10.1126/science.aaz9463>.
- McGee, G.G., Birmingham, J.P., 1997. Decaying logs as germination sites in northern hardwood forests. *North. J. Appl. For.* 14, 178–182. <https://doi.org/10.1093/njaf/14.4.178>.
- McWilliams, W.H., Stout, S.L., Bowersox, T.W., McCormick, L.H., 1995. Adequacy of Advance Tree-Seedling Regeneration in Pennsylvania's Forests. *Northern Journal of Applied Forestry* 12, 187–191. doi:10.1093/njaf/12.4.187.
- McWilliams, W.H., Westfall, J.A., Brose, P.H., Dey, D.C., Hatfield, M., Johnson, K., Laustsen, K.M., Lehman, S.L., Morin, R.S., Nelson, M.D., Ristau, T.E., Royo, A.A., Stout, S.L., Willard, T., Woodall, C.W., 2015. A regeneration indicator for forest inventory and analysis: history, sampling, estimation, analytics, and potential use in the midwest and Northeast United States. U.S. Department of Agriculture, Forest Service, General Technical Report NRS-148 74pp.
- Messier, C., Bauhus, J., Sousa-Silva, R., Auge, H., Baeten, L., Barsoum, N., Bruelheide, H., Caldwell, B., Cavender-Bares, J., Dhiedt, E., Eisenhauer, N., Ganade, G., Gravel, D., Guillemot, J., Hall, J.S., Hector, A., Hérault, B., Jactel, H., Koricheva, J., Kreft, H., Mereu, S., Muys, B., Nock, C.A., Paquette, A., Parker, J.D., Perring, M.P., Ponette, Q., Potvin, C., Reich, P.B., Scherer-Lorenzen, M., Schnabel, F., Verheyen, K., Weih, M., Wollni, M., Zemp, D.C., 2022. For the sake of resilience and multifunctionality, let's diversify planted forests! *Conserv. Lett.* 15, 1–8. <https://doi.org/10.1111/conl.12829>.
- Millar, C.I., Stephenson, N.L., 2015. Temperate forest health in an era of emerging megadisturbance. *Science* 349, 823–826. <https://doi.org/10.1126/science.aaa9933>.
- Minott, J.A., Kolb, T.E., 2020. Regeneration patterns reveal contraction of ponderosa forests and little upward migration of pinyon-juniper woodlands. *For. Ecol. Manage.* 458, 117640 <https://doi.org/10.1016/j.foreco.2019.117640>.
- Muffler, L., Schmeddes, J., Weigel, R., Barbeta, A., Beil, I., Bolte, A., Buhk, C., Holm, S., Klein, G., Klisz, M., Löff, M., Peñuelas, J., Schneider, L., Vitasse, Y., Kreyling, J., 2021. High plasticity in germination and establishment success in the dominant forest tree *Fagus sylvatica* across Europe. *Glob. Ecol. Biogeogr.* 30, 1583–1596. <https://doi.org/10.1111/geb.13320>.
- Nyland, R.D., Bashant, A.L., Bohn, K.K., Verostek, J.M., 2006. Interference to hardwood regeneration in northeastern North America: Controlling effects of American Beech, striped maple, and hobblebush. *North. J. Appl. For.* 23, 122–132. <https://doi.org/10.1093/njaf/23.2.122>.
- Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Rey, C.P.O., 2017. Forest disturbances under climate change. *Nat. Clim. Change* 7, 395–402. <https://doi.org/10.1038/nclimate3303>.
- Seidl, R., Turner, M.G., 2022. Post-disturbance reorganization of forest ecosystems in a changing world. *Proc. Natl. Acad. Sci.* 119, 1–10. <https://doi.org/10.1073/pnas.2202190119>.
- Solomon, D.S., Blum, B.M., 1967. Stump sprouting of four northern hardwoods. USDA Forest Service Northeastern Forest Experiment Station Research Paper NE-59, Upper Darby, Pennsylvania, USA.
- Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D. C., Morgan, P., Veblen, T.T., 2018. Evidence for declining forest resilience to wildfires under climate change. *Ecol. Lett.* 21, 243–252. <https://doi.org/10.1111/ele.12889>.
- Stevens-Rumann, C.S., Prichard, S., Whitman, E., Parisien, M.-A., Meddens, A.J.H., 2022. Considering regeneration failure in the context of changing climate and disturbance regimes in western North America. *Can. J. For. Res.* 1–39 <https://doi.org/10.1139/cjfr-2022-0054>.
- Trumbore, S., Brando, P., Hartmann, H., Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z., Schepaschenko, D.G., 2015. Forest health and global change. *Science* 349. <https://doi.org/10.1126/science.aaa9092>.
- Vickers, L.A., McWilliams, W.H., Knapp, B.O., D'Amato, A.W., Dey, D.C., Dickinson, Y.L., Kabrick, J.M., Kenefic, L.S., Kern, C.C., Larsen, D.R., Royo, A.A., Saunders, M.R., Shifley, S.R., Westfall, J.A., 2019a. Are current seedling demographics poised to regenerate northern US forests? *J. Forest.* 117, 592–612. <https://doi.org/10.1093/jofore/fvz046>.
- Vickers, L.A., McWilliams, W.H., Knapp, B.O., D'Amato, A.W., Saunders, M.R., Shifley, S. R., Kabrick, J.M., Dey, D.C., Larsen, D.R., Westfall, J.A., 2019b. Using a tree seedling mortality budget as an indicator of landscape-scale forest regeneration security. *Ecol. Ind.* 96, 718–727. <https://doi.org/10.1016/j.ecolind.2018.06.028>.
- Vidal, C., Alberdi, I., Redmond, J., Vestman, M., Lanz, A., Schadauer, K., 2016. The role of European National Forest Inventories for international forestry reporting. *Ann. Forest Sci.* 73, 793–806. <https://doi.org/10.1007/s13595-016-0545-6>.
- Walters, M.B., Farinosi, E.J., Willis, J.L., Gottschalk, K.W., 2016. Managing for diversity: Harvest gap size drives complex light, vegetation, and deer herbivory impacts on tree seedlings. *Ecosphere* 7, 1–29. <https://doi.org/10.1002/ecs2.1397>.
- Walters, M.B., Farinosi, E.J., Willis, J.L., 2020. Deer browsing and shrub competition set sapling recruitment height and interact with light to shape recruitment niches for temperate forest tree species. *For. Ecol. Manage.* 467, 118134 <https://doi.org/10.1016/j.foreco.2020.118134>.
- Walters, R.S., Yawney, H.W., 1990. *Acer rubrum* L. Red Maple. In: *Silvics of North America*. USDA Forest Service Agriculture Handbook 654, Washington, DC, USA, pp. 60–69.
- Woodall, C.W., Westfall, J.A., D'Amato, A.W., Foster, J.R., Walters, B.F., 2018. Decadal changes in tree range stability across forests of the eastern U.S. *For. Ecol. Manage.* 429, 503–510. <https://doi.org/10.1016/j.foreco.2018.07.049>.
- Wu, X., McCormick, J.F., Busing, R.T., 1999. Growth pattern of *Picea rubens* prior to canopy recruitment. *Plant Ecol.* 140, 245–253. <https://doi.org/10.1023/A:1009723326707>.
- Yamazaki, M., Iwamoto, S., Seiwa, K., 2009. Distance- and density-dependent seedling mortality caused by several diseases in eight tree species co-occurring in a temperate forest. *Plant Ecol.* 201, 181–196. <https://doi.org/10.1007/s11258-008-9531-x>.
- Zhu, K., Woodall, C.W., Monteiro, J.V.D., Clark, J.S., 2015. Prevalence and strength of density-dependent tree recruitment. *Ecology* 96, 2319–2327. <https://doi.org/10.1890/14-1780.1>.