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Drivers of Tree Growth and Mortality in an Uneven-Aged, Mixed-Species Conifer Forest of Northeastern United States

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DRIVERS OF TREE GROWTH AND MORTALITY IN AN

UNEVEN-AGED, MIXED-SPECIES CONIFER FOREST

OF NORTHEASTERN UNITED STATES

By

Erin Katherine Pattison Fien

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An Abstract of the Thesis Presented
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Individual tree growth and mortality drive forest stand dynamics and are important, universal metrics of tree success. Studying the factors that affect growth and mortality is particularly challenging in mixed-species, uneven-aged systems due to their defining heterogeneity and strong temporal and spatial variability. However a better understanding of the factors driving growth and mortality in mixed-species, uneven-aged forest is crucial to managing and maintaining these valuable systems for the future.

The goal of this study was to determine the relative importance of individual tree attributes (e.g., species, size, neighborhood crowding, crown position) and environmental characteristics (e.g., soil moisture) in driving growth and survival. In particular we aimed to test if the factors regulating growth were the same as those regulating mortality, as is often assumed. Due to its large size and intensive sampling, the 3-ha, stem-mapped plot (established in 1989) at Howland Research Forest in central Maine allowed us to address additional relevant questions regarding the influence of sapling crowding, neighbor species identity, and past disturbance.

Growth and survival of over 3000 plot trees was assessed after 25 years and modeled using multiple linear regression (growth) and binary logistic regression (survival). We found that species, neighborhood crowding, and diameter, in that order, were the top predictors of both growth and survival. Growth, but not survival, was inhibited by soil moisture, especially in poorly-drained portions of the plot. Growth was also inhibited for individuals that grew in neighborhoods with more conspecific neighbors, which likely have more similar resource requirements when compared to those of heterospecific neighbors. In individual species growth analysis, we found that not all species are equivalent competitors, namely white pine (*Pinus strobus*) was more competitive, and red maple (*Acer rubrum)* was less competitive than would be expected if all species were equivalent competitors. Unexpectedly, we found that individuals with greater crowding from sapling neighbors were more likely to survive. For both growth and survival, we found a significant interaction between crowding and soil moisture, suggesting that within a single stand, individual success can be limited by both excess and insufficient water, depending on the crowding neighborhood. We also found that the growth of larger trees was enhanced when they were surrounded by more cut stumps, implying that the effects of a 100-year-old disturbance were surprisingly persistent.

These results demonstrate the broad range of variables driving growth and survival in uneven-aged mixed-species forests, as well as the benefit of differentiating between metrics of success when assessing stands and individuals. Given the importance of uneven-aged, mixed-species forests in storing and sequestering carbon, maintaining biodiversity, and providing resistance and resilience to an uncertain future, we suggest studies such as this that address a full range of interacting drivers of success are necessary to better manage and maintain these complex systems.

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PROLOGUE

Forest provide important ecosystem services by storing and sequestering carbon (Pan et al. 2011), sourcing forest products, protecting water resources (Welsch 1991) and acting as repositories for biodiversity (Liang et al. 2016). However, forests' continued ability to provide these services remains uncertain, given changing climate realities and novel disturbance regimes and is dependent in part on their composition and structure as well as their continued productivity.

In all forested systems, changes in composition, structure and productivity are driven by three major processes: growth, mortality and recruitment (Oliver 1981). This study focuses on two of these processes, namely growth and mortality. Variability in growth is inherently closely related to productivity but can also affect structure and composition by leading to differentiation in tree size and canopy position. Differentiation in size or canopy position (between individuals or species) can in turn alter access to resources and lead to variation in individual or species success (i.e., increased growth and survival). Tree mortality alters forest composition in a wide variety of ways. When individuals die they open space in the canopy, which may lead to the recruitment of new individuals or species (Watt 1947), which in turn increases structural diversity (Franklin et al. 2002, Stockland et al. 2012). Because of the major roles growth and mortality play in stand dynamics, continuing to improve our understanding of factors that drive these processes will allow us to better anticipate future forest change.

Driving factors of growth and mortality are possibly most uncertain in mature, uneven aged, mixed-species forests. These processes are challenging to study in these heterogeneous systems because of inherently high spatial and temporal variability; to capture this variability studies must to be spatially large and temporally long. Studies of mature, mixed-species forests

are particularly relevant as it becomes clear that their structural and compositional diversity may make them more successful under a changing climate. These heterogeneous forests may be more resilient, or have a greater ability to resist change, thus avoiding major loss of function (Thompson et al. 2009, Oliver et al. 2015, Cantarello et al. 2017). Uneven-aged, mixed-species forest are more resilient because the diversity of structures and species makes it unlikely that all individuals will be affected by changes or disturbances in the same way. Thus, if some individuals are catastrophically affected, others are likely to remain. Mixed-species forest may also be more likely to adapt, as their diversity acts as a repository of traits that have the potential to be equally or better suited to novel conditions (D'Amato et al. 2011). In addition, in some cases mixed-species forests have been found to be more productive (Paquette and Messier 2011, Zhang et al. 2012), and large, older trees of mature forests have the ability to store and sequester large amounts of carbon (Sillett et al. 2010, Keeton et al. 2011). These characteristics for climate adaptation and mitigation, as well as continued productivity, highlight the need for a better understanding of the factors governing growth and mortality of mature, mixed species forests.

The large mapped and intensively sampled permanent plot at Howland Research Forest of central Maine provides an ideal place to study the factors driving tree growth and mortality. Furthermore, the mixed-species composition is similar to other forests of the region, meaning that findings likely have implications for the broader region. This study can contribute to our understanding of interacting forest characteristics and processes, which may allow us to better anticipate forest productivity and carbon dynamics in an uncertain future.

1. INTRODUCTION

Variability in tree growth and mortality rates control the composition, structure, and productivity of forests stands as they develop through time (Oliver 1981, Franklin et al. 2002) and dictate distribution and abundance of individual trees across landscapes. In natural forests, individual tree growth and mortality rates vary considerably within and between species, as well as spatially within a stand. In uneven-aged, mixed-species forests, this variability is even more pronounced and is essential to maintaining heterogeneity in these systems. Improved understanding of the factors regulating variability in growth and mortality rates, as well as the interactions among these factors, can lead to better anticipation of individual tree success and community dynamics and allow us to better assess vulnerability of these systems to changing environmental conditions.

Numerous factors contribute to the variability in growth rate and mortality risk of individual trees in uneven-aged, mixed-species systems. Factors may include individual-tree characteristics such as species, size, crowding, or canopy position, or stand-level characteristics such as stand density, soil properties, or past disturbance. While the variability in individual success across species, sizes, and crowding has been extensively investigated (Biging and Dobbertin 1992, Canham et al. 2004, Coomes and Allen 2007a), more recent work has focused on the added influence of variability in climate (Rollinson et al. 2015, Copenhaver-Parry and Cannon 2016) and the species identity of crowding neighborhoods (Uriarte et al. 2004b, Fichtner et al. 2017, Vitali et al. 2018). However, due to the spatial and structural heterogeneity of mixed-species forests, as well as the time frame required to observe growth and mortality in these systems, studies addressing a full range of factors effecting an individual tree's success are uncommon. As a result, the relative importance of these factors is not fully understood.

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The broad range of tree sizes in late successional, mixed-species forests presents a particular challenge for identifying factors most strongly influencing growth and mortality. The detrimental influence of overstory trees on saplings growth and mortality is well documented (Lorimer et al. 2001, Ramage et al. 2017); however, the potential detrimental influence of saplings on overstory trees has not been well explored, despite suggestions that it could be substantial (Giuggiola et al. 2018). This lack of information is due, in part, to the scarcity of long-term studies that include mapped sapling and tree data needed to assess growth and mortality risk using standard spatially explicit crowding indices.

In addition, current tree growth and mortality risk may be influenced by disturbances that occurred in the past. Non-stand replacing disturbances create canopy gaps that increase resource availability and alter the growth of surrounding individuals (Whitmore 1989, Runkle 1998). Most studies of gap-forming disturbances are temporally limited to the short-term effects of gap formation or gap closure (Fraver et al. 1998, Gray et al. 2012). However, increasing interest in the legacy of past disturbance (e.g. Johnstone et al. 2016) suggests a need to better understand the long-term (i.e., many decades) effects canopy gaps may have on growth rates and mortality risks of the post-disturbance community. This topic may be addressed by incorporating structural legacies, such as stumps or standing dead trees, into crowding indices to assess the effects of associated disturbances on individual tree growth and mortality.

Finally, although both tree growth and mortality serve as useful proxies for forest vigor and productivity, the two metrics may be driven by distinct ecological factors (Brooks 1994, Zhu et al. 2017). The commonly accepted negative association between growth and mortality suggests that slow growing trees have an increased risk of mortality (Keane et al. 2001, Suarez et al. 2004, Battles et al. 2007). However, a positive association can be found, for example, on the

edge of canopy gaps where individuals experience both increased growth, due to more favorable light conditions, and increased risk of mortality, due to root damage or in environmental conditions that favor tree productivity but also favor insects and pathogens (Worrall et al. 2005, Gray et al. 2012, Das et al. 2016). Despite the indeterminate association between growth and mortality, as well as evidence of growth independent mortality (Wunder and Reineking 2007, Holzwarth et al. 2013), few studies have attempted to differentiate the factors driving growth and mortality. The need for this distinction may be particularly important in late-successional forests, due to the boarder range of both density-independent and density-dependent mortality agents (Larson et al. 2015). Given projections regarding future environmental change and novel disturbance regimes, a more detailed understanding of the factors influencing growth and mortality may be necessary to better address questions regarding individual-tree and stand-level dynamics (Bond-Lamberty et al. 2014).

Our primary objective was to identify the factors most strongly influencing tree growth and mortality rates in a red spruce (*Picea rubens*) – eastern hemlock (*Tsuga canadensis*) forest of the Acadian Forest region of northeastern North America. Specifically, we tested the relative influence of species, individual tree size, canopy position, neighborhood crowding, within-neighborhood species composition, soil moisture, disturbance legacies on tree growth and survival rates. Doing so allowed us to ask, are the factors that limit tree growth the same as those that increase mortality risk? We conducted this work using repeated inventories of a 3-ha, fully mapped plot (all tree stems ≥ 3 cm diameter, as well as decayed stumps) at the Howland Research Forest of central Maine, USA. The richness of this data set allowed us to ask additional question not typically addressed in otherwise similar studies of growth and mortality, namely (1) to what extent do saplings influence growth and mortality rates of canopy trees? and (2) can the

lingering effect of a long-ago harvest, now evident as decayed stumps, continue to influence growth and mortality of canopy trees? Answers to these questions can shed light on stand development in this forest type and allow us to better predict future changes by identifying areas of vulnerability.

2. METHODS

2.1 Study site

This work was conducted at the Howland Research Forest of central Maine, USA (45°12'N, 68°45'W) (Figure 1), where average annual precipitation is 1142 mm, and the average temperature is 6.2º C (Daly et al. 2008). Data was collected from a three-hectare (150 × 200 meter) permanent plot in Howland Forest established in 1989 by Laboratory for Terrestrial Physics at NASA's Goddard Space Flight Center (Weishampel et al. 1994); we refer to this as the NASA plot (Figure 2). The canopy is comprised mainly of red spruce (*Picea rubens)* and eastern hemlock (*Tsuga canadensis*) with scattered emergent white pine (*Pinus strobus)* (Table 1). Patches of advance regeneration of red spruce, eastern hemlock and balsam fir (*Abies balsamea*) are well developed in the understory.

Table 1: Descriptive statistics for the 3-ha Howland Forest NASA plot based on the initial (1989) inventory. Includes all trees ≥ 10 cm DBH. (N = number of trees, BA = basal area, DBH = diameter at breast height, sd = standard deviation, CI = neighbor crowding index).

Species	N (ha^{-1})	BA ($m^2\,ha^{-1}$)	Mean DBH (sd) (cm)	Mean CI (sd)
Picea rubens	511	13.3	17.2 (5.8)	8.4 (4.0)
Tsuga canadensis	265	7.6	17.9 (6.6)	8.1 (4.2)
Thuja occidentalis	111	2.9	17.3 (5.9)	8.2 (3.5)
Acer rubrum	77	1.9	16.8 (5.9)	8.8 (4.2)
Pinus strobus	36	2.7	28.7 (10.8)	5.5 (3.3)
Abies balsamea	14	0.3	14.7 (3.7)	9.7 (4.2)
Betula papyrifera	5	0.1	15.1 (4.4)	11.0 (4.0)
Betula alleghaniensis	4	0.2	24.9 (13.5)	6.6 (2.5)
Total	1023	29.0	17.8 (6.6)	8.3 (4.0)
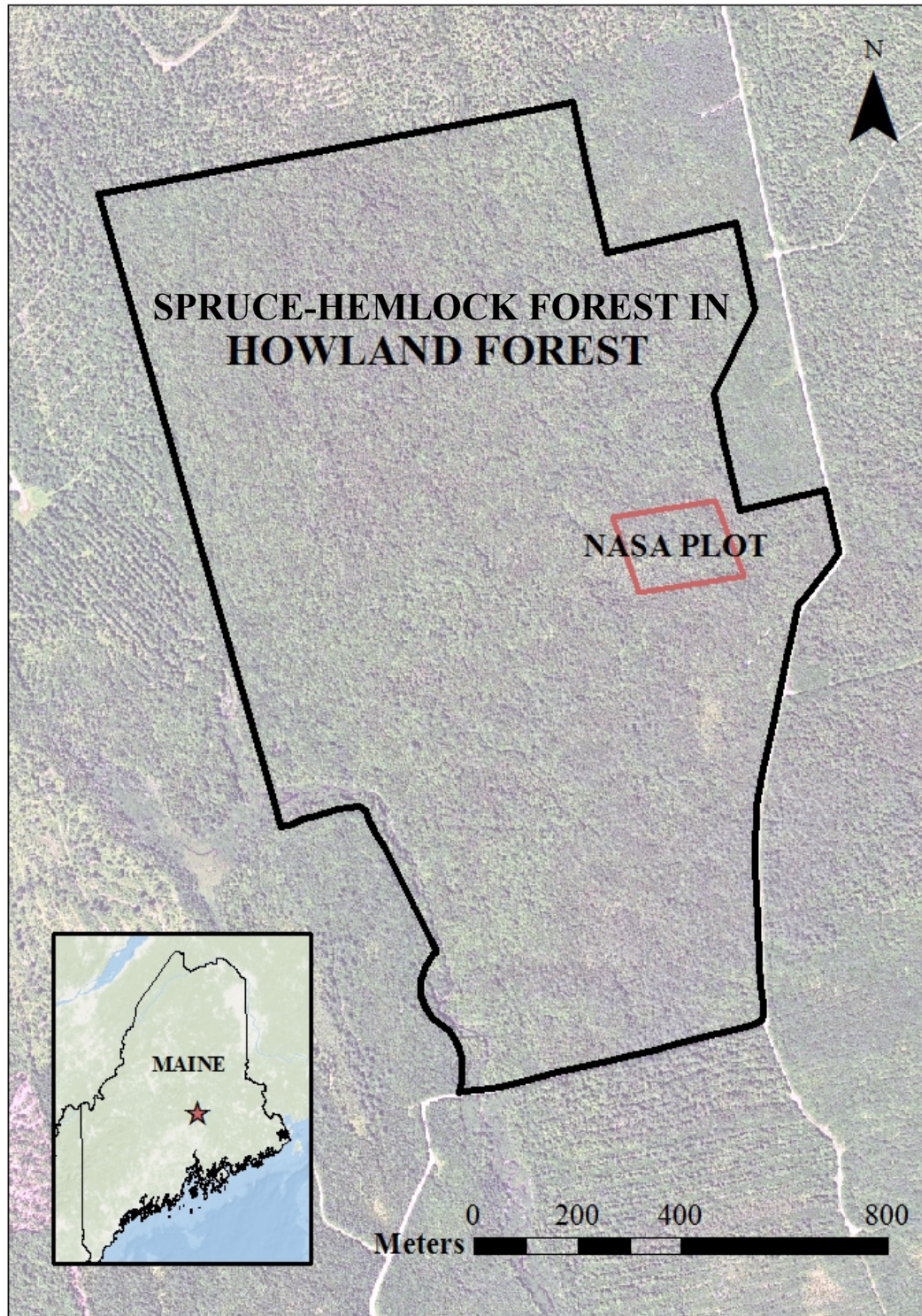
Figure 1: Howland Research Forest is located in the Acadian forest region in central Maine. The NASA plot is a 3-ha stem-mapped permanent plot established in in 1989. Black boarder surrounds contiguous minimally disturbed spruce-hemlock forest with in the boundary of the Research Forest.

Growth releases evident in tree-ring records, as well as well-decayed cut stumps, suggest partial harvests occurred in the 1890s and the 1920s (unpublished data). No other major disturbances have occurred since these harvests, and the stand has since developed characteristics typical of late successional forests including large old trees (> 200 years), a range of tree diameters, and abundant coarse woody debris. At the plot level, soil drainage ranges from large well drained areas to poorly drained forested wetlands (Figure 2). At a smaller scale, hummock and hollow topography results in more localized variability in soil moisture.
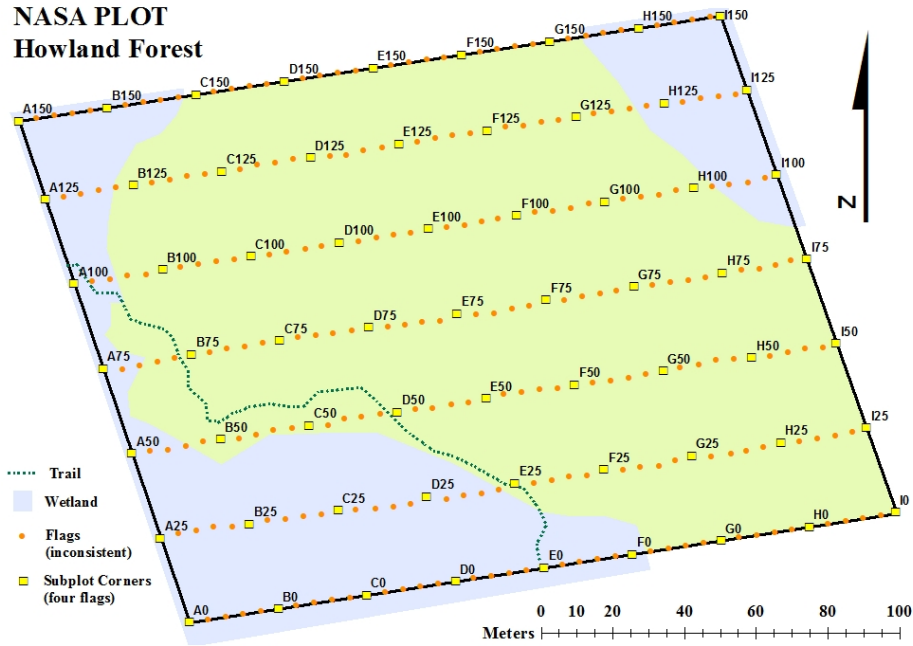
Figure 2: Map of NASA plot at Howland Research Forest showing plot boarders, subplot corners, transect markers, and wetland delineation. We note that the plot was established as a slight parallelogram and was not oriented directly north-south, east-west; however, for ease of presentation in subsequent Figures, we show it as a rectangle with standard orientation (north toward top).

2.2 Field procedures

In 1989 when the NASA plot was established, all trees greater than 3 cm in diameter at breast height (1.37m, DBH), approximately 7800 individuals living and standing dead, were mapped and tagged with a unique identifier (Figures 3 & 4). Species, DBH, height, and position in the canopy were recorded for all trees. Canopy position was visually classified into seven categories; however, for this study those classes were collapsed to match the more conventional four-class system of dominant, codominant, intermediate, and suppressed positions (Smith et al. 1997).
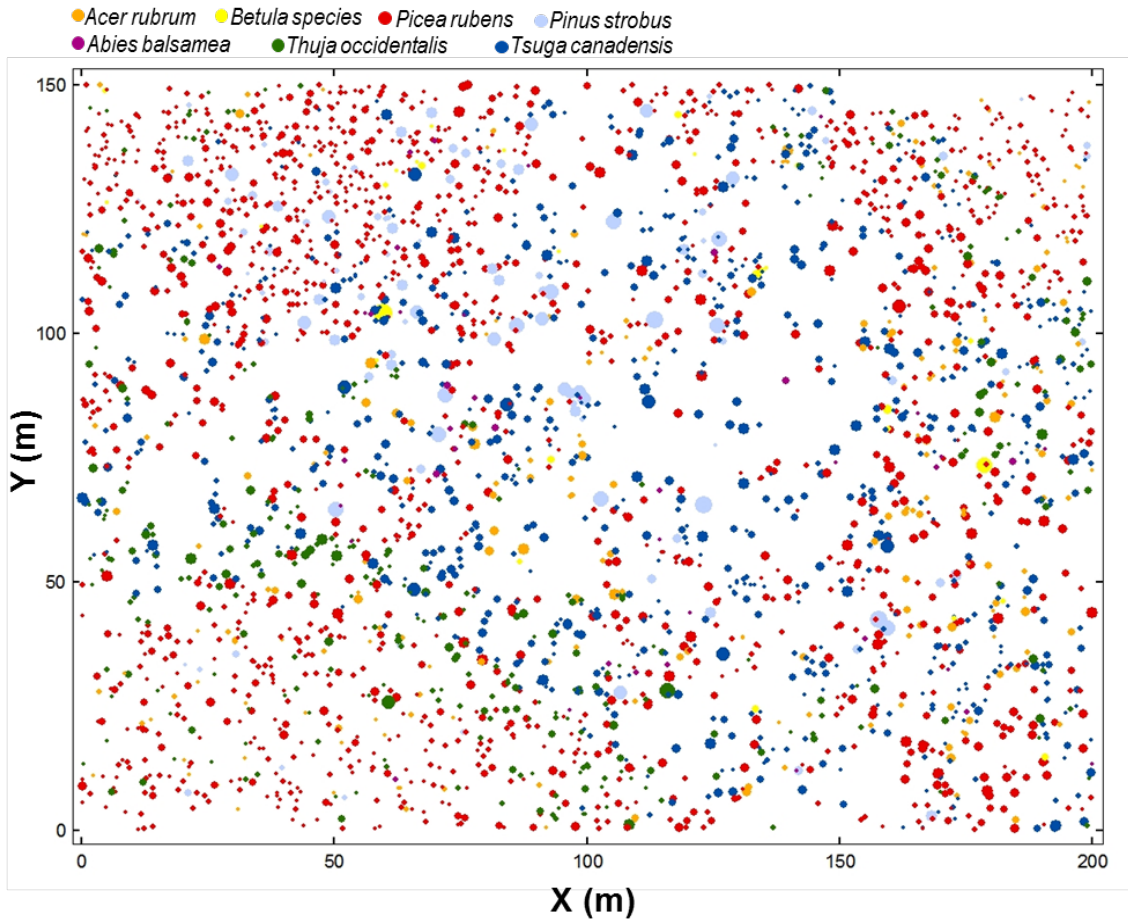
Figure 3: Spatial location of all NASA plot trees with diameter greater than 10 cm in 1989 when the plot was established. Point size is proportional to diameter in 1989 (north toward top).
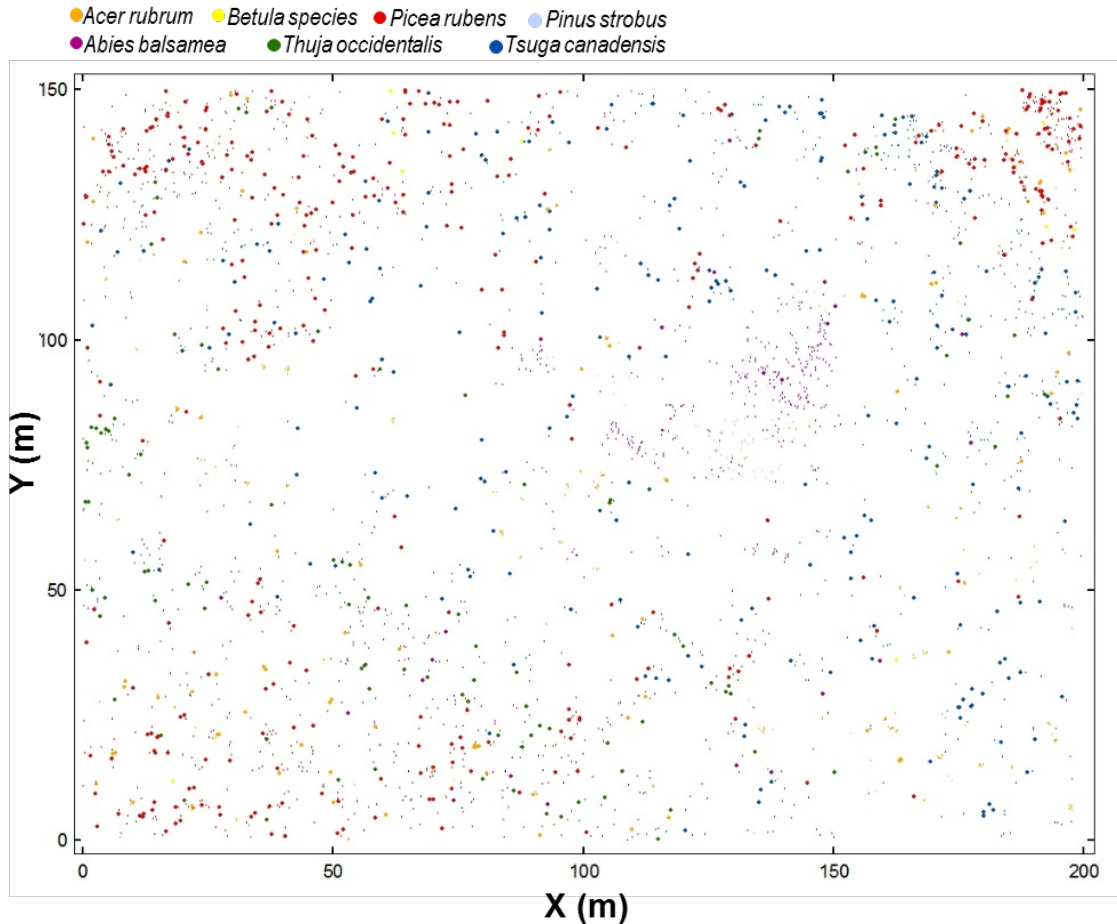
Figure 4: Spatial location of all NASA plot saplings (diameter less than 10 cm and greater than 3 cm) in 1989 when the plot was established. These saplings were used to develop a sapling crowding index but were not included as focal trees in models of growth and survival. Point size is proportional to DBH.

Between 2015 and 2017, we re-inventoried all trees and saplings to assess growth and mortality (Figure 5). DBH and canopy position were recorded, and species assignments and mapped locations were corrected when necessary. We relocated the larger trees, whether standing or fallen, with remarkable success; however, many of the dead and fallen smaller (generally < 10 cm DBH) trees had become moss-covered and partially decayed (Figure 4). Preliminary field work using a metal detector and forest floor excavations demonstrated that tags from these smaller trees could be found, but were buried as deep as 5 cm below litter and moss.

Therefore, to avoid disturbing the forest floor on this permanent plot, we assumed if a previously tagged tree could not be found after a thorough search, the tree had died, fallen, and its tag was buried. In order to better understand the influence of past harvests, we measured (top diameter, height) and mapped all cut stumps (N=722). We attempted to identify stump species; however, this was possible for only *ca.* 25% of the stumps, owing to advanced decay.
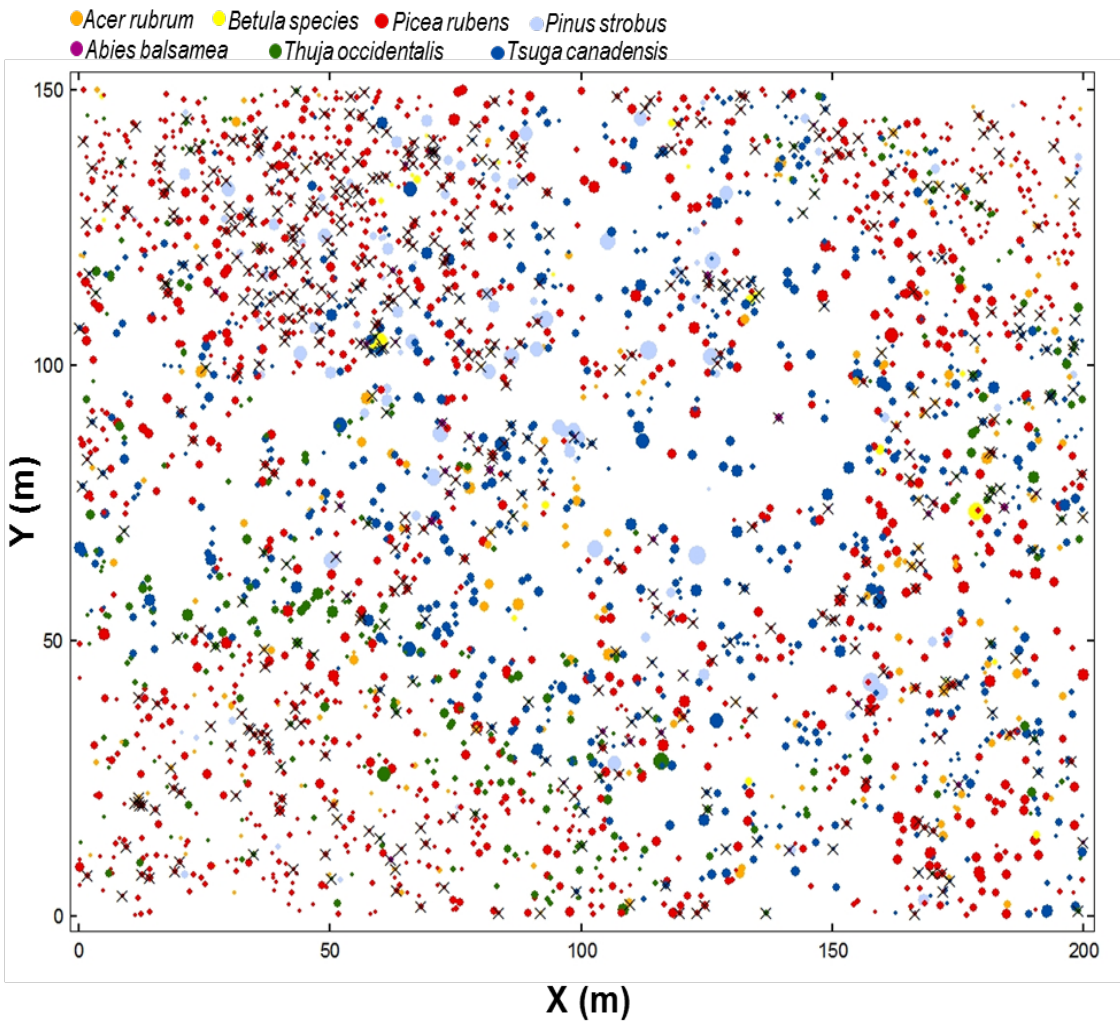
Figure 5: Spatial location of all NASA plot trees, living and dead, with diameter greater than 10 cm DBH. Point size is proportional to diameter in 1989. X symbol placed over individuals that died between 1989 and 2015.

2.3 Explanatory variables

Previous work has shown tree size to be a strong predictor of both growth (Enquist et al. 1999) and mortality (Coomes and Allen 2007b). In the current study, diagnostics of preliminary candidate models indicated that tree diameter provided the best size metric for directly predicting both growth (basal area increment, see below) and mortality, based on Akaike's information criterion (AIC) (Burnham and Anderson 2003), as well as graphs of residual-*versus*-predicted values. Other size metrics tested included tree basal area, and tree stem volume derived from Honer's (1967) regional allometric equations. All size metrics refer to the initial (1989) size.

The detailed mapping of the NASA plot allowed us to use spatially explicit indices to estimate the crowding intensity any tree may experience from its neighbors. Based on its success in previous work, as well as preliminary analyses of NASA plot data, we chose the crowding index (CI) proposed by Heygi (1974), which incorporates both the size and proximity of neighboring trees relative to a focal tree. The CI is calculated as follows:

$$CI_f = \sum_{n=1}^{N} \left(\frac{S_n/S_f}{Distance_{nf}} \right)$$

where CI_f is the crowding index for an individual focal tree, with larger CIs indicating greater crowding; N is number of trees in a fixed-radius neighborhood around the focal tree, S_n and S_f are the size of a neighboring tree and the focal tree, respectively; and $Distance_{nf}$ is the distance between the focal tree and a neighboring tree. All trees ≥ 10 cm DBH (in 1989) were used as focal and neighbor trees (Figure 3). DBH, basal area, and volume estimated using Honer's (1967) regional allometric equations were considered as potential size metrics for the CI (S_n and S_f). Preliminary candidate model diagnostics, including AIC and graphs of residual-*versus*-predicted values, indicated that CIs with DBH as the size metric yielded the best model

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performance regarding tree growth. DBH has been used commonly in past studies of crowding (Lorimer 1983, Canham et al. 2004, Coomes and Allen 2007a).

To determine the optimal neighborhood radius for the index above, we compared the goodness of fit (R^2) for a series of regression models predicting growth with CIs using a range of radii from 4 to 24 meters in 2-meter increments, following a procedure similar to that of Lorimer (1983). We ultimately chose a 10-m radius, as little predictive power was gained by further increasing the neighborhood size (Figure 6). CIs for focal trees located within 10 m of the plot border required edge correction; thus, their CIs were adjusted upward based on the proportion of their neighborhood that fell outside the plot (Haase 1995). Preliminary analyses demonstrated that models including this edge correction produced results similar to those in which edge trees (those within 10 m of plot border) were excluded as focal trees, thus providing support for this correction method.
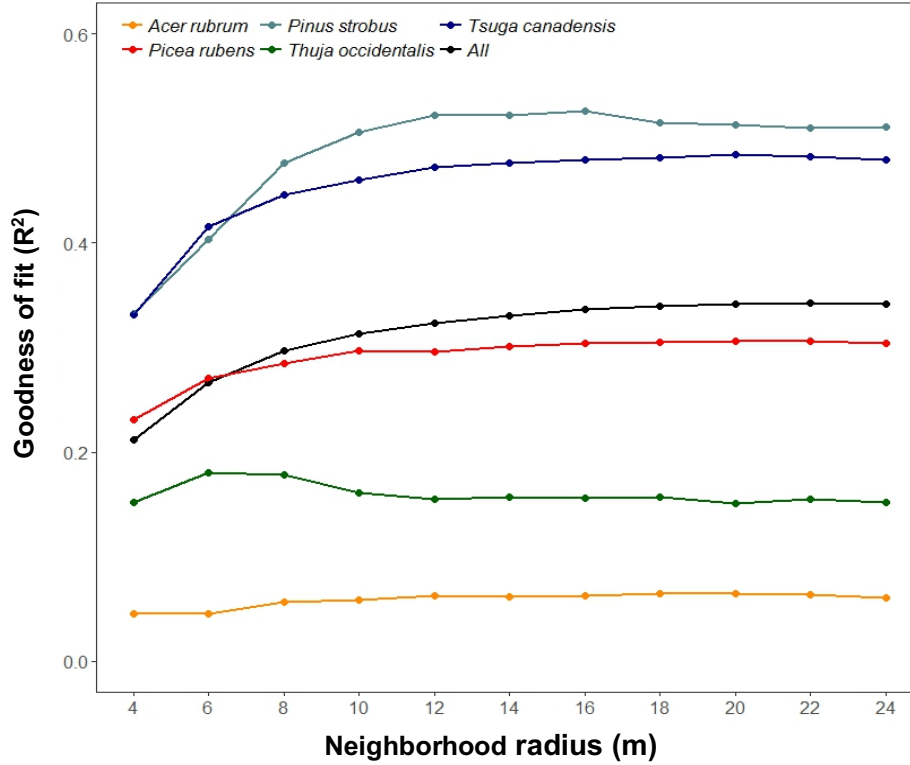
Figure 6: Goodness of fit (R^2) relating basal area growth and the Hegyi crowding index (CI) across a range of neighborhood radii. Demonstrating the marginal benefit of increasing the radius beyond ca. 10 m.

To test the potential crowding effect that neighboring saplings have on focal trees, we calculated an additional CI (as above) that included saplings only as neighbors. Saplings are defined here as stems < 10 cm DBH (He and Duncan 2000) (Figure 4). To account for high sapling mortality rates over the study period, crowding effects of sapling neighbors that died during the study period (1989 – 2017) were down-weighted using the following structure (Fraver et al. 2014).

$$CI_w = \sum_{n=1}^{N} \left(\frac{S_n/S_f}{Distance_{nf}} * w_m \right)$$

where w_m is the estimated proportion of the study period the neighbor tree survived, based on intermediate inventories conducted in 2010 and 2011 and the most recent inventories. An

individual's mortality date was taken as the midpoint of the inventory interval in which it died. The crowding effect of larger trees was not down-weighted as such because preliminary analysis suggested it did not improve model performance, perhaps because far fewer larger trees died and because large standing-dead trees, particularly conifers that retain needles, may still shade their neighbors (Fraver et al. 2014).

Given that previous studies in mixed-species forests report that neighbors of different species can exert varying crowding effects on the focal tree (Goldberg and Landa 1991, Uriarte et al. 2004b, Vitali et al. 2018), we calculated an additional explanatory variable to test this effect. To avoid a more complex species-by-species analysis when comparing all explanatory variables, we simply calculated for each focal tree the conspecific proportion of CI intensity as follows:

$$P_c = CI_c/CI_f$$

where P_c represents the proportion of a focal tree's crowding neighborhood associated with conspecific neighbors; CI_c is the CI based on conspecific neighbors only; and CI_f is as shown above. As such, focal trees with larger P_c values are growing with a greater proportion of conspecific neighbors; a P_c equal to 1 means all neighbors are conspecific. Because this intraspecific crowding index differentiates between conspecific and heterospecific neighbors it allowed us to assess potential differences between intra- and interspecific species interactions.

To assess the potential lingering influence of long-ago harvests on recent growth and mortality, we developed an index based on the mapped cut stumps. Diagnostics of preliminary candidate models indicated that the number of cut stumps within the neighborhood (10-m radius) of each focal tree provided the best index, based on AIC scores, as well as graphs of residual-

versus-predicted values. Other potential indices included stump proximity and size metrics tested in the form of Hegyi's index.

We developed a soil moisture index for each tree location based on moisture measurements taken at subplot corners forming a 25-m grid covering the entire plot, including borders, for a total of 63 locations (Figure 2). During the summer of 2017, we measured soil moisture at 10-cm depth using Fieldscout TDR 100 (Spectrum Technologies, Inc.) at each location on seven dates, ranging from 1 June to 29 August. To account for seasonal dry-down over the sampling period, moisture measurements at each location were converted to Z-scores (units of standard deviation) for each sampling date. The mean Z-scores at each location for all seven sampling dates were then used to create an interpolated soil moisture surface, and a mean Z-score was extracted at each tree location. Z-scores were taken as a relative index of soil moisture, with higher values indicating greater moisture. Interpolation, for this portion on the analysis, was done using a simple kriging method in ArcGIS (v. 10.4.1, ESRI, Redlands, CA, USA).

2.4 Growth and survival model analysis

We chose annual basal area increment (BAI, $cm^2 \ yr^{-1}$) as our growth metric, instead of radial growth, to minimize the confounding effects of assessing growth among trees with markedly different diameters (Biondi 1999). BAI was estimated by subtracting initial basal area (1989 inventory) from the final basal area (recent inventories) for each tree and dividing by the number of years in the study period. Individuals that slightly decreased in diameter (suggesting measurement error) were assumed to have zero growth.

The annual mortality rate was calculated by dividing the percent of trees that died by the length of the study period. We recognize that this method for calculating mortality rate is not

independent of the study period length; however, our purpose was simply to summarize mortality for this study, and not to make comparisons with other studies of different lengths (Sheil and May 1996). For clarity in presentation we chose to model survival (the complement of mortality) to better parallel our growth analyses, so that an increase in either metric is associated with greater individual success. Individual survival was based on whether trees living in 1989 were still living at the end of the inventory period.

Individuals that died during the study period were not included in growth models, such that we modeled survival of 3043 individuals and growth of 2552 individuals. Birch species (*Betula alleghaniensis* and *B. papyrifera*) were not included in either analyses given their low abundance (N < 20).

To assess the importance of our potential explanatory variables, we developed a series of candidate models using multiple linear regression for growth and binary logistic regression for survival. A modified hierarchical (or sequential) modeling approach was followed due to strong collinearity between explanatory variables (correlations coefficients of r > 0.6) (Graham 2003). Any degree of collinearity confounds our ability to assess the importance of individual explanatory variables because the partitioning of their shared explanatory power effects each explanatory variable's marginal statistics (such as the regression coefficient) and the ability to test for significance. With the common stepwise modeling approach, shared explanatory power is assigned arbitrarily, which may lead to the exclusion of important but highly collinear variables (Harrell 2015). To avoid this problem, we followed a hierarchical modeling approach whereby explanatory variables were added sequentially based on a pre-established order of importance. With this approach any shared explanatory power among collinear variables is assigned to the variable that was added first (the more important variable) (Graham 2003). This approach allows

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us to determine what additional variability can be explained by each added explanatory variable that was not already explained by previously added, more important explanatory variables. We note that this approach would not be necessary if our intent were to develop an optimal, parsimonious model for predicting growth and mortality for other sites. Our intent was rather to address the importance of specific explanatory variables of interest, some of which have not been well tested in previous studies. The initial ranked importance of the explanatory variables was established using a random forest algorithm, relying on regression and classification techniques to assess growth and mortality, respectively (Grömping 2009). The parameters for random forest regression and classification were the same, such that importance values were calculated based on 500 regression trees with three variables per node. Random forest procedures were conducted in R software package 'randomForest' (Liaw and Wiener 2002). Finally, given the importance of species in these analyses, all significant explanatory variables for growth and mortality were also evaluated separately by species.

Plots of residuals *versus* explanatory variables from the regression models constructed as above showed no clear trends that would demand the inclusion of interactions among explanatory variables (Zuur et al. 2009). However, we chose to include two biologically relevant interaction terms to test specific questions and to assist in the interpretation of the results. First, we tested the interaction between crowding and soil moisture, as recent studies have demonstrated that competition may modify the relationship between a tree's success and local environmental variables (Martin-Benito et al. 2011, Rollinson et al. 2015, Buechling et al. 2017, Gleason et al. 2017). Second, we tested the interaction between the number of neighborhood stumps and tree diameter. Given that the harvest occurred nearly 100 years ago, we reasoned that

a tree's recent size (as of the first inventory in 1989) may reflect its previous response to this long-ago harvest, which could be explored through this interaction.

In all analyses, BAI, DBH, tree CI, soil moisture and number of stumps were natural log transformed to better meet assumptions of normality and heterogeneity. Spatial correlation structures were added to all multiple linear regression (for growth) and binary logistic regression (for survival) models using the 'nlme' package (Pinheiro et al. 2017) in R software to test for spatial autocorrelation; however, no violations of residual independence were found. All models were compared using Akaike information criterion (AIC) (Burnham and Anderson 2003) to determine which models were best supported by the data. ΔAIC was calculated in reference to the model with the lowest AIC (top model). P values ≤ 0.05 were deemed statistically significant. All analyses were conducted using R statistical software (R Core Team 2016).

2.5 Spatial pattern analysis

To better understand plot-level variability and the importance of explanatory variables, we produced interpolated surfaces of all explanatory and response variables. Visually comparing the spatial patterns of growth variability with those of explanatory variables allowed us to better assess the strength of these relationships. We used ordinary kriging as our method of interpolation, conducted in R using packages 'sp' and 'gstat' (Pebesma and Graeler 2018, Pebesma et al. 2018). All default parameters were retained, and semivariograms were used to compare and select the best model shape (spherical, exponential or Gaussian) for each variable.

2.6 Neighbor species identity analysis

The mixed-species nature of this forest also allowed us to test for interspecific interactions related to crowding, asking if the success of a focal tree of a given species is influenced by the species identity of its neighbors. The large number of species–species

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combinations in the NASA plot led us to use a simplified method when identifying the most important explanatory variables of growth and survival (as outlined above). Given the significance of intraspecific CI in predicting growth, we fit growth models for species individually to further address the influence of neighbor identity. Each species model included all the top explanatory variables as determined by the previous analysis. We then added neighbor species-specific CIs to these top models one at a time to test the added explanatory ability of neighbor identity. The neighbor species-specific CIs were simply subsets of Hegyi's index calculated independently for each neighbor species around the focal tree, such that all neighbor species-specific CIs would sum to the to the original Hegyi's index (CI) for that focal tree. To evaluate the effect of neighbor identity, each model with an added neighbor species-specific CI was compared to the top models from the previous analysis using AIC. That is, if the growth model of species A were improved by adding the CI associated with neighbor B, it would suggest that the influence of neighbor species B on focal species A was not fully explained by neighborhood crowding that included all species. This approach of adding the crowding of each neighbor species as independent explanatory variables is similar to that used by Vitali et al. (2018), and it allowed us to efficiently assess all species pair-wise combinations.

3. RESULTS

3.1 Plot overview

Total plot-level basal area growth equaled 0.29 $m^2 ha^{-1} yr^{-1}$ for the study period. Mean annual tree growth rates differed markedly among species, ranging from 2.9 $cm^2 yr^{-1}$ for northern white-cedar to 30.0 $cm^2 yr^{-1}$ for white pine (Table 2). In fact, despite representing only 9.4% of the total plot basal area, white pine growth accounted for 22.8% of total plot basal area growth during the study period (Table 2). Despite the presence of some larger trees, the diameter distribution is skewed towards smaller size classes, particularly in 1989 (Figure 7).

Table 2: Summary of growth (basal area increment) and mortality for most abundant species.

Species	Growth		Mortality	
	Mean (sd) (cm^2yr^{-1})	Total ($m^2ha^{-1}yr^{-1}$)	Rate (%)	Mean DBH (sd) (cm)
Picea rubens	4.0 (3.7)	0.17	19	14.2 (4.2)
Tsuga canadensis	5.4 (4.5)	0.13	9	14.6 (4.7)
Thuja occidentalis	2.9 (2.4)	0.03	15	14.8 (4.2)
Acer rubrum	4.2 (2.8)	0.03	16	13.9 (4.0)
Pinus strobus	30.0 (17.3)	0.10	5	20.1 (9.6)
Abies balsamea	-	-	100	14.7 (3.7)
Total	5.3(7.2)	0.29	19	14.4 (4.4)

(DBH: diameter at breast height of trees that died between 1989 and 2015, sd: standard deviation)

Of the original 3043 individuals >10 cm DBH, 490 (16.1%) died during the study period (Figure: 5), equivalent to a loss of 0.11 $m^2 ha^{-1} yr^{-1}$ of basal area. As with growth, mortality rates varied markedly among species, ranging from 4.6% mortality for white pine to 100% mortality for balsam fir. Mortality occurred primarily in the smaller size classes; the mean and median DBH of trees that died were 14.4 (sd=4.4) and 13.1 cm respectively. Yet, we found no U-shaped

mortality trend (i.e., high mortality rates for both small and very large trees) associated with increased mortality probability of very large individuals (Figure 8). For all species except white pine, the mean diameter of trees that died was significantly smaller than that of trees that survived, based on t-tests (Figure 9).
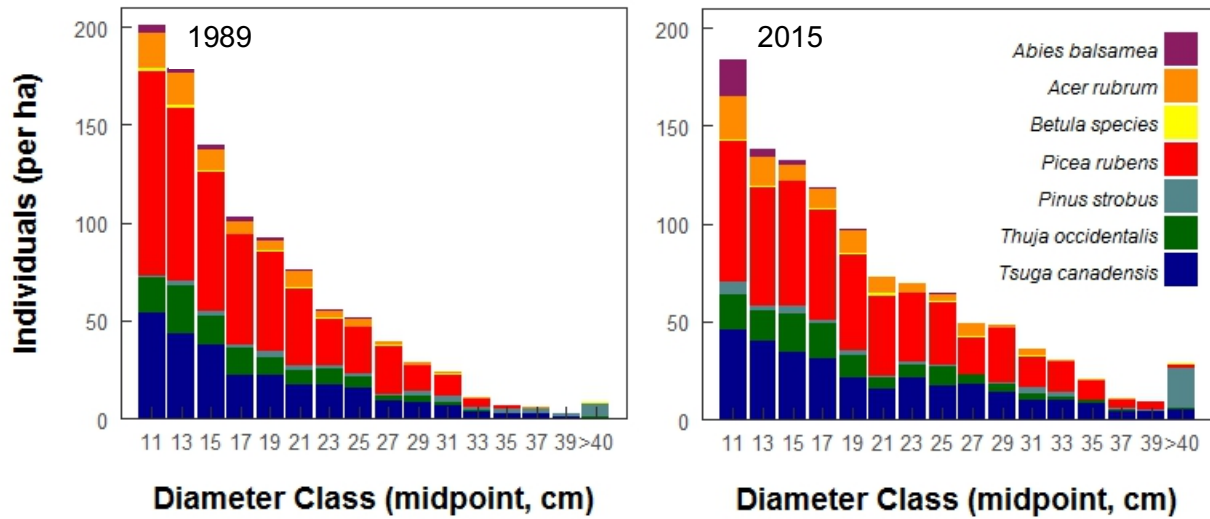
Figure 7: Diameter distribution of living trees in 1989 and 2015, by species.
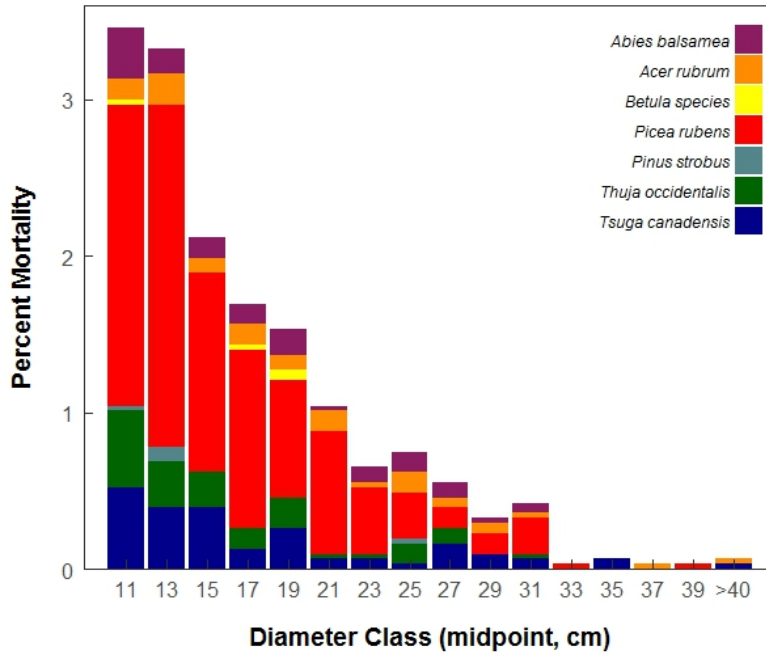
Figure 8: Diameter distribution of mortality. Demonstrating that smaller diameter classes had higher percent mortality in the NASA plot. No evidence for the theoretical U-shaped mortality pattern (high mortality rates for small and very large trees) was found, perhaps because this stand has not reached the developmental stage in which this trend becomes evident.
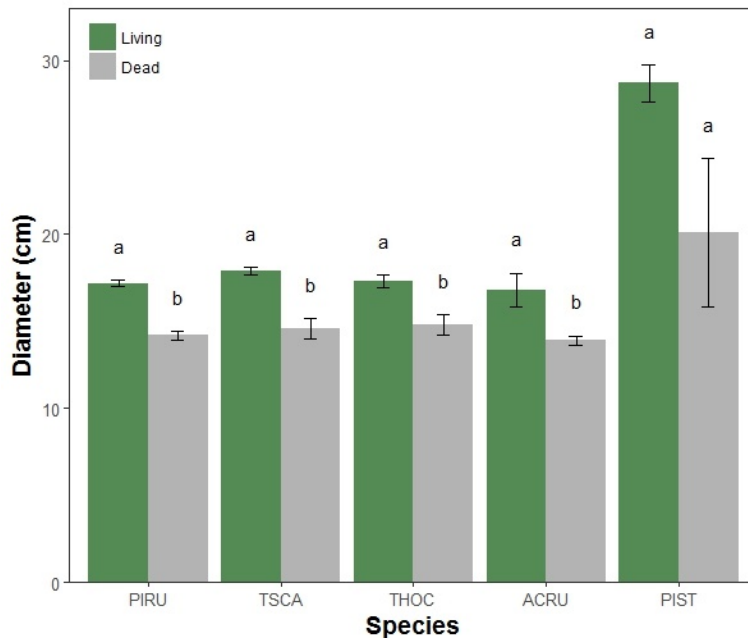
Figure 9: Diameter of all living and dead individuals by species. Mean diameter of trees that survived the study period (living in 2015) was larger than the mean diameter of trees that died for all species except white pine. Error bars represent standard errors. (PIRU: *Picea rubens*, TSCA: *Tsuga canadensis*, THOC: *Thuja occidentalis,* ACRU: *Acer rubrum*, PIST: *Pinus strobus*.)

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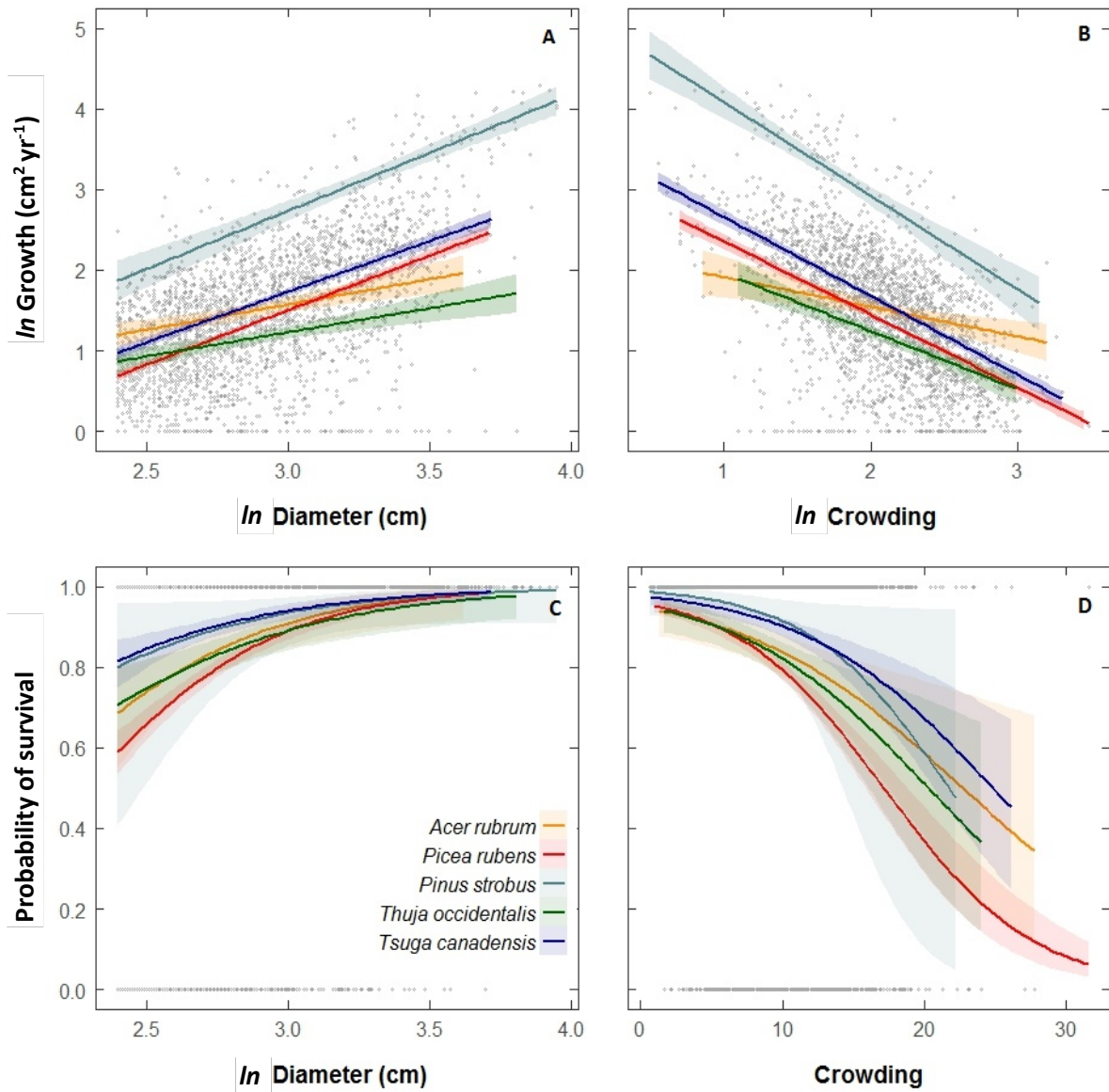
Figure 10: Relationship between growth (A, B) and survival (C, D) and the three most important explanatory variables: species, crowding (B, D) and initial diameter (A, C). Generally larger and less crowded individuals grow faster and are more likely survive, but not all species responses are identical.

3.2 Explanatory variables

All species showed a significant positive relationship between basal area growth and initial diameter (Figure 10A). As above, eastern white pine had the greatest growth across all diameters. Of the two most abundant species, eastern hemlock grew faster than red spruce across all diameters. Eastern hemlock was also more likely to survive than red spruce in smaller size classes (Figure 10C). With the exception of balsam fir, which experienced complete mortality, all species were more likely to survive with increasing initial diameter. Trees located toward the center of the plot, away from the wetter areas (Figure 11), were generally larger (Figure 11), which corresponded with greater growth rates toward the center of the plot (Figure 11). After species, tree crowding was the most important explanatory variable of growth (Table 3) and mortality (Table 4). Tree crowding had a significant negative effect on both growth and survival (Figure 10B&D). Again, eastern white pine had the greatest basal area growth across all levels of crowding. Eastern hemlock outgrew red spruce across all levels of crowding and was the species most likely to survive at high levels of crowding. Crowding intensity varied spatially across the plot, with areas of very high and very low intensity (Figure 11).

Crowding from saplings did not explain any additional variability in growth (Table 3), but was significantly positively related to survival (Table 4). Surprisingly, this finding suggests that focal trees with more sapling crowding in their neighborhood were more likely to survive. Generally, sapling crowding was relatively evenly distributed across the plot, except for the northeast corner where it was very intense (Figure 11).

Canopy class explained significant variability in both growth and mortality (Table 3, Table 4). Growth rates increased with increasing canopy class, from 2.3 (sd = 2.4) cm^2 yr^{-1} for suppressed trees to 7.4 (sd = 9.0) cm^2 yr^{-1} for dominant trees.

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Table 3: Models of growth (basal area increment, cm^2 yr^{-1}). Models were developed by sequentially adding explanatory variables compared using Akaike information criterion (AIC). Δ AIC shows differences in model performance as compared to top model (model with lowest AIC, bold). Model predictive power estimated with R^2. (CI: crowding index, N stumps: number of cut stumps within a neighborhood, β: estimated coefficient, se: standard error; β and se provided for continuous variables only.)

Growth Models	k	β (se)	AIC	Δ AIC	R^2
Species	1		5434	1178	0.23
+ Crowding (CI)*	2	-0.9 (0.0)	4537	281	0.46
+ Diameter*	3	0.6 (0.1)	4384	128	0.49
+ Soil Moisture*	4	-0.1 (0.0)	4350	94	0.50
+ Canopy Class*	5		4272	16	0.51
+ Intraspecific CI*	**6**	**-0.3 (0.1)**	**4256**	**-**	**0.52**
+ Sapling CI	7	0.0 (0.0)	4256	0	0.52
+ N Stumps	8	0.0 (0.0)	4256	0	0.52

*significant explanatory variables (p-value < 0.01)

Table 4: Logistic regression models of survival. Models were developed by sequentially adding explanatory variables compared using Akaike information criterion (AIC). Δ AIC shows differences in model performance as compared to top model (model with lowest AIC, bold). Model predictive power estimated with area under the receiver operating curve (AUC). (CI: crowding index, N stumps: number of cut stumps within a neighborhood β: estimated coefficient, se: standard error; β and se provided for continuous variables only.)

Survival Models	k	β (se)	AIC	Δ AIC	AUC
Species	1		2691	510	0.63
+ Crowding (CI)*	2	-1.8 (0.1)	2489	308	0.75
+ Diameter*	3	1.3 (0.3)	2301	120	0.76
+ Sapling CI*	4	0.7 (0.1)	2275	94	0.76
+ Canopy Class*	**5**		**2181**	**-**	**0.78**
+ Soil Moisture	6	-0.1 (0.1)	2182	1	0.78
+ Intraspecific CI	7	-0.4 (0.3)	2183	2	0.78
+ N Stumps	8	0.2 (0.1)	2182	1	0.79

*significant explanatory variables (p-value < 0.01)
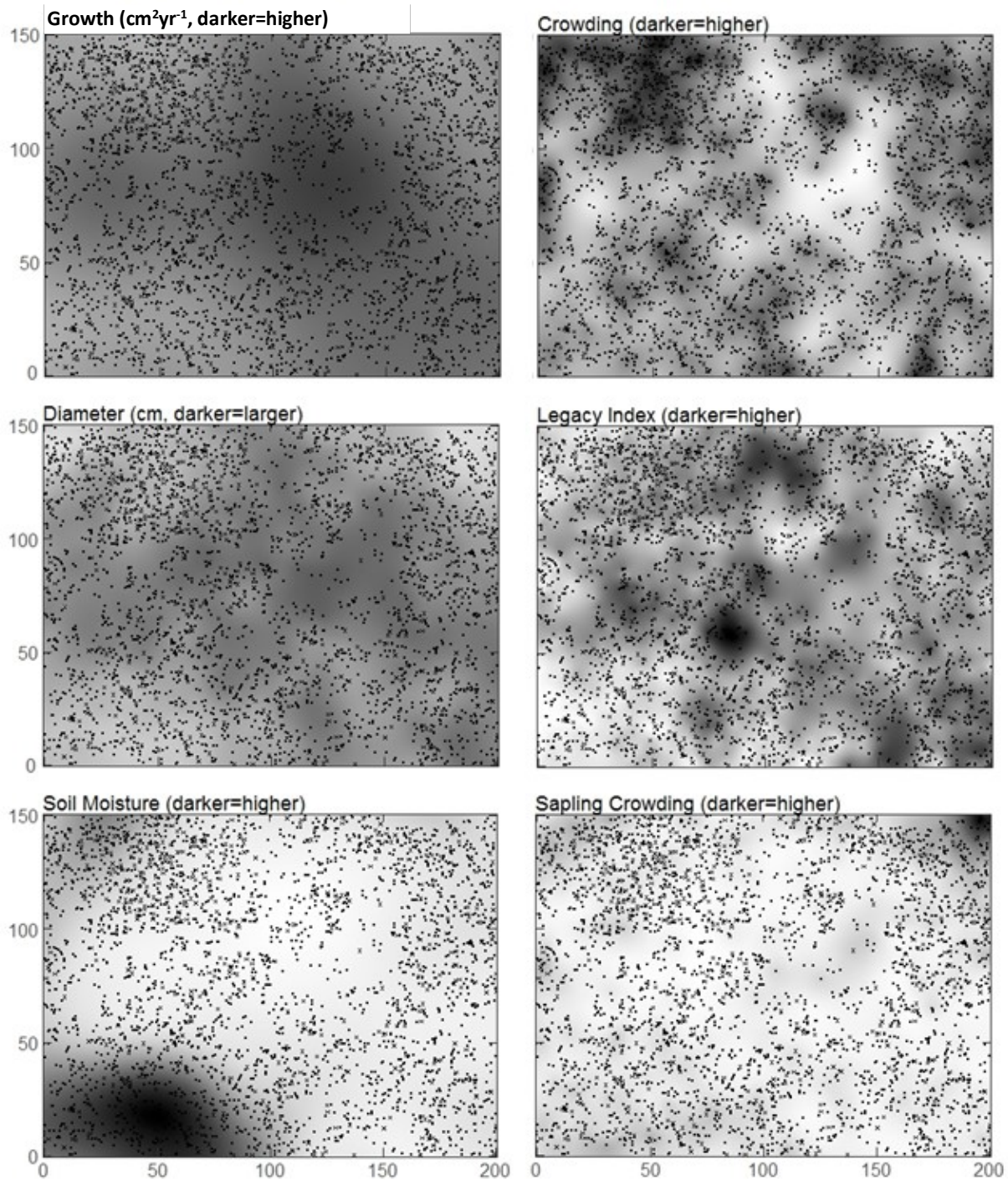
Figure 11: Interpolation of NASA plot variables. Kriged images provide a visual assessment of the strength of the relationships between growth and diameter, soil moisture, crowding, number of cut stumps in 10-m neighborhood, and sapling crowding on the NASA plot in Howland Research Forest. Dots indicate location of trees ≥ 10 cm diameter.

In most cases, tree growth was negatively related to the proportion of crowding due to conspecific neighbors (Table 3), meaning that focal tree growth improved in neighborhoods comprised of species different from that of the focal. However, this general finding did not hold for all species. Eastern hemlock grew better in neighborhoods comprised of hemlock, and northern white-cedar showed no significant response related to neighborhood species composition (Figure 12). In contrast to growth, neighborhood species composition was not significantly correlated with survival.
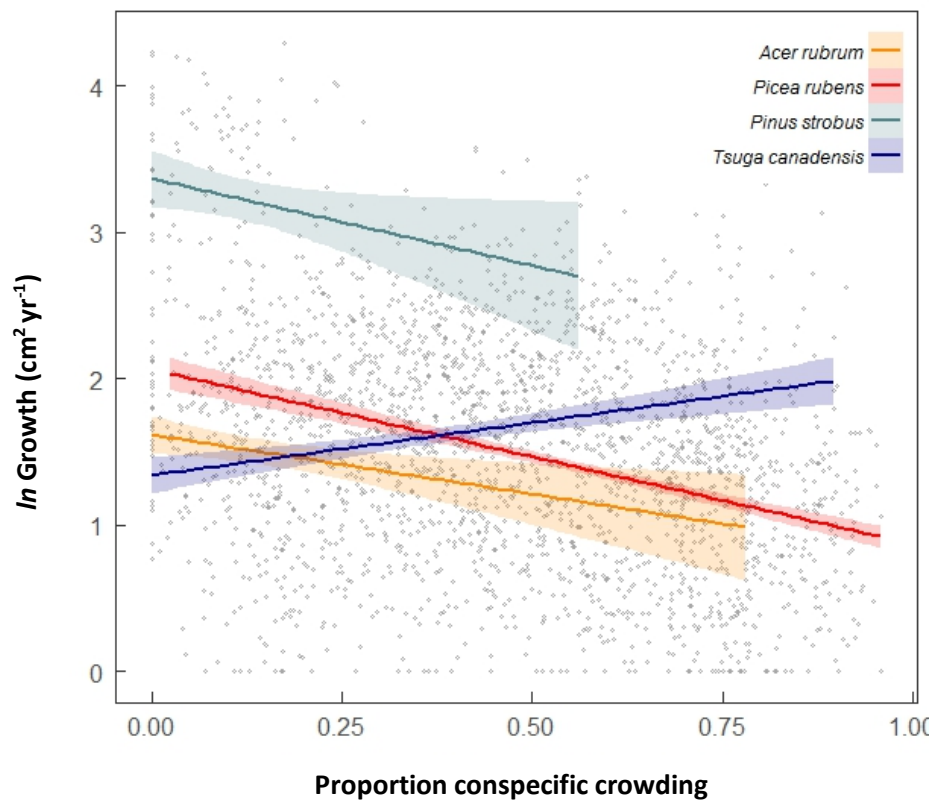
Figure 12: Relationship between growth and the proportion of an individual's crowding neighborhood associated with conspecific neighbors. Growth is expressed as basal area increment (BAI) and crowding is estimated with the Heygi index. Most species grew best with more heterospecific neighbors, while hemlock grew best with more conspecific neighbors.

The number of cut stumps in a 10-m neighborhood around each focal tree ranged from 0 to 21. We found no significant relationship between growth or survival and the number of stumps (Table 4). However, the interaction between initial diameter and number of stumps was significant for both growth (p-value < 0.01) and mortality (p-value < 0.05) (Figure 13). Adding the number of stumps and the stumps × diameter interaction resulted in a large (>10 unit) decrease in AIC in the growth model but not the survival model (Table 5).

Tree growth was significantly negatively related to soil moisture (Table 3). Mortality was not related to soil moisture alone; however, adding the soil moisture × crowding interaction improved model performance for both growth and mortality (Table 5). Soil moisture interacts with crowding such that at high levels of crowding, growth and survival are positively related to soil moisture, but at low levels of crowding, growth and survival are negatively related to soil moisture (Figure 13). Interpolated surfaces of growth and soil moisture clearly show the trend of lower growth where soil moisture is higher (Figure 11).

Table 5: Significant biologically relevant interactions. Interactions demonstrate that the relationship between an individual's successes (growth and survival) and soil moisture varies according to crowding environments, and the relationship between an individual's success and the number of cut stumps in its neighborhood (indicating past disturbance) varies with individual size. Models compared using Akaike information criterion (AIC). (CI: crowding index, AUC: area under curve)

Model	Growth				Survival			
	AIC	ΔAIC	p-value	R^2	AIC	ΔAIC	p-value	AUC
Full Model	4256	-	-	0.52	2181	-	-	0.78
CI × Soil Moisture	4114	-142	<0.01	0.54	2173	-8	<0.01	0.79
Diameter × N Stumps	4209	-47	<0.01	0.52	2179	-2	0.04	0.78
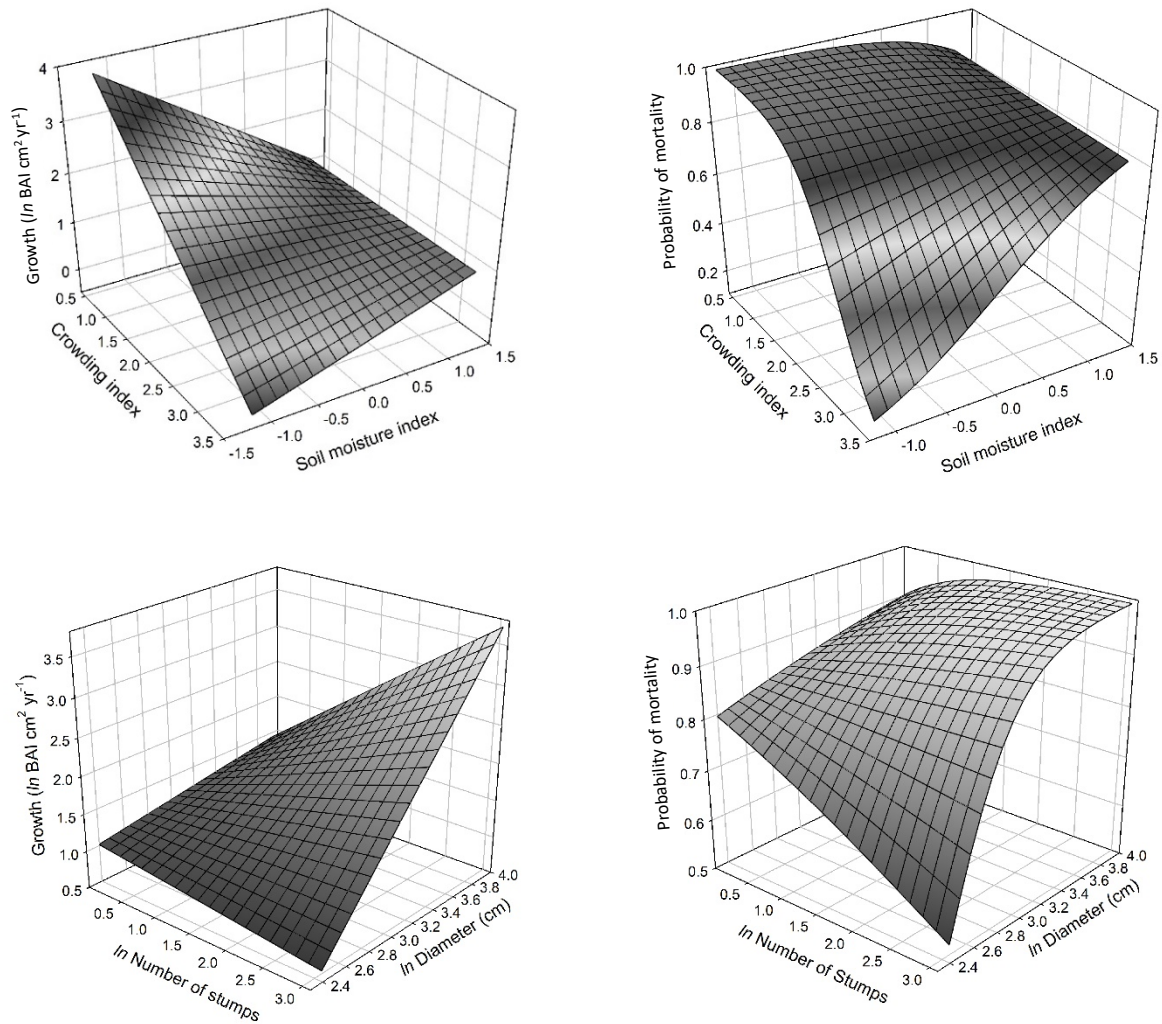
Figure 13: Depiction of biologically relevant interactions in the NASA plot. Where neighborhood crowding (based on Heygi index) is low, high soil moisture is associated with decreased individual growth and survival; however, where crowding is high, low soil moisture is associated with decreased individual growth and survival. The growth and survival of small trees decrease with increasing number of neighborhood cut stumps, while the growth and survival of large trees increases with the number of cut stumps. An individual's size may reflect its past and/or present ability to respond to the increase in available resources following harvest.

3.3 Comparing growth and survival models

The top three explanatory variables for growth and survival models were identical: species followed be crowding, then size. Canopy class was also in the top models of growth and survival and was the fifth ranked variable in both. Soil moisture and intraspecific neighborhood crowding were both in the top model of growth but not survival, while sapling crowding was in the top model of survival but not growth.

3.4 Neighbor species identity effect

Our analyses of species-specific interactions revealed striking differences among species. As a focal tree, red spruce was most effected by the identity of its neighbors: its growth was significantly inhibited by red spruce and white pine neighbors but enhanced by northern white-cedar and red maple neighbors (Table 6). Hemlock neighbors had no additional effect (i.e., effect beyond what would be expected if all neighbor species competed equivalently) on red spruce. Like red spruce, hemlock and white pine growth was both additionally inhibited by conspecific neighbors and enhanced by red maple neighbors. White pine growth was also additionally enhanced by hemlock neighbors. Northern white-cedar and red maple were less affected by the identity of their neighbors; the only significant relationship was the additional inhibition of northern white-cedar growth by white pine neighbors. These results can be viewed both from the perspective of the responsiveness of focal tree species to the identity of their neighbors, as stated above, and from the influence of each species as neighbors. From this latter perspective, white pine generally had the most additional negative effect as a neighbor, while red maple most often had an additional competitive reduction or complementary effect as a neighbor.

Table 6: Added influence of neighbor species identity on growth of focal tree species. (+) indicates the focal species grew better than expected when more crowded by the stated neighbor species, while (–) indicates the focal species grew less than expected when more crowded by the stated neighbor species.

Focal Species	Neighbor Species				
	P. rubens	*T. canadensis*	*P. strobus*	*A. rubrum*	*T. occidentalis*
Picea rubens	-		-	+	+
Tsuga canadensis		-		+	
Pinus strobus		+	-	+	
Acer rubrum					
Thuja occidentalis			-		

4. DISCUSSION

4.1 Effects of species, size and neighborhood crowding

This study capitalized on a large, fully-mapped permanent plot to assess and compare the factors driving growth and survival in an uneven-aged, mixed species forest. As in previous studies, we found that the most important factors for predicting both growth and survival were tree species, neighborhood crowding and tree size (Canham et al. 2004, Zhao et al. 2006, Coomes and Allen 2007a, Das et al. 2011, Gómez-Aparicio et al. 2011, Das 2012).

We found large differences in growth and survival by species, likely associated with species' autecologies in relation to continued stand development. For red spruce and hemlock, the two most abundant species, we found that in all size classes and crowding environments hemlock grew faster than red spruce. This finding may be explained by the slightly more shade-tolerant advantage of hemlock (Baker 1949), particularly when both species are growing among canopy-dominant white pines, as in this study. These differences in shade tolerance would also explain our finding that in high crowding environments, where there may be more competition for light, hemlock was much more likely to survive than red spruce. Due to its rapid growth and lower shade tolerance (relative to red spruce and hemlock), white pine often attains canopy dominant or emergent positions in these mixed species stands (Fajvan and Seymour 1993, Abrams and Orwig 1996), as we found in our study. The extremely high mortality rate of balsam fir may be attributed to balsam fir's much shorter longevity as compared to all co-occurring species (Hett and Loucks 1976, Seymour 1992), as well as the non-native balsam fir woolly adelgid (*Adelges piceae*) (Hain 1988). Given its expected longevity, had balsam fir become established following harvests of the 1890s or 1920s (see Methods), we would expect it to now be dropping out of the sta nd.

For all species, we found that larger trees grew faster and were more likely to survive, a finding well supported by previous studies (MacFarlane and Kobe 2006, Russo et al. 2007). Increasing growth of larger trees is likely associated with increased access to resources; for example, larger trees generally have a more prominent position in the canopy and greater leaf area and therefore have more access to light. Several previous studies of mature or old-growth forests report that very large or old trees may experience growth declines or high rates of mortality as a result of reduced efficiency, accumulated stress, or senescence (Larson and Franklin 2010, Holzwarth et al. 2013, Fraver et al. 2014). However, despite the presence of several larger (presumably older) trees, we did not find a decrease in growth or survival of the largest individuals, perhaps because this stand has not reached the advanced developmental stage in which such trends become evident.

We found that for all species, reduced growth and lower probability of survival were related to increased crowding. These findings are in agreement with abundant evidence that neighboring plants compete for growing space and resources including light, water and soil nutrients (Welden and Slauson 1986, Keddy 2001). Our findings support the ability of distance-dependent crowding indices to explain significant variability in growth and mortality. Although more complex crowding indices have been proposed (Stadt et al. 2007, Weiskittel et al. 2011), we chose the distance-dependent Hegyi index because of its simplicity and strong performance in numerous previous studies (Biging and Dobbertin 1992, Contreras et al. 2011, Fraver et al. 2014). Further, our intent was not to identify an ideal crowding index for these data, but rather to assess the importance of crowding relative to a set of other explanatory variables of growth and survival; the simplicity of the Hegyi index made it appropriate for this purpose. One persistent challenge in constructing spatially-explicit crowding indices is the selection of the neighborhood

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radius. By testing the goodness-of-fit for a series of models with increasing neighborhood radii, we demonstrated that radii greater than 10 m conferred little additional improvement in model fit, and that this finding was fairly consistent among species. However, we note that the ideal neighborhood radius may be a function of canopy radius and therefore may vary among systems (Lorimer 1983).

4.2 Additional effects

Though our research was limited to one plot, the large size, heterogeneity, and sampling intensity of the plot allowed us to answer a series of less frequently addressed and currently relevant questions to add to previous understanding of variability in growth and survival.

First, we assessed how crowding from understory saplings may affect overstory tree success, as few previous studies have quantified this effect with spatially explicit indices. Although we found no effect of sapling crowding on tree growth, we found that trees with greater sapling crowding were more likely to survive. This finding was contrary to our expectation that saplings would decrease overstory tree success due to competition for below-ground resources. Some understory removal studies have found limited benefits for the overstory (Kelty et al. 1987), while other studies have demonstrated that removal of the understory can increase soil moisture resulting in more favorable conditions for the overstory (Kelliher et al. 1986, Giuggiola et al. 2018). These findings suggests one possible explanation for the facilitative effects of saplings. In more mesic forests, such as the one under study here, saplings may draw down soil moisture *via* transpiration, thereby ameliorating the detrimental effects of saturated soils and thus increasing overstory tree success. However it is also possible that high sapling crowding is associated with some other beneficial factors we have not measured. Additional and

more-detailed studies of the understory are needed to better differentiate these effects, especially given the influence of changing water availability on tree mortality (Allen et al. 2010).

Second, we attempted to understand how species identity within a neighborhood affects focal tree growth and survival. The dynamics of mixed-species stands has recently gained interest given the growing recognition that stands with more mixed-species may provide structural diversity and elevated productivity (Paquette and Messier 2011, Zhang et al. 2012, Forrester and Bauhus 2016, Liang et al. 2016) and confer resistance and resilience to climate fluctuations (Thompson et al. 2009, D'Amato et al. 2011, Oliver et al. 2015, Cantarello et al. 2017). Our findings suggest that the species identity within a neighborhood is not correlated with focal tree survival. However, species identity did affect growth – for most species, focal trees with heterospecific neighbors grew better than those with conspecific neighbors. This finding may be attributed to complementary functional traits and resources requirements, such that potentially competing species with slightly different requirements, heterospecific individuals, can better share resources (Uriarte et al. 2004b, Canham et al. 2006, Ramage et al. 2017). However, this finding did not hold true for eastern hemlock, which grew better in neighborhoods with more hemlock. As an explanation, we found that increases in hemlock neighbors was associated with decreased crowding; therefore, a neighborhood with abundant hemlock would tend to be less crowded and presumably favor growth. Hemlock may be associated with less crowded environments because of the soil moisture conditions in those sites as hemlock grows most successfully on moist but well-drained sites (Rogers 1978), a requirement that might exclude hemlock from the poorly drained, lower elevation areas here that tended to have higher crowding.

Third, we assessed the extent to which soil moisture affected individual tree success over the study period. In general water is less limiting in northeastern U.S. forests than in other parts of the world, due to abundant precipitation that is evenly distributed throughout the year. We found that tree growth was inhibited by abundant soil moisture in the wettest areas of our study area. The lack of oxygen in water-saturated forests restricts root and microbial respiration, thereby limiting root functioning and microbial organic matter decomposition (Ernst 1990, Davidson et al. 1998). By addressing the interacting effect of soil moisture and crowding on both growth and survival, we found that even within this three hectares of contiguous forest, tree success is negatively correlated with both excess and insufficient moisture. That is, when crowding is low and soil moisture is elevated, tree growth and survival may be inhibited. However, when crowding (and potentially competition for water) is high, tree growth and survival may be inhibited by a lack of soil moisture. Interestingly, this interaction suggests inherent resilience in this system to uncertain environmental change (Trenberth 2011), as some individuals would be more successful in drier conditions while others would be more successful in wetter conditions.

Finally, given evidence of partial harvesting in the distant past (i.e., presence of scattered cut stumps), we tested if the legacy of such harvests that occurred over 100 years ago (harvests in the 1890s and 1920s) was still evident as persistent increased tree growth and survival. The short-term growth increases following gap creation are quite well studied (Watt 1947, Brokaw 1982, Runkle 1982); however, the long-term responses have rarely been addressed (but see Hytteborn and Verwijst 2014). Small canopy gaps, such as those likely created by the past partial harvests at our study site, affect forest structure and species composition and are therefore important drivers of forest stand dynamics in this forest type (Fraver and White 2005, Worrall et

al. 2005). By testing the interacting effects of tree size and number of stumps on growth and survival, we found that larger trees were more successful with more cut stumps in their neighborhood. In contrast, smaller trees were less successful with more cut stumps in their neighborhood. The favorable association between cut stumps and success for some trees, but not all, suggests that presently, larger trees had superior ability to take advantage of increased resource availability following gap creation (Uriarte et al. 2004a). The variability in response to gap formation may be associated with tree size at the time of the harvest. That is, trees that were larger than their neighbors immediately following harvest were apparently better able to take advantage of newly available resources and remain larger and more successful at present, when compared to smaller trees less able to take advantage of increased resource availability. The persistent elevated growth and survival (1989 to present) of trees able to take advantage of canopy gaps – even ca. 100 years following gap creation – highlights a remarkable legacy of past disturbance on current forest dynamics, and the interaction of size and number of cut stumps suggests this legacy is context dependent.

4.3 Neighbor species identity

In mixed-species forests, the numerous pair-wise combinations of focal tree species and neighbor species makes it difficult to comprehensively address the extent to which multiple species interact. This is further confounded by the dual roles each species may play in these interactions. That is, species can vary both in their response to the identity of neighbor species and in the effect they have as neighbors on a given focal tree species (Goldberg and Landa 1991). By modeling the growth of each species individually, we were able to determine how much additional variability neighbor identity explained beyond overall crowding alone (i.e., ignoring neighbor identity). By doing so, we are able to answer the question, if crowding were

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held constant, would species A grow better or worse with more abundant species B in its neighborhood?

Our findings support our intraspecific crowding analysis (above) in that three of the five species (red spruce, hemlock and white pine) were more negatively affected by crowding from conspecific neighbors than would be expected with crowding alone. Conspecific neighbors surrounding a given focal tree may be more inhibitory to focal tree growth than are heterospecific neighbors, simply because heterospecifics likely differ more in their resource requirements (Uriarte et al. 2004b, Ramage et al. 2017). This beneficial interaction between heterospecific neighbors has been referred to as a complementary or a competitive reduction interaction, because it is not necessarily the result of facilitation between individuals, rather the result of less competition than would be expected if all species competed equivalently (Forrester and Bauhus 2016). White pine had the greatest inhibitory effect, which is likely associated with its tendency, on this plot and in this region, to occupy dominant and often emergent canopy positions, making it a strong competitor for light (Fajvan and Seymour 1993). Red maple neighbors commonly had a complementary effect on focal tree growth: red spruce, white pine and hemlock trees growing in equal crowding environments grew better if more of their neighbors were red maple. This finding could possibly be explained by the observed tendency for red maple to occur in small clumps in this plot. If neighbors are clumped in one portion of a neighborhood, available growing space for the focal trees may not be as severely restricted as when neighbors are dispersed throughout the neighborhood. The inclusion of a metric describing arrangement of competitors within a neighborhood has been shown to improve models for focal tree growth (Fraver et al. 2014). We note that the lack of a significant neighbor-identity effect between two species should not be taken as evidence against competition between those two

species; instead, it simply means that species identity does not add additional explanatory ability beyond what we would expect if neighbor species were equivalent competitors. Species-by-species analyses such as these represent a rather simple approach for exploring the potentially complex interactions among species. Our findings suggest more work is needed to better understand how competitive interactions play out within mixed-species forests.

4.4 Conclusions

The inherent heterogeneity of uneven-aged, mixed-species forests makes them well suited to meet a variety of environmental and societal expectations of forests ecosystems; however, this heterogeneity also presents analytical and interpretive challenges. Our findings demonstrate the variety of ways in which individuals of various species and sizes may respond to their surroundings. We found that the most influential factors driving individual tree growth and survival (species, crowding, and size) were the same, yet additional factors, including soil moisture, sapling crowding and neighbor identity, suggest dissimilarities. This finding warns against conflating growth and survival (as well as recruitment) as metrics of success. Understanding the factors affecting dynamic and complex processes, such as growth and mortality, are necessary to successfully manage uneven-aged, mixed-species forest systems for continued resilience and productivity.

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Erin Fien was born in Webster, NY and grew up in the maple, beech, basswood forests of upstate New York. She graduated from Webster Thomas High school in 2011 and went on to earn a Bachelors of Science from the State University of New York at Geneseo, graduating magna cum laude in 2015. Erin majored in Biology with a minor in Environmental Studies and was inducted into the National Tri Beta Biological honor society. While at Geneseo, Erin worked in the lab of Dr. Ray Spear using paleoecological techniques to compare past and present forests of western New York and became increasingly interested in forest and landscape ecology.

While attending Geneseo, Erin worked for the Wisconsin Farmers Union as an assistant director of youth programs and community outreach and developed a passion for science education and community science projects. After graduating Erin worked for the US Forest Service at the Oconto River Seed orchard in northern Wisconsin and learned to appreciate the species of northern forests.

Erin's interests and experiences lead her to pursue forest ecology research advised by Dr. Shawn Fraver. Erin is a candidate for the Master of Science degree in Ecology and Environmental Science from the University of Maine in August 2018.