



Drivers of individual tree growth and mortality in an uneven-aged, mixed-species conifer forest



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ABSTRACT

Individual tree growth and mortality drive forest stand dynamics and are universally important metrics of tree success. Studying 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. The goal of this study was to determine the relative importance of individual tree attributes (i.e., species, size, neighborhood crowding, crown position) and environmental characteristics (i.e., soil moisture) in driving tree growth and survival in an uneven-aged, mixed species forest. In particular we tested 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, USA, allowed us to address additional questions regarding the influence of sapling crowding, neighbor species identity, and legacies of 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). As expected, species, neighborhood crowding, and tree diameter were top predictors of growth and survival. Specifically, growth and survival decreased with greater crowding, and increased with larger diameters. We also found that the identity of neighbors influenced focal tree growth: growth generally 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 hemlock neighborhoods, and northern white-cedar showed no response related to neighbor identities. In contrast to growth, neighborhood identity was not related to survival. Crowding from saplings did not explain any additional variability in growth; however, unexpectedly, individuals with greater sapling crowding were more likely to survive. For both growth and survival, we found an interaction between crowding and soil moisture, suggesting that within a single stand, individual success can be limited by both excess and insufficient moisture. We found no relationship between neighborhood cut stumps (legacy of past disturbance) and recent growth or survival. These results highlight the many variables driving growth and survival in uneven-aged, mixed-species forests. The top predictors for growth were identical to those for survival; however, other predictors differed in their relative importance. Given the recent emphasis on promoting uneven-aged, mixed-species forests, we suggest that studies addressing a full range of predictors of individual tree success are necessary to better manage and maintain these complex systems.

1. Introduction

Variability in tree growth and mortality drives changes in the composition, structure, and productivity of forests stands as they develop through time (Oliver, 1981; Franklin et al., 2002). In natural forests, these rates vary considerably within and among species, as well as spatially within a stand. In uneven-aged, mixed-species forests, this variability is especially pronounced, and it 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. Factors may include individual tree

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characteristics such as species, size, crowding, or canopy position, as well as stand-level characteristics such as stand density, soil properties, or past disturbance. Variability in individual success across species, sizes, and crowding has been well studied for many years (Biging & Dobbertin, 1992; Canham et al., 2004; Coomes & Allen, 2007a; Castagneri et al., 2008). More recent work has focused on the added influence of climate variability (Rollinson et al., 2015; Copenhagen-Parry and Cannon, 2016), the distinction between above- and below-ground competitive interactions (Canham et al., 2004; Coates et al., 2009), the influence of within-neighborhood spatial patterning (Fraver et al., 2014), and the influence of stand cohort structure (Aakala et al., 2013). However, studies addressing a full range of factors affecting individual tree success are relatively uncommon because they require long-term and large-scale observations to capture the spatial and temporal heterogeneity of forest stands. As a result, the relative importance of these factors is not fully understood.

The range of tree species in mixed-species, uneven-aged forests raises questions regarding the importance of neighborhood species identity on growth rates and mortality risk. Several previous studies in mixed-species forests report that neighbors of different species can exert varying crowding effects on the focal tree (Goldberg & Landa, 1991; Uriarte et al., 2004; Vitali et al., 2018). This issue has recently gained attention given the recognition that mixed-species assemblages can confer resistance and resilience to climate fluctuations (D'Amato et al., 2011; Oliver et al., 2015; Cantarello et al., 2017), as well as increases in productivity (Fichtner et al., 2018).

Similarly, the broad range of tree sizes in such forests presents a particular challenge for identifying factors most strongly influencing growth and mortality. The detrimental influence of overstory trees on sapling growth and survival is well documented (Lorimer et al., 2001; Ramage et al., 2017); however, the potential influence of saplings on overstory trees has not been well explored, despite suggestions that the effect of below-ground sapling interactions 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 the legacy of past partial disturbances. Non-stand-replacing disturbances create canopy gaps that increase resource availability and alter the growth of surviving individuals (Whitmore, 1989; Runkle, 1998). Most studies of canopy disturbances are 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 of canopy disturbance 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 lingering effects of partial 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 environmental conditions that favor insects and pathogens (Worrall et al., 2005; Gray et al., 2012; Das et al., 2016). Despite the uncertain 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 broader range of both density-independent and density-dependent mortality agents (Larson et al., 2015). Given projections of future environmental change, novel disturbance regimes and globally increasing tree mortality, 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; Allen et al., 2010).

Our primary objective was to identify the factors most strongly influencing tree growth and mortality rates in a red spruce (*Picea rubens* Sarg.) – eastern hemlock (*Tsuga canadensis* (L.) Carrière) forest of the Acadian Forest region of northeastern North America. Specifically, we tested the relative influence of tree species, tree size, neighborhood crowding, within-neighborhood species composition, and soil moisture on individual tree growth and mortality 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 three-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 explore additional questions 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 located in central Maine, USA (45°12'N, 68°45'W), where average annual precipitation is 1142 mm, and the average temperature is 6.2°C (Daly et al., 2008). Data were collected from a three-hectare (150 × 200 m) permanent plot established in the Howland Forest in 1989 by the Laboratory for Terrestrial Physics at NASA's Goddard Space Flight Center (Weishampel et al., 1994); we refer to this as the NASA plot. The canopy is comprised mainly of red spruce (*Picea rubens* Sarg.) and eastern hemlock (*Tsuga canadensis* (L.) Carrière) with scattered emergent white pine (*Pinus strobus* L.) (Table 1). Patches of advance regeneration of red spruce, eastern hemlock and balsam fir (*Abies balsamea* (L.) Mill.) are well developed in the understory.

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

Table 1

Descriptive statistics for the three-ha Howland Forest NASA plot in central Maine, US, 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)
<i>Picea rubens</i>	511	13.3	17.2 (5.8)	8.4 (4.0)
<i>Tsuga canadensis</i>	265	7.6	17.9 (6.6)	8.1 (4.2)
<i>Thuja occidentalis</i>	111	2.9	17.3 (5.9)	8.2 (3.5)
<i>Acer rubrum</i>	77	1.9	16.8 (5.9)	8.8 (4.2)
<i>Pinus strobus</i>	36	2.7	28.7 (10.8)	5.5 (3.3)
<i>Abies balsamea</i>	14	0.3	14.7 (3.7)	9.7 (4.2)
<i>Betula papyrifera</i>	5	0.1	15.1 (4.4)	11.0 (4.0)
<i>Betula alleghaniensis</i>	4	0.2	24.9 (13.5)	6.6 (2.5)
Total	1023	29.0	17.8 (6.6)	8.3 (4.0)

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 well drained uplands to poorly drained forested wetlands. At a smaller scale, hummock and hollow microtopography results in more localized variability in soil moisture.

2.2. Field procedures

In 1989 when the NASA plot was established, all trees ≥ 3 cm diameter at breast height (1.37 m, DBH), approximately 7800 individuals living and standing dead, were mapped and tagged with a unique identifier (Figs. A.1 & A.2). Species, DBH, total height, and canopy position were recorded for all individuals. Canopy position was visually classified into seven categories; however, those classes were collapsed to match the more conventional four-class system of dominant, codominant, intermediate, and suppressed positions in this analysis (Smith et al., 1997).

We re-inventoried all trees (stems ≥ 10 cm DBH) in 2015 and saplings (stems ≥ 3 cm and < 10 cm DBH) in 2017 to assess growth and mortality (Fig. A.3). 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. 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 five 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.

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 & Allen, 2007b). In the current study, diagnostics of several 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 & Anderson, 2002), 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 individual's initial size in 1989.

The detailed mapping of the NASA plot allowed us to use spatially explicit indices to estimate the crowding intensity each tree experienced 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 the 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, and

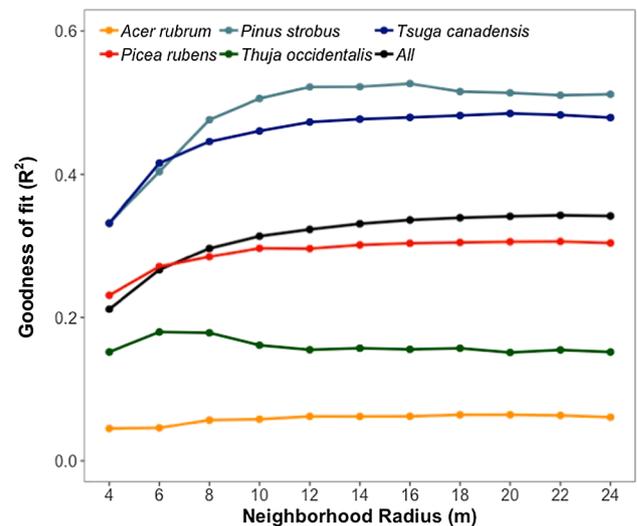


Fig. 1. Goodness of fit (R^2) relating basal area growth and the Hegyi crowding index (CI) by species across a range of neighborhood radii (Lorimer, 1983), demonstrating the marginal benefit of increasing the radius beyond ca. 10 m.

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 performance regarding tree growth. DBH has been used commonly in past studies of crowding (Lorimer, 1983; Canham et al., 2004; Coomes & 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 radii ranging from 4 to 24 m in 2-m 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 (Fig. 1). 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.

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. 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. Given the lack of visual evidence of major disturbances or discrete mortality events during the study period, we believe the midpoint is the best approximation available, considering the lack of more frequent intermediate inventories. The crowding effect of trees (i.e., individuals ≥ 10 cm) was not down-weighted as such because preliminary analysis suggested it did not improve model performance, perhaps because, compared to saplings, far fewer 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 & Landa, 1991; Uriarte et al., 2004; 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 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 the crowding index of the focal tree as shown above. As such, focal trees with larger P_c values were growing with a greater proportion of conspecific neighbors; a P_c equal to 1 means all neighbors were conspecific. Because this 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, as stumps represent the removal of a neighboring individual and the formation of a canopy gap. Diagnostics of preliminary candidate models indicated that simply 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.

Lastly, we developed a soil moisture index for each tree location based on moisture measurements taken at grid corners from a 25-m grid covering the entire plot, including borders, for a total of 63 locations. 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 of the analysis, was done using a simple kriging method in ArcGIS (v. 10.4.1, ESRI, Redlands, CA, USA). We believe these index values to be relatively stable over the study period, given their strong correlation with a LiDAR derived digital elevation model (correlation coefficient = -0.70). Further, in preliminary analyses, elevation was used as a surrogate for moisture at each tree location, but we found that our interpolated moisture indices improved model performance, relative to LiDAR data.

2.4. Growth and survival model analysis

We chose annual basal area increment (BAI, $\text{cm}^2 \text{yr}^{-1}$) 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 between 1989 and 2015 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.

Trees (stems ≥ 10 cm DBH) that died during the study period were not included in growth models, such that we modeled survival of 3043 trees and growth of 2552 trees across six species. Birch species (*Betula alleghaniensis* Britton and *B. papyrifera* Marshall) 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 (response variable) and binary logistic regression for survival (response variable). A modified hierarchical (or sequential) modeling approach was followed due to strong collinearity among explanatory variables (correlation 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 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 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 using the 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.

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. Plots of residuals *versus* explanatory variables from the regression models constructed as above showed no clear trends that would require the inclusion of interactions among explanatory variables (Zuur et al., 2009). Nevertheless, to explore the unexpected result ultimately found regarding soil moisture, we chose to analyze the interaction between crowding and soil moisture. Indeed, 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).

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 & Anderson, 2002) to determine which models were best supported by the data. ΔAIC was calculated in reference to the model with the lowest AIC (top model); models with a ΔAIC greater than 10 were considered significantly different (Weiskittel

et al., 2011). P values < 0.05 were deemed statistically significant. Finally, given the limitation of studying one plot and a relatively large sample size, bootstrapping regression analysis was conducted to better assess the uncertainty around estimated model coefficients and to address the potential effects of highly influential trees (Fox and Weisberg, 2017). Bootstrapping was conducted in the R software package 'car' to estimate model coefficients from 2000 bootstrap samples and construct 95% confidence intervals using the bootstrap percentile interval approach (Fox and Weisberg, 2011). All analyses were conducted using R statistical software (R Core Team 2016).

3. Results

3.1. Plot overview

Total plot-level basal area growth equaled $0.29 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ for the study period. Mean annual tree growth rates differed markedly among species, ranging from $2.9 \text{ cm}^2 \text{ yr}^{-1}$ for northern white-cedar (*Thuja occidentalis* L.) to $30.0 \text{ cm}^2 \text{ yr}^{-1}$ for white pine (Table A.1). In fact, despite representing only 9.4% of the total plot basal area, white pine accounted for 22.8% of total plot basal area growth during the study period (Table A.1). Despite the presence of larger trees, the diameter distribution was skewed towards smaller size classes, particularly in 1989 (Fig. A.4).

Of the original 3043 individuals ≥ 10 cm DBH, 490 (16.1%) died during the study period (Fig. A.3), equivalent to an approximate loss of $0.11 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$ 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. 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 (Fig. A.5). For all species except white pine, the mean diameter of trees that died was significantly smaller than that of trees that survived (t -tests, P values < 0.05 , Fig. A.6).

3.2. Growth and survival models

All species showed a significant positive relationship between initial diameter and basal area growth (Fig. 2A). 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 (Fig. 2C). With the exception of balsam fir, which experienced 100% mortality, all species were more likely to survive with increasing initial diameter. After species, tree crowding accounted for the most variance in growth and mortality (Table 2). Tree crowding had a significant negative effect on both growth and survival (Fig. 2B & 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 from saplings did not explain any additional variability in growth but was significantly positively related to survival (Table 2). Surprisingly, this finding suggests that focal trees with more sapling crowding in their neighborhood were more likely to survive.

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

Generally, tree growth was negatively related to the proportion of crowding due to conspecific neighbors (Table 2), 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 (Fig. 3). In contrast to growth, neighborhood species composition was not significantly related to survival.

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 2). Tree growth was significantly negatively related to soil moisture (Table 2). Mortality was not related to soil moisture alone; however, adding the soil moisture \times crowding interaction improved model performance for both growth and mortality (Table 3). The sign of this interaction coefficient is positive. Soil moisture interacted with crowding such that at high levels of crowding, growth and survival were positively related to soil moisture, but at low levels of crowding, growth and survival were negatively related to soil moisture (Fig. 4).

All explanatory variables whose bootstrapped β intervals did not contain zero were also indicated as significant by regression analysis (β term equal to zero suggests no relationship between growth or survival and the explanatory variable) (Table 2).

3.3. Comparing growth and survival models

The top three explanatory variables for growth and survival models were identical: species followed by crowding, and 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 (Table 2).

4. Discussion

4.1. Effects of species, size and neighborhood crowding

Our study capitalized on a large, fully-mapped permanent plot to identify the factors driving individual tree growth and survival in an uneven-aged, mixed species forest. The limitation of having only one large plot was addressed via bootstrapping, which allowed us to calculate error in the estimate of model coefficients and thus validate conclusions drawn from model results. We acknowledge that our study would have benefitted from complete, intermediate inventories (between 1989 and 2017); however, these data were not available. Nevertheless, 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; Castagneri et al., 2008; Gómez-Aparicio et al., 2011; Das, 2012).

We found large differences in growth and survival among 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 higher shade tolerance 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 & Seymour, 1993), as we found in our study. The complete mortality rate of balsam fir (100%) may be attributed to its much shorter longevity as compared to co-occurring species (Hett and Loucks, 1976; Seymour, 1992), as well as the non-native balsam fir woolly adelgid (*Adelges piceae* (Ratzeburg)) (Hain, 1988). That is, had balsam fir become established following harvests of the 1890s or 1920s (see Methods), we would expect it to now be

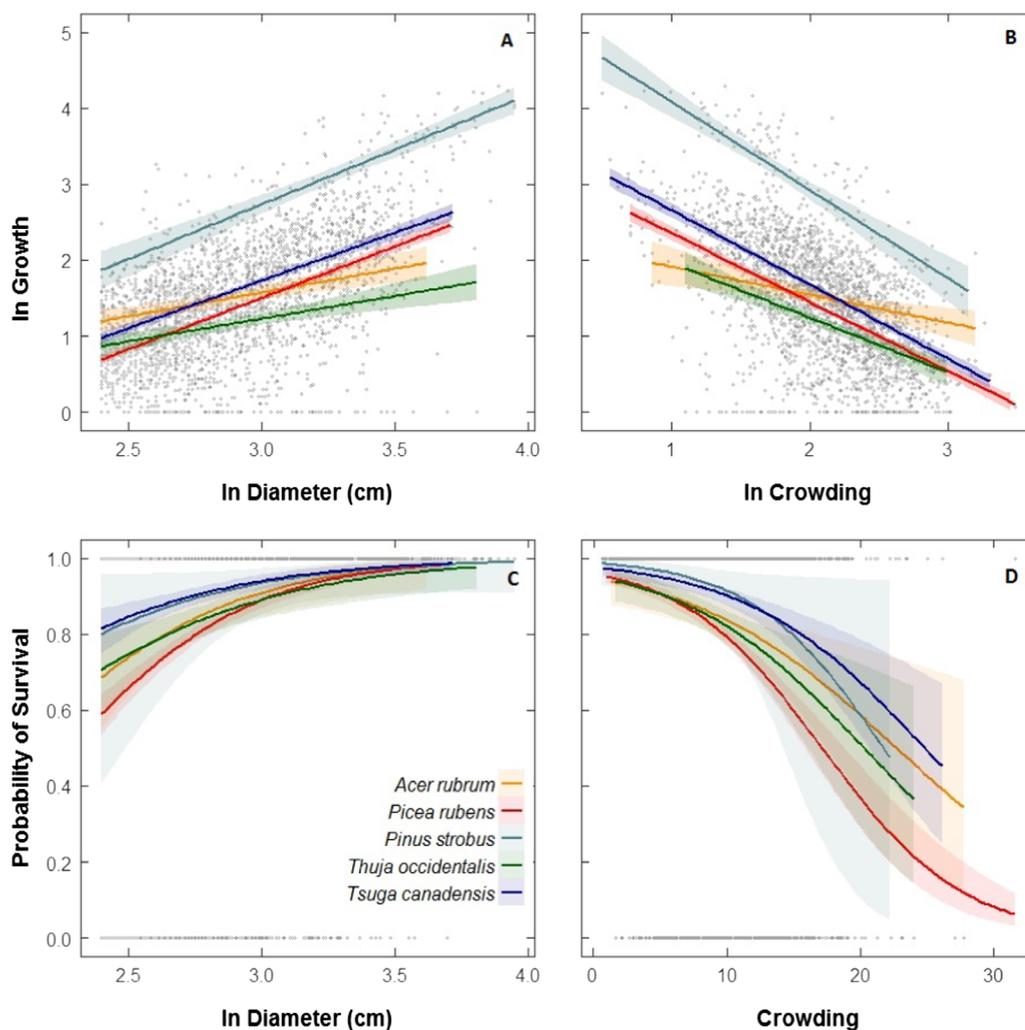


Fig. 2. Relationship between growth (A, B; basal area increment; $\text{cm}^2 \text{yr}^{-1}$) and probability of survival (C, D) and the three most important explanatory variables: species, crowding (B, D) and initial diameter (A, C). Generally larger and less crowded individuals grew faster and were more likely survive, but not all species responses were identical.

dropping out of the stand, given its expected longevity.

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). Higher growth rates of larger trees are likely associated with increased access to resources; for example, larger trees generally have prominent position in the canopy, greater leaf area, and therefore have more access to light. Other studies on the growth and mortality of large (and presumably old) trees in mature forests report 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 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). 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. One persistent challenge in constructing spatially-explicit crowding indices is the selection of the neighborhood 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 on growth and survival

Our large, heterogeneous, stem-mapped plot allowed us to address a number of less frequently addressed but currently relevant research questions. However, we note that given the restriction of this research to one study site, more research will be needed to determine if our findings apply more broadly. 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 focal 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. Several understory removal studies found limited

Table 2

Multiple linear regression models of growth (basal area increment, $\text{cm}^2 \text{yr}^{-1}$, upper portion of table) and logistic regression models of survival (lower portion) developed by sequentially adding explanatory variables and compared using Akaike information criterion (AIC). ΔAIC shows differences in model performance as compared to top model (model with lowest AIC, shaded). Model predictive power estimated with R^2 (growth models) or area under the receiver operating curve (AUC, survival models). Row containing top model is shaded. CI = crowding index, N stumps = number of cut stumps within a neighborhood, β = estimated bootstrapped coefficient, se = standard error, β Interval = bootstrapped 95% interval; β , se, and confidence interval provided for continuous variables only.

Growth Models						
Model	k	AIC	ΔAIC	R^2	β (se)	β Interval
Species	1	5434	1178	0.23		
+ Crowding (CI)*	2	4537	281	0.46	-0.9 (0.0)	-0.95, -0.84
+ Diameter*	3	4384	128	0.49	0.6 (0.1)	0.47, 0.68
+ Soil Moisture*	4	4350	94	0.50	-0.1 (0.0)	-0.18, -0.07
+ Canopy Class*	5	4272	16	0.51		
+ Intraspecific CI*	6	4256	-	0.52	-0.3 (0.1)	-0.43, -0.17
+ Sapling CI	7	4256	0	0.52	0.0 (0.0)	-0.04, 0.08
+ N Stumps	8	4256	0	0.52	0.0 (0.0)	-0.01, 0.09

Survival Models						
Model	k	AIC	ΔAIC	AUC	β (se)	β Interval
Species	1	2691	510	0.63		
+ Crowding (CI)*	2	2489	308	0.75	-1.8 (0.1)	-2.12, -1.54
+ Diameter*	3	2301	120	0.76	1.3 (0.3)	0.81, 1.94
+ Sapling CI*	4	2275	94	0.76	0.7 (0.1)	0.49, 1.00
+ Canopy Class*	5	2181	-	0.78		
+ Soil Moisture	6	2182	1	0.78	-0.1 (0.1)	-0.36, 0.15
+ Intraspecific CI	7	2183	2	0.78	-0.4 (0.3)	-1.08, 0.12
+ N Stumps	8	2182	1	0.79	0.2 (0.1)	-0.05, 0.58

*significant explanatory variables (p -value < 0.01).

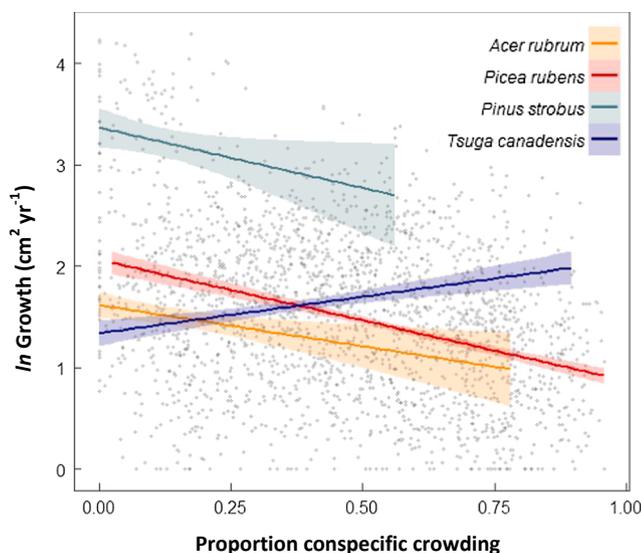


Fig. 3. Relationship between growth (basal area increment, BAI, $\text{cm}^2 \text{yr}^{-1}$) and the proportion of an individual's crowding neighborhood (based on Heygi index) associated with conspecific neighbors. Most species grew best with more heterospecific neighbors, while hemlock grew best with more conspecific neighbors.

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). Additional and more-detailed studies of the understory are needed to better differentiate these unexpected relationships.

Second, we tested 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 such stands may provide structural diversity and higher productivity (Paquette and Messier, 2011; Zhang et al., 2012; Forrester & Bauhus,

Table 3

This significant biologically relevant interaction demonstrates that the relationship between an individual's successes (growth and survival) and soil moisture varies according to crowding environments. 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 \times Soil Moisture	4114	-142	< 0.01	0.54	2173	-8	< 0.01	0.79

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 related to 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 (i.e., heterospecific individuals) can better share resources (Uriarte et al., 2004; 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 higher proportion of hemlock neighbors was associated with lower levels of crowding; therefore, a neighborhood with abundant hemlock would tend to be less crowded and presumably favor hemlock growth. Hemlock may be associated with less crowded environments because of the soil moisture conditions in those locations, as hemlock tends to occur on moist but well-drained sites (Rogers, 1978), a requirement that might exclude hemlock from the poorly drained, lower elevation areas that tended to have higher crowding. We acknowledge that studies of species interactions in mixed-species systems are inherently complex; however, our finding that neighbor identity influences tree growth highlights the importance of including species identity when modelling growth in such systems.

In addition, these results generally support recent work demonstrating that individual tree growth increases with increasing neighborhood tree species richness, and this increase in turn leads to greater stand-level productivity in species-rich stands (Fichtner et al., 2018). Similarly, mixed-species stands have been shown to support higher tree densities (Pretzsch and Biber, 2016), enhance structural heterogeneity (Riofrío et al., 2017), and reduce climate sensitivity (Thurm et al., 2016). The recognized benefits of mixed-species stands are now being used to develop silvicultural prescriptions that create or maintain such mixtures; however, additional work is needed to determine which species, in what proportions, and what spatial patterns provide the appropriate conditions for a given region (Pretzsch and Zenner, 2017).

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 many other parts of the world, due to abundant precipitation that is evenly distributed throughout the year. We found that tree growth was lower in the wettest areas of our study site. The lack of oxygen in water-saturated soils restricts root and microbial respiration, thereby limiting root functioning and microbial organic matter decomposition (Ernst, 1990; Davidson et al., 1998). By addressing the interaction of soil moisture and crowding on both growth and survival, we found that even within these three ha of contiguous forest, tree success is negatively related to both excess and insufficient moisture. That is, when crowding is low and soil moisture is elevated, tree growth and survival may be inhibited. In contrast, when crowding (and potentially competition for water) is high, tree growth and survival may be inhibited by a lack of

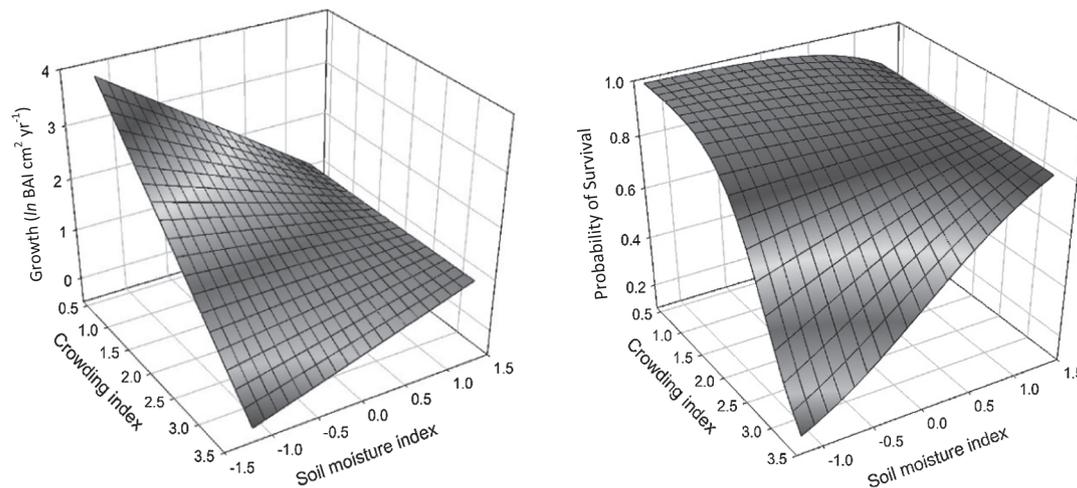


Fig. 4. Depiction of biologically relevant interactions. Where neighborhood crowding (based on Heygi index) is low, high soil moisture is associated with decreased individual growth and survival; however, where crowding is high, low soil moisture is associated with decreased individual growth and survival.

soil moisture. Interestingly, this interaction suggests inherent resilience in this system to uncertain future environmental conditions (Trenberth, 2011), as some individuals would be more successful in drier conditions, while others would be more successful in wetter conditions. Though further research is needed to affirm the applicability of these findings, they suggest a more nuanced approach to modeling the effects of soil moisture may be beneficial, particularly in the face of global changes in soil moisture availability (Allen et al., 2010).

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). However, at this site we found that the canopy disturbance that occurred ca. 100 years ago had no lingering effects on recent tree growth or survival, suggesting that as time passes the influence of disturbance dissipates and is replaced by other factors.

5. 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, interpretive, and management 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 (species, crowding, and size) were the same as those driving survival, yet additional factors, including soil moisture, sapling crowding and neighbor identity, suggest dissimilarities. This finding warns against conflating growth and survival 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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Declaration of Competing Interest

None.

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Data accessibility

The data described in the manuscript will be freely available upon request from the corresponding author.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.06.043>.

References

- Aakala, T., Fraver, S., D'Amato, A.W., Palik, B.J., 2013. Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. *For. Ecol. Manage.* 308, 128–135.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259 (4), 660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>.
- Baker, F.S., 1949. A revised tolerance table. *J. Forest.* 47, 179–181.
- Battles, J.J., Robards, T., Das, A., Waring, K., Gilless, J.K., Biging, G., Schurr, F., 2007. Climate change impacts on forest growth and tree mortality: a data-driven modeling study in the mixedconifer forest of the Sierra Nevada, California. *Clim. Change* 87 (1 Suppl.), s193–s213. <https://doi.org/10.1007/s10584-007-9358-9>.
- Biging, G.S., Dobbertin, M., 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual. *Forest Sci.* 38 (3), 695–720. <http://www.ingentaconnect.com/content/saf/fs/1992/00000038/00000003/art00015>.
- Biondi, F., 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. *Ecol. Appl.* 9 (1), 216–227. <https://doi.org/10.1890/1051->

- 0761(1999) 009[0216:CTRCAR]2.0.CO;2.
- Bond-Lamberty, B., Rocha, A.V., Calvin, K., Holmes, B., Wang, C., Goulden, M.L., 2014. Disturbance legacies and climate jointly drive tree growth and mortality in an intensively studied boreal forest. *Glob. Change Biol.* 20 (1), 216–227. <https://doi.org/10.1111/gcb.12404>.
- Brokaw, N.V.L., 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14 (2), 158. <https://doi.org/10.2307/2387750>.
- Brooks, R.T., 1994. A regional-scale survey and analysis of forest growth and mortality as affected by site and stand factors and acidic deposition. *Forest Sci.* 40 (3), 543–557. <https://doi.org/10.1111/1365-2745.12782>.
- Buechling, A., Martin, P.H., Canham, C.D., 2017. Climate and competition effects on tree growth in Rocky Mountain forests. *J. Ecol.* 105 (6), 1636–1647. <https://doi.org/10.1111/1365-2745.12782>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A practical Information-Theoretic-Approach*. Springer Science & Business Media, New York.
- Canham, C.D., Lepage, P.T., Coates, K.D., 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. *Can. J. For. Res.* 34, 778–787. <https://doi.org/10.1139/X03-232>.
- Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., Twery, M.J., 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. *Ecol. Appl.* 16 (2), 540–554. [https://doi.org/10.1890/1051-0761\(2006\)016\[0540:NAOCTC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[0540:NAOCTC]2.0.CO;2).
- Cantarello, E., Newton, A.C., Martin, P.A., Evans, P.M., Gosal, A., Lucash, M.S., 2017. Quantifying resilience of multiple ecosystem services and biodiversity in a temperate forest landscape. *Ecol. Evol.* 7 (22), 9661–9675. <https://doi.org/10.1002/ece3.3491>.
- Castagneri, D., Vacchiano, G., Lingua, E., Motta, R., 2008. Analysis of intraspecific competition in two subalpine Norway spruce (*Picea abies* (L.) Karst.) stands in Paneveggio (Trento, Italy). *For. Ecol. Manage.* 255 (3–4), 651–659.
- Coates, K.D., Canham, C.D., LePage, P.T., 2009. Above-versus below-ground competitive effects and responses of a guild of temperate tree species. *J. Ecol.* 97 (1), 118–130.
- Contreras, M.A., Affleck, D., Chung, W., 2011. Evaluating tree competition indices as predictors of basal area increment in western Montana forests. *For. Ecol. Manage.* 262 (11), 1939–1949. <https://doi.org/10.1016/j.foreco.2011.08.031>.
- Coomes, D.A., Allen, R.B., 2007a. Effects of size, competition and altitude on tree growth. *J. Ecol.* 95 (5), 1084–1097. <https://doi.org/10.1111/j.1365-2745.2007.01280.x>.
- Coomes, D.A., Allen, R.B., 2007b. Mortality and tree-size distributions in natural mixed-age forests. *J. Ecol.* 95 (1), 27–40. <https://doi.org/10.1111/j.1365-2745.2006.01179.x>.
- Copenhaver-Parry, P.E., Cannon, E., 2016. The relative influences of climate and competition on tree growth along montane ecotones in the Rocky Mountains. *Oecologia* 182 (1), 13–25. <https://doi.org/10.1007/s00442-016-3565-x>.
- D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J., 2011. Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments. *For. Ecol. Manage.* 262 (5), 803–816. <https://doi.org/10.1016/j.foreco.2011.05.014>.
- Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., 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>.
- Das, A., 2012. The effect of size and competition on tree growth rate in old-growth coniferous forests. *Can. J. For. Res.* 42 (11), 1983–1995. <https://doi.org/10.1139/x2012-142>.
- Das, A.J., Stephenson, N.L., Davis, K.P., 2016. Why do trees die? Characterizing the drivers of background tree mortality. *Ecology* 97 (10), 2616–2627. <https://doi.org/10.1002/ecy.1497>.
- Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Glob. Change Biol.* 4, 217–227.
- Enquist, B.J., West, G.B., Charnov, E.L., Brown, J.H., 1999. Allometric scaling of production and life history variation in vascular plants. *Nature* 401, 907–911. <https://doi.org/10.1038/44819>.
- Ernst, W.H.O., 1990. *Ecophysiology of plants in waterlogged and flooded environments*. *Aquat. Bot.* 38, 73–90.
- Fajvan, M.A., Seymour, R.S., 1993. Canopy stratification, age structure, and development or multicohort stands of eastern white pine, eastern hemlock, and red spruce. *Can. J. For. Res.* 23, 1799–1809.
- Fichtner, A., Härdtle, W., Bruehlheide, H., Kunz, M., Li, Y., von Oheimb, G., 2018. Neighborhood interactions drive overyielding in mixed-species tree communities. *Nat. Commun.* 9 (1144). <https://doi.org/10.1038/s41467-018-03529-w>.
- Forrester, D.I., Bauhus, J., 2016. A Review of processes behind diversity—productivity relationships in forests. *Curr. Forest. Rep.* 2 (1), 45–61. <https://doi.org/10.1007/s40725-016-0031-2>.
- Fox, J., Weisberg, S., 2011. *An R Companion to Applied Regression*. Retrieved from Sage, Thousand Oaks CA. <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>.
- Fox, J., and Weisberg, S., 2017. Appendix: Bootstrapping Regression Models in R. *An R Companion to Applied Regression*, (June), 1–17. Retrieved from <https://socserv.socsci.mcmaster.ca/jfox/Books/Companion/appendix/Appendix-Bootstrapping.pdf>.
- Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* 155, 399–423. [https://doi.org/10.1016/S0378-1127\(01\)00575-8](https://doi.org/10.1016/S0378-1127(01)00575-8).
- Fraver, S., Brokaw, N.V.L., Smith, A.P., 1998. Delimiting the gap phase in the growth cycle of a Panamanian forest. *J. Trop. Ecol.* 14, 673–681.
- Fraver, S., D'Amato, A.W., Bradford, J.B., Jonsson, B.G., Jönsson, M., Esseen, P.A., 2014. Tree growth and competition in an old-growth *Picea abies* forest of boreal Sweden: influence of tree spatial patterning. *J. Veg. Sci.* 25 (2), 374–385. <https://doi.org/10.1111/jvs.12096>.
- Fraver, S., White, A., 2005. Disturbance dynamics of old-growth *Picea rubens* forests of northern Maine. *J. Veg. Sci.* 16 (5), 597–610. [https://doi.org/10.1658/1100-9233\(2005\)16\[597:DDOOPR\]2.0.CO;2](https://doi.org/10.1658/1100-9233(2005)16[597:DDOOPR]2.0.CO;2).
- Giuggiola, A., Zweifel, R., Feichtinger, L.M., Vollenweider, P., Bugmann, H., Haeni, M., Rigling, A., 2018. Competition for water in a xeric forest ecosystem – effects of understorey removal on soil micro-climate, growth and physiology of dominant Scots pine trees. *For. Ecol. Manage.* 409 (December 2017), 241–249. <https://doi.org/10.1016/j.foreco.2017.11.002>.
- Gleason, K.E., Bradford, J.B., Bottero, A., D'Amato, A.W., Fraver, S., Palik, B.J., Kern, C.C., 2017. Competition amplifies drought stress in forests across broad climatic and compositional gradients. *Ecosphere* 8 (7). <https://doi.org/10.1002/ecs2.1849>.
- Goldberg, D.E., Landa, K., 1991. Competitive effect and response – hierarchies and correlated traits in the early stages of competition. *J. Ecol.* 79 (4), 1013–1030. <https://doi.org/10.2307/2261095>.
- Gómez-Aparicio, L., García-Valdés, R., Ruíz-Benito, P., Zavala, M.A., 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: Implications for forest management under global change. *Glob. Change Biol.* 17 (7), 2400–2414. <https://doi.org/10.1111/j.1365-2486.2011.02421.x>.
- Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* 84 (11), 2809–2815. <https://doi.org/10.1890/02-3114>.
- Gray, A.N., Spies, T.A., Pabst, R.J., 2012. Canopy gaps affect long-term patterns of tree growth and mortality in mature and old-growth forests in the Pacific Northwest. *For. Ecol. Manage.* 281, 111–120. <https://doi.org/10.1016/j.foreco.2012.06.035>.
- Grömping, U., 2009. Variable importance assessment in regression: Linear regression versus random forest. *Am. Stat.* 63 (4), 308–319. <https://doi.org/10.1198/tast.2009.08199>.
- Haase, P., 1995. Spatial pattern analysis in ecology based on Ripley's K-function: Introduction and methods of edge correction. *J. Veg. Sci.* 6 (4), 575–582. <https://doi.org/10.2307/3236356>.
- Hain, F.P., 1988. *The balsam woolly adelgid in North America*. In: Berryman, A.A. (Ed.), *Dynamics of Forest Insect Populations. Population Ecology (Theory and Application)*. Springer, Boston, MA.
- Harrell, F.E., 2015. *Regression Modeling Strategies*. Springer Series in Statistics, vol. 64. <https://doi.org/10.1007/978-1-4757-3462-1>.
- Hett, J.M., Loucks, O.L., 1976. Age structure models of Balsam Fir and Eastern Hemlock. *J. Ecol.* 64 (3), 1029–1044.
- Heygi, F., 1974. A simulation model for managing jack-pine stands. In: Fries, J. (Ed.), *Growth models for tree and stand simulations (Research N)*. Royal College of Forestry, Uppsala, SE.
- Holzwarth, F., Kahl, A., Bauhus, J., Wirth, C., 2013. Many ways to die – partitioning tree mortality dynamics in a near-natural mixed deciduous forest. *J. Ecol.* 101 (1), 220–230. <https://doi.org/10.1111/1365-2745.12015>.
- Honer, T., 1967. *Standard volume tables and merchantable conversion factors for the commercial tree species of central and eastern Canada*.
- Hyttborn, H., Verwijst, T., 2014. Small-scale disturbance and stand structure dynamics in an old-growth *Picea abies* forest over 54 yr in central Sweden. *J. Veg. Sci.* 25 (1), 100–112. <https://doi.org/10.1111/jvs.12057>.
- Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Turner, M.G., 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* 14 (7), 369–378. <https://doi.org/10.1002/fee.1311>.
- Keane, R.E., Austin, M., Field, C., Huth, A., Lexer, M.J., Peters, D., Wyckoff, P., 2001. Tree mortality in gap models: application to climate change. *Clim. Change* 51 (3–4), 509–540. <https://doi.org/10.1023/A:1012539409854>.
- Keddy, P., 2001. *Competition*, second ed. Springer Science & Business Media.
- Kelliher, F.M., Black, T.A., Price, D.T., 1986. Estimating the effects of understorey removal from a Douglas Fir forest using a two-layer canopy evapotranspiration model. *Water Resour. Res.* 22 (13), 1891–1899.
- Kelty, M.J., Gould, E.M., Twery, M.J., 1987. Effect of understorey removal in hardwood stands. *North. J. Appl. For.* 4 (3), 162–164.
- Larson, A.J., Franklin, J.F., 2010. The tree mortality regime in temperate old-growth coniferous forests: the role of physical damage. *Can. J. For. Res.* 40 (11), 2091–2103. <https://doi.org/10.1139/X10-149>.
- Larson, A.J., Lutz, J.A., Donato, D.C., Freund, J.A., Swanson, M.E., HilleRisLambers, J., Franklin, J.F., 2015. Spatial aspects of tree mortality strongly differ between young and old-growth forests. *Ecology* 96 (11), 2855–2861. <https://doi.org/10.1890/15-0628.1.sm>.
- Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Reich, P.B., 2016. Positive biodiversity-productivity relationship predominant in global forests. *Science* 354 (6309). <https://doi.org/10.1126/science.aaf8957>.
- Liaw, A., Wiener, M., 2002. Classification and regression by randomForest. *R News* 2 (3), 18–22.
- Lorimer, C.G., 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. *For. Ecol. Manage.* 6 (4), 343–360. [https://doi.org/10.1016/0378-1127\(83\)90042-7](https://doi.org/10.1016/0378-1127(83)90042-7).
- Lorimer, C.G., Dahir, S.E., Nordheim, E.V., 2001. Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. *J. Ecol.* 89 (6), 960–971. <https://doi.org/10.1046/j.0022-0477.2001.00619.x>.
- MacFarlane, D.W., Kobe, R.K., 2006. Selecting models for capturing tree-size effects on growth-resource relationships. *Can. J. For. Res.* 36 (7), 1695–1704. <https://doi.org/10.1139/x06-054>.
- Martin-Benito, D., Kint, V., del Río, M., Muys, B., Cañellas, I., 2011. Growth responses of West-Mediterranean *Pinus nigra* to climate change are modulated by competition and productivity: past trends and future perspectives. *For. Ecol. Manage.* 262 (6),

- 1030–1040. <https://doi.org/10.1016/j.foreco.2011.05.038>.
- Oliver, C.D., 1981. Forest development in North America following major disturbances. *For. Ecol. Manage.* 3 (3), 153–168. [https://doi.org/10.1016/0378-1127\(80\)90013-4](https://doi.org/10.1016/0378-1127(80)90013-4).
- Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F., Bullock, J.M., 2015. Biodiversity and resilience of ecosystem functions. *Trends Ecol. Evol.* 30 (11), 673–684. <https://doi.org/10.1016/j.tree.2015.08.009>.
- Paquette, A., Messier, C., 2011. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Glob. Ecol. Biogeogr.* 20 (1), 170–180. <https://doi.org/10.1111/j.1466-8238.2010.00592.x>.
- Pinheiro, J., Bates, D., DebRoy, S., and R Core Team, 2017. nlme: linear and nonlinear mixed effects models. Retrieved from <https://cran.r-project.org/package=nlme>.
- Pretzsch, H., Biber, P., 2016. Tree species mixing can increase maximum stand density. *Can. J. For. Res.* 46 (10), 1179–1193.
- Pretzsch, H., Zenner, E.K., 2017. Toward managing mixed-species stands: from parametrization to prescription. *Forest Ecosystems* 4 (1), 19. <https://doi.org/10.1186/s40663-017-0105-z>.
- Ramage, B.S., Johnson, D.J., Gonzalez-Akre, E., McShea, W.J., Anderson-Teixeira, K.J., Bourg, N.A., Clay, K., 2017. Sapling growth rates reveal conspecific negative density dependence in a temperate forest. *Ecol. Evol.* 7 (19), 7661–7671. <https://doi.org/10.1002/ece3.3298>.
- Riofrio, J., del Río, M., Pretzsch, H., Bravo, F., 2017. Changes in structural heterogeneity and stand productivity by mixing Scots pine and Maritime pine. *For. Ecol. Manage.* 405, 219–228.
- Rogers, R.S., 1978. Forests dominated by hemlock (*Tsuga canadensis*): distribution as related to site and postsettlement history. *Can. J. Bot.* 56, 843–854. <https://doi.org/10.1139/b78-096>.
- Rollinson, C.R., Kaye, M.W., Canham, C.D., 2015. Interspecific variation in growth responses to climate and competition of five eastern tree species. *Ecology* 97 (4), 1003–1011. <https://doi.org/10.1890/15-1549.1>.
- Runkle, J.R., 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63 (5), 1533–1546.
- Runkle, J.R., 1998. Changes in southern Appalachian canopy tree gaps sampled thrice. *Ecology* 79 (5), 1768–1780.
- Russo, S.E., Wiser, S.K., Coomes, D.A., 2007. Growth-size scaling relationships of woody plant species differ from predictions of the Metabolic Ecology Model. *Ecol. Lett.* 10 (10), 889–901. <https://doi.org/10.1111/j.1461-0248.2007.01079.x>.
- Seymour, R.S., 1992. The red spruce-balsam fir forest of Maine: Evolution of silvicultural practice in response to stand development patterns and disturbances. In: Kelty, M.J., Larson, B.C., Oliver, C.D. (Eds.), *The Ecology and Silviculture of Mixed-Species Forests* (Forest Sci). Springer, Dordrecht, pp. 217–244.
- Sheil, D., May, R.M., 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *J. Ecol.* 84 (1), 91–100.
- Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. *The Practice of Silviculture: Applied Forest Ecology*, ninth ed. John Wiley & Sons Inc., New York.
- Stadt, K.J., Huston, C., Coates, D.K., Feng, Z., Dale, M.R.T., Lieffers, V.J., Victor, J.L., 2007. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. *Ann. Forest Sci.* 64, 477–490. <https://doi.org/10.1051/forest:2007025>.
- Suarez, M.L., Ghermandi, L., Kitzberger, T., 2004. Factors predisposing episodic drought induced tree mortality in *Nothofagus*-site, climatic sensitivity and growth trends. *J. Ecol.* 92 (6), 954–966. <https://doi.org/10.1111/j.1365-2745.2004.00941.x>.
- Team R Core, 2016. R: A Language and Environment for Statistical Computing. Retrieved from R Foundation for Statistical Computing, Vienna, Austria.
- Thompson, I., Mackey, B., McNulty, S., Mosseler, A., 2009. Forest resilience, biodiversity, and climate change. A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems, vol. 43. Montreal.
- Thurm, E.A., Uhl, E., Pretzsch, H., 2016. Mixture reduces climate sensitivity of Douglas-fir stem growth. *For. Ecol. Manage.* 376, 205–220.
- Trenberth, K.E., 2011. Changes in precipitation with climate change. *Clim. Res.* 47, 123–138. <https://doi.org/10.3354/cr00953>.
- Uriarte, M., Condit, R., Canham, C.D., Hubbell, S.P., 2004. A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbors matter. *J. Ecol.* 92, 348–360. <https://doi.org/10.1111/j.0022-0477.2004.00867.x>.
- Vitali, V., Forrester, D.I., Bauhus, J., 2018. Know your neighbours: drought response of Norway Spruce, Silver Fir and Douglas Fir in mixed forests depends on species identity and diversity of tree neighbourhoods. *Ecosystems* 1–15. <https://doi.org/10.1007/s10021-017-0214-0>.
- Watt, A.S., 1947. Pattern and process in the plant community. *J. Ecol.* 35 (1/2), 1–22.
- Weishampel, J.F., Sung, G., Ransom, K.J., LeJeune, K.D., Shugart, H.H., 1994. Forest textural properties from simulated microwave backscatter: The influence of spatial resolution. *Remote Sens. Environ.* 47 (2), 120–131. [https://doi.org/10.1016/0034-4257\(94\)90149-X](https://doi.org/10.1016/0034-4257(94)90149-X).
- Weiskittel, A.R., Hann, D.W., Kershaw, J.A., Vanclay, J.K., 2011. *Forest Growth and Yield Modeling*. John Wiley & Sons.
- Welden, C.W., Slauson, W.L., 1986. The Intensity of competition versus its importance: an Overlooked distinction and some implications. *Q. Rev. Biol.* 61 (1), 23–44.
- Whitmore, T.C., 1989. Canopy gaps and the two major groups of forest trees. *Ecology* 70 (3), 536–538.
- Worrall, J.J., Lee, T.D., Harrington, T.C., 2005. Forest dynamics and agents that initiate and expand canopy gaps in *Picea* – *Abies* forests of Crawford Notch, New Hampshire, USA. *J. Ecol.* 93, 178–190. <https://doi.org/10.1111/j.1365-2745.2004.00937.x>.
- Wunder, J., Reineking, B., 2007. Predicting tree death for *Fagus sylvatica* and *Abies alba* using permanent plot data. *J. Veg. Sci.* 18 (4), 525–534. <https://doi.org/10.1111/j.1654-1103.2007.tb02567.x>.
- Zhang, Y., Chen, H.Y.H., Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *J. Ecol.* 100 (3), 742–749. <https://doi.org/10.1111/j.1365-2745.2011.01944.x>.
- Zhu, Y., Hogan, J.A., Cai, H., Xun, Y., Jiang, F., Jin, G., 2017. Biotic and abiotic drivers of the tree growth and mortality trade-off in an old-growth temperate forest. *For. Ecol. Manage.* 404 (June), 354–360. <https://doi.org/10.1016/j.foreco.2017.09.004>.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*, vol. 36. <https://doi.org/10.1016/B978-0-12-387667-6.00013-0>.