**Development and evaluation of individual tree- and stand-level approaches for predicting
spruce-fir response to commercial thinning in Maine, USA**

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Abstract

Commercial thinning is a widely used silvicultural method in the spruce-fir (*Picea-Abies*) forests of the northeastern USA, but limited work has been done on predicting both short- and long-term individual tree- and stand-level responses to this treatment. Based on annual inventories of permanent plots from a replicated thinning experiment in Maine, USA, stand- and individual tree-level treatment response functions for spruce-fir stands were developed and evaluated. The developed thinning modifiers were shown to significantly improve predictions of annual stand-level basal area growth and mortality as well as species-specific, individual tree-level annual diameter increment, height to crown base increment, and mortality. For these response variables, duration and magnitude of the response functions were significantly influenced by thinning intensity and to a lesser extent by thinning method. In contrast, modifiers for stand-level dominant height increment as well as tree-level height increment did not show significant improvement when compared to the baseline model. When the developed modifiers were included in stand- and individual-tree growth models, a significant improvement in prediction over the baseline models was achieved, but the individual-tree approach was superior to predicting long-term response to various alternative thinning treatments. Overall, the study highlights the advantage of including thinning modifiers in growth and yield models, even for relatively shade-tolerant species, and the effectiveness of an individual-tree approach in structurally diverse and mixed-species stands.

Keywords: growth modelling, thinning response, multiplicative modifiers, balsam fir, red spruce

1. Introduction

Throughout the last 30 years forestry in many regions of the world has seen a dramatic shift from intensive, large-scale management operations to spatially more restricted partial harvest activities (Puettmann et al. 2015). As a result, clearcutting followed by site preparation and artificial reforestation have been replaced by selection or retention silviculture that favors natural regeneration (Gustafsson et al. 2012). The shift has often been initiated and driven by public concerns regarding the effects of conventional forest management procedures on the sustainable and long-term provision of forest goods and services other than timber production such as biodiversity conservation, water supply, and recreational opportunities (Bliss 2000). Societal engagement has also often triggered legislative amendment, which has accelerated the shift towards more extensive forest management practices (Thomas et al. 2006, Bauhus et al. 2013). More recently, sustainable forest certification became the impetus for the transition in forest management philosophy and practices (Sheil et al. 2010).

The Acadian Forest of Maine, USA is an exemplary region demonstrating the forestry paradigm shift described above (Seymour 1992). In response to public concern about the common practice of very large clearcuts (>1000 ha) in the aftermath of the spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak of the 1970's and 80's (Irland 1988), a Forest Practices Act (FPA) was passed in 1989. Since the FPA does not regulate partial harvesting above a specific residual basal area while heavily regulating clearcuts, the latter has decreased dramatically within several years to less than 5% of the total harvest area today, the lowest level recorded statewide since data collection began in the early 1980s (Maine Forest Service 2015). In contrast, the area of partial and selection harvesting has more than doubled from about

100,000 ha year⁻¹ in the mid-1980s to over 200,000 ha year⁻¹ from 2003-07 (Maine Forest Service 2015). In fact, partial harvesting is the largest and most widespread disturbance on Maine's forest today, accounting for approximately 90% of harvested hectares (Maine Forest Service 2015). In addition, stand response to partial harvest treatments were among the factors most influential with regard to the outcomes of the last wood supply assessment for Maine (Wagner et al. 2003). Partial harvesting practices in the Acadian Forest of Maine most often mechanically remove a portion of the stand volume from trails or aggregated patches (Arsenault and Saunders 2012, Lombardo 2014) but also include traditional silvicultural operations such as shelterwood and thinning. Pre-commercial and commercial thinning treatments have been important management activities in Maine's coniferous forests, but limited evaluation has been conducted on stand and individual tree response to these treatments (Bataineh et al. 2013, Clune 2013).

A variety of approaches have been used to model short- and long-term response to thinning at both the stand- and individual-tree levels (Weiskittel et al. 2011, Weiskittel 2014). Commonly, modifiers are developed to alter predicted stand- (e.g. Bailey et al. 1985, Gyawali and Burkhart 2015) and tree-level (e.g. Hann et al. 2003; Hynynen et al. 1995) dynamics following thinning. These modifiers can be either additive or multiplicative (with the latter being preferred for a variety of reasons such as greater flexibility and accuracy), and rely on an array of factors describing the thinning treatment such as time since treatment, % basal area removed, and thinning method (Weiskittel et al. 2011). Despite several investigations which developed thinning modifiers, most of these previous studies have focused on pure stands of primarily species of low or intermediate shade tolerance such as loblolly pine (*Pinus taeda* L; e.g. Gyawali

and Burkhart 2015), slash pine (*Pinus elliottii* Engelm.; Bailey et al. 1985), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; Hann et al. 2003), and Scots pine (*Pinus sylvestris* L.; Hynynen et al. 1995). Relatively few examples exist for mixed-species stands of shade tolerant conifer species such as those which are dominant in the northeastern USA. In addition and to our knowledge, no study has compared the effectiveness of modeling thinning response at the stand- or individual tree-level to date.

In the northeastern US, the Forest Vegetation Simulator (FVS; Crookston and Dixon 2005) is widely used, but has been shown to be biased in stands receiving either pre-commercial or commercial thinning treatments (Saunders et al. 2007). This outcome is likely because FVS assumes that growth and yield of thinned stands is similar to non-thinned stands of the similar stand characteristics such as age, site index, and stocking. Thinning responses are therefore only reflected and hence predicted via model equations through changes in stand density (Hynynen 1995, Hann et al. 2003). This, however, proved to be not sufficient to capture modified stand and tree growth dynamics after thinning in loblolly pine (Westfall and Burkhart 2001). Given the wide use of, and importance placed on growth models such as FVS to evaluate the long-term financial return on alternative silvicultural treatments (e.g. Bataineh et al. 2013) or the assessment of carbon storage (e.g. Nunery and Keeton 2010), the development of regional modifiers is critical. Moreover, regional modifiers that are independent of a particular growth model would be specifically beneficial as they could be used in various forest growth simulators after testing their performance within each system of equations.

Consequently, the aim of this study was to develop and evaluate stand and individual tree-level growth and mortality modifiers for commercially thinned spruce-fir (*Picea-Abies*)

forests of the Acadian Region using a series of regional, comprehensive, multi-year, and replicated thinning studies. Specific objectives were to: (1) develop annual thinning response modifiers for stand-level basal area growth, dominant height increment, and mortality; (2) establish annual and species-specific thinning response modifiers for individual-tree diameter, height, and height to crown base increment as well as mortality; and (3) evaluate predictions of thinning response across a range of treatments using both the stand- and individual tree-level modifiers.

2. Material and methods

2.1 Study Area

Measurements from 16 study locations across northern Maine, which are part of the University of Maine's Cooperative Forestry Research Unit's Commercial Thinning Research Network (CTRN) were used for this investigation (Table 1, Figure 1). Maine has a diverse climate, consisting of nine climatic zones (Briggs and Lemin 1992). Locations of this study represented five climatic zones. The delineations have strong influence on site conditions and forest structure (Briggs and Lemin 1992). The parent material of soils is glacial till and alluvium (Ferwerda et al. 1997). All locations lie within the Acadian forest, a conifer-dominated mixedwood ecosystem covering much of Maine and the Canadian Maritimes (Rowe and Halliday 1972). Forest stands usually consist of naturally-regenerated balsam fir (*Abies balsamea* [L.] Mill.) and red spruce (*Picea rubens* Sarg.). Other conifer species present include white spruce (*Picea glauca*), eastern white pine (*Pinus strobus* L.), black spruce (*Picea mariana*),

eastern hemlock (*Tsuga canadensis* (L.) Carrière) and northern white-cedar (*Thuja occidentalis* L.). Hardwood species include red maple (*Acer rubrum* L.), yellow birch (*Betula alleghanensis* Britt.), paper birch (*Betula papyrifera* Marshall), and quaking aspen (*Populus tremuloides* Michx.). Mean stand age at the start of the study across all locations ranged from 14 to 68 years, while site index (red spruce dominant height at base age 50) varied between 13 and 24 m (Table 1, DeRose and Seymour 2010).

2.2 Data

Pre-commercial thinning (PCT) contrasted with non-PCT (NoPCT) was conducted in six and nine study locations respectively, during the mid- and late-1980's. One additional location, Austin Pond, was comprised of both PCT and NoPCT plots. In locations with PCT stands, subsequent crown thinning treatments included a 3 x 2 factorial combination of time of thinning (immediate, 5, and 10 year delay) and level of relative density reduction (33 or 50%) in addition to an non-thinned control. Thinning treatments in locations with NoPCT stands included a 3 x 2 factorial combination of thinning method (low, dominant, or crown) and level of relative density reduction (33 or 50%) in addition to an non-thinned control (McConville et al. 2005). The low and dominant thinning treatments were defined as the removal of trees beginning at the lower or upper end of the diameter distribution, respectively, until target residual relative density was reached. Competitors of selected dominant and co-dominant crop trees were harvested in the crown thinning treatment until target residual density was reached. Each PCT and NoPCT study location comprised a total of seven treatment plots (3 x 2 factorial including control) with locations serving as blocks (DeRose and Seymour 2010). However, the Austin Pond location had

3 and 4 replicate blocks of NoPCT and PCT, respectively, with an additional 66% relative density reduction treatment and further control plots.

Thinning operations were carried out in various years on PCT and NoPCT locations (Table 1). During harvest operations, larger balsam fir trees (DBH > 20 cm) were preferentially removed in all thinning treatments because of high stem rot susceptibility in these larger DBH classes and the resulting increased risk of stem breakage (Frank 1990). Due to variation in thinning method, targeted relative density, initial stand density, and tree size distribution across the study locations, thinning intensity expressed as basal area removed for the 33% reduction treatments ranged from 23 to 64%, from 48 to 73% for the 50% treatments, and between 63 and 81% for the 66% treatments. Post-treatment tree mortality occurred particularly in the crown and dominant thinning treatments of the NoPCT stands (Pekol 2011).

The sampling units for each treatment consisted of a 26.6 x 30.5 m (0.08 ha) permanent measurement plots with a forwarder trail running through the plot center and in alignment with the plot's width (except control treatment). These measurement plots were established in the center of each of the 61 x 61 m (0.37 ha) treatment units within each study location and considered representative of the stand growing conditions. Prior to treatment, temporary plots were established to quantify species composition, stand density, and the diameter distribution. Following treatment, diameter at breast height (DBH) of all live trees as well as newly established ingrowth trees taller than 1.3 m were measured on an annual basis starting in the first year after thinning on the permanent measurement plots. DBH measurements at PCT plots with a delayed thinning entry also started at the beginning of the study in 2002. Consequently, these plots were considered untreated control replicates up to the year when harvesting finally took

place. In addition to DBH, tree height (HT) and height to crown base (HCB) were recorded for a varying, randomly selected subsample (61% on average) of trees every year. Data were collected for a total time period of up to 13 and 12 years for NoPCT and PCT locations, respectively (Table 1). Overall, the available data included over 20,000 individual trees and a total of approximately 145,000 observations across 16 installations and 132 measurement plots.

2.3 Data analysis

Imputation of missing data

Predicting and imputing missing values prior to simulations is a common procedure in forest growth and yield modeling (Weiskittel et al. 2011). Using modeled values as predictors in subsequent modeling approaches, however, likely underestimates true variability, which can make error estimates optimistic. HT and HCB values for approximately half of all observations had to be calculated in our study. Missing HT and HCB were predicted using the ‘nlme’ package (Pinheiro et al. 2014) in R (version 3.2.2, R Core Team 2015) and the following individual-tree static equations:

$$(1) \quad HT = e^{\left(\alpha_{10} + a_{1i} + a_{1j} + a_{1k} + a_{1l} + \left(\frac{\alpha_{11}}{1+DBH}\right)\right)}$$

$$(2) \quad HCB = \frac{HT}{e^{\left(\alpha_{20} + a_{2i} + a_{2j} + a_{2k} + a_{2l} + \alpha_{21} \cdot DBH\right)}}$$

where α_{ij} are model fixed parameters, a_{xi} , a_{xj} , a_{xk} , and a_{xl} are random terms for the i th species, j th study location, k th plot, and l th year, and all other variables are described above. The

mixed effects models had a variance structure to account for the increasing residual spread along the major explanatory variable DBH. Crown ratio (CR) was subsequently calculated as follows:

$$(3) \quad CR = \frac{HT - HCB}{HT}.$$

Growth response modeling

Given adequate treatment data, stand- or individual tree-level response to silvicultural manipulations ($\hat{y}$) including thinning has been preferably modeled as a treatment modifier equation (f_{res}) that is either added to or a multiplier upon a separately developed untreated equation (f_{base}), i.e. a baseline model not including thinning treatment variables ($\hat{y} = f_{\text{base}} + f_{\text{res}}$ or $\hat{y} = f_{\text{base}} * f_{\text{res}}$; Weiskittel et al. 2011, Gyawali and Burkhart 2015). We followed this general approach by using the combined data of non-thinned and thinned CTRN plots and simultaneously fitting a baseline model multiplied by a thinning-response equation. As a result, the final treatment modifiers f_{res} may be suitable for individual inclusion in different growth simulators as generalized response functions. However, their impact on the overall system should always be evaluated.

Stand-level baseline models

Stand-level f_{base} were developed for annual basal area growth of survivor trees (ΔBA), annual dominant height growth in balsam fir or red spruce ($\Delta\text{HT}_{\text{DOM}}$), and annual mortality quantified as accumulated basal area of dead trees (BA_{MORT}). ΔBA and BA_{MORT} f_{base} were derived from plots with a combined post-treatment basal area proportion of at least 66% in balsam fir and red spruce. Using exponential equation forms and the ‘nlme’ package in R, realized ΔBA , $\Delta\text{HT}_{\text{DOM}}$, and BA_{MORT} mixed effects f_{base} can be expressed as follows:

$$(4) \quad \Delta BA = e^{\left(\beta_{10} + b_{1j} + b_{1k} + \frac{\beta_{11}}{BA} + \beta_{12} \cdot \log(SI)\right)}$$

$$(5) \quad \Delta HT_{DOM} = e^{\left(\beta_{20} + b_{2j} + b_{2k} + \frac{\beta_{21}}{HT_{DOM}} + \beta_{22} \cdot \log(SI)\right)}$$

$$(6) \quad BA_{MORT} = e^{\left(\beta_{30} + b_{3j} + b_{3k} + \frac{\beta_{31}}{BA} + \beta_{32} \cdot PCT + \beta_{33} \cdot \sqrt{\frac{BA_{BF}}{BA}}\right)}$$

where BA is initial basal area ($\text{m}^2 \text{ ha}^{-1}$), SI is site index (red spruce dominant height at base age 50, m), HT_{DOM} is initial dominant height (m), PCT is an indicator variable such that PCT = 1 for stands that were pre-commercially thinned and PCT = 0 for stands that were not, BA_{BF} is BA in balsam fir, β_{ij} s are fixed-effects parameters, b_{xj} and b_{xk} are random intercept terms for the j th study location and k th plot. The models had a variance structure to account for the increasing residual spread along major explanatory variables of each equation (BA for ΔBA and P_{MORT} , HT_{DOM} for ΔHT_{DOM}). Model development followed a forward step-wise procedure. Starting with a null model consisting of an intercept only, potential explanatory variables were sequentially added to evaluate their influence on model accuracy. Predictors were included in the model if a biologically plausible significant effect (P-value < 0.05) was observed and model performance improved. Model performance was assessed using Akaike's information criterion (AIC).

Individual tree-level baseline models

Individual tree f_{base} for the two most common conifer species of the CTRN data base, balsam fir and red spruce, were developed for annual diameter increment (ΔDBH), annual height increment (ΔHT), annual height-to-crown base increment (ΔHCB), and individual tree mortality (probability of a tree dying, P_{MORT}). Existing literature on realized individual-tree dynamic equations was reviewed to obtain potential equation forms for each modeled dependent variable

(e.g. Hann et al. 2003, Weiskittel et al. 2007, Russell et al. 2014). The final individual tree-level f_{base} were of the following form:

$$(7) \quad \Delta DBH =$$

$$e^{(\beta_{40} + b_{4j} + b_{4k} + \beta_{41} \cdot \log(DBH) + \beta_{42} \cdot DBH + \beta_{43} \cdot \log(CR) + \beta_{44} \cdot BAL^2 + \beta_{45} \cdot \sqrt{BA} + \beta_{46} \cdot SI)}$$

$$(8) \quad \Delta HT = e^{(\beta_{50} + b_{5j} + b_{5k} + \beta_{51} \cdot \log(HT) + \beta_{52} \cdot HT + \frac{\beta_{53}}{DBH} + \beta_{54} \cdot BA)}$$

$$(9) \quad \Delta HCB = e^{(\beta_{60} + b_{6j} + b_{6k} + \frac{\beta_{61}}{CR} + \beta_{62} \cdot HT)}$$

$$(10) \quad P_{MORT} = \left(1 + e^{-(\beta_{70} + b_{7j} + b_{7k} + \beta_{71} \cdot DBH + \beta_{72} \cdot DBH^2 + \beta_{73} \cdot \log(CR) + \beta_{74} \cdot BAL)}\right)^{-1}$$

where BAL is basal area in larger trees ($\text{m}^2 \text{ha}^{-1}$) and all other variables are described above while parameter indexing conventions follow those given previously. PCT was not included in the list of potential explanatory variables for individual tree-level baseline models as preliminary analysis had revealed that a clear PCT effect was reflected and hence captured in the potential predictors CR and HT-to-DBH ratio. Models were again derived as nonlinear mixed effects models with a variance structure to account for the variability in the most influential explanatory variable of each equation (DBH, HT, CR, and DBH for ΔDBH , ΔHT , ΔHCB , and P_{MORT} , respectively). Model development followed the procedure for stand-level baseline models described above.

Thinning-response functions

Additive or multiplicative thinning modifiers developed in previous studies usually followed a Type 1 response over time, i.e. they produced a short-term effect of the treatment (Snowdon 2002). As such, they predict no response at the time of thinning, a relatively rapid increase and often early maximum of the thinning effect shortly after the thinning followed by a more gradual lessening of the response over time after thinning until the thinning effect eventually diminishes and becomes zero again (Gyawali & Burkhart 2015). To correspond with this general response pattern, multiplicative modifiers (thinning treatment response functions f_{thin}) of this study were modeled based on a Type I combined exponential - power function of the following form (Sit and Poulin-Costello 1994):

$$(11) \quad f_{thin} = 1 \pm (\gamma_1 \cdot \gamma_2^{Y_t} \cdot Y_t^{\gamma_3})$$

where Y_t is time since thinning (with $Y_t = 0$ for non-thinned plots) and γ_i 's are fixed-effects parameters. Depending on the response variable and hence the kind of expected response to thinning, the modeled modifier component would be added to (ΔBA , ΔDBH) or subtracted from one (ΔHT_{DOM} , ΔHT , ΔHCB). In contrast to previous modeling efforts (Hamilton 1986), thinning in our study mostly increased overall mortality levels due to high competition-independent (catastrophic) mortality rates due to windstorm events (Pekol 2011). In fact, observed mortality rates in the control plots were lowest among PCT treatments and second lowest only to the 33% reduction low thinning treatment plots of NoPCT locations. Consequently, BA_{MORT} and P_{MORT} were modeled following the approach applied for ΔBA and ΔDBH .

Previously developed thinning modifiers are often comprised of treatment related predictor variables other than just Y_t such as stand or tree age at the time of thinning, the ratio of

stand basal area removed in thinning (BA_t) to basal area before thinning (BA_b), and the ratio of the quadratic mean diameter (QMD) of trees removed in thinning (QMD_t) to QMD of all trees before thinning (QMD_b) (Weiskittel et al. 2011). Including age at the time of thinning in treatment modifiers should reflect the decreasing response potential (or maximum response) of aging trees and hence stands (Amateis et al. 1989, Liu et al. 1995, but see also Jonson 1995). In contrast, the inclusion of basal area removed and QMD ratio was assumed to better represent varying response to thinning operations that differ in the amount and kind of trees removed, i.e. thinning intensity and thinning method, respectively (Bailey and Ware 1983, Short and Burkhart 1992). Age at the time of thinning was not included in our modifier equation as the two species analyzed here have been characterized as very shade-tolerant (Niinemets and Valladares 2006) and hence, are capable of responding to release irrespective of age and duration of suppression or neighborhood competition (Morris 1948, Blum 1990, Clune 2013). In addition, preliminary results revealed that age was not a significant predictor in ΔDBH and ΔHT *f*base.

To better represent varying response of stands (or trees in stands) thinned with the same intensity but at different prior basal areas, we also added BA_b to the percentage of basal area removed. The additional inclusion of BA_b allows for the prediction of a stronger and longer lasting thinning effect in stands fully stocked prior tree removal compared to understocked ones. Since information on DBH of trees removed in thinning were incomplete in the CTRN database, we used a modified QMD ratio. To assure compliance with the outcome of the classical approach, QMD_b became the numerator while QMD of remaining trees after thinning (QMD_a) formed the denominator. Assuming that thinning from below ($QMD_b/QMD_a < 1$) causes a weaker treatment response compared with dominant and crown thinnings that primarily remove

dominant individuals ($QMD_b/QMD_a > 1$), we multiplied our modified QMD ratio with the combined measure of thinning intensity. This resulted in the following extended f_{thin} :

$$(12) \quad f_{thin} = 1 \pm \left(e^{\left(\gamma_0 + \frac{\gamma_1}{\left(\left(100 \cdot \frac{BA_t}{BA_b} + BA_b \right) \cdot \frac{QMD_b}{QMD_a} \right) + 0.01} \right)} \cdot \gamma_2^{Y_t} \cdot Y_t^{\gamma_3} \right)$$

where all variables and parameters are described above, BA_t was set to zero and QMD_a was set equal to QMD_b for non-thinned plots. Random terms for the j th study location and k th plot were added to γ_2 or γ_3 if the inclusion improved the predictive ability of the model. Because f_{thin} for each f_{base} was developed in a forward stepwise manner by adding the various treatment related predictors successively starting with Y_t , we were able to evaluate the importance of each variable as well as model performance of various predictor combinations. As a result, insignificant predictors were omitted and simplified equation forms were considered and used when appropriate. The simplified equation forms were as follows:

$$(13) \quad f_{thin} = 1 \pm \left(e^{\left(\gamma_0 + \frac{\gamma_1}{100 \cdot \frac{BA_t}{BA_b} + 0.01} \right)} \cdot \gamma_2^{Y_t} \cdot Y_t^{\gamma_3} \right)$$

$$(14) \quad f_{thin} = 1 \pm \left(e^{\left(\gamma_0 + \frac{\gamma_1}{\left(100 \cdot \frac{BA_t}{BA_b} + BA_b \right) + 0.01} \right)} \cdot \gamma_2^{Y_t} \cdot Y_t^{\gamma_3} \right)$$

$$(15) \quad f_{thin} = 1 \pm \left(e^{\left(\gamma_0 + \frac{\gamma_1}{\left(100 \cdot \frac{BA_t}{BA_b} \cdot \frac{QMD_b}{QMD_a} \right) + 0.01} \right)} \cdot \gamma_2^{Y_t} \cdot Y_t^{\gamma_3} \right)$$

Model forms were compared and final models selected based on parameter significance (P-value < 0.05) and model performance, which was evaluated using AIC, mean bias (MB; observed - predicted), mean absolute bias (MAB), root mean squared error (RMSE), and area under the curve (AUC). AUC is a measure of performance for models with a binary outcome. AUC values lower than 0.6 suggest poor model performance while values larger than 0.6, 0.7, or 0.8 present acceptable, good, and excellent discrimination, respectively (Hein and Weiskittel 2010).

To further evaluate the predictive ability of the thinning-response functions short- and long-term predictions of stand-level BA increment from the first to last post-treatment measurement (1-12 growing seasons depending on location and treatment) were derived using tree- and stand-level equations with and without the developed modifiers. We applied the probability multiplier method in the tree-level approach for BA increment predictions by converting P_{MORT} into a probability of survival ($1 - P_{\text{MORT}}$) and then multiplying it by each tree's expansion factor (Weiskittel et al. 2011). As a result, decreasing probability of tree survival leads to lower expansion factors and in turn to a reduced individual tree contribution to total stand BA increment. Only thinned plots with a combined initial post-treatment basal area proportion of at least 90% balsam fir and red spruce were considered for this analysis ($n = 78$). The thinning modifier predictions were compared with f_{base} predictions using MB, MAB, and RMSE.

3. Results

The 16 locations in the CTRN study and the resulting varying initial stand conditions ensured a wide range of values for all stand- and individual tree-level predictor and response

variables (Tables 1-3). Differences between species-specific individual-tree datasets were marginal, with the exception of DBH, which was a direct result of the preferred removal of large balsam fir (Table 3). In general, PCT stands were younger and were more dominated by red spruce when compared to NoPCT stands.

Stand-level response variables

For the stand-level response variables ΔBA and BA_{MORT} , a f_{thin} of the form depicted in equations (13) and (14), respectively, could be derived (Table 4). Thinning increased ΔBA and BA_{MORT} strongly and thus, combining f_{base} and f_{thin} resulted in a better model performance (Table 7). In contrast, adding a treatment modifier of equation (12) to ΔHT_{DOM} did not improve model prediction accuracy (Table 7) as evident in the insignificance of parameter γ_3 (Table 4). The inclusion of the random effects parameters proved to be highly significant, improving performance of all derived models.

The predictor variables that were initially considered for thinning intensity and thinning method improved overall prediction accuracy, however their contributions were comparatively small as Y_t turned out to be the most important f_{thin} predictor (data not shown). Thinning intensity still had a pronounced effect on the shape of the response function as depicted in Figure 2.

Individual tree-level response variables

Combining individual-tree level f_{base} with a treatment modifier of equation (15) improved prediction accuracy in ΔDBH and ΔHCB of both species (Table 7, Figure 3). However, improvement in model performance in ΔHCB was minor and not all estimated parameters were

significant in balsam fir (Tables 5 and 6). When adding f_{thin} of equations (12) and (14) to balsam fir and red spruce P_{MORT} , respectively (Tables 5 and 6, Figure 3), improvement in model accuracy was again more pronounced in the latter one (Table 7). Y_t and the ratio of BA_t to BA_b were the most influential f_{thin} predictors (data not shown). In contrast, no thinning effect (equation 13) was found in ΔHT for either species as again reflected in insignificant estimates for parameter γ_3 (Tables 5, 6, and 7). The inclusion of the random effects structure again proved to be highly significant, improving performance of all derived models.

Comparison of modeling approaches

Regardless of approach, the accuracy of post-treatment predictions for stand-level basal area increment were mostly greater for f_{thin} model outcomes when compared to f_{base} results (Table 8). Tree-level based predictions outperformed predictions derived in the stand-level approach, which was especially evident for NoPCT plots.

4. Discussion

Using an extensive and regional database, multiplicative modifiers (f_{thin}) were successfully derived for stand-level annual basal area growth (ΔBA) and annual mortality (BA_{MORT}) as well as species-specific individual tree-level annual diameter increment (ΔDBH), annual height to crown base increment (ΔHCB) and annual mortality (P_{MORT}). The magnitude and duration of these response functions were influenced by thinning intensity and to a lesser extent by thinning method. In contrast, stand-level annual dominant height growth (ΔHT_{DOM}) and individual tree-level annual height growth (ΔHT) appeared to be relatively insensitive to

thinning. The developed modifiers were also generally consistent with prior findings from the CTRN (Clune 2013, Pekol 2011), and significantly improved long-term predictions of stand-level response to alternative thinning treatments when compared to unmodified equations. The individual-tree approach was generally superior to the stand-level approach for NoPCT plots.

Changes in stand- and tree-level growth and mortality patterns after thinning primarily result from increased individual tree growing space per tree, thus allowing residual trees to exploit newly available resources (e.g. light, water, nutrients, and growing space). However, increased diameter increment and thus basal area growth have also been related to thinning triggered fertilization and selection effects (Hynynen 1995). Decomposition of organic material including logging slash following thinning is often accelerated as openings in the canopy result in more favorable temperature and moisture regimes on the ground (e.g. Vesterdal et al. 1995, Thibodeau et al. 2000). Supply of nutrients may be improved in thinned stands which holds especially true for forests in higher latitudes as with those in our study. In addition, conventional thinning usually removes unhealthy, damaged, and less vigorous trees irrespective of the thinning method. Remaining trees not only grew at higher rates before thinning, but are able to better respond to modified growing conditions after thinning (Hynynen 1995).

Fertilization and selection effects are the principal reasons why thinned forests and trees in thinned stands exhibit increased growth rates when compared with non-thinned stands and trees with similar characteristics (age, basal area, site productivity), respectively (Weiskittel et al. 2011). However, ranges obtained in this analysis for ΔBA and $\Delta DBH f_{thin}$ with values of 1.5 and close to 2.0 for heavy dominant thinnings, respectively, appear comparatively high. For example, Hann et al. (2003) only found five-year $\Delta DBH f_{thin}$ values >1.4 for Douglas-fir and

western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) when more than 50% of the basal area was removed, but these values diminished rapidly with time since treatment. However, previous studies also found a close relationship between thinning intensity and response function magnitude (e.g. Pienaar and Shiver 1986, Hasenauer et al. 1997) and thus reported similar modifier value ranges especially for high thinning intensities (Hynynen 1995, Jonson 1995). Overall, this analysis highlights the responsiveness of these two species to thinning.

Likewise, duration of the predicted thinning effect in this study were similar in magnitude but were generally longer than those reported in other studies (e.g. Hann et al. 2003, Gyawali and Burkhart 2015). For example, f_{thin} generally peaked by year five since treatment and then declined, and stayed greater than 1.0 until approximately twenty years post treatment. Hann et al. (2003) also found five-year ΔDBH f_{thin} to remain above 1.0 until approximately twenty years after treatment for Douglas-fir and western hemlock, while their peak was always immediately following the treatment with a rapid decline thereafter.

Besides time since thinning and the percentage of basal area removed, our final ΔDBH f_{thin} also included the ratio of QMD before to QMD after thinning. Variables such as QMD ratio and basal area prior thinning, are theoretically important in determining thinning response because they represent the stand conditions at time of thinning and the type of thinning method (e.g. low, crown, high), respectively. The inclusion of these variables did improve the predictive capability of some modifier functions, however, the effect was relatively marginal. This result suggests that simpler f_{thin} forms can be pursued in future modelling efforts. The significance and importance of time since thinning and thinning intensity as essential modifier components have been demonstrated in other studies (Weiskittel et al. 2011).

Insensitivity of tree height growth to thinning as deduced from ΔHT_{DOM} and ΔHT analyses of our study has been reported in several other investigations. However, these studies focused primarily on shade-intolerant species such as Scots pine and loblolly pine (e.g. Hynynen 1995, Westfall 1998), yet the lack of height response to thinning has also been observed in more shade tolerant species like Douglas-fir and western hemlock (e.g. Hann et al. 2003). Tree height growth of dominant and co-dominant individuals usually does not vary much across a wide range of stand densities (Lanner 1985). A sudden reduction in stand density, however, can cause immediate and short-term modifications in within-tree photosynthate resource allocation patterns favoring crown expansion over leader growth (Ginn et al. 1991). Consequently, some studies have found a small negative thinning effect on stand ΔHT_{DOM} , but concluded that it was negligible due to the observed small magnitude and the short-term duration (Sharma et al. 2006, Gyawali and Burkhart 2015).

In contrast, observed ΔHCB of spruce and fir trees in this analysis appeared to be influenced by thinning. This finding is consistent with previous studies that reported a negative effect of thinning on individual-tree height-to-crown base recession (Liu et al. 1995, Westfall 1998). However, these studies investigated shade-intolerant loblolly pine whose foliage is not capable of coping with low light levels (Short and Burkhart 1992). As a result, branches of the lower, shaded crown are shed early and swiftly. However, increased light levels due to harvest operations such as thinning can slow crown recession significantly or may even bring it to a near total halt for a few years (Ginn et al. 1991, Peterson et al. 1997). In contrast, balsam fir and red spruce are among the most shade-tolerant conifer tree species of temperate and boreal forest ecosystems of the northern hemisphere (Niinemets and Valladares 2006). Their capability to

persist in deep shade is an indication that individuals of these species will self-prune at a much slower rate (Barnes et al. 1998). This observation may explain the less pronounced modifier effect detected in our models, which holds especially true for the very shade-tolerant balsam fir. However, previous studies analyzing crown growth dynamics after thinning in trees of shade-tolerant species including red spruce and balsam fir also reported a slowing in crown height recession (Kramer 1966, Clune 2013).

As expected and supported by findings from previous studies, thinning substantially increased stand mortality as reflected in the derived f_{thin} for stand-level BA_{MORT} and individual tree P_{MORT} (Ruel et al. 2000, Achim et al. 2005). Higher mortality rates in thinned spruce-fir stands of the Acadian forest are a direct result of increased risk of windthrow and breakage (Pekol 2011). Shallow soils, high seasonal groundwater table, and shallow rooting patterns of the studied conifer species are associated with stem losses due to high intensity windstorms (Seymour 1992, Ruel 2000). In addition, storm related stem breakage in balsam fir frequently occurs because of the species proneness to stem rot (Frank 1990). The basic effect of increased risk of catastrophic mortality in thinned spruce-fir stands is counterbalanced by a similar fundamental effect, a lower risk of density-dependent mortality resulting from a reduced number of trees and thus lowered inter-tree competition. We assume that these opposing influences caused a mixed mortality signal at the individual tree-level, which hindered our ability to detect a much more significant effect of f_{thin} on P_{MORT} prediction accuracy, particularly in red spruce.

Thinning modifiers have been developed at both the stand- and individual tree-levels, however, to our knowledge the effectiveness of these two alternative approaches has yet to be compared. The developed modifiers improved predictions at both the stand- and individual tree-

levels when compared to the baseline models, but there were substantial differences between the approaches when used to project stand-level basal area increment from the first to last measurement of each plot. With and without the modifiers, the individual tree-level approach was superior with MAB and RMSE lower when compared to the stand-level approach. The RMSE was further improved with the inclusion of both the individual-tree Δ DBH and P_{MORT} thinning modifiers. Likely, this result highlights the high within-stand composition and structural variability of individual tree response to thinning, which is not fully captured by the stand-level approach, particularly in the structurally diverse NoPCT stands. For example, Kuehne et al. (in review) found high spatial variability in the individual-tree response to the NoPCT thinning treatments of this analysis due to differences in the residual competitive environment and distance from the harvester trail. A stand-level approach would generally be more robust in stands dominated by a single-species, that have not been naturally-regenerated, or were thinned for a more regular distribution of comparatively similar-sized trees.

5. Conclusions

Our findings generally confirmed results from similar studies that found thinning-response functions to be beneficial for the prediction of Δ BA and Δ DBH, while Δ HT_{DOM} and Δ HT models did not improve from inclusion of such modifiers. In addition, Δ HCB of the analyzed shade-tolerant species of our study was only slightly affected by thinning which is in contrast to previous works. Mortality modifiers did improve long-term predictions of basal area increment.

Due to the varying characteristics of the studied stands and the broad range of thinning treatments examined, the derived modifiers are assumed to be suitable for growth response predictions over a wide range of contemporary partial harvest practices in spruce-fir stands of the Acadian Region. While we believe that there is greater applicability, data used in this study were clearly constrained within the state of Maine. Furthermore, we did not test the efficacy of adding the derived thinning modifiers into an existing simulation system. Overall system performance therefore needs to be thoroughly evaluated when the presented modifiers are embedded in other forest growth simulators.

Overall, there are a limited number of studies that have developed thinning response functions. Most of these studies analyzed plantation grown trees and stands of shade-intolerant species (Weiskittel 2014). Consequently, the current study is one of the first to use data from mixed, naturally regenerated stands that consist primarily of two highly shade-tolerant species. Future work will focus on better quantifying individual-tree responses using distance-dependent competition indices that can effectively capture the spatial and compositional variability created by thinning.

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Table 1. Stand and thinning treatment characteristics (mean, standard deviation, and range where applicable) of Commercial Thinning Research Network (CTRN) study locations that were (PCT) and were not pre-commercially thinned (NoPCT)

Characteristic	PCT	NoPCT
Number of locations	10	7
Number of annual post-treatment inventories	3-13	2-12
Breast height age (2000, years)	24 ± 8 (14-40)	46 ± 18 (18-68)
Site index (m)	21 ± 2 (18-24)	17 ± 4 (13-22)
Pre-treatment basal area (m ² ha ⁻¹)	30 ± 5 (21-42)	44 ± 6 (32-56)
Pre-treatment spruce/fir proportion (%) ¹	90 ± 12 (29-100)	84 ± 14 (34-99)
Year of commercial thinning	2002/07/09/10/12/13	2000/01/02/14
Thinning method(s)	Crown	Crown, dominant, low
Basal area reduction (%)	49 ± 10 (32-74)	55 ± 13 (23-81)
Post-treatment spruce/fir proportion (%) ¹	93 ± 13 (29-100)	90 ± 15 (34-100)

¹ basal area based, including non-thinned controls

Table 2. Description of stand-level Commercial Thinning Research Network (CTRN) data that were (PCT) and were not pre-commercially thinned (NoPCT)

Variable ¹	PCT				NoPCT			
	N	Mean	SD	Range	N	Mean	SD	Range
ΔBA ($m^2 ha^{-1}$)	571	1.28	0.55	0-5.47	472	0.87	0.48	0.12-4.68
BA ($m^2 ha^{-1}$)		26.6	8.3	8.1-46.2		25.5	12.2	3.6-56.6
ΔHT_{DOM} (m)	355	0.37	0.24	0-1.49	90	0.20	0.17	0-0.66
HT_{DOM} (m)		16.7	1.6	12.8-21.5		17.6	1.9	13.7-23.0
BA_{MORT} ($m^2 ha^{-1}$)	571	0.19	0.41	0-3.7	472	0.64	0.85	0-5.44
BA ($m^2 ha^{-1}$)		26.7	8.3	8.7-46.2		26.2	12.1	4.5-56.7
$BA_{BF} BA^{-1}$		0.80	0.20	0.05-1		0.28	0.36	0-1

¹ ΔBA : annual basal area increment of survivor trees, BA: initial stand-level basal area of survivor trees (ΔBA) or of all trees (BA_{MORT}), ΔHT_{DOM} : annual dominant height increment, HT_{DOM} : initial dominant height, BA_{MORT} : annual mortality (basal area of dead trees), BA_{BF} : basal area proportion in balsam fir

Table 3. Description of Commercial Thinning Research Network (CTRN) data for individual tree-level response variables by species.

Variable ¹	Balsam fir				Red spruce			
	N	Mean	SD	Range	N	Mean	SD	Range
Δ DBH (cm)	69,358	0.32	0.29	0-2.29	44,237	0.19	0.22	0-2.03
DBH (cm)		14.3	5.2	1.0-34.7		14.2	5.2	1.0-40.4
CR (m m ⁻¹)		0.44	0.14	0.01-1		0.32	0.13	0.01-1
BAL (m ² ha ⁻¹)		20.1	11.3	0-56.7		21.8	13.0	0-56.6
BA (m ² ha ⁻¹)		31.4	9.1	5.2-56.7		32.3	13.3	3.4-56.7
Δ HT (m)	28,109	0.38	0.30	0-1.98	9,821	0.29	0.28	0-1.98
HT (m)		12.4	2.6	1.5-23.0		11.5	3.0	1.5-20.4
DBH (cm)		14.8	4.8	1.3-33.8		13.8	4.7	1.5-40.4
BA (m ² ha ⁻¹)		30.4	7.6	5.2-55.0		30.0	11.7	5.2-55.0
Δ HCB (m)	27,051	0.56	0.57	0-3.96	9,191	0.45	0.55	0-3.99
CR (m m ⁻¹)		0.49	0.13	0.01-0.92		0.39	0.15	0.02-0.90
HT (m)		12.4	2.6	1.5-23.1		11.6	3.0	1.5-20.4
P _{MORT} ²	73,410	2.82	1.90	0.18-7.15	47,230	3.11	2.71	0.03-8.57
DBH (cm)		14.1	5.3	0.8-34.7		14.0	5.2	1.0-40.4
CR (m m ⁻¹)		0.44	0.14	0.01-1		0.32	0.13	0.01-1
BAL (m ² ha ⁻¹)		20.5	11.4	0-56.7		21.9	13.1	0-56.6

¹ Δ DBH: annual DBH increment, DBH: diameter at breast height, CR: crown ratio, BA: basal area, BAL: basal area in larger trees, Δ HT: annual height increment, HT: tree height, Δ HCB: height-to-crown base increment (crown recession), P_{MORT}: annual tree mortality (probability of a tree's dying)

² Here: annual proportion of dead trees (%)

Table 4. Baseline model (f_{base}) and baseline model multiplied by a thinning-response function (f_{base} & f_{thin}) parameters for estimating plot-level annual basal area growth of survivor trees (ΔBA), annual dominant height increment ($\Delta\text{HT}_{\text{DOM}}$), and annual mortality (BA_{MORT}) fitted with measurements from thinned and non-thinned plots.

Variable	Parameter	f_{base}				$f_{\text{base}} \& f_{\text{thin}}$				
		Estimate	SE	F-value	P-value	f_{thin} equation	Estimate	SE	F-value	P-value
ΔBA	β_{10}	-3.6820	0.4294	22.4	<0.0001	13	-4.1094	0.4439	475.4	<0.0001
	β_{11}	-7.6135	0.8101	105.6	<0.0001		-11.7458	1.2234	11.1	0.0009
	β_{12}	1.3938	0.1429	95.1	<0.0001		1.5525	0.1483	8.3	0.0041
	γ_0	-					-0.2321	0.5908	1111.6	<0.0001
	γ_1	-					-43.7104	23.0449	33.8	<0.0001
	γ_2	-					0.6736	0.0704	1479.2	<0.0001
	γ_3	-					1.3259	0.3873	11.7	0.0006
$\Delta\text{HT}_{\text{DOM}}$	β_{10}	-4.6474	1.1174	400.9	<0.0001	12	-3.0244	0.8652	1269.2	<0.0001
	β_{11}	-17.4463	5.3724	6.1	0.0140		-21.0615	5.7173	0.0	0.9895
	β_{12}	1.5189	0.3789	16.1	0.0001		1.0904	0.2893	47.9	<0.0001
	γ_0						0.3224	1.2521	63.8	<0.0001
	γ_1						-155.9706	99.0596	2.7	0.1025
	γ_2						1.0016	0.1406	85.2	<0.0001
	γ_3						0.0000	0.2434	0.0	1
BA_{MORT}	β_{10}	-1.2647	0.5606	10.0	0.0016	14	-1.2402	0.2994	57.6	<0.0001
	β_{11}	-17.9412	2.9308	40.3	<0.0001		-24.5202	3.0175	846.9	<0.0001
	β_{12}	-3.6941	0.7722	4.0	0.0462		-1.1302	0.3196	33.7	<0.0001
	β_{13}	4.4858	0.6998	41.1	<0.0001		1.5884	0.4397	65.9	<0.0001
	γ_0	-					8.3385	1.0725	143.7	<0.0001
	γ_1	-					-601.3096	96.9259	11.6	0.0007
	γ_2	-					0.5507	0.0349	3295.2	<0.0001
	γ_3	-					1.5795	0.1633	93.5	<0.0001

Table 5. Baseline model (f_{base}) and baseline model multiplied by a thinning-response function ($f_{\text{base}} \& f_{\text{thin}}$) parameters for estimating balsam fir individual tree-level annual DBH increment (ΔDBH), annual height increment (ΔHT), annual height-to-crown base increment (ΔHCB), and mortality (P_{MORT}) fitted with measurements from thinned and non-thinned plots.

Variable	Parameter	f_{base}				$f_{\text{base}} \& f_{\text{thin}}$				
		Estimate	SE	F-value	P-value	f_{thin} equation	Estimate	SE	F-value	P-value
ΔDBH	β_{40}	-1.9217	0.4946	147.4	<0.0001	15	-2.6640	0.3881	11.4	0.0007
	β_{41}	1.3766	0.0344	10571.3	<0.0001		1.3088	0.0329	38581.0	<0.0001
	β_{42}	-0.0471	0.0024	807.7	<0.0001		-0.0621	0.0024	1737.7	<0.0001
	β_{43}	0.5259	0.0135	2011.9	<0.0001		0.6921	0.0139	202.4	<0.0001
	β_{44}	-0.0002	0.0000	1260.9	<0.0001		-0.0003	0.0000	10188.3	<0.0001
	β_{45}	-0.2721	0.0067	1626.4	<0.0001		-0.1264	0.0099	58.3	<0.0001
	β_{46}	-0.0112	0.0248	0.2	<0.5986		0.0083	0.0193	149.1	<0.0001
	γ_0	-					-0.2566	0.1414	38452.8	<0.0001
	γ_1	-					-22.7609	5.0085	860.5	<0.0001
	γ_2	-					0.7745	0.0103	56340.5	<0.0001
ΔHT	β_{50}	0.0210	0.2608	270.3	<0.0001	13	-1.7201	0.2121	211.6	<0.0001
	β_{51}	0.1506	0.1530	21.1	<0.0001		0.8303	0.1210	111.4	<0.0001
	β_{52}	-0.0850	0.0125	101.8	<0.0001		-0.0699	0.0095	914.8	<0.0001
	β_{53}	-8.5331	0.3445	578.6	<0.0001		-4.5104	0.2564	486.0	<0.0001
	β_{54}	0.0075	0.0013	35.6	<0.0001		0.0096	0.0011	189.6	<0.0001
	γ_0	-					-1.8443	0.3810	7678.8	<0.0001
	γ_1	-					5.2969	15.2399	101.7	<0.0001
	γ_2	-					1.0532	0.0122	7550.9	<0.0001
	γ_3	-					0.0000	0.0039	0.0	1
ΔHCB	β_{60}	0.0459	0.1166	36.9	<0.0001	15	0.1148	0.1234	40.5	<0.0001
	β_{61}	-0.4114	0.0120	1246.7	<0.0001		-0.4025	0.0121	1401.8	<0.0001
	β_{62}	0.0143	0.0023	39.4	<0.0001		0.0172	0.0024	1.6	0.2091
	γ_0	-					-0.4208	0.4216	74.0	<0.0001
	γ_1	-					-17.0998	16.2840	2.0	0.1598
	γ_2	-					0.7986	0.0413	709.6	<0.0001
	γ_3	-					0.0521	0.0390	1.8	0.1819
P_{MORT}	β_{70}	-4.4816	0.3283	186.6	<0.0001	12	-8.2074	0.3860	8.5	0.0035
	β_{71}	-0.0788	0.0150	926.0	<0.0001		0.0400	0.0129	27.7	<0.0001
	β_{72}	0.0014	0.0004	77.2	<0.0001		0.0016	0.0003	55.6	<0.0001
	β_{73}	-1.0394	0.0287	1341.9	<0.0001		-0.5487	0.0176	978.6	<0.0001
	β_{74}	0.0188	0.0041	21.4	<0.0001		0.1033	0.0050	53.1	<0.0001
	γ_0	-					1.7414	0.4736	28.4	<0.0001
	γ_1	-					7.0805	37.5842	284.3	<0.0001
	γ_2	-					0.6677	0.0188	16266.5	<0.0001
	γ_3	-					0.8474	0.0600	199.5	<0.0001

Table 6. Baseline model (f_{base}) and baseline model multiplied by a thinning-response function ($f_{\text{base}} \& f_{\text{thin}}$) parameters for estimating red spruce individual tree-level annual DBH increment (ΔDBH), annual height increment (ΔHT), annual height-to-crown base increment (ΔHCB), and mortality (P_{MORT}) fitted with measurements from thinned and non-thinned plots.

Variable	Parameter	f_{base}				$f_{\text{base}} \& f_{\text{thin}}$				
		Estimate	SE	F-value	P-value	f_{thin} equation	Estimate	SE	F-value	P-value
ΔDBH	β_{40}	-5.0749	0.2121	2148.6	<0.0001	15	-5.4336	0.2366	24.3	<0.0001
	β_{41}	1.8522	0.0706	6415.2	<0.0001		1.6033	0.0665	20116.3	<0.0001
	β_{42}	-0.0615	0.0043	220.1	<0.0001		-0.0608	0.0041	130.1	<0.0001
	β_{43}	0.4775	0.0189	749.6	<0.0001		0.5812	0.0189	38.1	<0.0001
	β_{44}	-0.0002	0.0000	197.2	<0.0001		-0.0003	0.0000	5528.0	<0.0001
	β_{45}	-0.1545	0.0123	151.3	<0.0001		-0.0442	0.0152	18.0	<0.0001
	β_{46}	0.0501	0.0078	41.0	<0.0001		0.0670	0.0093	53.1	<0.0001
	γ_0						-0.5010	0.2002	33221.1	<0.0001
	γ_1						-20.1147	6.4607	990.3	<0.0001
	γ_2						0.8067	0.0141	54626.5	<0.0001
ΔHT	β_{50}	-2.2596	0.4249	300.4	<0.0001	13	-2.9635	0.4419	4456.3	<0.0001
	β_{51}	1.4263	0.2812	70.3	<0.0001		1.9330	0.2947	39.7	<0.0001
	β_{52}	-0.1875	0.0258	60.2	<0.0001		-0.2327	0.0273	92.2	<0.0001
	β_{53}	-9.1753	0.6042	210.5	<0.0001		-7.8372	0.5997	148.1	<0.0001
	β_{54}	0.0139	0.0025	30.7	<0.0001		0.0135	0.0032	83.0	<0.0001
	γ_0						-1.8426	0.3225	315.4	<0.0001
	γ_1						6.2781	11.8327	0.4	0.5125
	γ_2						1.1596	0.0466	620.3	<0.0001
	γ_3						0.0000	0.0314	0.0	1
ΔHCB	β_{60}	0.1860	0.1190	75.9	<0.0001	15	0.3737	0.0924	875.9	<0.0001
	β_{61}	-0.4957	0.0184	814.1	<0.0001		-0.4949	0.0182	1258.9	<0.0001
	β_{62}	0.0189	0.0049	14.8	0.0001		0.0255	0.0050	32.5	<0.0001
	γ_0						-1.0778	0.4811	1859.8	<0.0001
	γ_1						-14.7694	15.0320	8.6	0.0034
	γ_2						0.7758	0.1099	670.9	<0.0001
	γ_3						1.1164	0.5399	4.3	0.0387
P_{MORT}	β_{70}	-3.3936	0.3341	338.0	<0.0001	14	-7.6648	0.4453	100.2	<0.0001
	β_{71}	-0.2945	0.0239	1347.8	<0.0001		-0.1441	0.0198	1370.6	<0.0001
	β_{72}	0.0062	0.0008	49.8	<0.0001		0.0043	0.0006	46.7	<0.0001
	β_{73}	-0.9377	0.0332	773.6	<0.0001		-0.5257	0.0215	637.4	<0.0001
	β_{74}	0.0411	0.0064	41.8	<0.0001		0.1066	0.0072	41.4	<0.0001
	γ_0	-					10.5057	0.9952	323.2	<0.0001
	γ_1	-					-650.8260	90.7762	51.8	<0.0001
	γ_2	-					0.6948	0.0308	919.1	<0.0001
	γ_3	-					0.6429	0.0463	193.0	<0.0001

Table 7. Fit statistics (AIC: Akaike's information criterion, MB: mean bias, MAB: mean absolute bias, RMSE: root mean squared error, AUC: area under the curve) for stand-level and species-specific (BF: balsam fir, RS: red spruce) individual tree-level baseline models (f_{base}) and baseline models multiplied by a thinning-response function ($f_{\text{base}} \& f_{\text{thin}}$) for estimating annual basal area growth of survivor trees (ΔBA), annual dominant height increment ($\Delta\text{HT}_{\text{DOM}}$), annual stand mortality (BA_{MORT}), annual DBH increment (ΔDBH), annual height increment (ΔHT), annual height-to-crown base increment (ΔHCB), and annual tree mortality (P_{MORT}) fitted with measurements from thinned and non-thinned plots.

Response	Species	Model	AIC	MB	MAB	RMSE	AUC
Stand-level							
ΔBA	—	f_{base}	1,221	-0.0089	0.2636	0.4030	—
		$f_{\text{base}} \ \& \ f_{\text{thin}}$	1,153	-0.0037	0.2528	0.3985	—
$\Delta\text{HT}_{\text{DOM}}$	—	f_{base}	-85	-0.0132	0.1287	0.1841	—
		$f_{\text{base}} \ \& \ f_{\text{thin}}$	-48	-0.0001	0.1608	0.2239	—
BA_{MORT}	—	f_{base}	1,821	-0.0015	0.3299	0.5354	—
		$f_{\text{base}} \ \& \ f_{\text{thin}}$	1,583	-0.0249	0.2854	0.4587	—
Tree-level							
ΔDBH	BF	f_{base}	-17,769	-0.0007	0.1666	0.2198	—
		$f_{\text{base}} \ \& \ f_{\text{thin}}$	-20,159	0.0002	0.1644	0.2161	—
	RS	f_{base}	-29,028	-0.0012	0.1325	0.1774	—
		$f_{\text{base}} \ \& \ f_{\text{thin}}$	-30,211	-0.0008	0.1304	0.1748	—
ΔHT	BF	f_{base}	8,471	-0.0006	0.2055	0.2792	—
		$f_{\text{base}} \ \& \ f_{\text{thin}}$	8,528	-0.1888	0.2891	0.3474	—
	RS	f_{base}	1,313	-0.0022	0.1830	0.2548	—
		$f_{\text{base}} \ \& \ f_{\text{thin}}$	1,335	0.0157	0.1837	0.2582	—
ΔHCB	BF	f_{base}	37,027	0.0005	0.3465	0.4879	—
		$f_{\text{base}} \ \& \ f_{\text{thin}}$	36,917	0.0001	0.3455	0.4869	—
	RS	f_{base}	10,667	0.0011	0.3186	0.4479	—
		$f_{\text{base}} \ \& \ f_{\text{thin}}$	10,650	0.0018	0.3180	0.4471	—
P_{MORT}	BF	f_{base}	-90,469	—	—	—	0.8457
		$f_{\text{base}} \ \& \ f_{\text{thin}}$	-111,607	—	—	—	0.8408
	RS	f_{base}	-48,564	—	—	—	0.8516
		$f_{\text{base}} \ \& \ f_{\text{thin}}$	-49,129	—	—	—	0.8622

Table 8. Annual stand-level basal area increment ($\text{m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$) predictions using observed data from commercially thinned spruce fir stands of the Acadian forest that were (PCT) and were not pre-commercially thinned (NoPCT), baseline models (f_{base}), and baseline models multiplied by stand- (ΔBA , BA_{MORT}) or tree-level (ΔDBH , P_{MORT}) thinning-response functions (f_{base} & f_{thin}).

	N	Observed (Mean $\pm$ SD)	Approach	Model	Predicted (Mean $\pm$ SD)	MB	MAB	RMSE
PCT	43	0.70 ± 0.67	Stand-level	f_{base}	1.09 ± 0.35	-0.3937	0.5790	0.7621
				$f_{\text{base}} \& f_{\text{thin}}$	1.20 ± 0.35	-0.5005	0.5897	0.7736
			Tree-level	f_{base}	0.80 ± 0.22	-0.1013	0.4701	0.6159
				$f_{\text{base}} \& f_{\text{thin}}$	0.65 ± 0.35	0.0451	0.4635	0.6009
NoPCT	35	0.01 ± 0.66	Stand-level	f_{base}	-0.64 ± 1.31	0.6527	1.2177	1.6024
				$f_{\text{base}} \& f_{\text{thin}}$	0.81 ± 0.28	-0.7955	0.8297	0.9854
			Tree-level	f_{base}	0.50 ± 0.19	-0.4857	0.5676	0.7331
				$f_{\text{base}} \& f_{\text{thin}}$	0.38 ± 0.38	-0.3707	0.5177	0.6616

Figure 1. Position of Commercial Thinning Research Network (CTRN) study locations in Maine, USA. Lines depict Maine's climate zones of Briggs and Lemin (1992).

Figure 2. Stand-level thinning-response functions for exemplary moderate and heavy thinnings (25% or 50% basal area removal, respectively) for a) annual basal area increment of survivor trees (ΔBA) and b) annual stand mortality (BA_{MORT}) of Acadian spruce-fir forests.

Figure 3. Individual tree-level annual DBH increment (Δ DBH), annual height to crown base increment (Δ HCB), and annual tree mortality (P_{MORT}) thinning-response functions for exemplary moderate and heavy (25% or 50% basal area removal, respectively) low or dominant thinnings (QMD ratio = 0.7 or 1.1, respectively) for a) balsam fir and b) red spruce.