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Differential declines in Alaskan boreal forest vitality related to climate and competition

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Abstract

Rapid warming and changes in water availability at high latitudes alter resource abundance, tree competition, and disturbance regimes. While these changes are expected to disrupt the functioning of boreal forests, their ultimate implications for forest composition are uncertain. In particular, recent site-level studies of the Alaskan boreal forest have reported both increases and decreases in productivity over the past few decades. Here, we test the idea that variations in Alaskan forest growth and mortality rates are contingent on species composition. Using forest inventory measurements and climate data from plots located throughout interior and south-central Alaska, we show significant growth and mortality responses associated with competition, midsummer vapor pressure deficit, and increased growing season length. The governing climate and competition processes differed substantially across species. Surprisingly, the most dramatic climate response occurred in the drought tolerant angiosperm species, trembling aspen, and linked high midsummer vapor pressure deficits to decreased growth and increased insect-related mortality. Given that species composition in the Alaskan and western Canadian boreal forests is projected to shift toward early-successional angiosperm species due to fire regime, these results underscore the potential for a reduction in boreal productivity stemming from increases in midsummer evaporative demand.

KEYWORDS

Alaska, boreal forest, climate change, drought, forest inventory, growth decline, insect-induced mortality, terrestrial carbon cycle, vapor pressure deficit

1 | INTRODUCTION

Boreal forests are rapidly changing. Increased temperatures, lengthening of the growing season, changes in water availability, and increased disturbance may disrupt the functioning, structure, and composition of these forests (Hinzman et al., 2013; Kasischke & Turetsky, 2006; Zhu & Mcguire, 2016). In recent decades, different parts of the North America boreal forest have experienced different changes. In Alaska, spring tree growth can be limited by temperature (Euskirchen et al., 2006), and observational studies have reported increased vegetation productivity concurrent with warming in some locations (Welp, Randerson, & Liu, 2007). In contrast, in interior

Alaska, remote sensing and tree ring studies of white spruce and black spruce trees document growth declines ascribed to warming-induced water stress (Barber, Juday, & Finney, 2000; Beck et al., 2011; Verbyla, 2015; Walker & Johnstone, 2014; Walker, Mack, & Johnstone, 2015). Canadian forest inventory analyses have disagreed on the observational trends in growth and mortality as well as the mechanisms driving the changes (Girardin et al., 2016; Luo & Chen, 2013, 2015; Peng et al., 2011; Zhang, Huang, & He, 2015).

These disparate changes suggest that boreal forest responses to climate change may strongly depend on the current state of the system, including current ecosystem composition. For example, temperature sensitivity of spring tree growth, water use, and successional

strategy vary dramatically between the dominant angiosperm and gymnosperm species (Drobyshev, Gewehr, Berninger, Bergeron, & Mcglone, 2013; Euskirchen, Carman, & McGuire, 2014; Hollingsworth, Johnstone, Bernhardt, & Chapin, 2013; Johnstone & Chapin, 2006; Trugman et al., 2016; Young-Robertson, Bolton, Bhatt, Cristobal, & Thoman, 2016). Site-level studies have shown that angiosperm water use greatly exceeds that of gymnosperm species in the Alaskan boreal forest, such that angiosperm species consume >20% of total snowmelt water in comparison to the <1% associated with gymnosperm species (Young-Robertson et al., 2016). Understanding angiosperm vs. gymnosperm responses to climate change is particularly important given that recent fires in Alaska have the potential to increase angiosperm coverage by up to 20% (Barrett, McGuire, Hoy, & Kasischke, 2011). However, few studies address how climate variability and change impact decadal-scale growth and mortality dynamics of Alaskan angiosperm species at broad spatial scales (Barber et al., 2000; Beck et al., 2011; Juday, Alix, & Grant, 2015; Nicklen, Roland, Ruess, Schmidt, & Lloyd, 2016; Walker & Johnstone, 2014; Walker et al., 2015).

In addition to the direct impacts of climate change, recent tree growth and mortality rates may have been affected by changes in competition and insect disturbance. In central and western Canada, investigations using forest inventory measurements have attributed increases in tree mortality to increased competition resultant from rising atmospheric CO₂, increased growing season length, and increased soil nutrient availability (Luo & Chen, 2015; Zhang et al., 2015). Sustained insect outbreaks in British Columbia (Kurz, Stinson, & Rampley, 2008) and interior Alaska (Doak & Wagner, 2015; Wagner & Doak, 2013) have also caused widespread species-specific tree mortality, likely amplified by an interaction between climate warming and insect life cycle and population dynamics (Raffa et al., 2008; Weed, Ayres, & Hicke, 2013).

In this study, we use forest inventory measurements to evaluate the relative importance of climate, competition, and insect disturbance on decadal-scale species-specific growth and mortality rates in interior and south-central Alaska. We use 323 plots from the Cooperative Alaska Forest Inventory (CAFI) (Malone, Liang, & Packee, 2009) that were repeatedly measured at 5-year intervals from 1994 to 2013 (Figures 1, S1). With variance decomposition and mixed effects model analyses (Grömping, 2015), we address four questions: (i) Have there been detectable changes in Alaskan tree growth and mortality rates over the last 15 years? (ii) What is the relative importance of different climate drivers with respect to growth and mortality rates? (iii) Do gymnosperm species exhibit different climate sensitivities, in magnitude or even sign, than angiosperm species? (iv) Is insect disturbance related to growth and mortality rates, and, if so, for what species?

2 | MATERIALS AND METHODS

2.1 | Study area and forest inventory data

This study was conducted in forests in interior and south-central Alaska (Figure 1). Temperature in interior Alaska ranges from -40°C in the winter to $>30^{\circ}\text{C}$ in the summer and mean annual precipitation is approximately 300 mm (Van Cleve, Oliver, Schlentner, Viereck, & Dyrness, 1983). In contrast, conditions in south-central Alaska are wetter with more moderate seasonal temperature changes. Throughout Alaska, the growing season is short (approximately 3–4 months), but up to 22 hr of sunlight are available during the summer months (Van Cleve et al., 1983).

The CAFI permanent sample plots (PSPs) are a network of fixed-sized PSPs established in 1994 to monitor growth, yield, and health of Alaskan forests (Malone et al., 2009). The layout, establishment,

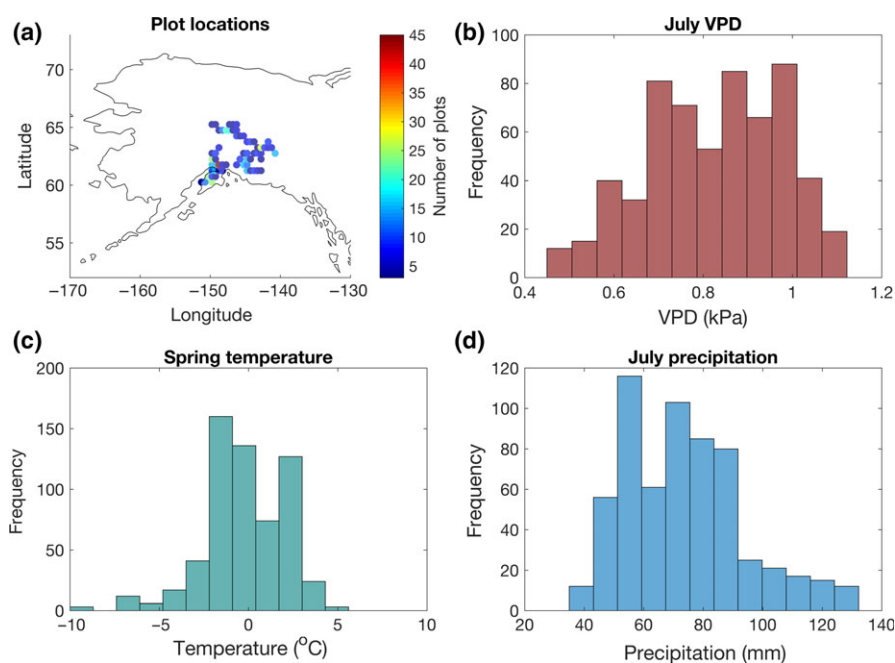


FIGURE 1 Spatial locations of the permanent sample plots in the Cooperative Alaska Forest Inventory binned by half degree (a). The number of plots in each half-degree grid cell is indicated by the color map. Distribution histograms of the July vapor pressure deficit (VPD) (b), March–May temperature (c), and July precipitation (d) showing the 10-year average over 2000–2009 across plots [Colour figure can be viewed at wileyonlinelibrary.com]

and maintenance of the PSPs follows conventional forest inventory procedures (Curtis, 1983). We selected 323 PSPs in our study (Figures 1, S1; Tables S1–S2) based on the following criteria: (i) PSPs with evidence of fire, tree cutting, or other manmade damage in the census periods were excluded; (ii) PSPs had at least three complete censuses, enabling us to compare demographic rates from a minimum of two different time intervals; (iii) because individual plots were our unit of analysis, we limited analyses to PSPs containing ≥ 30 trees at the first census according to the methods of previous inventory studies to reduce random variation in plot-level demographic rates (Peng et al., 2011; Van Mantgem et al., 2009; Zhang et al., 2015); (iv) only trees with diameter at breast height (DBH) > 3.8 cm were included to avoid biasing our results due to a change in the definition of minimum tree size during the study interval.

Selected PSPs were located in forests that experience a range of climate conditions, stand structures, species compositions, and site conditions representative of the region. All PSPs were square and 405 m². The initial census year ranged from 1994 to 2003 (mean 1999) and the final census year ranged from 2007 to 2013 (mean 2011). At the initial census, forests spanned ages from 32 to 276 years (determined through tree ring analysis of four dominant and/or codominant trees on a site), and the average age was approximately 95 years. The monitoring length for each PSP ranged from 10 to 15 years, averaging 12.2 years with number of censuses ranging from 3 to 4 (mean 3.4). Tree number per plot ranged from 30 to 265 at the initial census with a mean of 84. The 323 PSPs contained a total 27,057 living trees at the first census. Basal area ranged from 3.1 to 48.8 m²/ha with a mean of 23.9 m² ha. Summary statistics are available in Table S1 and Fig. S1. Finally, in addition to documenting growth, the CAFI records insect damage (Fig. S2) and intensity of damage inflicted on individual trees (minor (<11%), moderate (11–40%), severe (>40%), or unspecified) for 10 insect categories (unknown or unspecified, defoliators, bark beetles, sucking insects, aphids, spruce budworm, leaf roller, ants, leaf miner, ips beetle).

2.2 | Competition indices

To evaluate the effect of competition on tree growth and mortality, we used two metrics, (i) competition indices and (ii) tree canopy status. Furthermore, we used two competition indices, stand basal area and the stand density index (SDI) (Zhang et al., 2015). Stand basal area is a surrogate for stand crowding in each PSP as it factors in both tree size and density. SDI is another metric used to assess the degree of crowding within a stand (Reineke, 1933):

$$SDI = N \times \left(\frac{DBH_{\text{mean}}}{25.4} \right)^{1.605} \quad (1)$$

In equation (1), N represents the number of trees per hectare and DBH_{mean} represents the quadratic mean DBH in centimeters.

Second, we sorted trees based on canopy status (e.g., trees with a dominant or codominant crown class vs. intermediate, suppressed, or understory (Malone et al., 2009)) to isolate competition and climate effects in the absence and presence of light competition.

2.3 | Climate variables

The following climate variables were selected for initial consideration based on previously recognized biological significance (Barber et al., 2000; Beck et al., 2011; Luo & Chen, 2015; Parida & Buermann, 2014; Peng et al., 2011; Walker et al., 2015; Zhang et al., 2015): precipitation, vapor pressure deficit (VPD), summer frost-free period (FFP), and temperature. All climate variables were point-estimates derived from the locally downscaled CLIMATE_{NA} software package (Wang, Hamann, Spittlehouse, & Carroll, 2016). For all variables we tested both 5-year means and 5-year minimum/maximum in accordance with the inventory re-measurement interval. We did this for (i) annual, (ii) seasonal (previous December–February, March–May, June–August, and September–November), (iii) start of the growing season (May), and (iv) midsummer (July) meteorology. Based on previous studies of biologically relevant climate drivers, sensitivity tests, and to minimize collinearity between climate variables (Fig. S3), we selected two metrics of water availability, 5-year maximum July VPD and 5-year mean July precipitation, and also 5-year mean March–May temperature. The range in climate experienced by the CAFI is shown in Figure 1b–d, and temporal climate trends are shown in Fig. S4.

2.4 | Statistical analysis: competition, climate, and insects

First, we identified trends over time in growth, mortality, and insect infestation to evaluate possible declines in growth or increases in mortality during the study period. Trends in basal area growth were assessed using the following linear model:

$$\frac{\log(BA_{i,j}) - \log(BA_{i,j-1})}{5} = \beta_0 + \beta_1 Cl_j + \beta_2 Gyf_j + \beta_3 t_j + \gamma_i \quad (2a)$$

In equation (2a), $BA_{i,j}$ represents the basal area of the i th PSP of the j th census, and includes all trees with a diameter > 3.8 cm at the previous census. Cl_j is the competition index calculated using the total number of trees in a given plot. Gyf_j is a fixed effect associated with the forest gymnosperm fraction (calculated as gymnosperm basal area over total forest basal area) that controls for changes in demographic rates due to forest aging and/or succession, and t_j is the year of the j th census. The random effect of the i th PSP, γ_i , is assumed to follow a normal distribution with mean zero and standard deviation σ_γ . Each β coefficient represents the standardized fixed effect associated with an individual model parameter.

Similarly, we modeled the 5-year probability of tree mortality using the following logistic regression:

$$\text{logit}(p_{i,j}) = \beta_0 + \beta_1 Cl_j + \beta_2 Gyf_j + \beta_3 t_j + \gamma_i \quad (2b)$$

In equation (2b), $p_{i,j}$ is the 5-year tree mortality probability for the i th PSP of the j th census. All other parameters are identical to those specified in equation (2a).

We estimated 5-year trend in plot insect infestation fraction according to the following linear model:

$$\frac{\text{ninsect}_{i,j}}{n_{i,j}} = \beta_0 + \beta_1 \text{Cl}_j + \beta_2 \text{Gyf}_j + \beta_3 t_j + \gamma_i \quad (2c)$$

In equation (2c), $\text{ninsect}_{i,j}$ represents the number of trees infested with insects with an intensity >11%, and $n_{i,j}$ represents the total number of trees of the i th PSP of the j th census. All other parameters are identical to the growth model (equation 2a).

Next, we used mixed effects models to evaluate the dependence of tree growth and mortality on climate, competition, and insect drivers. We optimized growth, mortality, and insect models on all of the 323 CAFI PSPs used in this study. We found insect presence to be significantly associated with mortality but not growth (Cailleret et al., 2016). Including insect presence in our growth models increased the AIC, thus we used it only in our mortality models. The interactions between climate and competition variables were also considered; however, they did not contribute to reducing the AIC and were therefore excluded from the final models. We identified climate and competition effects associated with growth with the following model:

$$\frac{\log(\text{BA}_{i,j}) - \log(\text{BA}_{i,j-1})}{5} = \beta_0 + \beta_1 \text{Cl}_j + \beta_2 \text{Gyf}_j + \beta_3 \text{JVPD}_j + \beta_4 \text{JPrec}_j + \beta_5 \text{MAMT}_j + \gamma_i \quad (3a)$$

In equation (3a), JVPD_j is the July VPD, JPrec_j is the July precipitation, and MAMT_j is the March–May temperature. All other parameters are identical to equation (2a).

Similarly, we identified climate and competition effects associated with mortality with the following logistic regression (Luo & Chen, 2015; Van Mantgem et al., 2009):

$$\text{logit}(p_{i,j}) = \beta_0 + \beta_1 \text{Cl}_j + \beta_2 \text{Gyf}_j + \beta_3 \text{JVPD}_j + \beta_4 \text{JPrec}_j + \beta_5 \text{MAMT}_j + \beta_5 \text{insect}_j + \gamma_i \quad (3b)$$

In equation (3b), insect_j indicates the fraction of trees infested with insects with an intensity of >11%. All other parameters are identical to equations (2b, 3a).

Finally, we identified climate and competition effects associated with the plot insect infestation fraction using with the following model:

$$\frac{\text{ninsect}_{i,j}}{n_{i,j}} = \beta_0 + \beta_1 \text{Cl}_j + \beta_2 \text{Gyf}_j + \beta_3 \text{JVPD}_j + \beta_4 \text{JPrec}_j + \beta_5 \text{MAMT}_j + \gamma_i \quad (3c)$$

In equation (3c), all parameters are identical to equations (2c, 3a).

We next used models 3a–c on individual subclasses within the CAFI to further evaluate the effects of climate, competition, and insects on Alaskan forest demographic rates. We divided the CAFI into subclasses based on canopy status, size, and species. We divided PSPs by growing season length/light (latitude), mean annual precipitation (MAP), soil drainage conditions, topography (elevation, slope, aspect), and permafrost presence. For canopy status, trees were categorized as canopy or understory trees based on tree crown category in the CAFI. Trees were divided into three size classes with the following thresholds: $\text{DBH} < 9$ cm, $9 \text{ cm} \leq \text{DBH} < 20$, $\text{DBH} \geq 20$. We also categorized trees as angiosperm, gymnosperm,

trembling aspen (*Populus tremuloides* Michx.), birch (either *Betula kenaica* Evans and *Betula neolaska* Sarg.), black spruce (*Picea mariana* Mill.), or white spruce (*Picea glauca* Moench). PSPs were divided by latitude using 62.5° N as the dividing line. PSPs were also divided into low and high precipitation groups using $\text{MAP} > 400$ mm as the high precipitation group. Soils were divided into two moisture classes (indicated by the CAFI site description database): wet soils (encompassing peraquic, aquic, and subaquic soils) and dry soils (encompassing perhumid, humid, subhumid, subxeric, and xeric soils). PSP elevation ranged from ~16–920 m, and PSPs were divided into low elevation (<395 m) and high elevation groups (>395 m). PSPs were also divided by northern and southern aspect, by shallow (<9%), intermediate (9–20%), and steep (>20%) slope grade, and by permafrost presence or absence (indicated by CAFI site description database). We then recorded the range of values for significant ($p < .05$) fixed effects for all subclasses (Tables S2a–S4b) and computed the percent of subclasses for which each individual effect was significant (Figure 2b,d,f).

Changes in growth and mortality with age and successional status (Van Mantgem et al., 2009) were accounted for using two methods. First, we included gymnosperm fraction as a metric in all mixed models to control for changes in forest demographic rates due to the natural aging and/or successional process (Gyf, equations 2, 3a–c) (Luo & Chen, 2015). We also categorized PSPs based on stand age: young forests (33–80 years), mature forests (80–120 years), and old growth forests (>120 years) and examined demographic trends within each of these age groups (Luo & Chen, 2013; Zhang et al., 2015).

For our mixed models, we tested both SDI and basal area for the competition index parameter and found little difference in the significance or magnitude of the fixed effect. Our final analysis was performed using basal area. Similarly, both age and gymnosperm fraction behaved similarly in our model when controlling for changing demographic rates due to aging and/or succession. Because plot age is missing for ~4% of the PSPs used in our study, we used gymnosperm fraction in our final analysis.

Finally, we estimated the relative importance of each independent variable in our growth, mortality, and insect models in the time and climate models using variance decomposition (Chevan & Sutherland, 1991; Grömping, 2015). This method calculates goodness of fit measures for the entire hierarchy of linear (growth and insect fractions) and logistic (mortality) models using all combinations of variables to obtain the average independent contribution of climate, competition, insect effects, and time trends (Chevan & Sutherland, 1991).

Mixed effects model analyses were performed in MATLAB using fitglm. Our linear growth and insect models were fit assuming a normal distribution and identity link function. Our mortality models were fit using a binomial distribution and logistic link function. Standardized response coefficients in all mixed effects models were estimated using a maximum likelihood Laplace approximation. The relative importance of climate, competition, and insect factors to growth, mortality, and insect presence was calculated in R using

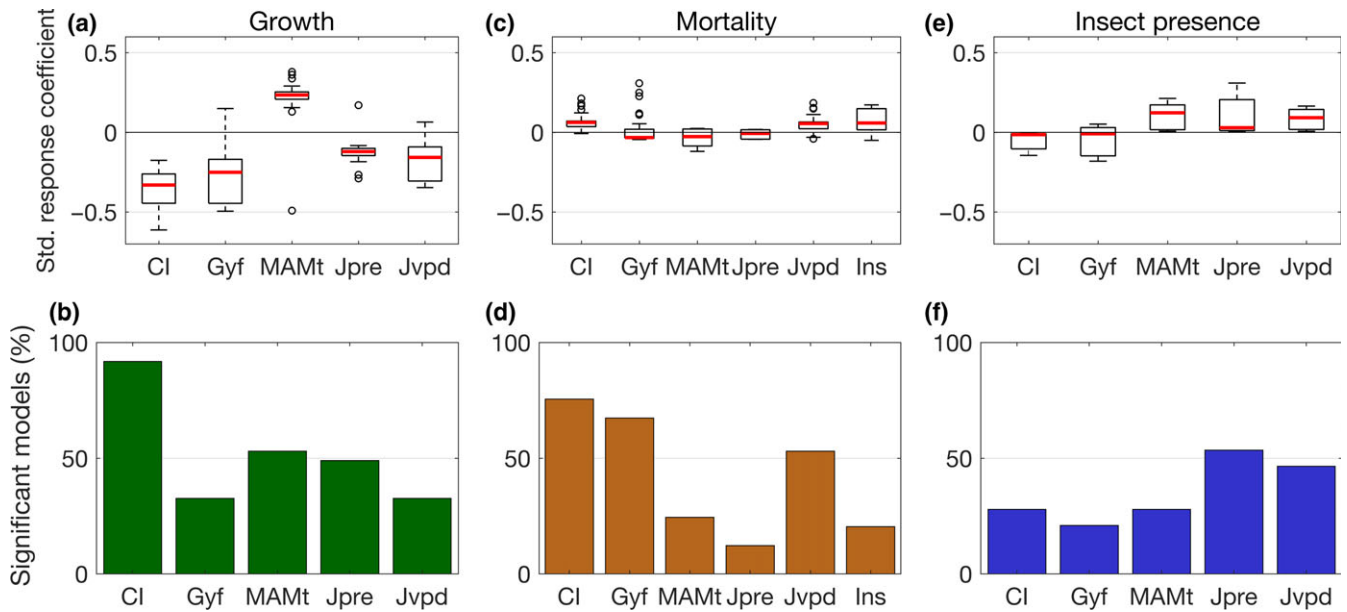


FIGURE 2 Climate, competition, and insect disturbance all affect tree demographic rates in interior and south-central Alaska. Standardized response coefficients for significant effects, and the corresponding percentage of mixed effects regression models in which each were significant ($p < 0.05$) for growth (a–b), mortality (c–d), and insect presence (e–f). Mortality probability was modeled as $\text{logit}(P) = \log\left(\frac{P}{1-P}\right)$, thus response coefficients for tree mortality were calculated as $\frac{\exp(\beta_0 + \beta_x)}{1 + \exp(\beta_0 + \beta_x)}$ where x corresponds to the standardized β coefficient fitted to CI, Gyf, MAMt, Jpre, Jvpd, or ins and where β_0 and β_x are from equations (3a–c) (Methods). Standardized response coefficients are shown for competition index (CI), forest gymnosperm fraction (Gyf), March–May temperature (MAMt), July precipitation (Jpre), July vapor pressure deficit (Jvpd), and insect presence (ins, mortality models only). For each model, we grouped inventory plots by stand age, geographic location, tree size, tree canopy status, soil moisture classification, topography, permafrost presence, MAP, and species (Tables S2a–S4b). In panels (a, c, e), red lines indicate the median explained variance; black boxes define the interquartile range; error bars represent 2.7 standard deviations [Colour figure can be viewed at wileyonlinelibrary.com]

hier.part. An equivalent analysis was performed to assess the importance of trends in growth, mortality, and insects with time. Our linear growth and insect models were fit assuming a normal distribution. Our mortality models were fit using a binomial distribution. Goodness of fit in all models was assessed using log likelihood. Model selection was based on minimum AIC and was tested on the inventory as a whole. We did not recalibrate or modify any models for individual subclasses within the CAFI. Codes are available upon request.

3 | RESULTS

We found significant declines in growth in two widespread boreal tree species, trembling aspen (*Populus tremuloides*) and black spruce (*Picea mariana*), and no significant change in growth in white spruce (*Picea glauca* Moench) and birch species (*Betula kenaica* Evans and *Betula neolaska* Sarg.) during the study interval, even after controlling for natural changes in demographic rates due succession and aging (see equation 2a) (Table 1). Contrary to expectations based on previous studies (Drobyshev et al., 2013), the relative strength of the growth decline was 3–5 times stronger in trembling aspen than in black spruce (Table 1) and was significantly associated with both competition and high summer VPD (Figures 2a–b, 3a–b).

Water availability, temperature, and competition all affected tree growth and mortality, though the relative importance of different drivers differed substantially between growth and mortality models (Figures 2,3; Tables S2a–b, S3a–b). Growth was negatively associated with increased competition, gymnosperm fraction, July VPD, and July precipitation, and positively associated with increased spring (March–May) temperature (Figure 2a–b). Of the factors tested, competition (~90% of growth models) followed by March–May temperature (~55% of growth models) were most frequently significant effects in our growth models. July precipitation and July VPD were significant in ~50% and ~35% of the growth models respectively (Figure 2b). Insect presence resulted in significant effects in fewer than 5% of our growth models and increased the AIC, thus we excluded insects from our growth analysis (Methods). Increased tree mortality was generally positively associated with competition, July VPD, and insect presence. The signs of the spring temperature and gymnosperm fraction effects were not consistent across species (Figure 2c–d, Tables S2a–b).

The relative importance of competition, water availability, and temperature to tree growth differed considerably between species (Figures 3b–c, 3e–f, S6). In particular, trembling aspen, an early-successional species adept at growing in dry conditions, recorded highly significant and negative associations between growth and both July VPD and competition, and a positive association between growth

TABLE 1 Changes in growth, mortality, and insect presence over the last two decades are evident but differ across species. The left column shows the relative importance (RI) (percent) determined from variance decomposition and the right column shows the standardized response coefficient (Std. RC) determined from mixed effect model analysis of trends in growth, mortality, and insect presence with time. Significance level is shown in parentheses. Nonsignificant effects ($p > .05$) are indicated by 'NS'

Model	Populus tremuloides		Betula kenaica/ nealaska		Picea glauca		Picea mariana	
	RI	Std. RC	RI	Std. RC	RI	Std. RC	RI	Std. RC
Growth	19.79	-0.28 ($\ll 0.0001$)	1.46	NS	0.97	NS	6.50	-0.056 (0.026)
Mortality	41.46	0.24 ($\ll 0.0001$)	3.23	NS	3.65	NS	3.34	NS
Insect	40.76	0.014 (0.013)	3.34	NS	51.64	-0.0026 (0.0031)	68.60	-0.0081 (0.044)

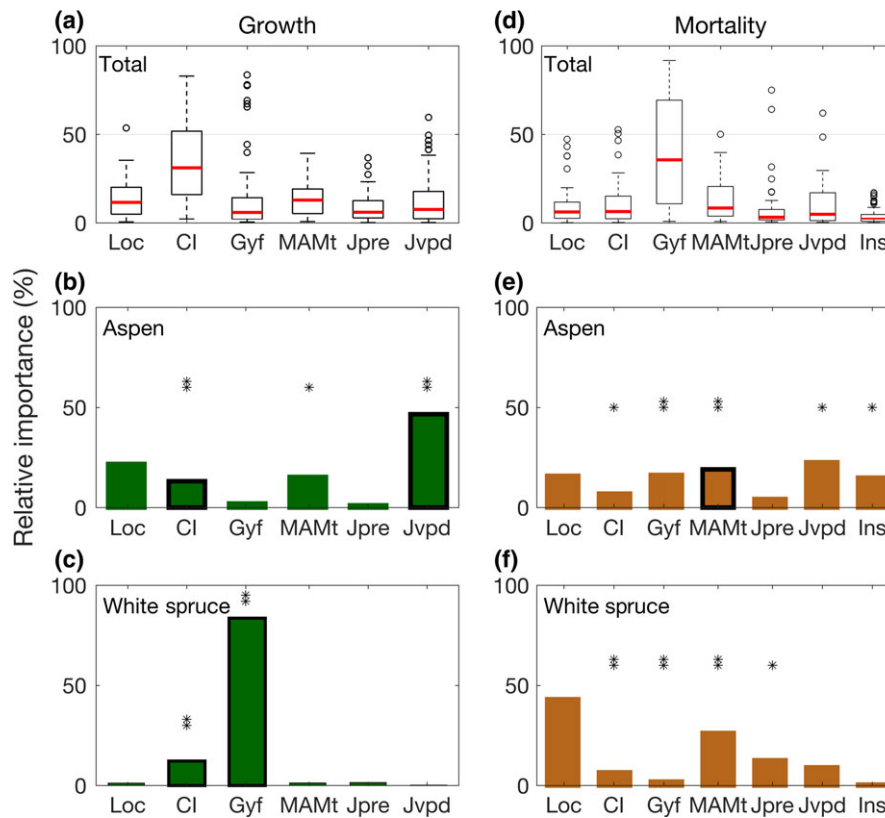


FIGURE 3 The relative importance of climate, competition, and insect disturbance differs substantially depending on species. Relative importance (%) of plot-specific location effects (Loc), competition index (CI), forest gymnosperm fraction (Gyf), March–May temperature (MAMt), July precipitation (Jpre), July vapor pressure deficit (Jvpd), and insect presence (ins, mortality models only) to the total explained variance in growth (a–c) and mortality (d–f) for all models (a, d) and end member species (b–c, e–f). For (a, d) we grouped inventory plots by stand age, geographic location, tree size, tree canopy status, soil moisture classification, topography, permafrost presence, MAP, and species (Tables S2a–S4b). In panels (a, d), red lines indicate the median explained variance; black boxes define the interquartile range; error bars represent 2.7 standard deviations. In panels (b–c, e–f), black outlines indicate a significant negative effect on growth or decreased mortality as indicated through the mixed effects model analysis. An asterisk indicates effects significant at $p < .05$ and a double asterisk indicates effects significant at $p < .001$ in mixed effects models [Colour figure can be viewed at wileyonlinelibrary.com]

and spring temperature (Figure 3b; Tables S2a–b). However, the negative July VPD association in aspen had a relative importance value 2–3 times larger compared the temperature and competition effects (Figure 3b). In contrast, growth variability in white spruce was predominantly associated with competition and gymnosperm fraction (Figure 2c).

The relative importance of different climate and competitions drivers associated with tree mortality differed substantially from

those that associated with growth. It was also more difficult to explain the variance in tree mortality compared to tree growth using the same climate and competition effects (the average R^2 for the growth models was 0.76, in contrast to an average R^2 of 0.54 for the mortality models). For mortality of trembling aspen, the relative importance of most drivers, including competition, climate (excluding July precipitation), and insect presence, was similar (Figure 3e). However, increased mortality in white spruce was primarily associated

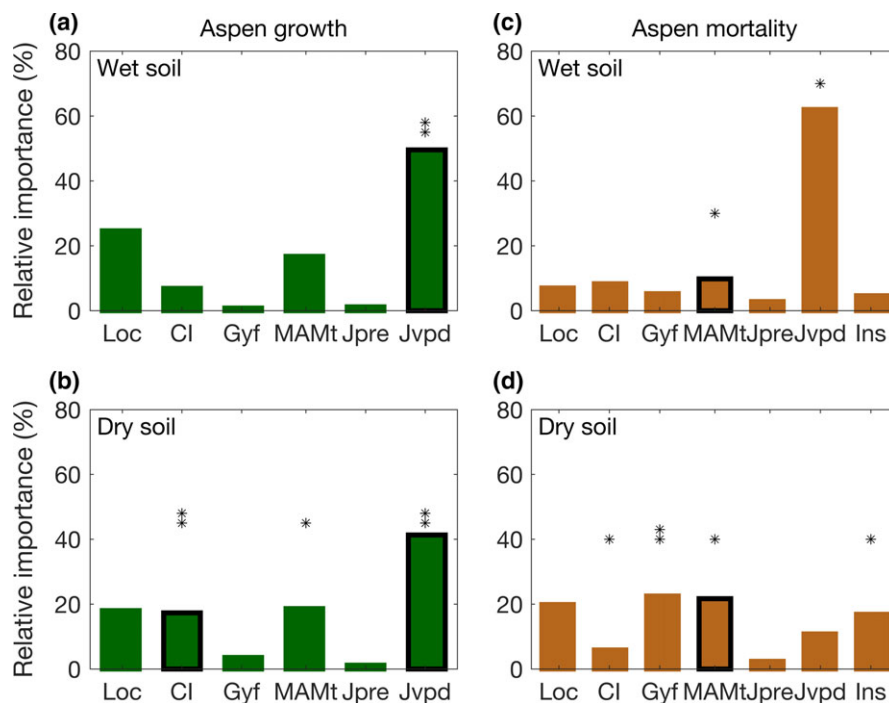


FIGURE 4 Midsummer vapor pressure deficit particularly affects trembling aspen growth in wetter soils. Relative importance (%) of plot-specific location effects (Loc), competition index (CI), forest gymnosperm fraction (Gyf), March–May temperature (MAMt), July precipitation (Jpre), July vapor pressure deficit (Jvpd), and insect presence (ins, mortality model only) to the total explained variance in growth and mortality for aspen trees in plots grouped by wet soils (encompassing paraquic, aquic, and subaquic soils) (a, c) and dry soils (encompassing perhumid, humid, subhumid, subxeric, and xeric soils) (b, d). Black outlines indicate a significant negative effect on growth or decreased mortality as indicated through the mixed effects model analysis. An asterisk indicates effects significant at $p < .05$ and a double asterisk indicates effects significant at $p < .001$ in mixed effects models [Colour figure can be viewed at wileyonlinelibrary.com]

with warmer spring temperatures, and to a lesser extent, July precipitation, July VPD, and competition (Figure 3f, Tables S3a–b). Of the other species tested, including birch and black spruce, the relative importance of climate and competition for tree growth and mortality varied along a spectrum between the responses observed for white spruce and aspen (Fig. S5).

High July VPD was associated with growth declines in aspen trees regardless of soil moisture conditions (Figure 4a–b). Furthermore, VPD effects were significantly more important than the influence of competition and spring temperature. However, the relative importance of July VPD decreased at higher MAP (Fig. S6a–b). The relative importance of July VPD was larger than that of July precipitation except at high MAP (Figures 3a, 4a–b, S6a–b). In contrast, warmer springs were associated with increased aspen growth; however, the relative importance of spring temperature was a factor of 2–5 smaller than July VPD under most conditions (Figures 3b, 4a–b, S6a–b; Tables S2a–b).

Significant increases in mortality were recorded only for aspen during the study period (Table 1). This increase corresponded to an increase in aspen insect pests (predominantly aspen leaf miners and defoliators), a smaller but significant decrease in white spruce and black spruce pests (primarily aphids and some spruce budworms and bark beetles), and no significant change in birch pests (predominantly defoliators and leaf rollers) (Table 1). There were also interactions between climate and insect presence. High July VPD and high spring

temperature were associated increased insect presence (Figure 2e; Tables S4a–b). Furthermore, increased aspen mortality was associated with both insect presence and high July VPD, depending on MAP and soil moisture conditions (Figure 4c–d, S6).

4 | DISCUSSION

We document here differential effects of climate drivers on dominant boreal tree species in Alaska, which have both similarities and differences with recent studies of Alaskan and Canadian forests. Previous site-level studies have recorded significant growth declines for white spruce trees in interior Alaska (Barber et al., 2000; Beck et al., 2011), and tree ring analyses have documented white spruce growth declines in western Canada (Hogg, Michaelian, Hook, & Undersultz, 2017); however, we did not find significant trends in white spruce growth during the study period (Table 1). It is possible that these different results arise from differences in sample location (Hogg et al., 2017), time period, or spatial scale (Nicklen et al., 2016). We also found no significant growth or mortality trends for birch species, contrary to an inventory study in central Canada (Zhang et al., 2015). However, earlier studies have found aspen, a typical early-successional canopy species, to be more moisture limited than birch, a more shade-tolerant subcanopy species (Huang et al., 2010). This difference in microenvironment could account for the different

climate responses of birch and aspen in the CAFI. Indeed, we do find the relative importance of July VPD in our growth models to be significant for canopy trees and not understory trees (Table S2a).

Pervasive increases in tree mortality spanning multiple species have been recorded in the lower latitude Canadian boreal forest (Luo & Chen, 2015; Michaelian, Hogg, Hall, & Arsenault, 2011; Peng et al., 2011; Zhang et al., 2015). Two studies attributed the increase in mortality predominantly to increased competition associated with climate change (Luo & Chen, 2015; Zhang et al., 2015). In contrast, Peng et al. (2011) attributed the increase in mortality to increasing drought conditions. In this study, we document that high midsummer evaporative demand and increased competition were associated with increased Alaskan tree mortality, yet results differed substantially by species. We also found significant declines in growth in both aspen and black spruce trees; perhaps precluding elevated mortality in the coming decade (Cailleret et al., 2016; Kane & Kolb, 2014). However, contrary to the overarching theme of declining forest vitality, we found that the climate-mortality response of angiosperms and gymnosperms was partially compensating at an ecosystem-level, such that the differential responses of these clades led to a less severe overall regional response in growth. Surprisingly, we also found that gymnosperm species had negative growth associations related to increased July precipitation, perhaps due to an interaction with solar insolation. Lastly, we found significant increases in July VPD and insect-driven mortality in aspen trees associated with a severe ongoing leaf miner outbreak (Doak & Wagner, 2015; Wagner & Doak, 2013; Wolken et al., 2011), and additional evidence that elevated leaf miner presence was associated with high midsummer evaporative demand (Tables S4a-b), perhaps due to decreased aspen insect defenses resulting from unfavorable climate conditions (Allen, Breshears, & McDowell, 2015).

Collectively, these results show that stress due to atmospheric water limitation is most evident in an early-successional angiosperm species, trembling aspen, irrespective of soil moisture conditions. This indicates that recorded growth declines were primarily related to higher evaporative demand associated with warmer summer temperatures, rather than decreased soil water availability (Hogg et al., 1999). Though no significant climate trends occurred in July VPD during the study period, increased variability in summer VPD, and particularly VPD during the summer of 2009 which exceeded 2 standard deviations above mean summer VPD, may have caused tree growth declines through structural overshoot and/or increased drought legacy effects (Anderegg et al., 2015; Jump et al., 2017). These findings are supported by observations that tree growth is becoming increasingly limited by atmospheric VPD in locations across latitudes ranging from Arizona to the Pacific Northwest (Restaino, Peterson, & Littell, 2016), hypotheses that atmospheric drought is causing declines in white spruce and black spruce productivity in interior Alaska (Beck et al., 2011; Walker et al., 2015), preliminary observations of increased aspen drought stress in interior Alaska (Juday, Grant, & Spencer, 2012), and documentation of major drought-induced aspen dieback in the lower Canadian boreal forest (Michaelian et al., 2011).

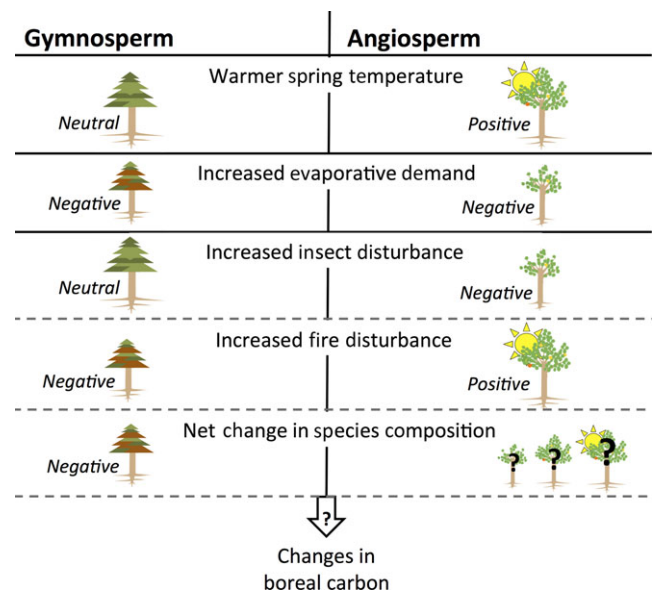


FIGURE 5 The competing effects of warmer springs, drier summers, and increased insect pests will determine future boreal productivity. Outcomes for gymnosperm (left) and angiosperm (right) vitality can differ. The bottom section shows the expected effect of changes in fire on species presence (Barrett et al., 2011; Hollingsworth et al., 2013; Johnstone & Chapin, 2006). Given that fire frequency and severity are expected to increase the prevalence of early-successional angiosperm species, it is particularly important to understand how changing climate conditions impact angiosperm demographic rates [Colour figure can be viewed at wileyonlinelibrary.com]

Site-level studies have documented declining tree growth associated with drought stress in interior Alaska. We demonstrate that these trends scale across broader areas and are additionally present in key angiosperm species. These climate impacts may hold even more ecological significance in the coming century if a strengthening of the fire regime causes aspen to become more prevalent across the Alaskan landscape (Barrett et al., 2011). With projected increases in temperature and evaporative demand, both spring warming and summer VPD will likely become increasingly important, affecting forest composition and carbon drawdown (Figure 5). Our analysis shows that increased midsummer VPD can counteract and often exceeds positive benefits of increased growing season length due to spring warming, resulting in a net negative trend in growth for early-successional aspen trees with current climate change. These results can help inform larger scale projections for the western North American boreal forest by quantifying the relative importance of spring warming, summer water limitation, and insect presence to tree growth and mortality, enabling better projections of the future vitality and carbon storage in the western boreal forest of North America.

Further data, in both time and space, would be useful to test the ideas presented here. Though the CAFI provides a thorough, well-sampled spatial extent, its census interval is shorter than other Canadian analyses (Luo & Chen, 2015; Zhang et al., 2015). However, the CAFI is the only inventory study with substantial temporal coverage over the past decade (Fig. S1) that spans a range of environmental

conditions from interior to south-central Alaska. The geographic extent of this analysis encompasses comparable or broader spatial scales than previous studies of the Alaskan boreal forest (Barber et al., 2000; Beck et al., 2011; Nicklen et al., 2016; Walker et al., 2015). Nevertheless, the inventory plots are all located within 10 miles of road ways and the plots do not sample the Arctic-boreal boundary, where some greening has been associated with warming temperatures (Beck & Goetz, 2012). The lack of coverage at the highest forest latitudes would preclude our detection of possible increases in productivity associated with greening (Beck & Goetz, 2012). On the other hand, satellite-observed greening trends in the North American boreal forest are fragmented and attribute substantial browning in Alaska to drought stress concurrent with warming (Xu et al., 2013; Zhou et al., 2001), results that are consistent with this analysis.

In conclusion, our analysis indicates that competition, climate, and insect disturbance interact to influence growth and mortality in the Alaskan boreal forest. However, the complexity of species-specific responses to spring temperature, midsummer water limitation, and insect-related mortality makes it difficult to anticipate the net effect of changes in climate on boreal forest vitality and carbon storage (Figure 5). The negative association between July VPD and trembling aspen growth is particularly surprising because aspen is a widespread boreal angiosperm species that is adept at growing in dry conditions. Given that recent fires in Alaska have the potential to increase angiosperm coverage by up to 20% in the Alaskan boreal forest in the near future (Barrett et al., 2011; Zhu & Mcguire, 2016), and that the negative effect of July VPD can be 2–5 times larger than the positive effect of spring warming under most environmental conditions, it is essential to better understand the climate drivers impacting boreal aspen growth to anticipate how future climate conditions may affect overall Alaskan forest health, resilience, and carbon drawdown.

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