




## RESEARCH ARTICLE

# Boreal tree growth exhibits decadal-scale ecological memory to drought and insect defoliation, but no negative response to their interaction

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**Abstract**

1. Interactions between drought and insect defoliation may dramatically alter forest function under novel climate and disturbance regimes, but remain poorly understood. We empirically tested two important hypotheses regarding tree responses to drought and insect defoliation: (a) trees exhibit delayed, persistent, and cumulative growth responses to these stressors; (b) physiological feedbacks in tree responses to these stressors exacerbate their impacts on tree growth. These hypotheses remain largely untested at a landscape scale, yet are critical for predicting forest function under novel future conditions, given the connection between tree growth and demographic processes such as mortality and regeneration.
2. We developed a Bayesian hierarchical model to quantify the ecological memory of tree growth to past water deficits and insect defoliation events, derive antecedent variables reflecting the persistent and cumulative effects of these stressors on current growth, and test for their interactive effects. The model was applied to extensive tree growth, weather, and defoliation survey data from western and eastern regions of the Canadian boreal forest impacted by recent drought and defoliation events and characterized by contrasting tree compositions, climates, and insect defoliators.
3. Results revealed persistent negative tree growth responses to past water (all trees) and defoliation (host trees) stress lasting 3–6 and 10–12 years, respectively, depending on study region. Accounting for the ecological memory of tree growth to water and defoliation stress allowed for detection of interactions not previously demonstrated. Contrary to expectations, we found evidence for positive interactions among non-host trees likely due to reduced water stress following defoliation events. Regional differences in ecological memory to water stress highlight the role of climate in shaping forest responses to drought.

4. *Synthesis.* Study results suggest negative feedbacks in tree responses to drought and insect attack may be weaker than predicted for defoliator-dominated boreal forest systems. Instead, insect defoliation may offset the impacts of water deficit on boreal tree growth by reducing transpirational water demand. This offset mimics increased resistance to drought following forest thinning and may lessen growth and mortality losses due to increased aridity and more severe insect damage forecast for the boreal forest under global change.

#### KEYWORDS

Bayesian hierarchical model, boreal forest, drought, ecological memory, ecophysiology, forest tent caterpillar, global change ecology, insect defoliation, spruce budworm, tree rings

## 1 | INTRODUCTION

The boreal forest is a disturbance-driven ecosystem, defined by the interplay of droughts, insect damage, pathogens/disease, and stand-replacing fire (Fleming, 2000; Girardin et al., 2013). Increased temperatures and aridity forecast for much of the boreal forest under global climate change have the potential to fundamentally alter historical boreal disturbance regimes (Allen, Breshears, & McDowell, 2015; Price et al., 2013). In particular, severe drought events characterized by high temperatures are already occurring in boreal regions of western North America (Hogg, Brandt, & Kochtubajda, 2002; Hogg, Brandt, & Michaelian, 2008; Michaelian, Hogg, Hall, & Arseneault, 2011; Peng et al., 2011). Further, the severity, extent, and duration of defoliating insect outbreaks have increased in recent decades (Blais, 1983; Pureswaran et al., 2015; Roland, 1993). Changing climatic conditions are likely an important contributor to changes in defoliator population dynamics (Cooke, Nealis, & Régnière, 2007; Price et al., 2013). Both drought and insect defoliation can severely impact boreal forest function causing growth reductions and large-scale forest mortality with lasting impacts on the global carbon cycle, regional timber supplies, and an array of other ecosystem services (Hicke et al., 2012; Kurz et al., 2008; Pothier, Elie, Auger, Mailly, & Gaudreault, 2012; Price et al., 2013).

A number of studies have demonstrated spatio-temporal synchrony between drought and defoliating insect damage in the boreal forest (De Grandpré et al., 2018; Flower, Gavin, Heyerdahl, Parsons, & Cohn, 2014; Hogg, Brandt, & Kochtubajda, 2005). Several physiological feedbacks in tree responses to drought and insect defoliation have been proposed to explain the synchrony of such events. First, insect defoliation may reduce tree growth and xylem formation making trees more susceptible to future drought (Anderegg & Callaway, 2012; Jacquet, Bosc, O'Grady, & Jactel, 2014). Second, limited available carbon and water in drought-stressed trees may reduce metabolic defences against defoliating insects (McDowell et al., 2008, 2011). Finally, reductions in carbon uptake due to the combination of drought and insect defoliation may deplete non-structural carbohydrates and increase the risk of carbon starvation (Hogg et al., 2008).

In contrast to negative physiological feedbacks in tree responses to drought and insect defoliation described above, positive interactions between these stressors have also been proposed. For example, water stress may increase the concentration of secondary metabolites in leaves making them less palatable to defoliating insects (Mattson & Haack, 1987). Further, moderate defoliation may decrease the impact of drought events by reducing tree density and leaf area (Jacquet et al., 2014). The nature of interactive effects of drought and insect defoliation on tree growth and mortality remain unclear (Kolb et al., 2016). Previous studies indicate both positive and negative impacts of drought on tree resistance to insect defoliation and vice versa depending on the severity of the drought or defoliation event (Jactel et al., 2012).

Uncertainty in physiological mechanisms underlying feedbacks between drought and insect defoliation stress highlights the importance of empirical studies to test for their interactive effects (Anderegg, Hicke, et al., 2015). To date, few studies have explicitly tested for empirical evidence of interactive effects of drought and defoliation—none of which found evidence of interactions (Chen et al., 2018; Jacquet et al., 2014; but, see Sangüesa-Barreda, Camarero, Oliva, Montes, & Gazol, 2015 for evidence of negative interactions between drought and fungal pathogens). Detecting interactive effects of drought and insect defoliation on tree growth and mortality is complicated given that physiological responses to these stressors may be delayed or persist following a disturbance event (Anderegg et al., 2013; Hogg et al., 2005; Pothier, Mailly, & Tremblay, 2005; Pothier et al., 2012; Worrall et al., 2010). Further, physiological responses to past disturbance events may weaken a tree's ability to respond to future disturbances (Anderegg et al., 2013; Camarero et al., 2018); that is, there is a cumulative effect of drought and insect defoliation.

Potential delayed, persistent, and cumulative responses make it difficult to model the interactive effects of drought and insect defoliation using only current observations of forest conditions. Classical approaches to overcome this issue involve applying lagged variables (e.g., water availability in the year previous to growth) to estimate tree growth or mortality or comparing growth trends before and after a disturbance event (Anderegg, Schwalm, et al., 2015; Camarero et al., 2018). An alternative approach, based on recent advances in

statistical ecology, is to quantify the ecological memory of a forest to drought and insect defoliation. As defined in Ogle et al. (2015), ecological memory describes the influence of past conditions on current ecosystem function and comprises three components: the length of memory (similar to legacy effects quantifying the persistence of ecosystem responses to a disturbance event—see Anderegg, Schwalm, et al., 2015), the relative importance of past conditions over the memory period, and the cumulative effect of past conditions on current function. Quantifying the ecological memory of study trees to drought and insect defoliation allows for novel insights into the nature of boreal forest responses to these stressors. Further, it improves our ability to detect interactions due to physiological feedbacks by providing temporally averaged estimates of drought and defoliation conditions over the period of forest responses.

In the current study, we developed a Bayesian hierarchical model to quantify the ecological memory of trees to water deficit and insect defoliation allowing for the detection of delayed, persistent, and cumulative growth responses to these stressors. Further, the model tests for interactive effects of antecedent water and insect defoliation stress on tree growth. The model was applied to extensive tree-ring width, interpolated climate, and aerial defoliation datasets from western and eastern regions of the Canadian boreal forest characterized by contrasting climates, species compositions, and primary defoliating insect species. The use of two contrasting boreal study systems highlights the generalizability of the model and allows for a robust interpretation of interactions between drought and insect defoliation. Our analysis focused on tree growth responses alone; however, there is evidence of strong connections between tree growth and vital forest demographic rates including tree mortality (Berdanier & Clark, 2016; Buechling, Martin, & Canham, 2017; Das, Battles, Stephenson, & van Mantgem, 2007; Das, Stephenson, & Davis, 2016; van Mantgem et al., 2003; Wyckoff & Clark, 2000, 2002).

Based on current physiological understanding, we hypothesized that in both boreal study regions: (1) tree growth would exhibit persistent negative responses to water deficit with deficits in the year previous to the current growing season having the greatest relative importance for growth; (2) host tree growth would exhibit persistent negative responses to insect defoliation for multiple years following a defoliation event; (3) antecedent water and insect defoliation stress would have a negative interactive effect on host tree growth. In addition to testing each of these hypotheses, we further compared the ecological memory of trees to water deficit and insect defoliation across the two study regions.

## 2 | MATERIALS AND METHODS

### 2.1 | Study Regions

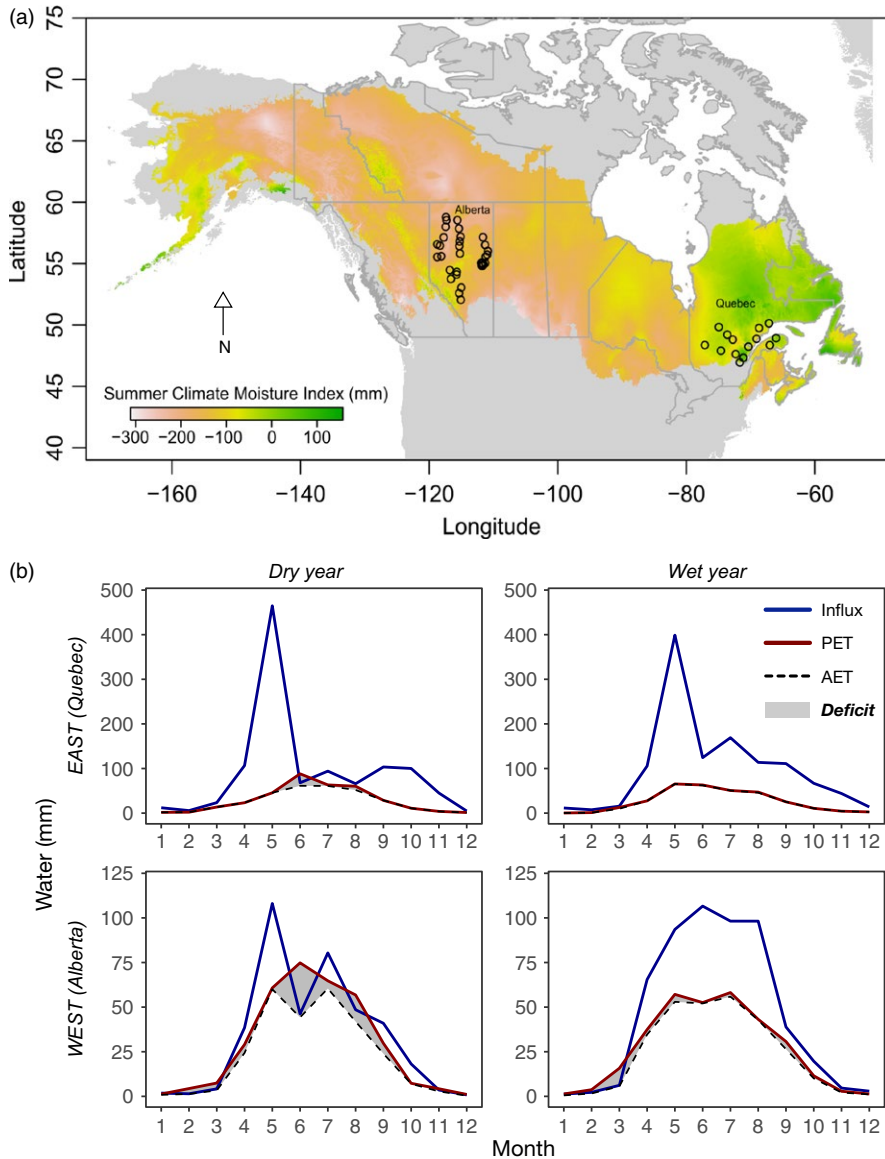
#### 2.1.1 | West

The western study region is located in Alberta, Canada and consists of 34 mixed-wood boreal stands in the interior plains

extending from 52.0 to 59.0°N and 111.0 to 119.5°W (Figure 1a). Study stands are predominantly composed of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* Moench) and established post stand-replacing fire. The higher growth rate of aspen relative to spruce leads to a bimodal diameter distribution early after stand establishment until spruce moves into the canopy as a co-dominant species (Huang, Stadt, Dawson, & Comeau, 2013). The region is defined by a continental climate (cold winters, hot and dry summers) with chronic summer water deficits (Figure 1b). Annual mean monthly temperature and total annual precipitation (1970–2000) ranged from  $-0.8$  to  $2.8^{\circ}\text{C}$  and 370–615 mm (25%–35% falling as snow) across the region (Fick & Hijmans, 2017). The study period for the West (1968–2010) includes the occurrence of a severe regional drought in 2001–2002, which led to widespread tree growth reductions (Chen, Huang, Alam, et al., 2017; Hogg et al., 2005, 2008; Hogg, Michaelian, Hook, & Undershultz, 2017). Forest soils in the western study region consist of orthic grey luvisols and brunisols with silty to clay-loam texture derived from glacial till and glaciolacustrine deposits (Huang et al., 2013). The forest tent caterpillar (*Malacosoma disstria* Hub., hereafter “FTC”) is the primary defoliating insect within western study stands attacking the regionally abundant trembling aspen (Brandt, Flannigan, Maynard, Thompson, & Volney, 2013). During its larval stage, the FTC, a univoltine lepidopteran, defoliates aspen shortly after leaf out for a 5–6 week period until pupations in mid-to-late June (Parry, Spence, & Volney, 1998). Outbreaks can last for one to several years (Price et al., 2013). Trees are able to produce a second flush of leaves after the FTC has pupated (Cooke et al., 2007). Outbreaks of the FTC have been linked to regional growth declines in aspen as well as large-scale mortality when outbreaks co-occur with droughts or extreme temperatures (Hogg et al., 2005).

#### 2.1.2 | East

The eastern study region is located in Quebec, Canada and comprises 14 coniferous boreal stands within the Forest Ecosystem Research and Monitoring Network, extending from 47.0 to 50.1°N and 66.1 to 75.0°W (Figure 1a). Stands are dominated by black spruce (*Picea mariana* Mill.) or balsam fir (*Abies balsamea* L.) accompanied by white birch (*Betula papyrifera* Marsh.), trembling aspen, white spruce, and jack pine (*Pinus banksiana* Lamb.). Annual mean monthly temperature (1970–2000) ranged from  $-0.3$  to  $3.2^{\circ}\text{C}$ , while total annual precipitation ranged from 860 to 1,600 mm (Fick & Hijmans, 2017). Spring snow melt is an important water source in the eastern study region replenishing soil water prior to the growing season (Girardin, Tardif, Flannigan, & Bergeron, 2004; Figure 1b). Soils in the eastern study region consist mainly of orthic ferro-humic podzols and gleysols derived from glacial till as well as glaci-oluvial and glaciolacustrine deposits with soil depths ranging from 30 to 60 cm (Ouimet, Duchesne, Houle, & Arp, 2001). Defoliation in the eastern study region is caused by outbreaks of the eastern spruce budworm (*Choristoneura fumiferana* Clem., hereafter “SBW”), which occur every circa 35 years and can persist 4–12 years or more in a given stand



**FIGURE 1** (a) Location of study stands within western (Alberta: 34 stands) and eastern (Quebec: 14 stands) study regions relative to mean summer (June to August) climate moisture index (CMI) values (1970–2000, Fick & Hijmans, 2017). (b) Mean monthly water balance for eastern (1968–1998) and western (1968–2010) study stands (dry and wet years correspond to the 10th and 90th percentiles of mean annual CMI respectively). Water balance terms are defined as Influx: precipitation + snow melt; PET: potential evapotranspiration; AET: actual evapotranspiration; Deficit: PET - AET

(Gray, 2008). Balsam fir is the primary SBW host in the East with white and black spruce also susceptible to attack during severe defoliation events (Nealis & Régnière, 2004). The larval feeding of the SBW, also a univoltine lepidopteran, is approximately 6 weeks from early-to-mid May until mid-to-late June depending on the region (Régnière, St-Amant, & Duval, 2012). Larvae feed primarily on current year foliage and require multiple years to kill a host tree (Gray, 2008). SBW outbreaks, given their extent and severity, are one of the most damaging natural disturbance types in the Canadian boreal forest (Fleming, 2000).

## 2.2 | Data

Variable-length belt transects were used to sample tree growth in the 34 western study stands between 2010 and 2011 (Figure 1a). Approximately 10 white spruce trees from a range of size classes and 15 dominant or co-dominant aspen trees were sampled within each transect. Either two radial increment cores were collected on opposite sides of a sampled tree or entire cross-sections were

obtained through harvesting. All radial growth sampling was done at breast height (1.3 m). Cores and cross-sections were dried, mounted, and sanded. Ring widths were measured using a Velmex measuring stage (increment cores) or WinDendro (cross-sections) to the closest 0.01 mm. A total of 919 tree growth series were used in the analysis: 471 white spruce and 448 trembling aspen. Additional details on the western tree growth data can be found in Chen, Huang, Alam, et al. (2017), Chen et al. (2018), and Chen, Huang, Stadt, et al. (2017)

Fixed area plots (0.25 ha) were established in each of the 14 eastern study stands in 1986–1998 (Figure 1a). Between 1996 and 1998, radial increment cores were collected at breast height from 25 to 50 healthy trees along the border of each plot. Two increment cores were taken from opposite sides of each tree. Cores were dried, mounted in wooden blocks, and sanded. Ring widths of all cores were measured to the nearest 0.01 mm under 40× magnification. A total of 622 tree growth series were used in the analysis, mostly black spruce (340) and balsam fir (207), as well as jack pine (35), white spruce (30), and white birch (10).

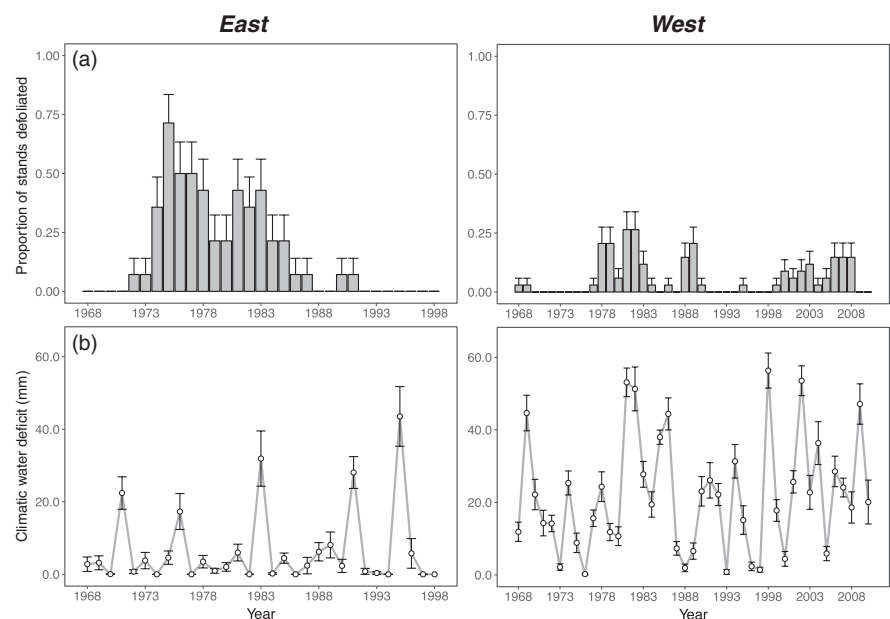
Tree-ring cross-dating in both study regions was done visually and verified statistically with COFECHA (Grissino-Mayer, 2001). Replicate ring widths resulting from the collection of multiple increment cores per tree were averaged to produce a single radial growth record for each sampled tree in the East and West. Trees were classified as hosts or non-hosts for the dominant regional defoliating insect based on species (SBW: balsam fir, black/white spruce; FTC: trembling aspen). Study stands are relatively young in both regions (Supporting Information Figure S2). As such, we included dominant/co-dominant (canopy) and intermediate/subordinate (understorey) trees in the analysis to account for the fact that current canopy trees may have been in the understorey within the study period. The inclusion of understorey trees is particularly important to assess defoliation impacts as understorey host trees in the boreal forest have been shown to suffer greater damage and mortality risk due to insect defoliation (Cooke et al., 2007). The provinces of Quebec and Alberta began conducting aerial defoliation surveys in 1967 and 1939, respectively, to estimate the extent and severity of damage caused by major forest pests (Ministère des Forêts, de la Faune et des Parcs, 2016; C. Whitehouse, Alberta Ministry of Agriculture and Forestry, pers. comm., March 21, 2017). Derived maps indicate annual defoliation attributable to regionally dominant defoliators in each region (SBW in the East, FTC in the West, note ~3% of defoliation in the West is due to the large aspen tortix [*Choristoneura conflictana* Walker] for which trembling aspen is the primary host). Defoliation is recorded using ordinal severity classes (approximate defoliation severity classes—Light: <35%, Moderate: 35%–70%, Severe: >70%, Mortality: clear signs of defoliation-related tree mortality; Government of Alberta, 2012; Ministère des Forêts, de la Faune et des Parcs, 2016). We defined a stand-scale annual binary defoliation variable with a value of 1 if a mapped defoliation event of moderate or higher severity (>35% defoliation) intersected a study stand, and 0 otherwise. The binary defoliation variable definition is based on

previous studies indicating increased risk of boreal tree mortality at stand-scale defoliation levels above 40% (Erdle & MacLean, 1999). Further, the accumulation of moderate-to-severe stand-scale defoliation across years has been shown to be a strong predictor of defoliation-related growth losses and increased risk of mortality (Chen, Weiskittel, Bataineh, & MacLean, 2017). The binary defoliation variable defined using a moderate severity threshold is consistent with previous studies of defoliation impacts in both study regions (Chen et al., 2018; Pothier et al., 2012). The start of the study period in the eastern and western regions was set to 1968 to be consistent with the availability of defoliation data in both study regions.

Host trees in eastern study stands experienced high levels of SBW defoliation between 1972 and 1986 (Figure 2a) coincident with the last major outbreak event when SBW defoliated 14 million ha per year on average in Quebec (Duchesne & Ouimet, 2008). Peak SBW defoliation damage occurred in 1975. Host trees in western study stands experienced FTC defoliation between 1978–1989 and 2000–2008 based on aerial defoliation surveys (Figure 2a). These periods are consistent with independent tree-ring reconstructions of FTC defoliation periods in the western study region (Hogg et al., 2005, 2008). There was no observable difference in the mean age of eastern and western study stands in defoliation versus non-defoliation years (Supporting Information Figure S2).

Monthly weather data (1950–2012) were generated for each study stand using the BioSim interpolation model (Régnière, 1996) based on a network of 365 weather stations in the East and 456 in the West. We applied a water balance model adapted from Lutz, Van Wagtenonk, and Franklin (2010) to estimate monthly potential evapotranspiration (PET), actual evapotranspiration (AET), and climatic water deficit (PET–AET). The model carries water balance over from month-to-month and accounts for spring soil water recharge. PET was estimated using a modified Hargreaves equation based on monthly averages of daily minimum/maximum temperature

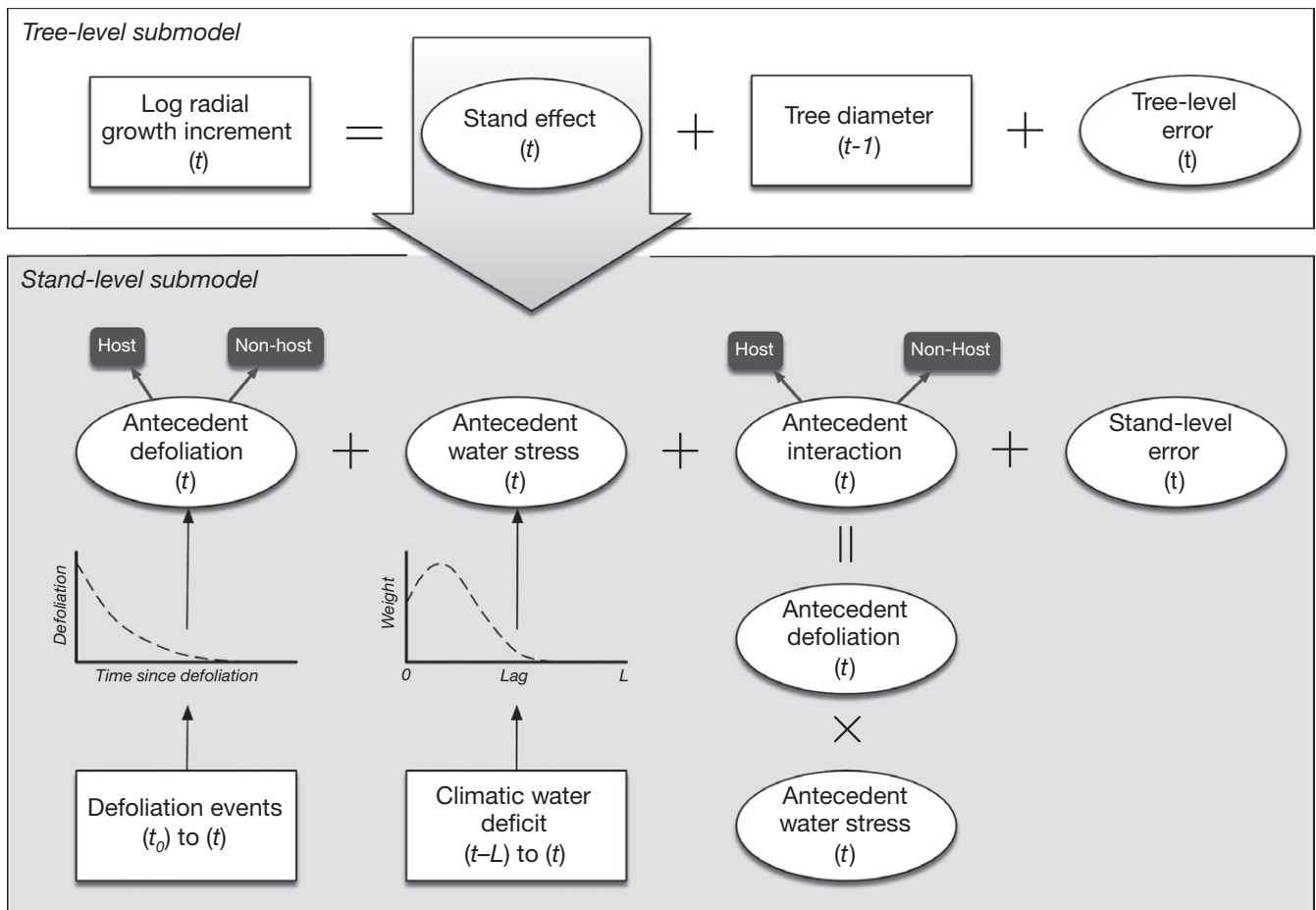
**FIGURE 2** Proportion of study stands (total number of stands equals 14 in East and 34 in West) with moderate-to-severe defoliation damage observed during annual aerial defoliation surveys (a) and mean climatic water deficit estimates across study stands (b). Error bars indicate standard error



and incoming solar radiation, total monthly precipitation, and latitude (Beguiría, Vicente-Serrano, Reig, & Latorre, 2014). Estimates of soil water holding capacity were necessary to derive AET. Mean soil water holding capacity was estimated for eastern study stands by converting granulometric content of unique soil horizons applying equations from Saxton & Rawls (2006) with weights corresponding to horizon thickness. Granulometric content was estimated based on laboratory analysis of four 1-m<sup>2</sup> soil pits dug in each study stand. Less detailed soil data were available for western study stands. Ordinal estimates of soil water holding capacity for western stands were obtained from the Canadian Soil Information Service (Soil Landscapes of Canada Working Group, 2010) and were converted to numeric estimates by taking the median value of each ordinal category. Monthly climatic water deficit estimates were summed across growing season months (June through August) to calculate a cumulative, annual water deficit, which was used as a driver of tree growth (see Section 2.3). High average climatic water deficits were observed in the East in 1983, 1991, 1995, and in the West in 1981–1982, 1998, 2002, intersecting a subset of years with high defoliation levels in both study regions (Figure 2).

### 2.3 | Model specification

Our Bayesian hierarchical model consists of tree- and stand-level submodels (Figure 3). The tree-level submodel estimates annual radial growth increment on the log scale as a function of a time-varying stand effect reflecting stand-level growing conditions, and a tree's diameter in the previous year. The stand-level submodel estimates the time-varying stand effect as a function of antecedent climatic water deficit and insect defoliation derived using ecological memory functions. The effects of antecedent variables within the stand-level submodel are based on mean tree growth after controlling for individual tree size averaging across individual growing conditions including competition and microclimates. Based on studies demonstrating forest growth responses to insect defoliation are modified by stand structure and composition (Bergeron, Leduc, Joyal, & Morin, 1995; Jactel & Brockerhoff, 2007; Nealis & Régnière, 2004), we allowed the effects of antecedent insect defoliation to vary by tree species categories (defoliator host vs. non-host). Primary inferential interest is in the stand-level submodel including the estimation of ecological



**FIGURE 3** Diagram of hierarchical model structure including tree- and stand-level submodels and the estimation of antecedent water deficit and antecedent insect defoliation variables. Rectangles delineate observations, while ovals delineate estimated quantities. Note  $t_0$  indicates the beginning of the study period and  $L$  indicates the maximum number of years before present for which ecological memory to past climatic water deficit is estimated

memory functions and regression coefficients for derived antecedent variables. The tree-level submodel is included to control for tree size and its effect on annual radial growth increment. Tree age may also affect radial growth rates. Although we do not include age in the tree-level submodel given its high correlation with tree size, extensive model checking indicated the tree-level submodel adequately controls for age effects. Combining the different model components results in the following regression equation for the radial growth increment ( $y$ ) of the  $i$ th tree in year  $t$ ,

$$\log(y_{ijh}(t)) = \alpha_{ijh}(t) + \mathbf{x}_{ijh}(t)^T \boldsymbol{\beta} + e_{ijh}(t),$$

where  $j$  indexes the study stand and  $h$  indexes whether the tree is from a host or non-host species for the dominant regional defoliating insect. Here,  $\mathbf{x}_{ijh}(t)$  includes observations of a tree's diameter at breast height (DBH) in the year previous to growth and its squared value (i.e.,  $\text{DBH}_{t-1}$ ,  $\text{DBH}_{t-1}^2$ ),  $\boldsymbol{\beta}$  includes estimated linear and quadratic DBH effect coefficients, and  $e_{ijh}(t)$  is a tree-level error term. The time-varying stand effect is estimated for each tree species (host/non-host) category applying the stand-level submodel,

$$\alpha_{ijh}(t) = \gamma_0 + \bar{z}_j(t)\gamma_1^{(h)} + \bar{f}_j(t)\gamma_2 + \tilde{z}\bar{f}_j(t)\gamma_3^{(h)} + u_{ijh}(t), \quad (1)$$

where  $\bar{z}_j(t)$  is the estimated antecedent defoliation value,  $\bar{f}_j(t)$  is the estimated antecedent climatic water deficit value,  $\tilde{z}\bar{f}_j(t)$  is an antecedent defoliation–water deficit interaction term ( $\tilde{z}\bar{f}_j(t) = \bar{z}_j(t) \times \bar{f}_j(t)$ ), the  $\gamma$ 's are estimated regression coefficients, and  $u_{ijh}(t)$  is a stand-level error term.

Ecological memory is quantified by estimating weights reflecting the relative importance of past environmental conditions on current ecosystem function (Ogle et al., 2015). We build on the Bayesian framework presented in Ogle et al. (2015) to estimate ecological memory using splines and temporal decay functions. Our approach to estimate ecological memory is different for climatic water deficit and insect defoliation reflecting hypothesized differences in forest growth responses to these disturbance types.

We used penalized regression splines to estimate antecedent weights for past climatic water deficit. Use of penalized regression splines in the current analysis allows the antecedent weight function for water deficit to be entirely determined based on the data (i.e., no pre-specified functional form). Splines were constructed as a function of time before present up to a maximum lag of  $L$  years. We set  $L = 10$  years, but other values can be applied depending on region and knowledge of forest ecosystem responses to water stress. The antecedent weight value ( $w$ ) for a given time-lag ( $\ell$ ) is estimated as,

$$w_\ell = \frac{\exp\left\{\sum_{i=1}^p h_i(\ell)\eta_i\right\}}{\sum_{\ell=0}^L \exp\left\{\sum_{i=1}^p h_i(\ell)\eta_i\right\}},$$

where  $h_i(\ell)$  is the value of the  $i$ th spline function evaluated at lag  $\ell$  and  $\eta_i$  is its corresponding regression coefficient ( $i = 1, 2, \dots, p$ ). The exponential term (equivalent to modelling weights on the log scale) constrains weights to be positive, while the sum over  $\ell$  in the denominator imposes a sum-to-one constraint among the weights,  $\sum_{\ell=0}^L w_\ell = 1$ . The antecedent water deficit value (reflecting

cumulative water stress) for stand  $j$  in year  $t$  is then estimated as the weighted sum of past water deficit observations,

$$\bar{f}_j(t) = \sum_{\ell=0}^L w_\ell f_j(t-\ell),$$

where  $f_j(t-\ell)$  is the observed climatic water deficit in stand  $j$ ,  $\ell$  years before year  $t$  (see Supporting Information Figures S3–S5 for an illustration of the application of weight functions to construct antecedent water deficit variables).

We applied a temporal decay function to model ecological memory to past insect defoliation given peak defoliation stress levels are expected to occur when a defoliating insect population is present in a stand. The decay function begins in the year of a defoliation event and decays to zero as a function of years since defoliation. We applied a spherical decay function in the current analysis because it achieves a value of zero within a finite interval of time (see Supporting Information). The function is conditional on an estimated temporal range parameter ( $\phi$ ), which reflects the length of ecological memory to past defoliation events. Defoliating insect outbreaks can last more than a single year and, in some cases, an additional defoliation event can occur before host trees have fully recovered from a previous defoliation event. To account for defoliator dynamics, we estimated antecedent insect defoliation as the sum of the decay function values for all defoliation events preceding or coincident with the current year to capture their cumulative effects. Specifically, antecedent defoliation is given by,

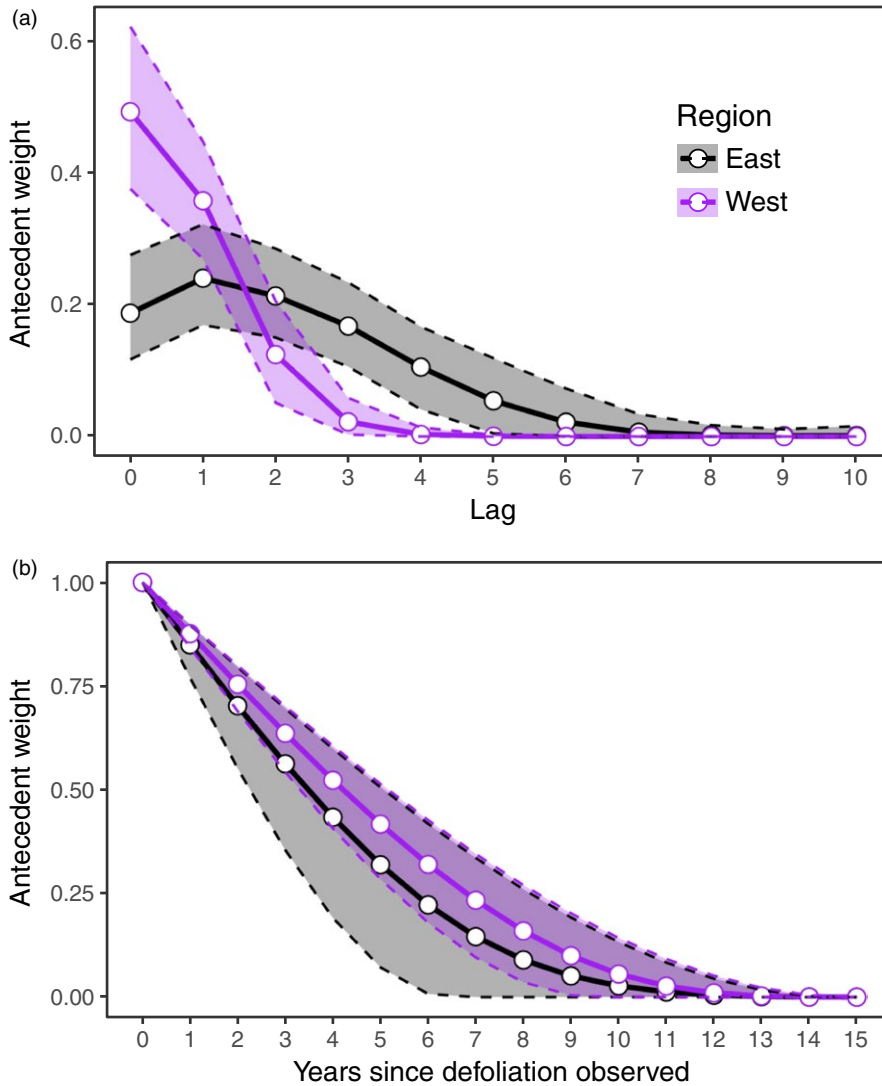
$$\bar{z}_j(t) = \sum_{i=1}^{D_j(t)} g(t-t(d_i); \phi),$$

where  $D_j(t)$  is the total number of defoliation events in stand  $j$  from the beginning of the study period through year  $t$ ,  $g(\cdot; \phi)$  is the spherical decay function,  $t(d)$  indicates the year of a defoliation event, and  $i$  indexes individual defoliation events (see Supporting Information Figures S6 and S7 for illustration of antecedent defoliation variables). Additional details on the modelling approach and Bayesian inference used to estimate model parameters including the specification of prior distributions and the MCMC sampler used are provided in the Supporting Information.

## 3 | RESULTS

### 3.1 | Ecological memory

Ecological memory is characterized by the length of responses to past conditions as well as their relative importance and cumulative effects on current ecosystem function. Boreal tree growth exhibited different ecological memory to past climatic water deficit in the two study regions (Figure 4a). The length of memory to climatic water deficit was approximately 6 years in the East. Climatic water deficit in the year previous to the year of growth ( $\ell = 1$ ) had the greatest relative importance (posterior mean weight: 0.24 [0.17, 0.32]). Weight values for water deficit in the East were relatively flat—differences in posterior mean weights for the first four lags ( $\ell = 0, 1, 2, 3$ ) were less than



**FIGURE 4** Posterior mean antecedent weight values indicating ecological memory and corresponding 95% credible intervals for climatic water deficit (a) and insect defoliation (b) based on annual radial tree growth in eastern and western study regions. Lag indicates the number of years before current year growth

0.08 indicating a prolonged response to water deficit. The length of memory to climatic water deficit was only 3 years in the West with near zero weights estimated for lags 4 and greater. Water deficit in the year of growth ( $\ell=0$ ) had the greatest relative importance (posterior mean weight: 0.49 [0.38, 0.62]) with weights quickly decaying to zero over lags 1–3 indicating a short response to water deficit in the West. Differences in the relative importance of past water deficits in the two regions are particularly strong for lags 0, 3, 4, and 5 as evidenced by non-overlapping 95% credible intervals (Figure 4a).

The length of ecological memory to past insect defoliation events was similar in the two regions (Figure 4b). Based on the posterior distribution of the range parameter ( $\phi$ ), trees in eastern study stands exhibited ecological memory to SBW defoliation events occurring up to 10.3 (6.5, 14.6) years before present, while trees in western study stands exhibited memory to FTC defoliation events up to 12.3 (9.5, 14.9) years before present. The larger range estimated for the West led to slightly larger posterior mean weight values compared to the East, but there was large overlap in the 95% credible intervals for weights in both regions (Figure 4b). The magnitude of weight values are not indicative of the relative importance of time since defoliation

as we applied a monotonically decreasing temporal decay function for defoliation (Section 2).

### 3.2 | Antecedent effects

Antecedent variables are temporally weighted versions of raw water deficit and defoliation event observations constructed using the estimated weight values in Figure 4 (see Supporting Information Figures S4–S7 for examples). These variables reflect the accumulation of water and defoliation stress over the memory period (i.e., the period for which non-zero weights are estimated). The magnitude and direction of regression coefficients placed on antecedent variables (i.e., the  $\gamma$ 's in the stand-level submodel, Equation 1) indicate the cumulative effect of past climatic water deficit and insect defoliation on boreal tree growth.

Mean host tree growth was negatively related to antecedent insect defoliation in both study regions (Table 1). Specifically, after controlling for tree size and assuming zero antecedent water deficit, the average annual growth of host trees was reduced by 41% for a one-unit increase in antecedent FTC defoliation in



**TABLE 1** Posterior median coefficient values (and 95% credible intervals) for antecedent insect defoliation, antecedent climatic water deficit, and their interaction for each study region by tree species (defoliator host vs. non-host) categories

Parameter	Category	East	West
Antecedent defoliation			
$\gamma_1$	Host	<b>-0.141 (-0.226, -0.07)</b>	<b>-0.528 (-0.691, -0.404)</b>
	Non-host	-0.007 (-0.125, 0.094)	<b>0.162 (0.067, 0.265)</b>
Antecedent water deficit			
$\gamma_2$	NA	<b>-0.031 (-0.041, -0.021)</b>	<b>-6.0E-03 (-7.0E-03, -4.0E-03)</b>
Antecedent defoliation $\times$ antecedent water deficit			
$\gamma_3$	Host	7.0E-03 (-2.0E-03, 0.018)	2.0E-03 (-4.0E-04, 5.0E-03)
	Non-host	<b>0.022 (2.0E-03, 0.059)</b>	2.0E-03 (-1.0E-03, 5.0E-03)

Coefficients for which credible intervals do not include zero are bolded.

the West, and 13% for a one-unit increase in antecedent SBW defoliation in the East (e.g.,  $[e^{\gamma_1} - e^0] \cdot 100$ ). Mean non-host tree growth was positively related to antecedent insect defoliation in the West with a one-unit increase in FTC defoliation leading to an 18% increase in average annual growth after controlling for tree size and assuming zero antecedent water deficit. There was no evidence that mean annual growth of non-host trees was related to antecedent defoliation after controlling for tree size in the East.

Mean annual tree growth was negatively related to antecedent water deficit in both study regions (Table 1). Specifically, after controlling for tree size effects and assuming no antecedent insect defoliation, the mean annual growth of trees in the East experiencing a simulated antecedent climatic water deficit of 5 mm (equivalent to the regional average over the study period) was reduced by 14%. Under the same conditions in the West, the mean annual growth of trees experiencing a simulated climatic water deficit of 20 mm (again equal to the regional average over the study period) was reduced by 11%.

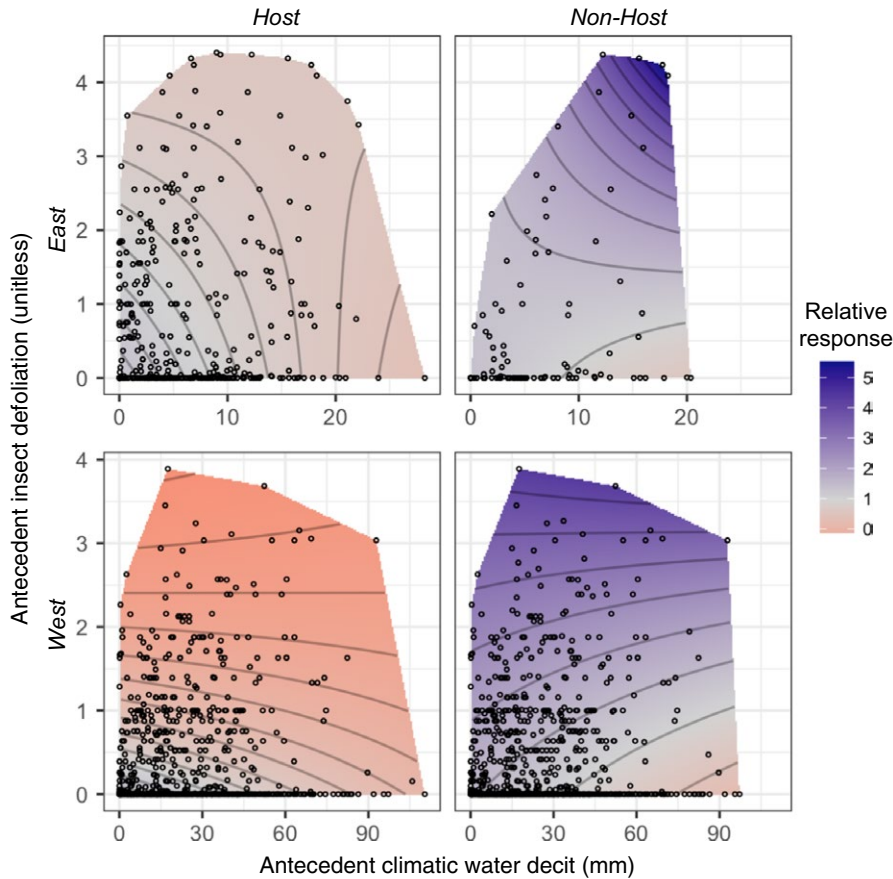
In general, mean annual tree growth in stands from both study regions was not strongly related to the interaction between antecedent insect defoliation and climatic water deficit (Table 1). The one exception was for non-host trees in the East where there was evidence that mean annual growth was positively related to the interaction between the antecedent variables. Specifically, mean annual growth among non-host trees experiencing 5 mm of antecedent water deficit was estimated to be 9% greater for an antecedent defoliation value of one versus zero after controlling for tree size. Figure 5 presents the sum of estimated effects for antecedent insect defoliation, antecedent climatic water deficit, and their interaction relative to regional mean annual tree growth over the study period after controlling for tree size. Based on Figure 5, the positive interaction between antecedent variables for non-host trees in the East was estimated to have the greatest impact at moderate antecedent water deficits and high antecedent defoliation levels. We observed no evidence of such an interaction in the West. Additional model coefficients of reduced inferential interest, including the effects of diameter on tree-level growth and tree- and stand-level variances for both regions are summarized in Table S1.

## 4 | DISCUSSION

### 4.1 | Ecological memory

The quantification of ecological memory allows for estimates of both the length of persistent responses to climatic water deficit and insect defoliation and the relative importance of past stress conditions on current tree function. Boreal tree growth in both study regions exhibited multi-year responses to water deficits consistent with hypothesis 1. There were significant differences in the ecological memory of tree growth to climatic water deficit between the two study regions. Specifically, tree growth was estimated to respond to climatic water deficit for up to 6 years in the East, but only 3 years in the West (Figure 4a). Water deficits in the year prior to growth had the greatest relative importance in the East consistent with hypothesis 1. Further, there was evidence water deficits 2–3 years before present had greater or equal importance for growth than water deficits in the current year consistent with previous studies indicating water availability in past years has greater impact on tree growth and mortality than current growing season conditions (D'Amato, Bradford, Fraver, & Palik, 2013; D'Orangeville, Côté, Houle, & Morin, 2013; Michaelian et al., 2011). The same dependence of tree growth on past water availability was not observed in the West where the relative importance of water deficit was estimated to be greatest in the year of growth and dropped off quickly over 1–3 years before present.

The specific drivers underlying regional differences in ecological memory to climatic water deficit are uncertain and warrant future analysis. It is likely regional tree species composition, stand structure, climate, and soils contribute to the different memory functions estimated for the eastern and western regions. In particular, chronic summer water deficits in the West may lead to drought-adapted stands in terms of stand density and structure, while favourable growing conditions punctuated by periodic water deficits in the East may cause structural overshoot contributing to longer term sensitivity to past deficits (Jump et al., 2017). Finally, differences in the tree growth sampling protocols between the East and West (see Section 2.2) may also contribute to observed regional differences in ecological memory to water deficit.



**FIGURE 5** Estimated effects of antecedent insect defoliation, antecedent climatic water deficit, and their interaction on host and non-host tree growth in eastern and western study regions. Points represent posterior mean antecedent variable values based on study data. Relative response surfaces correspond to mean tree growth under antecedent conditions relative to regional mean tree growth over the study period (East: 1968–1998, West: 1968–2010) after controlling for tree size. Response surfaces were generated by imposing a dense grid over the range of modelled antecedent variable values

Boreal tree growth exhibited persistent responses to insect defoliation in both study regions consistent with hypothesis 2. Specifically, we observed responses to SBW defoliation events 10 years in the past in the East, and FTC defoliation events 12 years in the past in the West (Figure 4b). Persistent tree growth responses contributed to the increase of antecedent defoliation values over the course of a multi-year insect attack or if the time between attacks was less than the memory period (Supporting Information Figures S6 and S7). Such increases in antecedent defoliation values reflect the accumulation of insect defoliation stress over the course of repeated attacks leading to reduced tree growth and potential mortality (Anderegg & Callaway, 2012; McDowell et al., 2008; Pothier et al., 2005, 2012). Although boreal tree growth exhibited slightly shorter responses to SBW defoliation in the East compared to responses to FTC defoliation in the West, there was insufficient evidence to suggest regional differences in defoliation responses (as indicated by overlapping 95% credible intervals for defoliation memory functions in Figure 4b).

More extensive tree growth and defoliation data can be used to further explore differences in boreal tree responses to SBW and FTC defoliation. In particular, a larger dataset would allow ordinal defoliation categories to be applied directly to account for differential tree responses to varying defoliation severity levels. More extensive data would also allow for the consideration of tree species or higher taxonomic-level differences in ecological memory to drought and insect defoliation. Recent studies indicate persistent responses to drought

may differ between coniferous and deciduous tree species (Anderegg, Schwalm, et al., 2015; Gazol et al., 2018).

## 4.2 | Antecedent effects

The lack of negative interactive effects observed for host trees even after accounting for persistent and cumulative responses to water and defoliation stress, combined with similar results from previous studies (Chen et al., 2018; Jacquet et al., 2014; Jactel et al., 2012; Kolb et al., 2016), implies physiological feedbacks in tree responses to drought and defoliating insects do not exacerbate their impacts on tree growth. These results run counter to current physiological theory and initial hypotheses (see hypothesis 3), which predict interactions between drought and insect defoliation should exacerbate their negative impacts on host tree function (Anderegg, Hicke, et al., 2015; McDowell et al., 2011). Instead, insect defoliation, though damaging to host trees, may offset the impacts of water stress leading to negative additive effects of water deficit and insect defoliation, but no interactive effects (Table 1).

The potential offsetting effect of insect defoliation on tree responses to water stress is highlighted by the positive effect of antecedent defoliation on non-host tree growth in the West and the positive interactive effect we observed for non-host trees in the East. Specifically, we found evidence of increased growth of non-host trees in western and eastern stands when there was high antecedent defoliation (Figure 5). Previous studies found SBW defoliation in the eastern Canadian boreal forest led to increased

abundance of early-successional, non-host species (Duchesne & Ouimet, 2008). Similar positive effects of defoliation have been hypothesized for non-host tree growth (Jacquet et al., 2014), but have not been empirically demonstrated. Accounting for ecological memory, our results provide evidence in support of the hypothesis that insect defoliation has a positive effect on non-host tree growth during droughts by lessening transpirational water demands through leaf area reduction.

Potential non-negative interactions between drought and defoliating insects on tree growth and mortality warrant further investigation. Several factors, in particular, may have contributed to the lack of observed negative interactive effects among host trees in the current study.

1. Despite study years with large climatic water deficits and high levels of insect defoliation in eastern and western study regions (Figure 2, see also Supporting Information Figure S8 for evidence of overlapping periods of high antecedent water deficit and insect defoliation in both study regions), chronic drought conditions (i.e., multiple consecutive years with high climatic water deficit) did not exist in either boreal region during the study periods. Supporting Information Figure S1 indicates study periods in the East and West coincide with periods of relative wetness over the past century. The climate was drier, on average, in both regions prior to circa 1960. Chronic water stress may trigger stronger tree growth responses leading to interactions with antecedent defoliation not observed in the current study. Indeed, ecological theory indicates there are likely drought thresholds beyond which tree responses occur, but below which, trees are able to maintain basic physiological function (Allen et al., 2015).
2. The current analysis utilizes tree-ring records collected from live trees alone. Trees that go on to suffer drought- or defoliation-induced mortality may exhibit different persistent responses to these disturbances and stronger responses to their interaction than surviving trees. The extensive research demonstrating prolonged radial growth suppression in trees that die during or following a drought relative to surviving trees suggests there is the potential for stronger interactions among trees suffering mortality (Berdanier & Clark, 2016; Das et al., 2007, 2016; van Mantgem et al., 2003; Wyckoff & Clark, 2002). Further, there is evidence past drought events may increase the susceptibility of trees to future mortality due to defoliation events in the eastern Canadian boreal forest (De Grandpré et al., 2018). Future work will focus on comparing live versus recently dead tree responses to antecedent water deficit and insect defoliation.
3. The lack of a mechanistic model for interactions between drought and insect defoliation may also contribute to no observable negative interactive effects among host trees. Once developed (see Anderegg, Hicke, et al., 2015), such models can be integrated into the Bayesian hierarchical model developed here taking the place of the empirical, linear interaction term between antecedent variables and may reveal negative interactions not identified in the current analysis.

## 5 | CONCLUSIONS

Growth of trees from western and eastern regions of the Canadian boreal forest characterized by different species compositions, climates, and primary defoliating insect populations exhibited decadal-scale ecological memory to climatic water deficit and insect defoliation. Accounting for the cumulative effects of water deficit and insect defoliation arising from persistent tree growth responses to these stressors, we were able to detect interactions between drought and defoliation not previously demonstrated. Counter to current physiological theory and initial hypotheses, however, we found no evidence of negative interactive effects between antecedent water and insect defoliation stress. This counter-intuitive result, combined with previous studies, suggests negative interactions between droughts and insect outbreaks may have minimal effects on tree growth in defoliator-dominated systems such as the boreal forest due to offsets in water stress caused by defoliation. The potential lack of negative interactive effects between drought and insect defoliation on boreal tree growth and mortality has important implications for our understanding of future impacts to the boreal forest under changing climate and insect disturbance regimes. Such understanding is critical given the global importance of the boreal system as both a carbon sink and valuable natural resource.

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## AUTHORS' CONTRIBUTIONS

M.S.I., L.D'O. and A.D. designed and performed the study; M.S.I. developed and ran the Bayesian hierarchical model with feedback from L.D'O. A.D., and A.O.F.; D.K. contributed to the interpretation of model results; L.Duchesne contributed to the collection of data; A.O.F. assisted in model design and analysis. All authors made significant contributions to the writing of the manuscript.

## DATA ACCESSIBILITY

Tree growth, defoliation, and weather data used in the current study are available at Dryad Digital Repository <https://doi.org/10.5061/dryad.f7bq534> (Itter et al., 2018).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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