



Continent-wide synthesis of the long-term population dynamics of quaking aspen in the face of accelerating human impacts

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Abstract

In recent decades, climate change has disrupted forest functioning by promoting large-scale mortality events, declines in productivity and reduced regeneration. Understanding the temporal dynamics and spatial extent of these changes is critical given the essential ecosystem services provided by forests. As the most widespread tree species in North America, quaking aspen (*Populus tremuloides*) is well suited for studying the dynamics of tree populations during a period of unprecedented climate change. Synthesizing continent-wide data, we show that mortality rates of mature aspen stems have increased over the past two-to-three decades, while relative gains in aspen basal area have decreased during the same period. Patterns were pervasive across multiple stand size classes and composition types in western North America biomes, suggesting that trends in demographic rates were not simply a reflection of stand development and succession. Our review of the literature revealed that increased aspen mortality and reduced growth rates were most often associated with hotter, drier conditions, whereas reduced recruitment was most often associated with herbivory. Furthermore, interactions between climate and competition, as well as climate and insect herbivory, had important, context-dependent effects on mortality and growth, respectively. Our analyses of aspen across its entire geographic range indicate that this important tree species is experiencing substantial increases in mortality and decreases in population growth rates across multiple biomes. If such trends are not accompanied by increased recruitment, we expect that the reduced dominance of aspen in forests will lead to major declines in the many essential ecosystem services it provides.

Keywords Distribution-wide patterns · Climate change · Mortality · Multiple stressors · *Populus tremuloides*

Introduction

Forests account for 45% of global terrestrial carbon stocks, serve a critical role in the maintenance of biodiversity (Myers et al. 2000), and are central to hydrological and nutrient cycles (Bonan 2008; Pan et al. 2011; Trumbore et al. 2015). Unfortunately, these services are at risk from increasing temperatures, shifts in precipitation patterns, and

more frequent and intense drought conditions, all of which have been linked to observed tree mortality in many regions (Breshears et al. 2005; van Mantgem et al. 2009; Allen et al. 2010, 2015; Anderegg et al. 2013; Reichstein et al. 2013; Cohen et al. 2016). Projected changes in climate and other environmental drivers are expected to further jeopardize forest ecosystems by promoting more widespread, severe, and frequent mortality events (Trenberth et al. 2014), with major consequences for biodiversity, ecosystem services, and feedbacks to climate change through loss of carbon sinks (Adams et al. 2010; Anderegg et al. 2013).

In addition to direct impacts of climate change, tree demographic rates also depend on interactions among abiotic and biotic controls (e.g., climate, topography, competition, and herbivory). Although much progress has been made in understanding the ecophysiological responses of trees to drought (Bréda et al. 2006; McDowell et al. 2011; Anderegg et al. 2012), many questions remain regarding the mediating influence of endogenous processes, including

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stand size structure, competition (Clark et al. 2011), and biotic mortality agents (Franklin et al. 1987; Zhang et al. 2015). Furthermore, these processes often depend on or interact with climate to determine long-term changes in demographic rates (Régnière and Nealis 2007; Raffa et al. 2008; Clark et al. 2011, 2014). Without accounting for endogenous or interacting drivers, research on the vulnerability of forests to climate change may result in erroneous or even contradictory conclusions. However, few syntheses have been conducted to assess the prevalence of multiple, interacting factors in driving the responses of tree species to climate change, especially across large geographic scales (but see Zhang et al. 2015; Meddens et al. 2015).

Although an improved mechanistic understanding of tree demographic performance has helped elucidate which tree species in a community are likely to be most vulnerable to decline (Anderegg et al. 2016; Greenwood et al. 2017; Trugman et al. 2018a; Menezes-Silva et al. 2019), our ability to identify vulnerable populations within a species remains poor (Anderegg et al. 2019). Addressing this limitation will require long-term data on demographic trends for tree species across their entire geographic ranges to capture the full extent of environmental variation that they experience and effects from ongoing anthropogenic climate change. Species will be unlikely to decline in all parts of their distribution, but at present we often lack a predictive understanding of the full range of responses that tree taxa exhibit across the often-heterogeneous environments they inhabit. In addition, we lack clarity on whether species are most vulnerable to changing climate conditions in the core parts of their range, or the drier areas where adaptations to drought may exist. For example, drought-driven mortality for tree species have been observed along the driest margins of their ranges (Worrall et al. 2008; Kulakowski et al. 2013; Fettig et al. 2019) as well as in the wetter, often core parts of their ranges (Lloret and Kitzberger 2018; Isaac-Renton et al. 2018), underscoring that intraspecific variation may drive broad, yet conflicting patterns in species responses to climate change. Identifying the spatial and temporal variation in tree demographic performance, as well as associated drivers, will be critical for determining the extent of tree decline and improving forecasts of species range shifts.

Among the many reports of tree decline globally, the dieback of quaking aspen (*Populus tremuloides*), the most widespread tree species in North America (Burns et al. 1990), has been of particular concern (Kay 1997; Frey et al. 2004; Worrall et al. 2008; Hogg et al. 2008; Rehfeldt et al. 2009; Michaelian et al. 2011). This species typically regenerates asexually after fire, varies in ploidy level across its range, and exists as both successional stands as well as relatively stable, persistent ones (Shinneman et al. 2013; Callahan et al. 2013; Rogers et al. 2014). As the most abundant broadleaved tree species in Canadian boreal forests (Peterson

and Peterson 1992) and one of the few deciduous tree species in western US forests, aspen is considered to be a foundation or even keystone species (Rogers et al. 2020) that serves a critical role in carbon cycling (Michaelian et al. 2011; Huang and Anderegg 2012) and supports high levels of biodiversity in boreal (Reich et al. 2001; Bartemucci et al. 2006) and temperate forests (Chong et al. 2001; Kuhn et al. 2011). Observations of large-scale, episodic dieback of aspen, especially after drought that is accompanied by warmer temperatures (i.e., ‘hotter drought’), have been concentrated in the drier margins of the species’ range, including the southern Rocky Mountains (e.g., Worrall et al. 2008, 2010; Huang and Anderegg 2012), the Arizona/New Mexico mountains (Zegler et al. 2012), and the prairie parkland region of western Canada (Hogg and Schwarz 1999; Hogg et al. 2002; Michaelian et al. 2011), but dieback has also been observed in wetter regions (Candau et al. 2002; Scarr et al. 2012; see review by Worrall et al. 2013). Despite these reports of decline, previous research has also shown that the demographic performance of aspen populations can be quite variable in both space and time (Yang et al. 2015; Shinneman and McIlroy 2019). For example, studies have shown that aspen cover has remained stable in some areas (Zier and Baker 2006; Kurzel et al. 2007), increased in others (Kaye et al. 2003; Elliott and Baker 2004; Kulakowski et al. 2004) and both expanded and contracted in the same landscape at different times (Elliott and Baker 2004; Kashian et al. 2007; Sankey 2008). Evaluating these temporal patterns will be aided by distinguishing disturbance-driven or successional losses of aspen from elevated mortality associated with climate change (sensu Worrall et al. 2013). Moreover, identifying the spatial and temporal drivers of this variability will be key for understanding the dynamics of aspen stands and improving their management during a period of unprecedented human-caused climate change (Yang et al. 2015).

Past reviews of aspen have summarized the spatial extent of more recent (2000–2010) dieback events across North America (Worrall et al. 2013), as well as the many factors that may amplify or prolong episodes of drought-driven mortality (Frey et al. 2004; Worrall et al. 2013), including fire history (Shinneman et al. 2013), competition and facilitation (St. Clair et al. 2013), and trophic interactions (Beschta and Ripple 2009; Eisenberg et al. 2013; Seager et al. 2013; Rogers and Mittanck 2014). Despite these substantial and valuable contributions, we still lack an understanding of the long-term trends in aspen demographic performance across its entire geographic range and whether recently observed patterns depart from expected, background demographic rates. Furthermore, the body of literature thus far presents an opportunity to synthesize both the individual and interacting factors associated with aspen mortality, growth and recruitment. Summarizing observations of aspen decline across its entire range, and the purported drivers of this change, will be

key for understanding the vulnerability of this foundational tree species to global change.

In this review, we analyze existing, long-term forest inventory data and assemble over 30 years of published literature to determine the extent of observed changes and synthesize the reported drivers of aspen population dynamics across its range in North America. Our focus was on studies that investigated the mortality, growth, and recruitment of aspen in response to climate, topography, stand structure and composition, herbivory, fungal pathogens, and disturbance. Our main objectives were to (1) analyze observed trends in the demographic performance of aspen over the past 10–30 years across the five biomes it inhabits in North America; (2) summarize geographic trends of research activity on aspen over the past 30 years; (3) synthesize study conclusions regarding the individual and interacting drivers most commonly associated with changes in aspen demographic rates across its geographic range; and (4) identify research areas that need greater attention in the future to improve our understanding of intraspecific variation in the susceptibility of tree populations to ongoing, climate change.

Analysis of long-term trends in aspen demographic rates

Data sources and plot selection criteria

To quantify changes in aspen demographic rates over time, we summarized the annual mortality rate and relative change in basal area (BA) of mature aspen stems from multiple forest inventory databases across North America (Table S1 in Online Resource 1). Although recruitment was also of interest, the assembled databases did not have the minimum number of repeat inventories required to calculate trends in recruitment across aspen's continent-wide range. Data sources included the British Columbia Ministry of Forests; Lands and Natural Resource Operations, Alberta Sustainable Resource Development; Saskatchewan Ministry of Environment Forest Service; Manitoba Conservation Forestry Branch; Ontario Ministry of Natural Resources and Forestry; Ministère des Ressources naturelles du Québec; Nova Scotia Department of Natural Resources; New Brunswick Department of Natural Resources and Energy; Newfoundland and Labrador Department of Fisheries and Land Resources; Yukon Energy, Mines and Resources; the Canadian Forest Service and the Climate Impacts on Productivity and Health of Aspen (CIPHA) Study; the Cooperative Alaska Forest Inventory; and the USDA Forest Service Forest Inventory and Analysis (FIA) Program.

We included plots in our analysis if they met the following criteria: (1) included censuses of at least five living, mature (≥ 12.7 cm diameter at breast height, dbh) aspen

stems at three or more dates (a requirement for comparing rates between time intervals); (2) the period between the initial (t_{initial}) and final (t_{final}) census was greater than or equal to 10 years; (3) plots had no evidence of fire, harvest or other silvicultural activities (e.g., planting, fertilization) prior to or during the measurement intervals; (4) plot dimensions and spatial coordinates were recorded; and (5) plots had an estimated stand age ≥ 40 years. Given that the forest inventory databases varied in their size-based definition of mature trees (≥ 7 to 12.7 cm dbh), we used ≥ 12.7 cm dbh as the most inclusive cutoff.

When studying the population dynamics of aspen through time, it is critical to address whether observed patterns are due to gradual stand development and/or successional processes, or the result of stress-induced decline (Worrall et al. 2013; Rogers et al. 2013). By restricting our analysis to mature stands (≥ 40 years old) with no evidence of recent disturbance, we sought to minimize the influence of successional dynamics and disturbance-driven catastrophic mortality on our estimates of annual mortality and relative rates of BA change through time. Such an approach, however, prevented us from explicitly capturing patterns of aspen recruitment through time, a key determinant of the species' resilience to changing environment conditions, and thus constrains our inference. That being said, we used the relative change in BA of mature aspen stems in plots through time to implicitly capture the net outcome of changing aspen mortality, growth and recruitment rates through time.

After applying these selection criteria, we had assembled two or more temporally-spaced inventories for 3962 plots distributed across five major biomes in North America, as categorized by Bailey (1998): boreal forest ($n=859$), montane coniferous forest ($n=874$), prairie parkland ($n=122$), mixed deciduous-coniferous forest ($n=1846$), and deciduous forest ($n=261$) (Fig. 1a). Plot sizes ranged from 90 m² (0.009 ha) to 8092 m² (0.81 ha), with an average of 595 m² (0.06 ha) (Table S1 in Online Resource 1). Data were collected between 1985 and 2018 and the measurement interval ranged from 3 to 16 years (mean 6.2 years). Plots had been remeasured two to six times (mean = 2.5 times). We confirmed that values for initial tree diameter and diameter change were reasonable—i.e., trees with diameter change less than -2.5 cm or greater than two standard deviations of the population mean were carefully inspected and excluded if inconsistencies were also found in species codes and/or height across repeat inventories (sensu Bradford and Bell 2017).

Due to an average remeasurement interval of 10 years for the FIA annual inventory program in the western US, there has been only a single remeasurement since plot establishment (t_{initial} , 2000–2007). Therefore, we used an approach based on Goeking (2015) to estimate trends in mortality and relative rates of aspen BA change across

this region. Specifically, we used field data collected during plot establishment in the Interior West Region of the FIA Program that distinguished between recently dead (≤ 5 years preceding t_{initial} , hereafter $t_{\text{initial}-1}$) and long-standing dead mature stems (USDA Forest Service 2013). Although a relatively rapid decaying species, aspen snags have been observed to remain standing for five years or more in west-central Canada (Hogg and Michaelian 2015) and Arizona (Ganey et al. 2015). Counting only those mature stems estimated to have recently died by t_{initial} , we calculated mortality for the census interval $t_{\text{initial}-1} - t_{\text{initial}}$. Consequently, our estimates of mortality rates during the first census interval for the western US are based on one-time observations rather than remeasurement. Therefore, an assumption of our analysis is that estimates of mortality in montane coniferous forests are not biased due to dead trees being missed or misidentified as recently, rather than long-standing, dead. We carefully compared estimates of mortality rates for the first and second census interval and did not detect any systematic bias that would affect our conclusions.

Calculation of demographic responses

Annual mortality rate (% year⁻¹) and relative change in live BA (% year⁻¹) of mature aspen stems were estimated over the census interval for each plot as follows:

$$\text{Mortality rate (\% yr}^{-1}\text{)} = \left(\frac{\text{number dead}_t}{\text{number live}_{t-1}} \right)^{1/c}, \quad (1)$$

$$\text{Relative change in BA (\% yr}^{-1}\text{)} = \frac{\log\left(\frac{\text{BA live}_t}{\text{BA live}_{t-1}}\right)}{c}, \quad (2)$$

where BA represents basal area of live, mature aspen stems in m² per ha and c represents the census interval length in years. Although not an explicit measure of the three demographic processes that determine population growth over time (i.e., mortality, growth and recruitment), our calculation of relative change in aspen BA implicitly integrates these processes. We mapped spatial variation in mean annual mortality rate and relative change in BA to confirm no major inconsistencies existed among the data sources (Fig. S1 and S2 in Online Resource 2).

Statistical models

Our goal was to use simple statistical models capable of detecting directional changes in aspen mortality and relative rates of BA change. Given this goal, we did not build and compare more complex, predictive models of aspen

demographic rates as a function of climate, as done in several past studies later discussed in this review (e.g., Zhang et al. 2015; Hember et al. 2017). We used generalized non-linear mixed-effects models (GNMM) and linear mixed-effects models (LMM) to assess temporal trends in annual mortality rate and relative change in BA, respectively, of aspen across plots in the five biomes. Specifically, we modeled annual mortality rates as a function of calendar year and biome using negative binomial regression (glmADMB package in R; Fournier et al. 2012), with number live_{*t-1*} * c as the offset term and plotID as the random intercept to account for differences among plots. We modeled the relative change in BA using LMM (lme4 package in R; Bates et al. 2015), with plotID as the random intercept. The estimated annual fractional change in aspen mortality (a) was calculated as $\exp(\beta_1) - 1$. To explore whether trends in mortality and relative rates of BA change were dependent on stand structure and composition, we used LMM to examine patterns as function of initial mean stem diameter of aspen (< 20 cm, 20–30 cm, ≥ 30 cm dbh) and initial relative abundance of aspen (i.e., as a proportion of total live stand BA, < 25%, 25–75%, $\geq 75\%$) for a more recent subset of years (1999–2018) when inventories had been conducted in all biomes. We also explored interactive effects between initial mean stem diameter and initial relative abundance of aspen on trends in mortality and relative rates of BA change, but no significant interactions were found. To evaluate how successional processes may have influenced demographic rates, we used LMM to assess plot-level trends in total stand density and BA over time within each biome.

Trends in aspen demographic rates across its geographic range

Over the past 10–30 years, the mean annual mortality rate of mature aspen stems has increased ($a=0.028$, $P<0.001$, GNMM, $n=3962$, where a is the estimated annual fractional change in mortality rate), with the magnitude and direction of change varying by biome (Fig. 1b). Mortality rates increased significantly for aspen stands in boreal forests ($P<0.001$, $n=859$), montane coniferous forests ($P<0.001$, $n=874$), and prairie parkland ($P=0.01$, $n=122$), with the estimated doubling periods for mortality ranging from 11 years (montane coniferous forests) to 33 years (boreal forests). In contrast, mortality rates decreased significantly for mixed deciduous-coniferous forests ($P=0.01$, $n=1846$) and did not change over time for deciduous forests ($P=0.96$, $n=261$) (Fig. 1b). Over a more recent study period (1999–2018) when data were available for all biomes, increased mortality was not consistently observed for stands of varying size structure and species composition. Specifically, mortality increased through time for stands initially composed of predominantly small- (< 20 cm

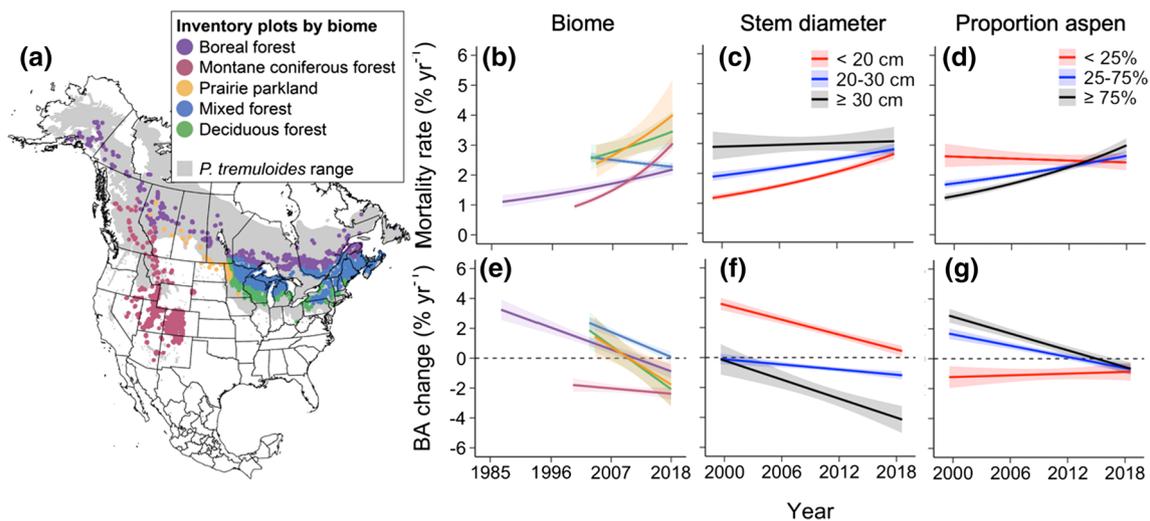


Fig. 1 **a** Spatial distribution of inventory plots ($n=3962$) containing quaking aspen (*P. tremuloides*), colored by biome (Bailey 1998). The background gray color represents the geographic range of aspen (Little 1971). The six panels show modeled trends in mean ($\pm 95\%$ CI) annual mortality rate and relative change in live basal area (BA) of mature ($\text{dbh} \geq 12.7$ cm) aspen stems by **b**, **e** biome, **c**, **f** initial mean diameter of aspen, and **d**, **g** initial relative abundance of aspen. Horizontal lines in **e**, **f**, and **g** represent no net change in live BA of

mature aspen through time. Plots contained at least five live mature aspen stems and were remeasured 2–6 times between 1985–2018. For stem size- and composition-dependent models, a more recent subset of years (1999–2018) was used to ensure trends were representative of all biomes. Sample sizes: boreal ($n=859$), montane coniferous ($n=874$), prairie parkland ($n=122$), mixed ($n=1846$), and deciduous ($n=261$)

dbh) and medium-sized (20–30 cm) mature aspen stems ($P < 0.001$, $n = 1776$; $P < 0.001$, $n = 1782$; respectively), but not large stems (≥ 30 cm) ($P = 0.36$, $n = 404$) (Fig. 1c). Mortality also increased for stands with moderate (25–75%) to high ($\geq 75\%$) initial aspen relative abundance ($P < 0.001$, $n = 2033$; $P < 0.001$, $n = 1189$; respectively), but not low ($< 25\%$) aspen relative abundance ($P = 0.84$, $n = 740$) (Fig. 1d). Examining patterns by biome revealed that increased mortality rates were pervasive across all stand size structures and composition types in montane coniferous forests, whereas in boreal forests, prairie parkland, and deciduous forests, increased mortality rates were limited to stands composed of moderate to high initial aspen relative abundance and small- and/or medium-sized mature aspen stems (Table S2 and S3, Fig. S3 in Online Resource 2).

The relative gain in live BA of aspen decreased significantly through time in all biomes ($\beta = -0.12\%$ per year, $P < 0.001$, LMM, $n = 3962$), resulting in a net loss of aspen BA in plots within all biomes except mixed deciduous-coniferous forests (Fig. 1e). Over the more recent study period (1999–2018), the relative gain in aspen BA decreased through time for stands of all aspen size classes, although the net reduction in aspen BA was only observed for stands initially composed of predominantly medium and large aspen stems ($P < 0.001$, $n = 1782$; $P < 0.001$, $n = 404$; respectively) (Fig. 1f). Decreased relative

gain in aspen BA through time was observed for stands with moderate to high initial aspen relative abundance ($P < 0.001$, $n = 2033$; $P < 0.001$, $n = 1189$; respectively), but not low relative abundance ($P = 0.41$, $n = 740$) (Fig. 1g). Assessing patterns by biome showed that decreased relative gain in aspen BA through time was pervasive across all stand size structures in boreal forests, whereas decreased relative gain in aspen BA was limited to stands composed of small stems in prairie parkland and deciduous forests, medium stems in montane coniferous forests, and small and large stems in mixed deciduous-coniferous forests (Table S4 and Fig. S4a in Online Resource 2). The decline in the relative gain of aspen BA through time was limited to stands composed of moderate to high initial aspen relative abundance in all biomes except prairie parkland, where only aspen-dominant stands experienced decreased gains in relative BA change (Table S5 and Fig. S4b in Online Resource 2).

Total stand density and BA declined during the study period for plots in montane coniferous forests ($P < 0.001$, LMM), whereas stand density, but not BA, declined for plots in boreal forest and prairie parkland ($P < 0.001$) (Fig. 4). In contrast, total stand density and BA increased during the study period for deciduous and mixed deciduous-coniferous forests ($P < 0.05$).

Synthesizing drivers of aspen demographic rates

Literature search

To synthesize our understanding of the factors that are most commonly associated with changes in aspen demographic rates, we surveyed the published literature search using Web of Science. On 26 August 2019, we conducted a search using keywords for the target species ('*Populus tremuloides*' OR 'aspen'), target response ('canopy dieback' OR 'crown dieback' OR 'crown loss' OR 'cover' OR 'growth' OR 'mortality' OR 'recruitment' OR 'regeneration'), and target methodology ('field sampling' OR 'survey' OR 'census' OR 'inventory' OR 'aerial' OR 'remote sensing'). Results were limited to primary research articles published in peer-reviewed journals between 1989 and 2019. After examining the abstracts of the retrieved articles and omitting any obviously irrelevant papers, our literature search yielded 600 articles.

The full text of each article was then examined and only papers that met the following criteria were retained: (1) empirical study that used field, aerial and/or remote sensing methods; (2) recorded data on aspen mortality, growth, and/or regeneration; and (3) reported statistical relationships between aspen performance and at least one predictor (general patterns or simple time series were not acceptable). As part of our synthesis of the literature, we opted for a vote-counting approach rather than a meta-analysis because of three key constraints: First, the definition and reporting of response variables (i.e., mortality, growth, and regeneration) differed greatly among studies, preventing the calculation of effect sizes. Second, predictor variables also varied across studies, resulting in few replicate studies reporting effects from the same predictor variable. Third, aspen size classes were inconsistently defined among studies (e.g., 'mature stems' defined using height or dbh criteria).

Of the 600 papers captured in our initial search, we identified 136 articles published between 1989 and 2019 that met these criteria (References in Online Resource 3). For each retained paper, we extracted the following: (1) study location classified by biome(s)—boreal forest, montane coniferous forest, prairie parkland, mixed deciduous-coniferous forest, or deciduous forest; (2) response variable(s) studied—mature stem mortality (i.e., defined either as a static count, e.g., number of dead stems, or a rate through time, e.g., probability of stem mortality or loss of basal area or aboveground biomass), mature stem growth (i.e., defined as annual change in stem diameter, tree ring width, basal area or aboveground biomass), and juvenile recruitment (i.e., defined as the survival, growth

or abundance of aspen seedlings, suckers or saplings); (3) the corresponding predictor variable(s) studied for each response—climate (temperature, precipitation, or drought index), topography (elevation, slope, aspect or topographic moisture index), competition (intraspecific, interspecific or total), tree age/size (including variables related to individual tree age and diameter, as well as stand age), herbivory (mammals or insects), fungal pathogens, and disturbance (fire, wind or harvest); (4) whether the predictor was a main effect or interaction and whether each predictor was found by the author(s) to be significantly associated with the response variable; and (5) the direction of the association or effect on each response variable (i.e., positive, negative, non-linear or neutral).

Because studies varied widely in their statistical approach, we deferred to the judgment of the author(s) of each paper when assigning the direction of effect and the significance of each predictor. When studies examined multiple variables for a given predictor category (e.g., competition approximated using both stand BA and stem density), the relationship between the response and each predictor variable was extracted, but only significant relationships were considered for review purposes. For example, if aspen growth was found significantly associated with stand BA but not stem density, we considered 'competition' a significant predictor of aspen growth for that study. Although several studies shared a dataset in common with at least one other study, we found most studies (85%) used independent datasets, and therefore defined each published paper as an independent study in our assessment.

Research activity on aspen mortality, growth and recruitment

The published literature that met our review criteria was widely distributed but spatially uneven across North America (Fig. 2a). Most studies on aspen were conducted within a single biome ($n = 117$, 86% of total) rather than across multiple biomes ($n = 19$; 14%). Of the studies occurring in a single biome, most were conducted in montane coniferous forests of western North America ($n = 66$; 56%), followed by boreal forests of Alaska and Canada ($n = 37$; 32%), mixed deciduous-coniferous forests of eastern North America ($n = 10$; 9%), and prairie parkland in western Canada ($n = 4$; 3%). Of the studies conducted in montane coniferous forests, the majority were conducted on aspen in the southern and middle Rockies ($n = 38$; 58%), followed by the Wasatch and Uinta Mountains in Utah ($n = 15$; 23%), semi-arid montane forests in Arizona and New Mexico ($n = 10$; 15%), seasonally dry forests in Sierra Nevada and Cascade Mountains ($n = 6$; 9%), and the semi-arid montane forests in the Great Basin ($n = 3$; 5%)

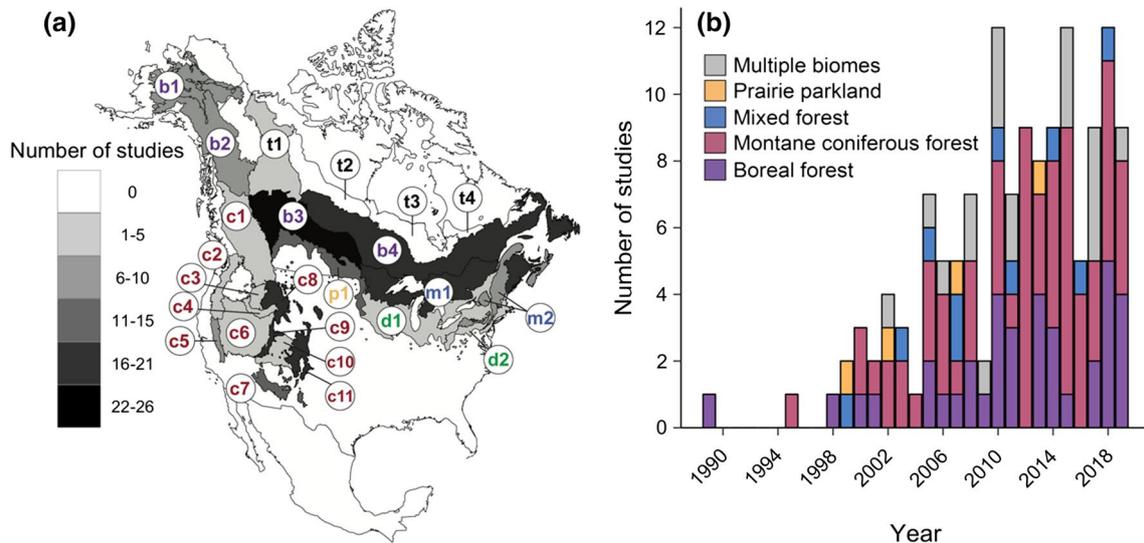


Fig. 2 **a** Total number of published studies by ecoregion (adapted from Wiken et al. 2011) on the drivers of quaking aspen (*P. tremuloides*) mortality, growth and recruitment. **b** Total number of studies published per year by biome(s) over the past thirty years (1989–2019) on the drivers of quaking aspen mortality, growth and recruitment. All studies of deciduous forests also included other biomes, so these articles are instead included in the ‘multiple biomes’ study count. Ecoregions are labeled as follows: (b1) Alaska interior, (b2) boreal cordillera, (b3) boreal plains, (b4) boreal shield, (t1) taiga plains, (t2)

western taiga shield, (t3) Hudson Plain, (t4) eastern taiga shield, (p1) prairie parkland, (c1) Canadian Rockies, (c2) Cascades, (c3) Idaho Batholith, (c4) Snake River Plain, (c5) Sierra Nevada, (c6) Great Basin, (c7) Arizona/New Mexico Mountains, (c8) Middle Rockies, (c9) Wasatch and Uinta Mountains, (c10) Colorado Plateaus, (c11) Southern Rockies, (m1) Northern Great Lakes and Southern Laurentians, (m2) Atlantic Highlands, (d1) interior and coastal lowlands, and (d2) Appalachian Plateau

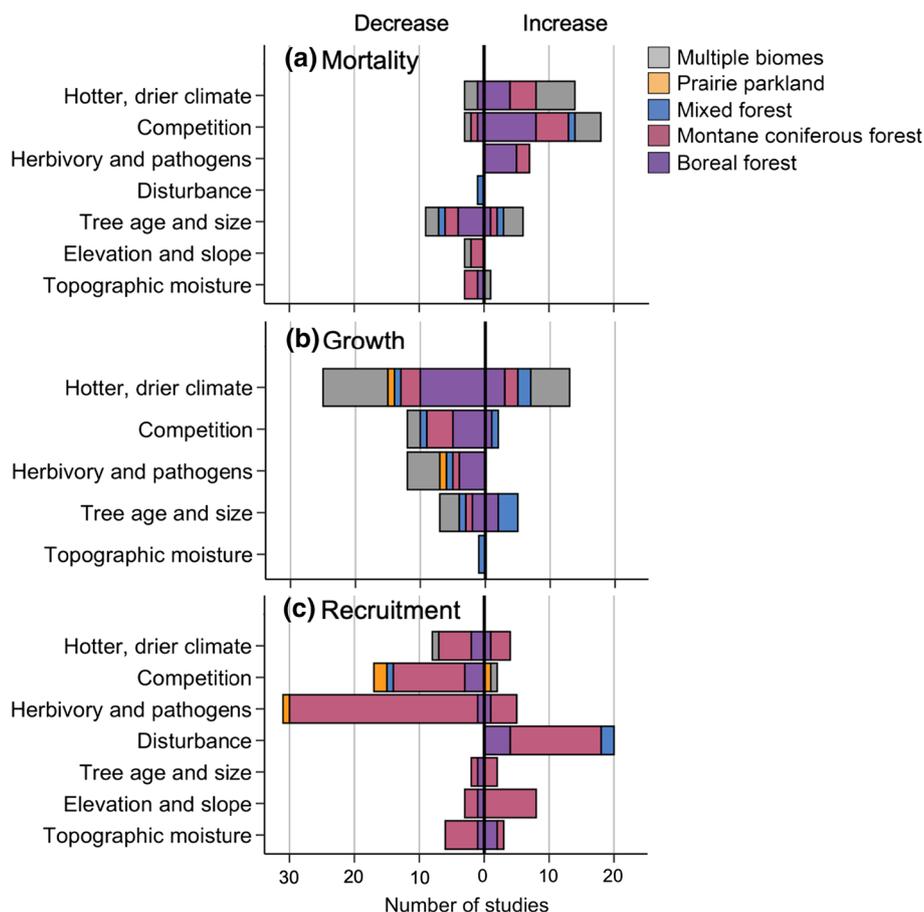
(Fig. 2a). Of the studies conducted in boreal forests, the majority were conducted in the boreal plains ($n = 14$; 38%) and boreal shield of Canada ($n = 13$; 35%), followed by the boreal cordillera ($n = 8$; 22%) and interior Alaska ($n = 7$; 19%) (Fig. 2a). Of the studies across multiple biomes, most were conducted in boreal and mixed deciduous-coniferous forests of Canada ($n = 7$; 37%), boreal forests and prairie parkland in western Canada ($n = 5$; 26%) and deciduous and mixed deciduous-coniferous forests in the eastern US ($n = 4$; 21%).

The number of published journal articles on aspen mortality, growth and recruitment generally increased over the past 30 years (1989–2019), with 35% of studies ($n = 47$) published in the past five years (2015–2019) (Fig. 2b). The increase was most notable for studies in boreal forests of Alaska and Canada, montane coniferous forests of western North America, and across multiple biomes, with each experiencing almost a five-fold increase in the number of studies published in 2006–2019 relative to 1989–2005. In contrast, the number of studies in prairie parkland and mixed deciduous-coniferous forests remained relatively small ($n = 4$ and 10 studies, respectively) and constant through time. The only published studies from deciduous forests that met our review criteria were conducted across multiple biomes (Fig. 2).

Individual drivers of aspen mortality, growth and recruitment

Our review of the literature revealed that among all individual drivers studied, competition and climate were most commonly associated with mature aspen mortality ($n = 18$ and 15 studies, respectively) (Fig. 3a). Of those studies reporting a significant relationship, the majority found mortality increased with greater competition ($n = 15$; 83%) and hotter, drier climate conditions ($n = 12$; 80%). Specifically, an equal number of studies found interspecific and intraspecific competition ($n = 4$ each) were associated with increased mortality. Of those that found a significant relationship between climate and mortality, most found elevated mortality with high temperatures ($n = 9$), followed by low precipitation ($n = 7$) and high evaporative demand relative to water supply, as indicated by various drought indices ($n = 7$). Several studies also found that increased mortality was frequently associated with tree age/size ($n = 12$) and herbivory and pathogens ($n = 7$) (Fig. 3a). The evidence was equivocal on the influence of tree age/size on mortality, with studies concluding mortality increased with increasing ($n = 3$) and decreasing age ($n = 4$), as well as with increasing ($n = 3$) and decreasing aspen stem

Fig. 3 Number of independent, published studies in the past thirty years (1989–2019) that reported a significant increase or decrease in **a** mortality, **b** growth, and **c** recruitment of quaking aspen (*P. tremuloides*) as a function of several abiotic and biotic stressors and endogenous factors



diameter ($n = 5$ each). Herbivory and pathogens were associated only with increased mortality, with effects reported for insect defoliators (*Malacosoma disstria*) and wood borers (e.g., *Agrilus liragus*) ($n = 4$), mammalian herbivory from elk (*Cervus canadensis*) and moose (*Alces alces*) ($n = 2$), and canker diseases (*Valsa sordida* and *Encoelia pruinosa*) ($n = 2$) (Table S6 in Online Resource 4).

Mature aspen growth was most commonly associated with climate ($n = 29$), followed by competition ($n = 14$), herbivory and pathogens ($n = 12$), and tree age/size ($n = 10$) (Fig. 3b). The relationship between climate and growth was more complex than with mortality. Although most studies found reduced growth under hotter, drier climate conditions ($n = 16$; 55%), several found mixed evidence of both increased and decreased growth ($n = 9$; 31%) or increased growth ($n = 4$; 14%) under hotter, drier conditions. Of those that found a significant relationship between climate and growth, most found reduced growth during periods of reduced precipitation ($n = 12$), high evaporative demand relative to water supply ($n = 12$), and high temperatures ($n = 7$). The minority of studies that found increased growth with warmer temperatures ($n = 4$), longer growing season ($n = 4$), or high evaporative demand relative to water supply ($n = 1$) were conducted primarily in high-latitude boreal and mixed

deciduous-coniferous forests, where aspen growth can benefit from longer growing seasons as well as drier conditions that may provide aspen a temporary, competitive advantage over many late-successional species. Studies on competition found reduced growth with higher interspecific ($n = 7$), intraspecific ($n = 1$) and total (inter- and intraspecific) competition ($n = 8$), with only two studies reporting increased growth with competition. All studies that considered herbivory and pathogens found a negative relationship with aspen growth. Specifically, growth was negatively associated with defoliation caused by forest tent caterpillars (*M. disstria*) ($n = 7$), leaf miners (*Phyllocnistis populiella*) ($n = 2$), and canopy leaf removal to simulate *M. disstria* ($n = 1$), as well as damage from wood borers (e.g., *Saperda calcarata*, *Agrilus liragus* and *Dicerca tenebrica*) ($n = 1$) and elk (*Cervus canadensis*) browse ($n = 1$). Finally, depending on the context, the relationship between tree age/size and aspen growth was either positive ($n = 3$), negative ($n = 5$), or both ($n = 2$) (Fig. 3b).

Aspen recruitment was most frequently associated with herbivory and pathogens ($n = 33$), followed by disturbance ($n = 20$), competition ($n = 18$) and climate ($n = 10$) (Fig. 3c). Recruitment was less commonly associated with elevation and slope ($n = 10$), topographic moisture ($n = 9$) and tree

age/size ($n=3$). Studies were almost unanimous in finding a negative relationship between recruitment and herbivory and pathogens, with the majority of studies finding reduced recruitment with increased mammalian herbivory from elk, mule deer (*Odocoileus hemionus*) and/or cattle ($n=27$; all but one study conducted in montane coniferous forests of the western US). A single study found insect herbivory from leaf miners (*P. populiella*) ($n=1$) as well as damage from wood borers (*A. liragus* and *D. tenebrica*) and canker diseases (*V. sordida* and *E. pruinosa*) ($n=1$) reduced aspen recruitment. Only four studies found increased recruitment with herbivory and pathogens. Specifically, the authors observed a pulse of recruitment after larger aspen stems were impacted by ungulate herbivory, forest tent caterpillars, leaf rust (*Melampsora* spp.) or blight (*Venturia tremulae*). Of those studies on disturbance, all found increased recruitment after disturbance ($n=20$), predominantly after fire ($n=15$; all studies conducted in montane and boreal forests of western North America). The majority of studies on competition found a negative relationship with recruitment ($n=16$), with most finding reduced recruitment with higher interspecific ($n=10$) or total ($n=5$) competition, rather than intraspecific ($n=1$). Of the studies that considered climate ($n=10$), recruitment was often negatively associated with hotter, drier climate conditions ($n=6$), but the limited number of studies on the effect of climate on recruitment relative to mortality and growth make generalizations difficult.

Interacting drivers of aspen mortality, growth and recruitment

Interacting drivers of aspen mortality

In addition to the individual drivers described previously, several studies found interactions among climate, competition, herbivory/pathogens and tree age/size as important determinants of aspen mortality (Table 1). The most commonly reported interaction was between climate and competition, such that aspen mortality was greatest in dense, competitive stands under hotter and/or drier conditions in montane coniferous (Bell et al. 2014, 2015) and boreal forests (Luo and Chen 2015; Trugman et al. 2018b). Patterns were inconsistent, however, with two studies in boreal forests reporting no interactive effect of competition and climate on aspen mortality (Luo and Chen 2013, 2015; Zhang et al. 2015). No consistent patterns emerged from studies that considered the influence of tree age/size on climate-associated mortality probability, with effects ranging from positive (Bell et al. 2014; Hember et al. 2017; Kweon and Comeau 2019) to negative (Luo and Chen 2013; Bell et al. 2014; Hember et al. 2017) to neutral (Luo and Chen 2015). There were only two studies that considered interactive

effects between spatial and temporal variation in climate on the mortality rates of aspen. In a continent-wide study of North America, Hember et al. (2017) found that the sensitivity of aspen mortality to drought was greater in more arid climates. However, at the regional scale, Trugman et al. (2018b) found the sensitivity of aspen mortality to intra-annual variation in evaporative demand was unaffected by mean annual precipitation in Alaska, suggesting that the dependence of climate-driven mortality on local climatic context may only be important at larger spatial scales.

Several studies reported climate and tree age/size as important in mediating the increased probability of mortality with competition and herbivory/pathogens (Table 1). Specifically, the effect of competition on mortality has been found to be stronger in more arid environments (Bell et al. 2014; Trugman et al. 2018b), whereas more mature and/or larger mature aspen stems have been found to have increased (Luo and Chen 2015) and decreased probability of mortality (Luo and Chen 2011; Bell et al. 2014, 2015; Kweon and Comeau 2019). The positive relationship between herbivore/pathogen presence and aspen mortality was stronger in more arid environments (Trugman et al. 2018b) and either decreased (Moulinier et al. 2014) or was unaffected by tree age/size (Pitt et al. 2001). Competition was not found to mediate the effects of herbivory/pathogens on aspen mortality (Pitt et al. 2001; Kaye et al. 2005).

Interacting drivers of aspen growth

The most commonly reported interaction in determining the growth of mature aspen stems was that between temporal and spatial variation in climate (Table 1), with regional to continental-scale studies generally finding that the response of aspen growth to inter-annual variation in climate was dependent on the larger climatic context (i.e., climate normals or latitude). Specifically, in boreal forests of Alaska, Trugman et al. (2018b) reported that declines in aspen growth during hotter, drier years were greater in drier than wetter sites. Although increased temperatures and/or growing season were positively associated with growth in high-latitude, boreal and mixed forests of Québec (Lapointe-Garant et al. 2010; Huang et al. 2010), aspen growth was also more susceptible to inter-annual variability in moisture availability in high-latitude forests (Huang et al. 2010; Chen et al. 2018). When patterns were examined across a wide latitudinal gradient comprising the prairie parkland-boreal forest ecotone, drought-associated declines in aspen growth were greatest near the ecotone boundary (Chen et al. 2017).

Of the studies that considered interactions among climate and insect herbivory in determining aspen growth (Table 1), all concerned the effects of forest tent caterpillar (*Malacosoma disstria*) defoliation on aspen in boreal forests. Haynes et al. (2018) reported that growth declines associated with

Table 1 Overview of aspen responses to the most frequently studied predictors and their interactions

Response	Predictor							References
	Hotter/drier climate (spatial)	Hotter/drier climate (temporal)	Competition	Herbivory and pathogens	Tree age/size	Disturbance	Interaction	
Mortality	~						~	1*
	=	↑					↑=	2
	=	↑					=	3
	↑↓=		↑				↑	3, 4
		↑=	↑				↑=	1, 5
		↑	↑=				=	6, 7
	↑↓=				↑		↑	3
	↑↓					↑↓=	↑	2, 4, 8
		↑↓				↓	↓	2, 4, 6
		↑				↑	=	5
			↑			↑↓=	↓	1, 4, 8, 9
			↑			↑	↑	5
			↑=	↑=			=	10, 11
				↑		=	↓	12
				↑		↓	=	10
Growth	↑=	↓=					↑	3, 13, 14
	↑=	↓					↓	14, 15
	↓	↓					~	16
		↑=					↑	17*
		↑=					=	18*
			↓				↓	3
		↓=	↓				=	7
		↑↓			↓		↓~	19
		↓=			↓		=	15, 20, 21
			=		↓		=	11
Recruitment		↑↓=	↓			=	↓	22
	↓=						=	7
	↓				=		↑=	23
					↓		=	24
					↓		↑	25
			=		↓		=	11
					↓=		↑=	26, 27, 28, 29, 30, 31, 32
						↑=	↑=	33*

↑, ↓, and ↑↓ indicate a positive, negative and context-dependent response, respectively. ~ and = indicate a non-linear response and no change, respectively. * indicates studies that examined interactions among predictors belonging to the same category, e.g., disturbance severity x disturbance area. Only studies that found a significant change in the response with at least one of the predictors are included. In cases where studies included multiple predictors of a given category when examining interactions, multiple responses may be reported from a single study

1. Bell et al. (2015); 2. Hember et al. (2017); 3. Trugman et al. (2018a, b); 4. Bell et al. (2014); 5. Luo et al. (2015); 6. Luo et al. (2013); 7. Zhang et al. (2015); 8. Kweon et al. (2019); 9. Luo and Chen (2011); 10. Pitt et al. (2001); 11. Kaye et al. (2005); 12. Moulinier et al. (2014); 13. Lapointe-Garant et al. (2010); 14. Huang et al. (2010); 15. Chen et al. (2018); 16. Chen et al. (2017); 17. Brown et al. (2006); 18. Foster et al. (2016); 19. Haynes et al. (2018); 20. Boyd et al. (2019); 21. Itter et al. (2019); 22. Canham et al. (2006); 23. Brodie et al. (2012); 24. Rhodes et al. (2017); 25. White et al. (2003); 26. Bailey and Whitham (2002); 27. Smith et al. (2016); 28. Conway and Johnstone (2017); 29. D'Amato et al. (2011); 30. Korb et al. (2012); 31. Kulakowski et al. (2013); 32. Wan et al. (2014b); 33. Wan et al. (2014a)

defoliation were mitigated by spring and moderate summer drought and exacerbated by severe summer drought. In contrast, several other studies found no mediating effect

of climate on defoliator-driven growth declines (Chen et al. 2018; Itter et al. 2019; Boyd et al. 2019). In terms of interactions between climate and competition, Trugman et al.

(2018b) reported growth was more negatively affected by conifer competition in dry than wet sites, while Zhang et al. (2015) found no significant effect of competition on climate-growth patterns. Canham et al. (2006) reported that competition-driven declines in growth decreased with tree age/size.

Interacting drivers of aspen recruitment

Previous studies primarily reported on interactions among mammalian herbivory, disturbance and competition in determining aspen recruitment (Table 1). Disturbance was a dominant driver of recruitment, with several studies reporting increased recruitment after multiple, compounded disturbances (e.g., windfall and wildfire; D'Amato et al. 2011; Korb et al. 2012; Kulakowski et al. 2013) or larger, more severe wildfires (Wan et al. 2014a). Most authors found that the negative effects of mammalian herbivory on recruitment were greater in post-fire than undisturbed stands (Bailey and Whitham 2002; Smith et al. 2016; Conway and Johnstone 2017), with one notable exception (Wan et al. 2014b). Specifically, in boreal forests of Alaska, aspen recruitment was impacted more by moose browsing after high than low-severity wildfire (Conway and Johnstone 2017). In montane coniferous forests, elk were found to selectively browse aspen ramets more after high- than intermediate-severity wildfires, negating the enhanced recruitment that typically occurs post-fire (Bailey and Whitham 2002). Similarly, Smith et al. (2016) found that the positive effect of elk exclosures on the height of aspen shoots was greater in post-wildfire than unburned areas. In contrast, Wan et al. (2014b) reported that mammalian browse intensity decreased with increasing fire severity, suggesting that aspen regeneration after severe wildfire can saturate herbivore impacts. Such findings are consistent with past studies in the western US that found that deer pellet density and overall browse intensity on post-fire aspen regeneration decrease with wildfire size (Wan et al. 2014a; Rhodes et al. 2018, respectively).

Competition and climate were found to have inconsistent effects on herbivory-driven declines in recruitment. Of several field studies conducted in montane coniferous forests, none reported a significant effect of competition on the sensitivity of aspen recruitment to herbivores (White et al. 2003; Romme et al. 2005; Kaye et al. 2005; Maxwell et al. 2019). Although such studies did not meet our review criteria, we note that evidence from greenhouse studies suggest that declines in light availability and changes in soil chemistry from increased conifer competition may constrain the production of defensive chemicals by aspen against herbivory (Calder et al. 2011).

In terms of climate mediating herbivore-driven declines in recruitment, Brodie et al. (2012) found that recruitment at wet sites with deep snowpack in montane coniferous forests of Wyoming benefited more from protection from

mammalian herbivory than dry sites. In contrast, Martin and Maron (2012) concluded that long-term declines in aspen recruitment associated with declining snowfall in montane Arizona were reversed by elk exclosures, suggesting sites with lack of deep snowpack, and therefore high over-winter herbivory, benefited most from protection from mammalian herbivory. In montane coniferous forests of Utah, however, Rhodes et al. (2017) found no evidence of winter precipitation mediating herbivory-related declines in aspen recruitment.

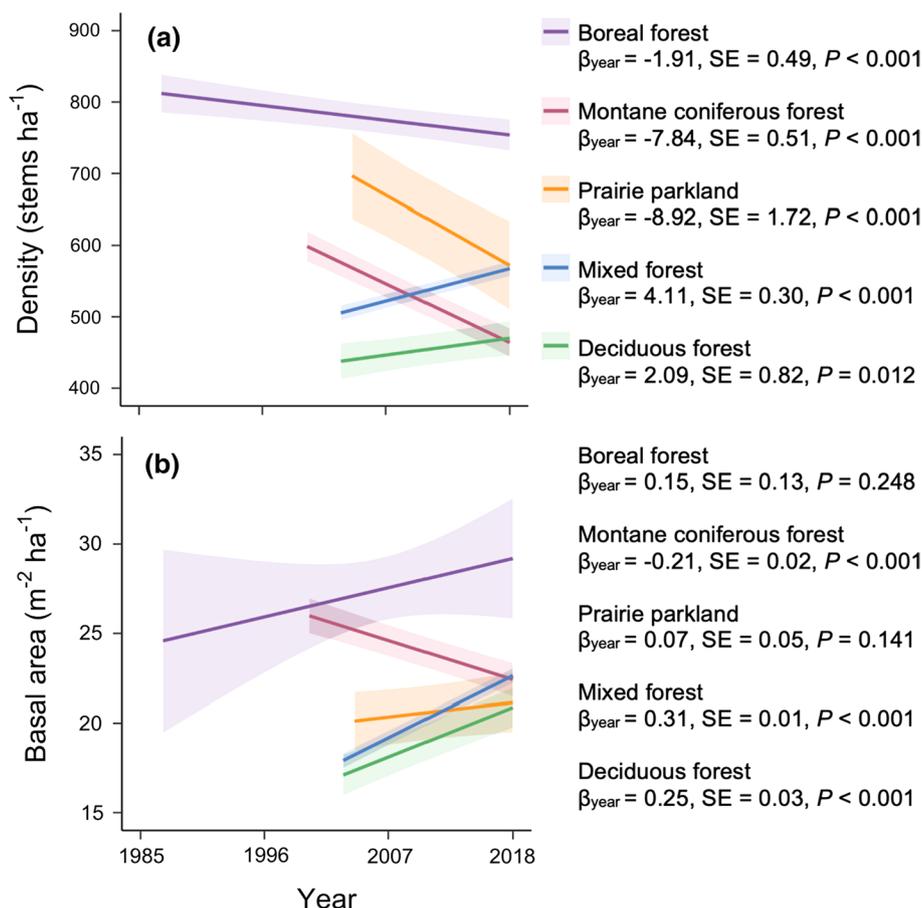
Synthesis of emerging patterns and future directions

In this paper, we have synthesized emerging patterns in mortality rates and the relative change in live BA of mature aspen stems within 3962 plots distributed across the species' entire geographic range in North America. Our analysis of such an extensive and spatially unbiased data set has allowed us to assess the demographic performance of aspen across multiple decades and all biomes that it inhabits. In addition, we have been able to evaluate how size structure and relative abundance of aspen mediates the spatial and temporal responses of this wide-ranging foundation species. Lastly, we have reviewed the published literature on aspen over the past three decades to synthesize our understanding of the individual and interactive drivers of its population dynamics.

Within a continent-wide network of plots in unmanaged, mature forests, we have shown that annual mortality rates of mature aspen stems have increased substantially over the past two-to-three decades across all biomes except mixed deciduous-coniferous forests, with doubling periods ranging from 11 years in montane coniferous forests to 33 years in boreal forests (Fig. 1b). During the same time period, relative gains in BA of mature aspen stems decreased across all biomes, reaching a net loss of live BA in all biomes except mixed deciduous-coniferous forests (Fig. 1e). These patterns are consistent with the broader literature on tree decline, where drought-induced mortality is often highest in the most arid or climatically variable regions of a species' distribution (Carnicer et al. 2011; Young et al. 2017; Anderegg et al. 2019). Our findings suggest that within the drier margins of its range, aspen may have a limited capacity to persist in the face of ongoing climate change.

For three reasons, we assert that the demographic declines reported here for aspen stands in boreal, montane coniferous and prairie parkland biomes of western North America cannot be explained simply by stand development or succession processes. First, we found total stand density and BA declined or remained stable through time in these biomes (Fig. 4), characteristics consistent with more late-successional forests (Odum 1969). Second, increased mortality

Fig. 4 Modeled trends in mean ($\pm 95\%$ CI) a) stem density and b) basal area of live, mature ($\text{dbh} \geq 12.7$ cm) trees of all species by biome from linear mixed models. Plots contained at least five live mature aspen stems and were remeasured 2–6 times between 1985–2018. Sample sizes: boreal ($n = 859$), montane coniferous ($n = 874$), prairie parkland ($n = 122$), mixed ($n = 1846$), and deciduous ($n = 261$)



and decreased gains in live BA through time were observed across multiple stand size structures in these biomes (Fig. S3a and S4a in Online Resource 2), suggesting that trends cannot be attributed solely to the aging of adult ramets (Bell et al. 2014; Chen and Luo 2015; Foster et al. 2016; Canham and Murphy 2017; Cortini et al. 2017). Finally, we found increased mortality and decreased gains in live BA through time for stands with moderate to high aspen abundance (Fig. S3b and S4b in Online Resource 2), suggesting that trends are not simply reflective of seral aspen stands being replaced by other tree species in the absence of disturbance (Shinneman et al. 2013). In contrast with the biomes of western North America, we found total stand density and BA generally increased through time in deciduous and mixed deciduous-coniferous forests (Fig. 4), characteristics that are more consistent with early-successional forests. Together, these patterns suggest that stand development and/or successional processes may play a dominant role in determining population dynamics of aspen stands in eastern North America, whereas stress-induced decline may be increasingly important in driving demographic decline of aspen in the drier regions of its range in western North America.

During the 30 years over which we present demographic rates for aspen across its range, global temperatures have

increased substantially due to anthropogenic climate change (Ratajczak et al. 2018). At the same time, precipitation regimes have also changed, although in less consistent ways—generally decreasing in the western portions of aspen's range and increasing in the eastern portions (IPCC 2018). Based on these well-documented changes, we postulate that the hotter and drier conditions in western North America were important drivers of the observed demographic declines in aspen performance. Furthermore, the warmer and wetter conditions in the eastern part of aspen's range may well explain the absence of such declines in these areas. Our review of the published literature generally supports this conclusion, with elevated mortality and reduced growth rates in aspen predominantly associated with hotter, drier climate conditions, followed by increased competition and insect herbivory (Fig. 3). Furthermore, interactions among climate and competition were important in determining mortality, whereas interactions among spatial and temporal variation in climate, as well as climate and insect herbivory, were important in determining growth (Table 1).

Our review of the published literature indicates that there is considerable spatial bias with respect to where aspen populations are studied. Research efforts have been concentrated in the core areas of aspen's range—specifically the boreal

plains and shield of Canada, temperate mixed forests near the Great Lakes, and coniferous forests in the southern and middle Rocky Mountains (Fig. 2a). Of the empirical studies that met our review criteria, relatively few were conducted along aspen's dry (e.g., Great Basin), cold (e.g., taiga) and wet (e.g., deciduous forest) range margins, where the species is less common (but see references in Table S6 in Online Resources 4). The shortage of studies in these areas is important because these regions represent the boundary between aspen's realized and fundamental niche (Hogg and Hurdle 1995; Hogg et al. 2002) and therefore documenting its response to global change in these regions may provide early insight into potential range shifts.

In addition to studying the demographic responses of tree species along their range margins, there is an urgent need to study the spatial and temporal drivers of population dynamics across the species' entire geographic range. Fortunately, we found that an increasing amount of research through time has been conducted on aspen across multiple biomes (Fig. 2b), studies which have contributed important insights on aspen growth and mortality along latitudinal gradients and ecotonal boundaries (Lapointe-Garant et al. 2010; Huang et al. 2010; e.g., Hember et al. 2017). Furthermore, by studying populations of species across their entire range, we can quantify intraspecific variation in adaptation and plasticity to environmental change that can buffer species from the impacts of stress-induced decline (Messier et al. 2010; Anderegg 2015). By doing so, we can better forecast range shifts and thus estimate the effects of climate change on biodiversity, species extinctions, ecosystem resilience, and to forecast forest carbon sinks (Anderegg et al. 2019).

Our review found only four studies that considered the influence of intraspecific variation on aspen demographic performance (Cole et al. 2009; Dixon and DeWald 2015; Latutrie et al. 2015; Grossman and Cavender-Bares 2019; Table S6 in Online Resource 4), yet phenotypic variation among and within aspen populations due to genotype, environmental conditions, and ontogeny is likely critically important in explaining variation in the performance of this species across its geographic range. Of the relatively few studies to consider genetic variation, previous investigators have shown that aspen genets can be either diploid or triploid (Kemperman and Barnes 1976), with diploids being more common in eastern and boreal populations and triploids being more common in the southwest regions of the range (Mock et al. 2008, 2012; Callahan et al. 2013). Mock et al. (2012) hypothesized that ploidy level, as well as clone size and age, could be important drivers of variation in aspen mortality for western populations. In northern Arizona, Dixon and DeWald (2015) showed that the proportion of triploid stems in a stand was positively correlated with mortality. The authors also found that site heterozygosity was positively associated with aspen mortality and crown

dieback. Additionally, age-related changes in phenotype within a single clone have been shown to affect defense chemistry in montane coniferous forests in Utah (Smith et al. 2011) and mixed deciduous forests in Wisconsin (Donaldson et al. 2006), suggesting that ontogenetic changes may have important implications for clone fitness. Thus, we assert that tremendous insight will be gained from future research that incorporates genetic and phenotypic variation to better understand the drivers of vulnerability of aspen populations to anthropogenic climate change and other environmental stressors.

As our synthesis has shown, aspen demographic performance is a product of multiple, often interacting drivers. To more fully understand the susceptibility of this foundation species to ongoing global change, especially along the margins of aspen's range, future studies need to consider multiple drivers operating simultaneously in the same system. In particular, greater insight will be gained if studies (1) quantify the relative importance of multiple factors in driving the dynamics of tree populations and (2) assess whether interactions among multiple drivers play an important role in predicting forest dynamics.

Conclusions

As a foundation species that inhabits topoclimatically heterogeneous environments and has experienced recent, stress-induced mortality events, quaking aspen is an ideal system in which to address the long-term dynamics of tree populations during a period of pronounced anthropogenic climate change. Our synthesis of the long-term dynamics of aspen populations across its entire geographic range indicates that this critically important tree species is experiencing increased mortality and reductions in BA through time in western North America, with increased water deficits and altered disturbance regimes being the most commonly reported drivers associated with these demographic trends. Our findings from a cross-continental plot network suggest that recruitment is not outpacing mortality rates and, in the absence of increased rates of colonization and/or regeneration elsewhere, our results signal a decline in aspen abundance in the western US. Our analyses demonstrate that the temporal changes in aspen mortality and live BA are widespread across multiple biomes, sometimes rapid, and at least in western North America, not explained by stand development or successional processes.

Anthropogenic climate change is an unavoidable reality, and our findings clearly indicate that it is a major driver of aspen demographic rates. Despite ongoing efforts at mitigation, all predictions suggest that climate change will intensify in the coming decades. Thus, it is highly probable that the trends in aspen demographic rates that we have reported

in this review will continue and likely intensify in the future. Indeed, we should expect to witness major changes in the structure and composition of aspen-inhabited forests, with these being especially important in the western US where aspen is the only dominant broadleaf tree species. The reduced dominance of aspen will lead to critical declines in many ecosystem services, including the maintenance of plant and animal biodiversity and effects on a range of ecosystem-level processes.

Like so many species on Earth, quaking aspen is confronted with an intensifying suite of human-induced changes to its environment. Human activities have increased global temperatures and led to more variable precipitation regimes (IPCC 2018), reduced or eliminated top predators that previously controlled large mammalian herbivores (Estes et al. 2011; Ripple et al. 2014), and promoted conifer expansion due to fire suppression (Singer et al. 2019). Operating individually and in concert, these global change drivers are causing significant declines in aspen demographic performance and consequently, will likely have cascading effects on biodiversity and ecosystem services.

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Declarations

Conflict of interest The authors declare that they have no conflicts of interest.

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Availability of data and material Data sources are summarized in Table S1 in Online Resource 1.

Code availability Not applicable.

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