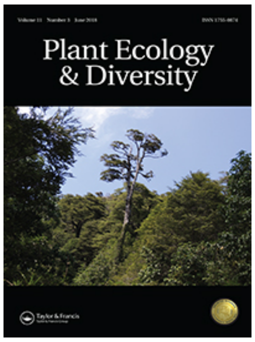

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ARTICLE

Tree recruitment at the treeline across the Continental Divide in the Northern Rocky Mountains, USA: the role of spring snow and autumn climate

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ABSTRACT

Background: Topoclimate can influence tree establishment within treeline ecotones. Yet much less is known about how regional topography, such as the Continental Divide, Rocky Mountains, mediates the role of climate in governing treeline dynamics.

Aims: To utilise the Continental Divide to test whether contrasts in growing-season moisture regimes to the west (summer-dry) and east (summer-wet) impact the spatio-temporal patterns of tree establishment and rates of treeline advance in the Northern Rocky Mountains.

Methods: We sampled trees at sites on north- and south-facing slopes, west and east of the Continental Divide. We used dendroecological techniques to reconstruct patterns of tree establishment. Age-structure data were quantitatively compared with climate to evaluate possible mechanistic linkages.

Results: Across all sites, 96% of trees established after 1950. There was a treeline advance (range = 39–140 m) accompanied by increases in tree density. Significantly more trees established during wet springs on both sides of the Divide.

Conclusions: Overall, snow duration in spring and autumn temperatures appear to influence patterns of tree recruitment at the treeline. Continued warming will likely amplify the role of autumn climate in regulating tree establishment throughout treeline ecotones in the Northern Rocky Mountains, particularly west of the Divide where summer-dry conditions persist.

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Autumn temperature; climate change; dendroecology; Idaho; Rocky Mountains; slope aspect; topoclimate; treeline

Introduction

Measuring the influence of rising temperatures on ecological processes at the treeline is challenging because mountain topography modifies radiation and moisture budgets across multiple spatial scales. At a local scale, for example, topography partitions the top-down influence of climate into topoclimates based on slope angle and aspect, which creates distinct temperature-moisture interactions on north- and south-facing slopes (Barry 2008). Global change ecology research from treeline ecotones suggests that these slope aspect-meditated variations in plant water availability have measurable impacts on the position/elevation of upper treeline (Brown 1994; Bader and Ruijten 2008; Kharuk et al. 2010; Stueve et al. 2011; Case and Buckley 2015; Chhetri et al. 2017), species composition (Elliott and Baker 2004; Schickhoff et al. 2015; Shrestha et al. 2015; Dearborn and Danby 2017), seedling establishment (Weisberg and Baker 1995; Germino et al. 2002; Elliott and Kipfmueller 2010; Shen et al. 2014; Millar et al. 2015) and the climate sensitivity of both annual tree growth (Leonelli et al. 2009; Bunn et al. 2011; Salzer et al. 2014; Zhang et al. 2015) and patterns of tree establishment required for upper treeline advance (Bunn et al. 2005; Danby and Hik 2007; Dang et al. 2015; Elliott and Cowell 2015; Alatalo and Ferrarini 2017; Young et al. 2017). Despite widespread study of how topoclimate influences upper treeline dynamics (but see Wang et al. 2013), surprisingly little is known about how regional topography, such as the Continental Divide, modifies the role of climate in governing tree recruitment at the treeline in the Rocky Mountains.

The Continental Divide is termed for the crest of the generally north-south trending Rocky Mountains that interrupts the flow of prevailing westerly winds to create separate regional climates to the west and east (Mitchell 1976; Mock 1996; Kittel et al. 2002). In the Northern Rocky Mountains (ca. 45° N), for instance, annual water budgets are dominated by cool season snowfall on both sides with disparate summer moisture regimes. To the west, subtropical high pressure creates summer-dry conditions (Brunelle et al. 2005), whereas

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frequent convective storms produce summer-wet conditions to the east (Crawford et al. 2015). Reconstructed climate-disturbance interactions from upper montane forests in the region suggest that these opposite growing season moisture regimes persisted throughout the Holocene (Brunelle et al. 2005), yet studies examining what these mean for treeline dynamics are lacking. This is notable because heat-induced drought stress is expected to impact trees in environments not currently considered moisture-limited, such as the treeline (Allen et al. 2015). In fact, recent research from the treeline east of the Divide in the Southern Rocky Mountains has suggested that these differences in regional climate and growing season moisture regimes could exert considerable control on treeline dynamics; seedling establishment was temperature-limited until drought stress began limiting tree function midway through the growing season (Moyes et al. 2013, 2015).

In this paper, we utilised the Continental Divide to test whether contrasts in growing-season moisture regimes to the west and east impact the spatio-temporal patterns of tree establishment and rates of treeline advance in the Northern Rocky Mountains. To achieve this, we used dendroecological techniques to reconstruct tree establishment which helps fill a sizable gap in tree-ring studies concerned with high-elevation climate-vegetation linkages along the American Cordillera. For example, results from previous research have underscored the key role that both temperature and moisture play in shaping tree demography at the treeline in the Andes Mountains of northern Patagonia (Villalba and Veblen 1997; Daniels and Veblen 2004; Srur et al. 2016), the Sierra Nevada (Lloyd and Graumlich 1997; Millar et al. 2004; Bunn et al. 2005), Great Basin (Millar et al. 2015), northern Cascades (Rochefort and Peterson 1996) and south-west Yukon, Canada (Danby and Hik 2007). Moreover, research from east of the Divide in the Southern (Weisberg and Baker 1995; Hessl and Baker 1997; Elliott and Kipfmueller 2011; Elliott 2012) and Northern (Alftine et al. 2003) Rocky Mountains corroborate these findings, but comparable data from regions west of the Divide are non-existent. Given these results, we hypothesised that both temperature and moisture would play a role in facilitating tree recruitment at the treeline. Taken at large, our motivation for this research was to generate empirical evidence that further elucidates the role of regional- and local-scale topoclimatic gradients in modifying the ecological response of upper treeline ecotones to global climate change.

Materials and methods

Study area

A total of four study sites were selected a priori through the use of satellite imagery, topographic maps and extensive field reconnaissance owing to the relative dearth of climatic treelines throughout this section of the Northern Rocky Mountains. Two of the study sites were west of the Continental Divide in the Lost River Range of east-central Idaho. Here, one site was on a north-facing slope (site code = WNF) and the other was on a south-facing slope (WSF). The other two study sites were east of the Continental Divide on the opposite north- and south-facing slope (ENF and ESF) of Sugarloaf Mountain in the Pioneer Range of south-west Montana (Table 1; Figure 1).

Temperature trends analysed from western Montana have indicated that this region has experienced a + 1.33°C increase in mean annual temperature from 1900 to 2006, which exceeds the global average of + 0.74°C (Pederson et al. 2010). On seasonal timescales, warming since the 1980s has caused an earlier spring thaw and delayed the first autumn frost (Pederson et al. 2010). Increases in mean summer temperature are more pronounced in Idaho, although nearly identical patterns of warming

Table 1. Study site characteristics, Northern Rocky Mountains, USA. Ecotone denotes the width of the treeline ecotone as measured from the elevational extent of the outpost tree downslope to timberline (m).

Site	Lat. (°N)	Long. (°W)	Elev. (m)	Aspect (°)	Slope (°)	Transect (m)	Ecotone (m)	Dominant tree species (%)
WNF	44.2	113.8	2863	350	22	140	109	*Pinus albicaulis* (77)
WSF	44.3	113.8	2995	172	24	70	37	*P. albicaulis* (84)
ENF	45.5	112.8	2700	0	26	39	39	*P. albicaulis* (100)
ESF	45.5	112.8	2539	220	10	96	79	*Pseudotsuga menziesii* (97)

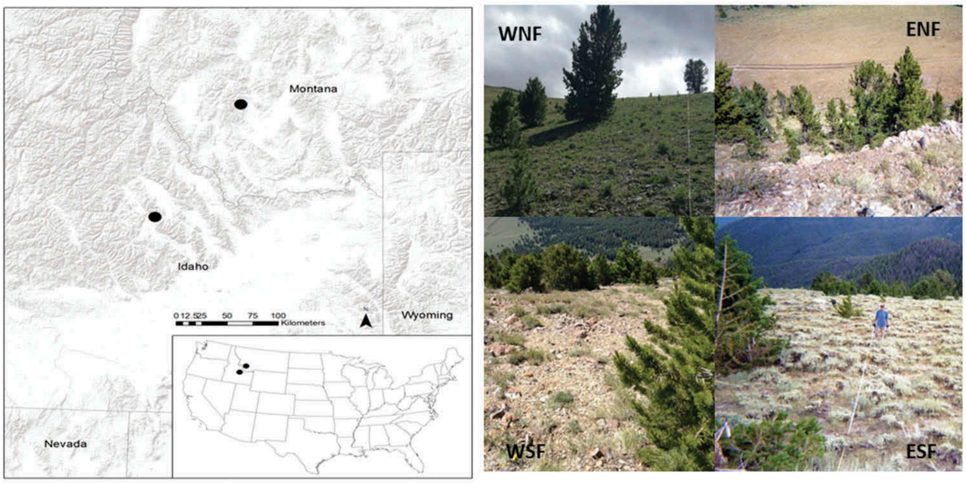

Figure 1. Study area map and representative images from each study site. Circles denote location of study sites.

are evident among sites since ca. 1980 (Figure 2). Precipitation regimes are dominated by snow, which is delivered most often by zonal flow off the Pacific during winter (Mitchell 1976). Snow cover typically persists into late spring and there has been an increase in the amount and variance since the late 1970s (Pederson et al. 2011).

The dominant tree species at our sites were whitebark pine (*Pinus albicaulis* Engelm.) and subalpine fir (*Abies lasiocarpa* [Hook] Nutt), with fewer Engelmann spruce (*Picea engelmannii* [Parry] Engelm.) and Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) confined to site ESF in Montana. Possible disturbance agents include grazing and fire, with outbreaks of native mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and invasions of exotic blister rust fungus *Cronartium ribicola* (J.C. Fisch.) on whitebark pine (Larson 2011; Smith-McKenna et al. 2013). Each of our study sites lacked a clear indication of these disturbances, but mountain pine beetle mortality was evident for whitebark pine in areas at and near the treeline throughout the eastern Pioneer Mountains.

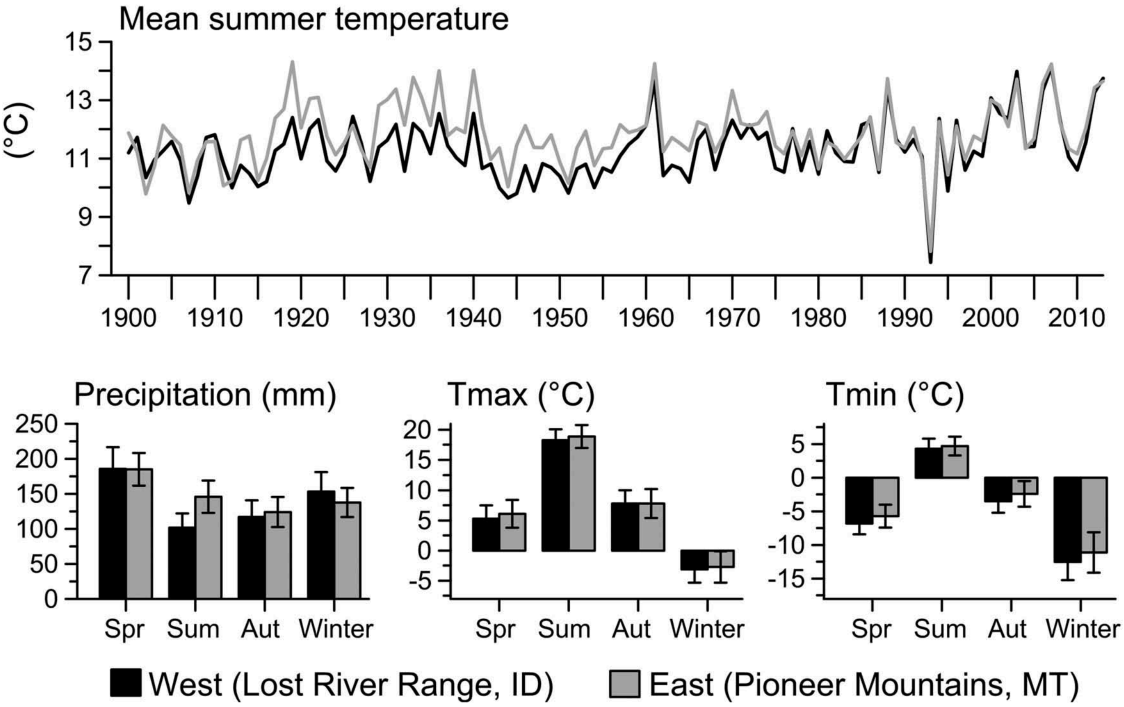

Figure 2. Mean growing-season temperature and seasonal differences in temperature and precipitation west and east of the Continental Divide.

Field methods

We carried out field work during the summer of 2013 and focused our study site selection on identifying climatic treeline boundaries. Climatic treelines refer to environments where tree establishment and potential treeline advance into alpine tundra are unimpeded by local topography or geomorphological conditions, such as steep and rocky slopes, often devoid of soil, or frequently disturbed avalanche tracks (see Holtmeier and Broll 2005; Butler et al. 2007). We refer to the treeline ecotone as the transition zone from the uppermost extent of closed-canopy upper montane forest (also called timberline or forest line) to alpine tundra (Malanson et al. 2007; Körner 2012). Depending on local topography and wind conditions, multi-stemmed *krummholz* were present, but we did not sample them because their low stature creates a different microclimate than that experienced by upright trees and thus may not reflect suitable conditions for tree establishment within the treeline ecotone (Holtmeier 2009).

At each site, we placed a nested-belt transect through the treeline ecotone. Transects began at the outpost tree (term after Paulsen et al. 2000), which was classified as the furthest upright tree (≥5 cm diameter at breast height [dbh]) or sapling (<5 cm dbh, ≥1.2 cm diameter at ground level [dgl]) existing within the treeline ecotone and then descended downslope perpendicular to slope contours, through the timberline boundary and 40 m into relatively closed-canopy upper montane forest. Transects were divided into two parts to ensure an adequate number of saplings were collected to analyse regeneration patterns. Above the timberline (ATL), we sampled all trees and saplings within a 40-m wide belt (20 m on each side of transect). Below the timberline (BTL), the total width was reduced to 20 m (10 m per side) to account for increasing stand density downslope. The only exception to this was on the north-facing slope of Sugarloaf Mountain (site ENF), where we were unable to sample BTL because of a precipitous cliff 39 m downslope from the outpost tree. As a result of variations in tree density and elevation of the outpost tree, overall transect length varied at each site (Table 1). We recorded local conditions at each site including elevation and geographic coordinates of the outpost tree, slope aspect, slope steepness and distance from the outpost tree to timberline (i.e. width of the ecotone; Table 1).

Age-structure data

For reconstructing tree colonisation within the treeline ecotones, we collected age-structure data by extracting increment cores as close to the base of each tree as possible to minimise error when assigning calendar dates of establishment. Every sapling was harvested at ground level and seedlings (<1.2 cm dgl) were inventoried by species and position relative to timberline (above or below) along the entire transect. All cores and cross-sections were processed following standard dendrochronological procedures (Stokes and Smiley 1996). All tree-ring samples were visually crossdated by identifying individual marker rings under a stereo microscope (Yamaguchi 1991). Pith estimators were used to geometrically determine the number of rings to centre when the pith was not obtained during field sampling (Applequist 1958). Considering the uncertainty involved in assigning an annual value for tree establishment, we combined our age-structure data (Table 2) into more conservative five-year age classes for the period 1900 to 2000 (Hessl and Baker 1997; Elliott and Kipfmueller 2011).

Table 2. Summary of dendroecological data, collected at the treeline ecotone, Northern Rocky Mountains, USA. Sapling cross-sections were not included when calculating age corrections. Cross-section (%) refers to the proportion of total trees sampled at each site (cross-sections/total trees).

Site	Total trees (*n*)	Core samples (*n*)	Mean age correction (*years*)	Age correction (*a*)	Pith (%)	Cross- sections (*n*)	Cross- sections (%)	Seedlings (*n*)
WNF	52	17	2.5	2.7	41.2	35	67.3	12
WSF	38	27	5.8	3.5	11.1	12	31.6	1
ENF	24	9	2.3	2.1	33.3	15	62.5	25
ESF	35	22	2.9	2.5	27.3	13	37.1	0
Mean	*37.3*	*18.8*	*3.4*	*2.7*	*28.2*	*18.8*	*49.6*	*9.5*

Climate data

To analyse climate-vegetation interactions at each site, we used Precipitation-elevation Regression on Independent Slopes Model (PRISM) climate data (PRISM Group, Oregon State University, www.prismclimate.org, created 5 May 2014). We used PRISM data because they account for physiographic variation and in the topographically complex western United States, these data more accurately represent mountain climate (Daly et al. 2008). To calculate seasonal climate values (temperature and precipitation), we used monthly PRISM data (1899–2000). For each climate variable, we calculated five-year means to align with the temporal resolution of our age-structure data and these included the following: (1) cool season (Oct–May) precipitation; (2) cool season maximum temperature (T_{max}); (3) cool season minimum temperature (T_{min}); (4) spring (March–May) precipitation; (5) spring T_{min}; (6) summer (June–August) precipitation; (7) summer T_{min}; (8) autumn (September–November) precipitation; (9) autumn T_{max} and (10) autumn T_{min}. Cool season data were used in lieu of winter data to more accurately capture the entire period of snowfall in this region.

Data analyses

We analysed the spatio-temporal patterns of treeline dynamics in three ways. To begin, we used a two-sample Kolmogorov-Smirnov test to quantitatively compare the temporal patterns of tree establishment west and east of the Divide. We then reconstructed the uppermost extent of the outpost tree (m) and tree density above and below timberline (trees ha^{-1}) at five-year intervals during the twentieth century. We used a natural-log transformation to standardise tree density data because ecotone size varied considerably between sites (Elliott and Kipfmueller 2011). Reconstructing the position of the outpost tree within the treeline ecotone was used as a general proxy for measuring treeline advance (Elliott 2012). This permits the comparison of outpost tree establishment with tree density data to determine if upslope advance was accompanied by site-wide increases in establishment or likely represents an artefact of a random regeneration event.

We examined the influence of climate on tree establishment during the twentieth century using three statistical measures. First, we compared age-structure data to identical pentads of key climate variables using Spearman's rank correlation coefficients (r_s) because the data were not normally distributed. Given the multitude of linear correlations analysed with this non-parametric method (n = 10), we used a Bonferroni correction ($\alpha = 0.05/10 = 0.005$) to measure statistical significance (Gamache and Payette 2005). Second, we used regime-shift analysis to identify statistically significant ($P \leq 0.05$) deviations in age structure and climate data (Rodionov 2004). This method identifies a stepwise regime shift when the cumulative sum of normalised deviations from the mean value of a potential new regime is significantly different from the mean of the current period (Rodionov and Overland 2005). We selected the default cut-off length of 10 years for the moving window of sequential *t*-tests. We used this technique to identify abrupt biotic (tree establishment) or abiotic changes in the time-series data that are potentially representative of a non-linear, threshold-type switch in climate-vegetation interactions at the treeline (Elliott 2012). Our rationale for employing this method in addition to correlation analysis was to examine how well the spatio-temporal patterns of tree establishment could be explained by both linear (e.g. correlation) and non-linear dynamics during the twentieth century. Finally, to gain a more complete understanding of how important moisture was over time in facilitating tree establishment, we carried out a chi-square goodness-of-fit test to determine if significantly more trees ($P \leq 0.05$) established during 'wet' conditions based on the proportion of wet spring pentads during the twentieth century (e.g. Ziegler et al. 2008). To do this, we standardised spring precipitation values relative to the 1900–1999 mean and averaged these into matching five-year bins for comparison with age-structure data. Wet periods were defined by a positive z-score anomaly and dry years by a negative z-score anomaly. We chose spring precipitation to account for snowmelt water available to trees during the onset of the relatively dry growing season, which has been shown to impact tree function into late summer (Hu et al. 2010).

Results

Tree regeneration dynamics

A total of 149 trees were crossdated, with a mean of 37.3 trees per site, of which 49.6% were sapling cross-sections harvested at ground level (Table 2). Among these trees, 96.4% (n = 141) established after 1950 (Figure 3). WSF is the only site where trees existed both above and below timberline before this time (1925–1950; Figure 3). Based on our sampling design, we excluded five krummholz groups based on the fact that although identical in height and dgl to the numerous saplings present at site ENF, they were formed by at least three stems (Table 2). Given the nearly ubiquitous existence of relatively young trees west and east of the Divide, no significant differences in the temporal patterns of establishment ($P > 0.05$) were detected using two-sample Kolmogorov-Smirnov tests. Tree seedlings were rare and almost exclusively confined to more mesic north-facing slopes (Table 2).

Dendroecological reconstructions of the outpost tree elevation at each site indicated considerable treeline advance during the twentieth century (mean = 86.2 m; range = 39–140 m), with the uppermost extent of present boundaries established between 1960 and 1985 (Figure 4). Increases in tree density above (ATL) and below (BTL) timberline accompanied initial colonisation at each site (Figure 4). Taken together, these results suggest a switch toward more favourable conditions for tree establishment both west and east of the Divide since 1950 (Figures 3 and 4).

Climate and tree establishment

Statistically significant correlations between climate and rates of tree establishment ($P \leq 0.005$)

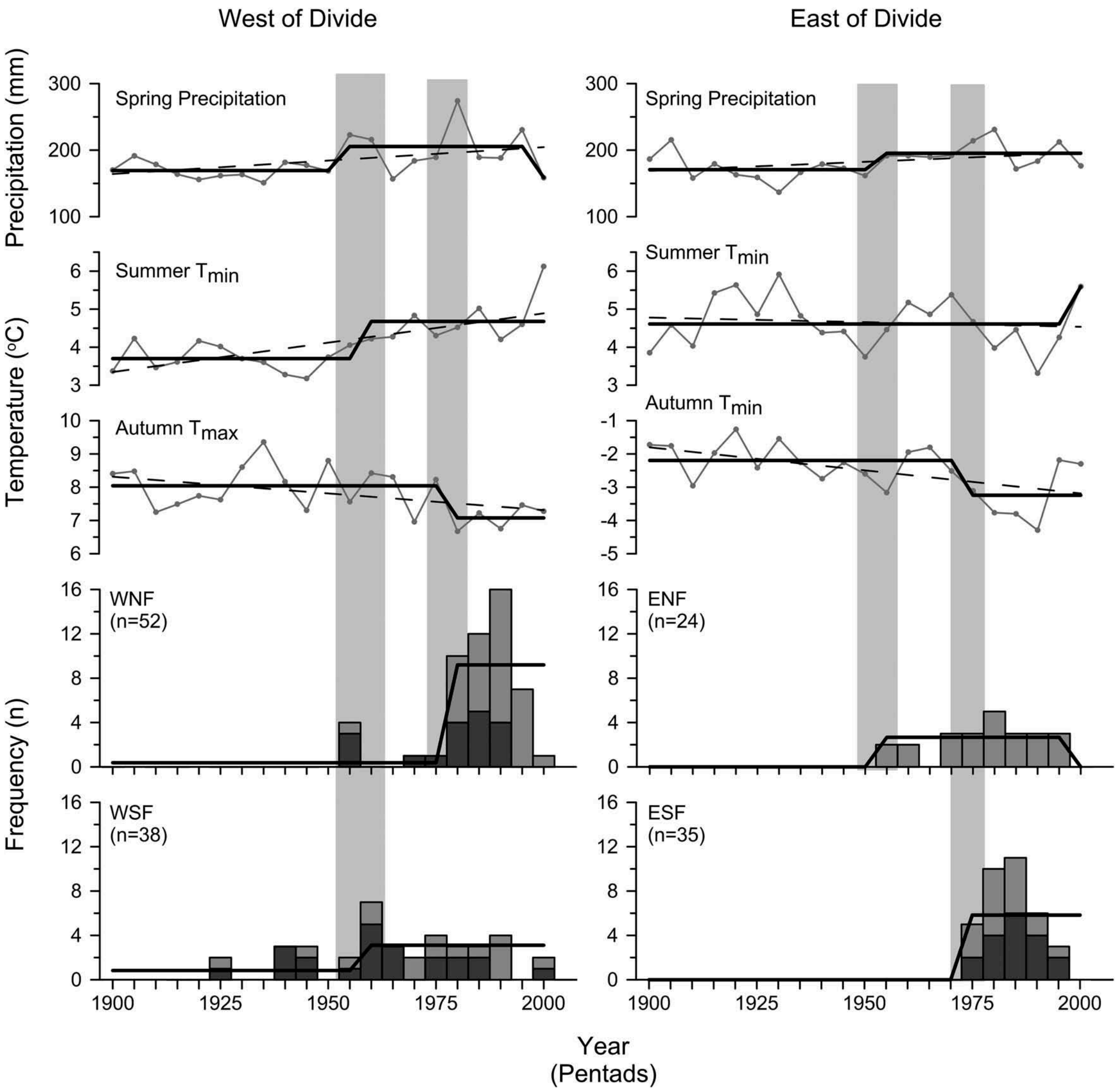

Figure 3. Age-structure data (1900–2000) in pentads for each study site. Climate data exhibit statistical ($P < 0.05$) or ecological significance with tree establishment. Bold lines denote quantitative results from regime-shift analysis. Grey boxes are used to highlight possible synchrony between abrupt shifts in establishment and climate. Refer to Table 1 for site abbreviations and note the non-uniform y-axes for climate variables.

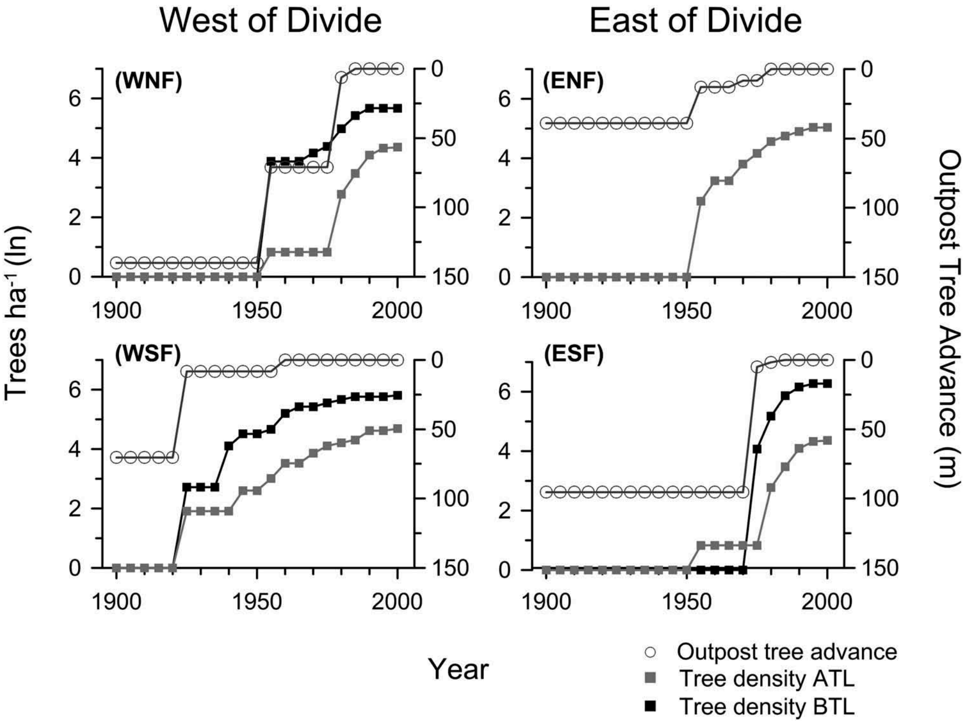

Figure 4. Reconstructed changes in tree density above (ATL) and below timberline (BTL) for five-year intervals during the twentieth century. Tree density data (trees ha-1) were normalised by a natural-log transformation to compensate for differences in ecotone area. Reconstructed distance of outpost tree advance is plotted so that the present extent of tree establishment was reached when the value equals zero (e.g. 1985 for WNF).

varied west and east of the Continental Divide and with slope aspect. For example, spring precipitation, which primarily falls as snow, was the only climate variable that produced a significant (and positive) correlation with tree establishment west and east of the Divide on north-facing slopes (WNF and ENF; Table 3). Tree establishment at WNF was also significantly and positively correlated with summer T_{min} and inversely correlated with autumn T_{max}. There were no significant correlations between climate and tree establishment at site WSF (Table 3). In addition to the aforementioned positive correlation with spring snowfall, rates of establishment east of the Divide were significantly and inversely correlated with autumn T_{min}, and this pertained to both aspects (ENF and ESF; Table 3).

The synchronous timing of regime shifts in tree establishment with significantly correlated climate variables provided insight into possible abiotic forcing mechanisms behind the observed increases in recruitment since 1950 (Figure 3). West of the Divide, this synchrony was preceded by a non-linear increase in spring snow (1955), which may have facilitated later biotic regime shifts coincident with an abrupt increase in summer T_{min} and decrease in autumn T_{max} at WSF (1960) and WNF (1980), respectively (Figure 3). East of the Divide, spring snow also exhibited a non-linear switch towards a new mean state in 1955, which was synchronous with the initiation of tree establishment at ENF. At ESF, the initiation of tree establishment coincided with a regime-shift towards cooler autumn T_{min} between 1975 and 1979 (1975 age class; Figure 3).

Plotting the cumulative percentage of tree establishment at each site over five-year intervals during the twentieth century indicated that the sharpest increases took place during wet springs from ca. 1950 to 1994 both west and east of the Divide (Figure 5). Quantitative results from chi-square analysis corroborated this superficial trend, with significantly more tree establishment during wet springs ($P < 0.05$). This was most apparent on north-facing slopes, where 96% and 88% of trees established during wet springs, which comprised only 38% and 48% of pentads during the twentieth century at sties WNF and ENF, respectively ([WNF] $\chi^2 = 74.64$, $P = 0.000$, df = 1; [ENF] $\chi^2 = 15.00$, $P = 0.000$, df = 1). During the period of maximum establishment from 1975 to 1990, the percentage of trees present more than doubled at three of four sites (excluding WSF; Figure 5). This period was characterised by above-average spring snow west and east of the Divide, with only a brief interlude of dry

Table 3. Spearman's rank coefficients (r_s) between five-year bins of tree establishment and climate variables at the treeline ecotone, Northern Rocky Mountains, USA. Significant correlations in bold and significance level (α) Bonferroni adjusted to 0.005. Seasonal climate variables calculated from monthly PRISM data available from www.prism.oregonstate.edu. Cool season data are measured from October to May.

	WNF		WSF		ENF		ESF	
Climate Variable	(r_s)	(P)	(r_s)	(P)	(r_s)	(P)	(r_s)	(P)
Cool season precipitation	0.308	0.174	0.374	0.095	0.524	0.015	0.215	0.350
Cool season T_{max}	−0.564	0.008	−0.054	0.816	−0.198	0.390	−0.015	0.949
Cool season T_{min}	0.372	0.097	0.230	0.315	−0.393	0.078	−0.543	0.011
Spring precipitation	**0.593**	**0.005**	0.371	0.098	**0.608**	**0.003**	0.367	0.102
Spring T_{min}	0.427	0.053	0.099	0.669	−0.101	0.663	−0.090	0.698
Summer precipitation	0.207	0.368	0.3112	0.169	0.272	0.233	0.382	0.087
Summer T_{min}	**0.676**	**0.001**	0.296	0.193	−0.264	0.247	−0.413	0.063
Autumn precipitation	−0.024	0.918	0.413	0.062	0.324	0.152	0.128	0.581
Autumn T_{max}	**−0.685**	**0.001**	−0.338	0.134	−0.247	0.281	−0.202	0.379
Autumn T_{min}	0.095	0.681	0.047	0.839	**−0.586**	**0.005**	**−0.593**	**0.005**

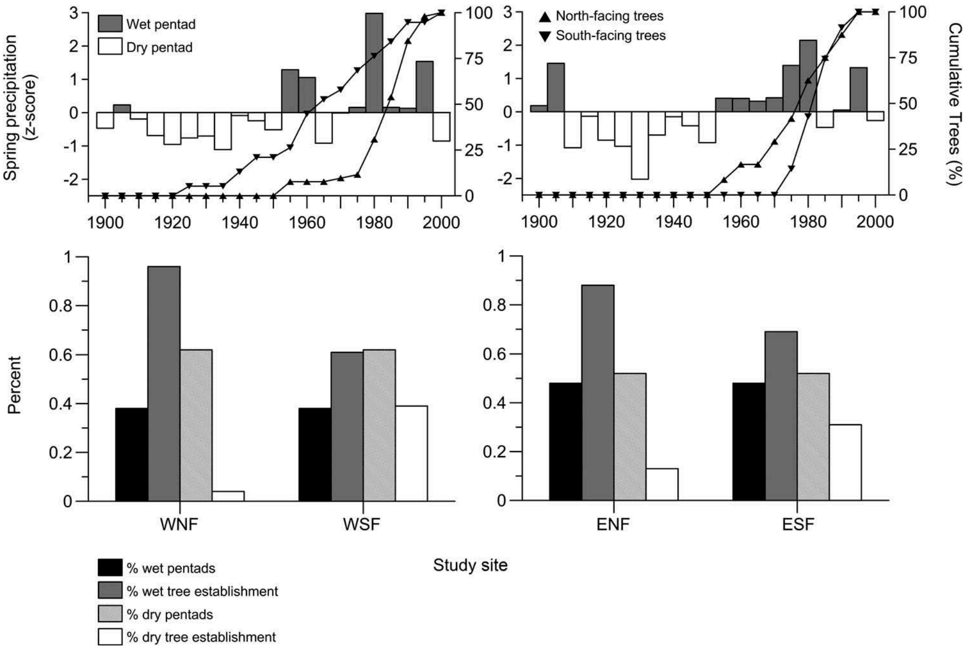

Figure 5. Proportion of tree recruitment during wet and dry springs. Wet and dry values based on positive and negative z-scores, respectively. Based on chi-square goodness-of-fit tests, significantly more trees established during wet springs ($P < 0.05$).

conditions from 1985 to 1989 to the east (Figure 5). Considered together, these three lines of evidence for evaluating possible mechanistic linkages between climate and tree establishment within upper treeline ecotones west and east of the Continental Divide imply that temperature-moisture interactions may be particularly influential during both the initiation (spring) and termination (autumn) of the growing season.

Discussion

This study included four distinct topoclimatic settings from two treeline sites west and east of the Continental Divide in the Northern Rocky Mountains. Our findings represent the first examination of how climate interacts with topographic moisture gradients at both a local (topoclimate) and regional scale (Continental Divide) to impact patterns of tree establishment within upper treeline ecotones. Below we discuss results within the context that more widespread dendroecological data are needed from climatic treelines in the Northern Rocky Mountains, especially west of the Continental Divide, to test proposed connections between seasonal climate and treeline dynamics.

Treeline type in the Rocky Mountains

Extensive field observations across the region have suggested that climatic treelines were relatively rare throughout much of central Idaho and portions of south-west Montana, particularly on the same mountain peak, which differs from the Southern Rocky Mountains, where it is more common for treeline ecotones to extend upslope into sizable expanses of alpine tundra (e.g. Elliott and Kipfmueller 2010). Further, we do not dispute the importance of low threshold temperatures in triggering tree function at the treeline (sensu Körner 2007), yet the position of ecotone boundaries was strongly dictated by local geologic and/or geomorphic constraints to tree establishment. This supports Butler et al. (2007) who argue for the subservient role of temperature in governing the position and structure of the treeline throughout much of the western United States. Other researchers have used the term *orographic/edaphic* treeline (Holtmeier and Broll 2005; Schickhoff et al. 2015) and *geologic* treeline (Elliott 2017) to reference instances when tree recruitment at the treeline is more of a function of local landform constraints than temperature alone (sensu Butler et al. 2007). Herein lies the arguably understated importance of study site selection because site-level conditions have been shown to override sufficient temperature regimes in determining whether treeline advance occurs (e.g. Macias-Fauria and Johnson 2013; McIntire et al. 2016) and/or create climate-pattern-feedback interactions that decouple linkages between climate and tree recruitment (Elliott 2011; Liang et al. 2016). In this study, the prevalence of non-climatic treeline ecotones contributed to our lack of replication from more study sites and, similar to most treeline studies, limits our ability to make generalisations beyond the site scale.

Changes in treeline structure

Dendroecological reconstructions of tree age revealed consistent and sometimes sharp increases in tree density accompanied by upper treeline advance between ca. 1950 and 1995. The densification or in-filling of treeline ecotones is the most commonly reported change in treeline structure as temperatures have warmed during the latter half of the twentieth century, with examples spanning the Northern Hemisphere (Szeicz and MacDonald 1995; Klasner and Fagre 2002; Alftine et al. 2003; Lloyd and Fastie 2003; Danby and Hik 2007; Batllori and Gutiérrez 2008; Kharuk et al. 2010; Liang et al. 2011; Fajardo and McIntire 2012; Mamet and Kershaw 2012; Mathisen et al. 2014; Trant and Hermanutz 2014; Chhetri and Cairns 2015; Sakulich 2015; Shrestha et al. 2015). Treeline advance, however, has only been reported by a slight majority of studies worldwide (52%) since A.D. 1900 and these episodes were attributed to pronounced winter warming (Harsch et al. 2009). Similar spatio-temporal patterns of tree establishment across a regional topographic barrier, such as the Continental Divide, indeed suggest that the broad-scale influence of rising temperatures may have contributed to changes in treeline structure since 1950. Yet based on quantitative analyses of dendroecological and climate data from this section of the Northern Rocky Mountains, we conclude that regional-scale changes in treeline structure (i.e. tree density and treeline advance) since 1950 were most likely driven by temperature-moisture interactions. As stated above, these findings align closely with other dendroecological studies at the treeline along the American Cordillera but perhaps, most importantly, raise questions about how seasonal climate variability influences patterns of tree establishment at treeline.

Role of spring climate

Despite a lack of site-level snow cover data, the apparent influence of snow in facilitating tree regeneration is evident across the region, as significantly more trees established during relatively wet springs at all four sites. Wet springs mean more snow (e.g. Pederson et al. 2011) and it is well recognised that temperature-snow interactions during this time exert considerable control on tree establishment and treeline advance by modifying the depth, distribution and duration of snowpack (Hättenschwiler and Smith 1999; Holtmeier 2005; Hiemstra et al. 2006; Barbeito et al. 2013). Simultaneous increases in temperature and snow during the past 65 years, for instance, facilitated treeline advance in north-western China (Wang et al. 2006) and in mountain ranges across Russia (Devi et al. 2008; Kirdyanov et al. 2012; Hagedorn et al. 2014). Plots of spring minimum and maximum temperature further support the likely interactive role temperature played in shaping patterns of tree recruitment (Figure 6). In the Southern Rocky Mountains, however, comparable changes in treeline structure were facilitated by warmer springs with less snow that accelerated the onset of amenable growing season conditions (Elliott 2012). Results from this work therefore highlight

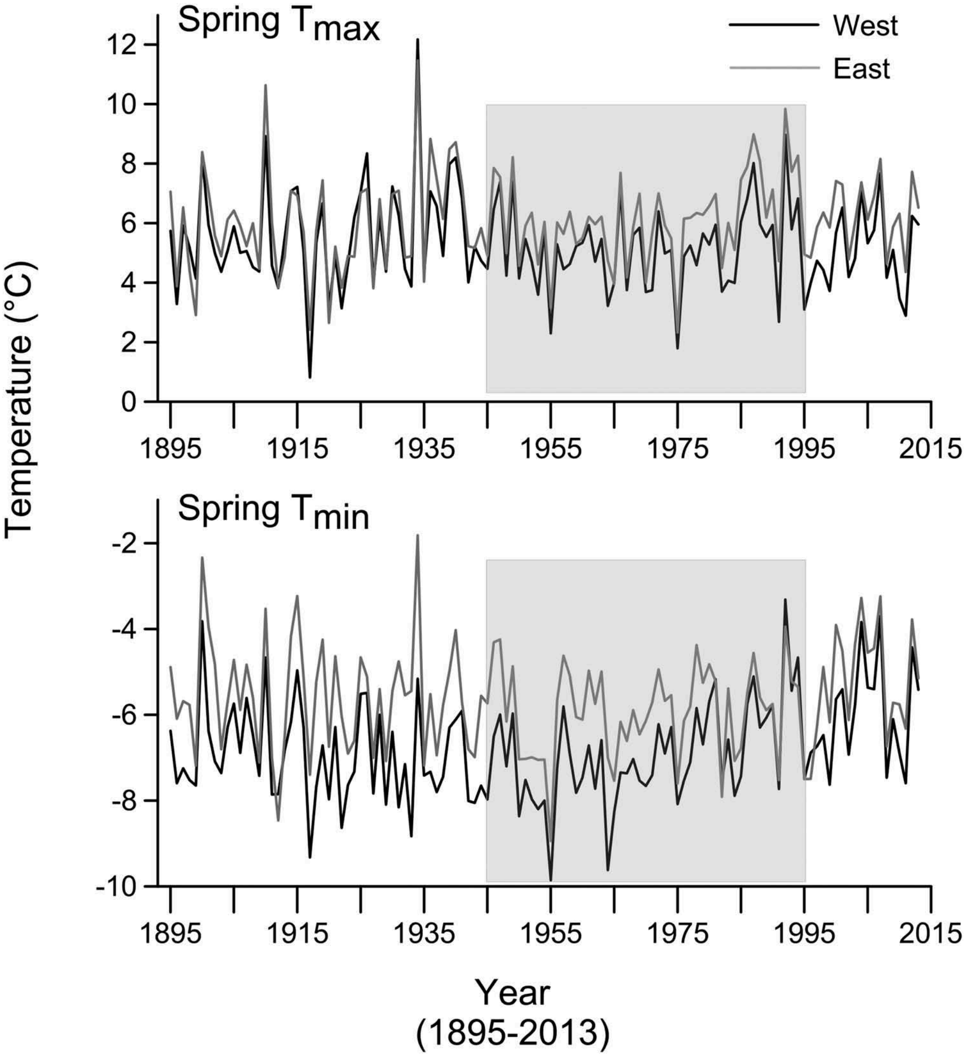

Figure 6. Spring maximum (T_{max}) and minimum (T_{min}) temperature for study sites west and east of the Continental Divide. Data are from PRISM (prism.oregonstate.edu) and grey boxes highlight period of time with maximum tree recruitment (1950–1995).

regional variability in how temperature-snow interactions during spring govern patterns of tree establishment at upper treeline along the U.S. Rocky Mountains, which has strong implications for how ongoing rises in temperature (Pepin et al. 2015), decreasing spring snowpack (Mote et al. 2018) and projected drought conditions (Allen et al. 2015) will impact treeline dynamics.

The role of autumn temperature

Cooler T_{max} during autumn appears to exert a strong influence on recruitment dynamics at the treeline west of the Continental Divide. Mechanistically, clouds effectively lower maximum temperature, especially during autumn when minimal latent heat is released from the normally dry soil (Dai et al. 1999). With respect to the treeline, experimental field research from the Medicine Bow Mountains in southern Wyoming suggests that cloud cover facilitates seedling establishment by reducing diurnal temperature range, increasing the likelihood of precipitation and enhancing carbon gain (Germino et al. 2002; Johnson et al. 2004). Taken together, we propose that cloud cover could ameliorate late in the growing season moisture stress, which would be expected to develop with rising summer temperatures (Figures 2 and 3) during the dry season, and ultimately facilitate tree establishment at treeline in central Idaho. In other words, a testable hypothesis worth exploring is that cooler autumns help to prolong soil moisture availability provided by spring snowpack, thus highlighting the importance of temperature-moisture interactions during the entire growing season.

East of the Divide, we interpret the significant and inverse correlation between autumn T_{min} and tree establishment to mean that autumn snow plays a crucial role by providing physical and thermal protection for tree seedlings because colder temperatures increase the likelihood of precipitation falling as snow rather than rain (Table 3; Figure 3). Unlike to the west, treeline environments along the eastern flank of the Rocky Mountains are exposed to arctic air masses that create exceptionally cold and dry conditions during the cool season (Barry 2008). This contributes to the formation of abrasive ice crystals that once windborne, physically damage trees and limit seedling survival/establishment at the treeline (Smith et al. 2003). In the absence of autumn snow cover, diurnal exposure to severe frosts and clear skies predisposes seedlings to temperature and moisture stress and has led to high seedling mortality in the Southern Rocky Mountains (Germino et al. 2002) and Tibet (Shen et al. 2014). Thus, it is certainly plausible that as continued warming exacerbates growing-season moisture stress, autumn temperature in general and a protective snow layer more specifically could become critical limiting factors to patterns of tree recruitment within upper treeline ecotones.

Alternative mechanisms for tree establishment

In addition to studying how climate influences tree physiology (e.g. Körner 2012) and annual ring-width formation (e.g. Salzer et al. 2014), examining patterns of successful tree establishment is a widely accepted method for determining the level of climate sensitivity at the treeline (Holtmeier and Broll 2005). Yet, it remains challenging to disentangle the role of climate because nearly identical spatio-temporal patterns of regeneration can result from the rapid onset of amenable climate conditions (Elliott 2012; Camarero et al. 2015) and/or forest regrowth following the cessation of grazing (e.g. Moen et al. 2008; Aakala et al. 2014; Ameztegui et al. 2016). To address this, Batllori et al. (2010) have compared disturbed versus undisturbed treeline ecotones in the Pyrenees and concluded that disturbance history was less influential on initial seedling establishment than local environmental conditions. The obvious influence of topoclimate on seedling establishment in this study, with 97% confined to north-facing slopes, likely offers further support for this (Table 2), although extrapolations from seedlings observed during a single growing season can be tenuous (see Lloyd and Fastie 2003). Additionally, further study is needed to rule out the possibility that pulses in tree establishment were not triggered by disturbance, or in the case of site ENF (an outcrop above the upper montane forest), from seed caching by Clark's nutcrackers (*Nucifraga columbiana* Wilson) who effectively disperse whitebark pine seeds in alpine tundra beyond treeline (Holtmeier 2009).

Conclusions

Key findings from this research are twofold. First, these results add further evidence that general climate warming trends since the middle of the twentieth century (e.g. Pederson et al. 2010) have played a role in facilitating sharp increases in tree density and treeline advance across the Northern Hemisphere. With respect to the Rocky Mountains, these results support our hypothesis and build on prior work (Elliott 2012) to provide empirical evidence for treeline advance since 1950 across a latitudinal gradient of ca. 1100 km (ca. 35–45°N). Second, and arguably most compelling, is that our findings suggest tree recruitment in the Northern Rockies was most likely to occur when growing seasons were bracketed by heavy snow in the spring and cooler temperatures in autumn to prolong soil moisture availability. This was most pronounced west of the Continental Divide where summer-dry conditions persist. These results are novel and worthy of further exploration, particularly since autumn temperature variability is poised to play an increasingly important role shaping demographic patterns at upper treeline as temperatures continue to rise and drought stress becomes more frequent during the growing season.

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