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Moisture availability limits subalpine tree establishment

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Abstract. In the absence of broad-scale disturbance, many temperate coniferous forests experience successful seedling establishment only when abundant seed production coincides with favorable climate. Identifying the frequency of past establishment events and the climate conditions favorable for seedling establishment is essential to understanding how climate warming could affect the frequency of future tree establishment events and therefore future forest composition or even persistence of a forest cover. In the southern Rocky Mountains, USA, research on the sensitivity of establishment of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*)—two widely distributed, co-occurring conifers in North America—to climate variability has focused on the alpine treeline ecotone, leaving uncertainty about the sensitivity of these species across much of their elevation distribution. We compared annual germination dates for >450 Engelmann spruce and >500 subalpine fir seedlings collected across a complex topographic-moisture gradient to climate variability in the Colorado Front Range. We found that Engelmann spruce and subalpine fir established episodically with strong synchrony in establishment events across the study area. Broad-scale establishment events occurred in years of high soil moisture availability, which were characterized by above-average snowpack and/or cool and wet summer climatic conditions. In the recent half of the study period (1975–2010), a decrease in the number of fir and spruce establishment events across their distribution coincided with declining snowpack and a multi-decadal trend of rising summer temperature and increasing moisture deficits. Counter to expected and observed increases in tree establishment with climate warming in maritime subalpine forests, our results show that recruitment declines will likely occur across the core of moisture-limited subalpine tree ranges as warming drives increased moisture deficits.

Key words: climate change; Colorado Front Range; Engelmann spruce; southern Rocky Mountains; subalpine fir; subalpine forest.

Introduction

Successful plant seedling establishment occurs when sufficient seed arrives in suitable sites and site conditions allow germination and survival (‘regeneration niche’, Grubb 1977). In the absence of broad-scale disturbance, many temperate coniferous forests experience periodic pulses of seedling establishment when strong seed production coincides with favorable climate conditions (Petrie et al. 2016)—two initial filters for seedling establishment (Malanson et al. 2007, Kroiss and HilleRisLambers 2015). Understanding how seedling establishment responds to climate variability is therefore essential to addressing uncertainty in forest trajectories and shifts in ecosystem structure and function under warming conditions (Anderson-Teixeira et al. 2013, Bell et al. 2014).

High-elevation mountain environments are expected to experience more rapid warming than lower elevations, increasing the vulnerability of high elevation forests to climate-induced changes in species composition and extent of forest cover (Langdon and Lawler 2015, Pepin et al. 2015). Demographic processes (e.g., reproduction, growth, and mortality) in subalpine forests across the western USA are sensitive to climate variability (van Mantgem et al. 2009, Kueppers et al. 2016) and are already impacted by a warming climate (Dolanc et al. 2013). For example, background rates of tree mortality are increasing in response to warming temperatures and moisture deficits (van Mantgem et al. 2009, Smith et al. 2015). For long-lived (>300 yr) subalpine tree species, infrequent episodes of establishment may be sufficient for population persistence. However, increasing climate-driven tree mortality and unfavorable climate conditions for new tree establishment may severely constrain population stability, therefore compromising forest persistence.

Evidence from multiple spatial scales (individual trees to watersheds) suggests a strong moisture limitation for the establishment of subalpine tree species in the southern Rocky Mountains, USA (Hessl and Baker 1997, Moyes et al. 2015, Kueppers et al. 2016). Yet previous research in the southern Rockies has primarily focused on the influence of climate on alpine treeline dynamics (Weisberg and Baker 1995, Maher and Germino 2006, Elliott and Cowell 2015, but see Kueppers et al. 2016, 2017), leaving uncertainty about how climate influences establishment across a majority of the area inhabited by subalpine tree species (i.e., “core” species range). Thus, research is needed to determine the frequency and trends in annual establishment events across the core range of subalpine tree species and to understand the sensitivity of establishment to interannual climate variability in the context of expected increases in temperature of 1.7°–2.8°C by mid-century (Lukas et al. 2014).

We assessed germination dates for >450 Engelmann spruce (*Picea engelmannii* Parry ex Engelmann) and >500 subalpine fir (*Abies lasiocarpa* (Hook) Nutt.) seedlings (<1 m in height) to investigate the frequency of broad-scale

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seedling establishment in the Colorado Front Range (CFR; Fig. 1). Then, we examined how broad-scale seedling establishment was influenced by climate variability, as measured by an instrumental climate record and observations of snowpack. Specifically, we asked, do broad-scale subalpine fir and Engelmann spruce establishment events coincide with years with anomalous moisture availability? We hypothesize that fir and spruce seedling establishment will be associated with above-average soil moisture availability, indicated by positive anomalies in snowpack and/or cooler and wetter summer conditions (Cui and Smith 1991, Kueppers et al. 2016). Our study improves upon and differs from previous on subalpine tree establishment in the southern Rocky Mountains because we (1) examine establishment frequency and sensitivity to climate across a broader range of abiotic and biotic environmental conditions within the core of each species' range, (2) use tree-ring analysis to determine the sensitivity of conifer establishment to interannual (e.g., summer moisture availability and winter snowpack) climate variability within the core of each species' range over a ~70 yr period, and (3) include both of the dominant species of the subalpine forest zone—Engelmann spruce and subalpine fir.

METHODS

Study area

We sampled ten plots (clustered in four sampling areas) in subalpine forests, spanning a 25-km north-south and ~400 m (2,980–3,370 m) elevation range on the eastern slope of the CFR (Fig. 1, Appendix S1: Table S1). The spatial distribution of plots captured the elevation distribution (~2,900–3,400 m) of subalpine forests and all spruce-fir forest types in the core range of subalpine forests in the CFR (subalpine forest types as described by Peet 1981). We included stands dominated by Engelmann spruce and subalpine fir as well as open stands of limber pine with spruce and fir in the understory. Plots were distributed across moisture gradients (hydric, mesic, xeric) inferred from topographic position and soil properties. Stand ages range from ~120 to >500 yr. Stands had not experienced recent disturbance (last two decades).

Much of the average annual precipitation (670 ± 130 mm, 1952–2010, Kittel et al. 2016) in the CFR falls as snow during the winter and spring months (November–May); moisture deficits are widespread in late summer months (McGuire et al. 2012). The combination of a persistent snowpack and cool temperatures [annual mean average temperature: 1.7°C, (C-1 climate station: 40.0362 N, −105.5434 W, 3,048 m, 1953–2008)] creates a short growing season; however, mean (0.2°C per decade) and maximum (0.44°C per decade) annual average temperatures are increasing in the in the study area (1950–2008, McGuire et al. 2012). Though total precipitation (1978–2010) in the subalpine zone in the CFR has not changed substantially, the early winter peak in precipitation shifted from November to October and the peak in spring precipitation shifted from May to April (Kittel et al. 2016). October–March precipitation at the C-1 climate station has declined over the 1978–2010 period (Kittel et al. 2016) which is consistent with a general decline in snow water equivalent (SWE) on April 1 in the subalpine zone across the Colorado Front Range (Clow 2010).

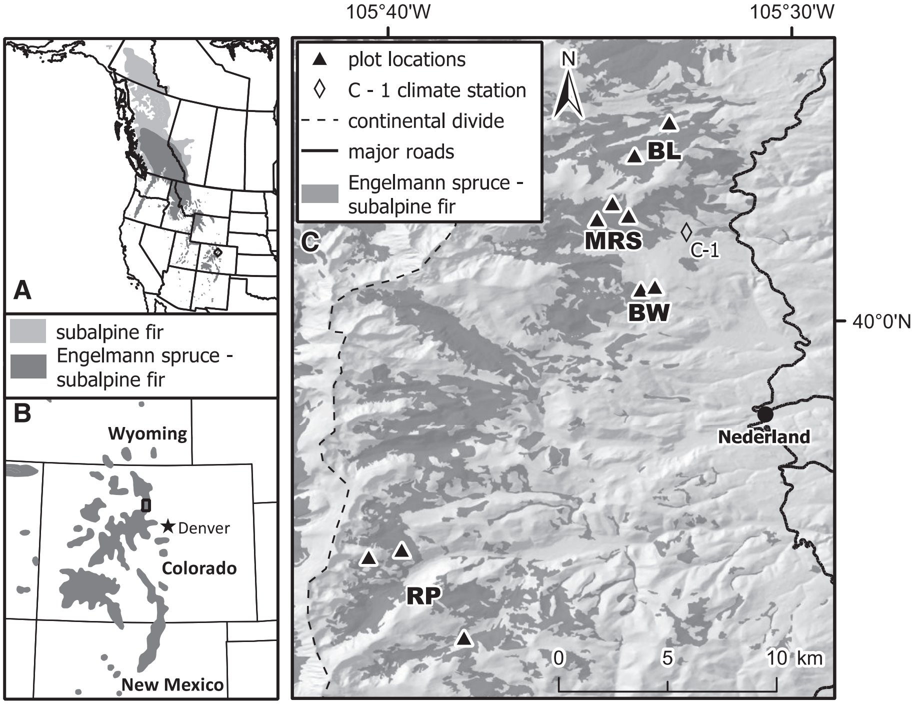

FIG. 1. Study area map. (A) Location of study area in Colorado in North America. Extent of Engelmann spruce—subalpine fir forest is shown in dark gray and the additional extent of subalpine fir is shown in light gray. (B) Location of study area in Colorado and extent of spruce-fir forest in the Colorado. (C) Location of study plots on the eastern slope of the Colorado Front Range and C-1 climate station in the Arapaho-Roosevelt National Forest. Sampling areas: (1) BL stands for Brainard Lakes Recreation Area, (2) MRS stands for University of Colorado's Mountain Research Station, (3) BW stands for Boulder Watershed, and (4) RP stands for Rollins Pass.

Field methods

To locate each sample plot, we selected a homogeneous area with abundant seedlings of both species (mean seedling density 5,300 seedlings/ha for fir and 3,900 seedlings for spruce) and then randomly located (random direction and distance) a 10 m wide and variable length plot (max length 50 m) (League and Veblen 2006). We increased the length of the plot by 1 m until a minimum of 50 seedlings ≥5 yr old (determined by bud scar count) and <1 m tall were identified. We excavated and cut each seedling to include at least 10 cm of the aerial portion of the stem and the subsurface stem and root (League and Veblen 2006). If a minimum of 50 seedlings of each species were not encountered in a 10 × 50 m area, we established a second plot within 50 m of the first plot. Previous destructive sampling of juveniles of the two-target species in the study area suggested that sampling seedlings up to a height of 1 m should capture abundant seedling ages up to ~70 yr (Veblen 1986) which was the case in the current study (Appendix S2). Seventy years approximately corresponds with the length of available snowpack record (see *Climate variables and indices* below). Stems originating from layering (i.e., multiple stems originating from and radiating out from a larger parent tree) were excluded in order to restrict our sampling to individuals that originated from seed. At each plot we recorded slope, aspect, canopy closure (spherical densiometer), site moisture, and elevation in the field.

Sample processing

We identified germination dates by selecting the maximum age from annual ring counts on a minimum of three 1–1.5 cm cross-sections cut from the root-shoot boundary on each tree seedling (Telewski 1993, League and Veblen 2006). Each cross-section was sanded with progressively finer sand paper and dated from the outer ring to the pith. For each cross-section, annual resolution was achieved with a clear view of the entire cross-section and multiple ring counts on each sample with a microscope (40× magnification). This allowed pinched or damaged rings to be detected following standard dendrochronological methods (Speer 2010). In order to be included in the analysis and to ensure accurate assessment of germination date, samples had to satisfy two criteria: (1) the cross-section with the maximum age must be bounded by cross-sections of lesser age, and (2) the cross-section below the maximum age cross-section must show an anatomical difference in ring formation, indicating root rather than the shoot (DesRochers and Gagnon 1997). We excluded 9% of the seedlings from our analysis because ring boundaries were not clear.

Data analysis

Identifying plot-level establishment peaks.—Annual seedling establishment was aggregated by species in each plot. We used a modified version of CharAnalysis (Higuera 2009, Tepley and Veblen 2015; Data S1)—a peak detection algorithm—to identify years of substantial seedling establishment (i.e., *establishment peaks*) for each species in each plot (Appendix S2). CharAnalysis is an improvement over previous methods used to identify establishment peaks in forest ecosystems because it does not rely on an arbitrary threshold for peak identification and accounts for differences in sample depth and seedling abundance across the time-series (Appendix S2).

Identifying broad-scale establishment events.—Since climate operates across a broad spatial extent, we expected that climate-driven establishment events would be synchronous across multiple plots. Thus, broad-scale *establishment events* were arbitrarily identified as those years in which ≥40% of the sampling plots from at least 3 of the 4 sampling areas recorded an establishment peak for a given year. This framework allowed us to identify establishment events that were synchronous across the study area rather than localized establishment driven by local factors.

Climate variables and indices.—In subalpine ecosystems in the CFR, soil moisture peaks immediately following snow disappearance and declines rapidly (Harpold et al. 2015). The rate of decline and the variability in soil moisture during the growing season is mediated by spring-summer weather conditions. We used SWE and the standardized precipitation-evaporation index (SPEI; Vicente-Serrano et al. 2010) to collectively describe annual climate—a key limitation to tree processes in the CFR (Villalba et al. 1994, Kueppers et al. 2016)—during the growing season (Appendix S3). We used 1 May SWE data from the University Camp snow course [(40.03 N, −105.57 W), 3,140 m, 1940–2010, NRCS 2016] because of the length of this record, proximity to our plots, and strong correlation (Spearman's r_s >0.75, P value <0.01) with other subalpine snow monitoring stations in the CFR (e.g., stations 05J05 and 05K14, NRCS 2016). To characterize the effect of summer climate conditions (1 June–30 September), we used SPEI—a multiscalar drought index which accounts for the combined effects of temperature and precipitation on moisture availability (Vicente-Serrano et al. 2010). To compute SPEI, we used monthly temperature and precipitation data from two strongly correlated climate records ($r_s > 0.75$, $P < 0.001$): (1) C1 climate station (monthly temperature and total precipitation from 1 October 1952 to 31 December 2010, NWT LTER 2016) and (2) PRISM (monthly temperature and precipitation from 1 January 1940 to 1 October 1952, PRISM 2016).

Testing the influence of climate variability on establishment.—We tested the importance of interannual climate variability during the year of establishment events (i.e., germination year) as well as years before and after establishment events (i.e., lagged years) and the relative importance of climate variables. To examine the influence of climate during the germination year and lagged years, we tested the bivariate interannual relationships between establishment events (by species) and climate variables (SWE and summer SPEI) using Superposed Epoch Analysis (SEA; Grissino-Mayer 1995) from 1940 to 2010. In using SEA, we tested the mean value of climate during establishment events (and at lags ±3 yr) with the expected climate if establishment years were randomly distributed across the time series. Climate variables were scaled by standard deviations to reduce the leverage of outliers. 5,000 bootstrap samples were used in randomly selected sets of '*lag* + 1' years from the dataset to estimate the significances for the departure from the mean (Bunn 2010). Statistical significance was evaluated using 90%, 95%, and 99% confidence intervals. Previous studies have identified that SEA is an inappropriate statistical technique when the serial autocorrelation is >0.60 for time lags greater than the window of analysis (Adams et al. 2003). Neither SWE nor SPEI were temporally autocorrelated ('acf' function in 'stats' package in R) for lags >3 yr (cross-correlation result SWE: <0.20, SPEI: <0.21), suggesting our application of SEA is statistically appropriate. We also compared climate conditions (SWE, SPEI by month) during establishment event years and years with low establishment (<1% of total sampled seedlings establishing [approximately ≤5 seedlings]) by species using a non-parametric Mann–Whitney *U* test ($\alpha = 0.05$). We did not correct for multiple comparisons (e.g., Bonferonni correction), because we were testing specific a priori hypotheses regarding differences between the typical climates of event years and years of low establishment.

To test the influence of interannual climate variability on years of widespread seedling establishment (1940–2010) and relative importance of climate variables (i.e., annual vs. monthly and seasonal variables), we used logistic regression with generalized linear models (binomial family and logit link function). Specifically, we modeled presence or absence of a broad-scale *establishment event* (dependent variable) as a function of species (spruce and fir) and climate variables (SWE and SPEI, individually and in combination). Predictor variables were scaled to allow direct comparison of model coefficients, and residuals were examined for temporal autocorrelation (R Core Team 2016). The explanatory power of each model was compared by examining the individual predictor variable coefficients, *P*-values, and model AIC values (Akaike Information Criterion).

RESULTS

Seedling establishment events

We assessed germination dates for 508 subalpine fir (93% of samples successfully aged) and 468 Engelmann spruce (91% of samples successfully aged) seedlings from ten plots in four sampling areas across the core range of subalpine forests in the CFR (Fig. 1). CharAnalysis identified between 4 and 12 plot-level *establishment peaks* for subalpine fir and between 6 and 12 plot-level *establishment peaks* for spruce in each plot (Appendix S2: Fig. S1, S2). Of the total plot-level establishment peaks identified by CharAnalysis (84 for spruce and 82 for fir), the majority coincided with a broad-scale *establishment event* for both spruce (56%) and fir (60%; Appendix S2), suggesting a broad-scale driver of establishment. Following our criteria for broad-scale establishment events (see *Methods*), we identified 10 fir and 9 spruce establishment events (Fig. 2), many of which occurred in the same year for both species ($r_s = 0.70$, $P < 0.001$). The temporal trend in establishment events shows that >75% of the spruce and ~70% of the fir establishment events occurred in the first half of the study period (1940–1974).

Influence of climate variability on seedling establishment events

Engelmann spruce and subalpine fir establishment events typically occurred in years of above-average snowpack (SWE SEA for spruce: $P < 0.10$, fir: $P < 0.05$, Fig. 3A, B) and with cooler and wetter summer conditions (SPEI SEA

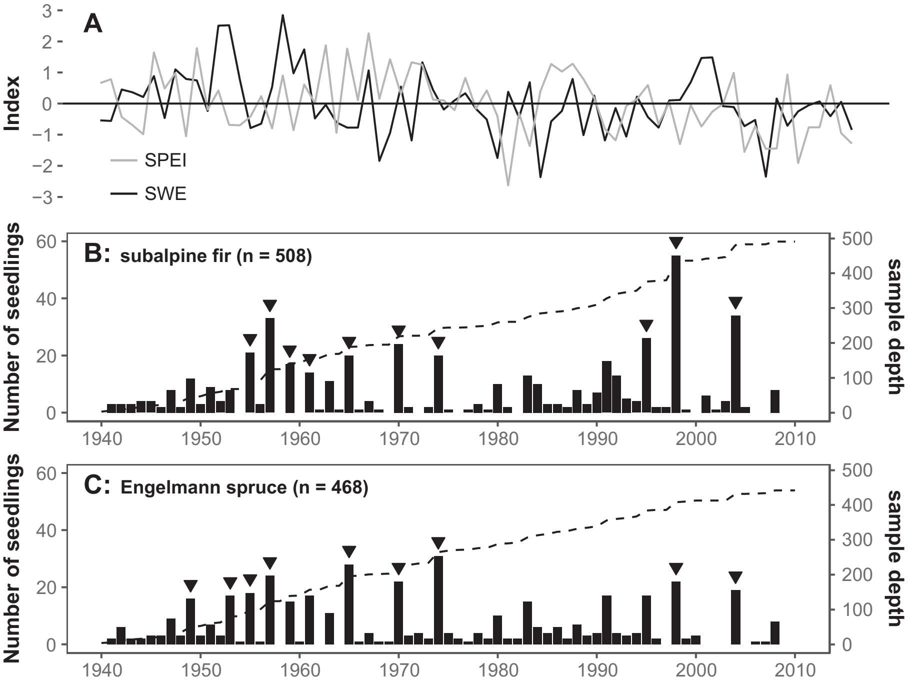

FIG. 2. Variability of annual June–September standardized precipitation evaporation index (SPEI, gray line) and 1 May snow-water equivalent (SWE, black line) from 1940 to 2010 (A), and establishment frequency distributions from all sampling locations for subalpine fir (B) and Engelmann spruce (C). Periods of cooler (warmer) and (drier) wetter conditions are represented by positive (negative) values of SPEI. Positive (negative) SWE anomalies indicate more (less) water available from snow. Triangles (B, C) indicate establishment events at >4 plots from 3 or more sampling areas. Sample depth (dashed line) is the cumulative number of samples.

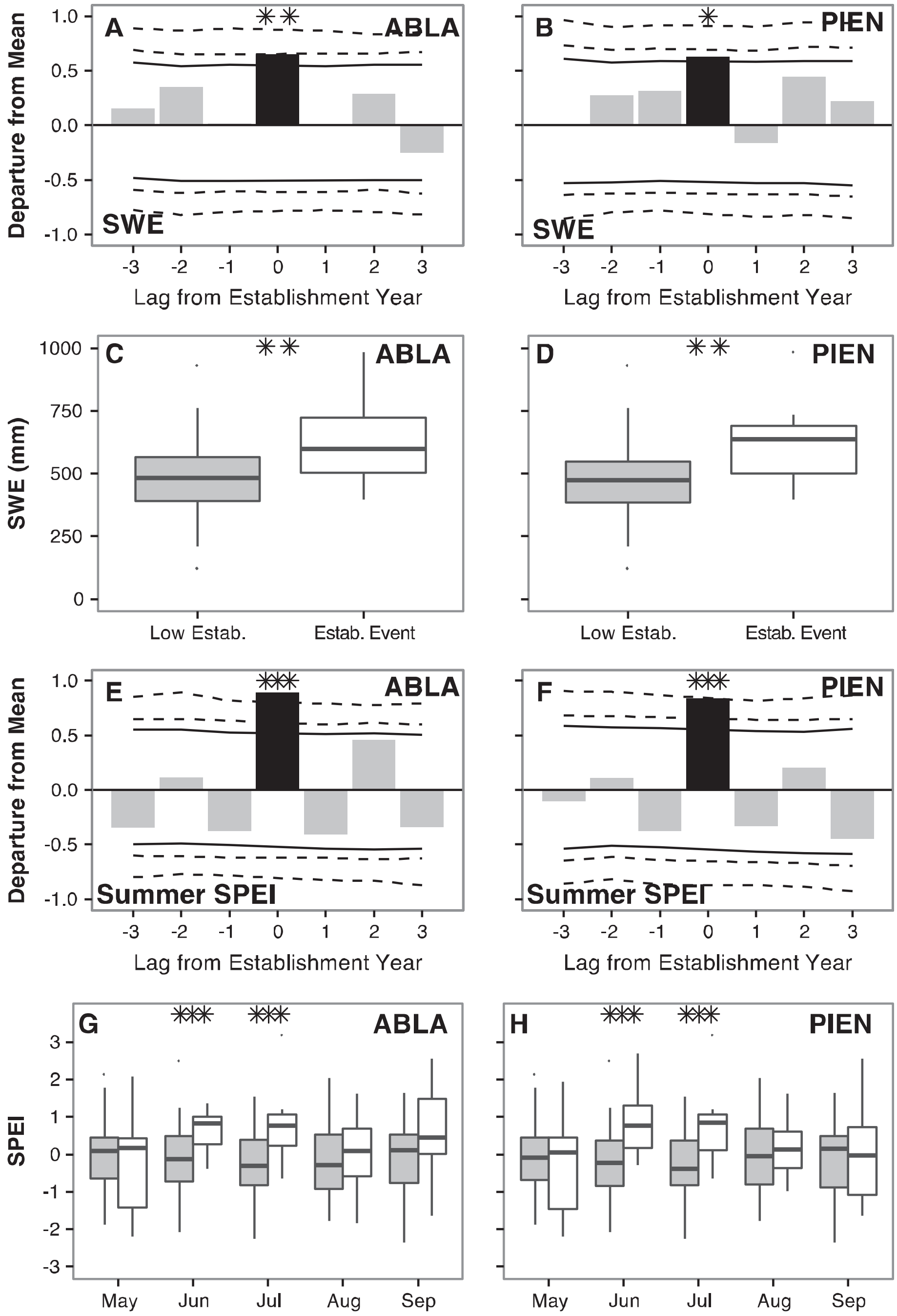

Fig. 3. Superposed epoch analysis (SEA) testing the influence of 1 May snow-water equivalent (SWE) on subalpine fir (ABLA, A, *n* = 10) and Engelmann spruce (PIEN, B, *n* = 9) establishment events, boxplots of the median value for SWE during establishment event years (white) and low establishment years (gray, <1% of total samples establishing) for subalpine fir (C) and Engelmann spruce (D), superposed epoch analysis (SEA) testing the influence of summer (June–September) standardized precipitation-evapotranspiration index (SPEI) on subalpine fir (E) and Engelmann spruce (F) establishment events, and boxplots of the median value for SPEI by month for establishment event years and low establishment years for subalpine fir (G) and Engelmann spruce (H) along the subalpine zone on the eastern slope of the Colorado Front Range. SEA departures are mean departures for ±3 years from the establishment event year. High SWE values indicate more water available from snow. High SPEI values indicate cooler and wetter conditions. In the boxplots, the thick black horizontal line within the box is the median, the box represents the interquartile range (25th–75th percentiles; IQR) of the distribution, the whiskers extend no further than ±1.5 times the IQR, and the solid black dots are outliers (i.e., data points beyond the whiskers). Solid lines (90%), dashed (95%), and dotted lines (99%) in SEA graphs indicate confidence intervals. Statistical significance between establishment event years and low establishment years for SWE (C, D) and SPEI (G, H) was tested with a Mann–Whittney test. Significance values: *<0.1; **<0.05; ***<0.01.

for spruce: $P < 0.01$, fir: $P < 0.01$, Fig. 3E, F) during the year of germination (lag 0). We did not identify any significant relationships between establishment events and climate in the years before or after germination. Climate conditions differed strongly between establishment event years and low establishment years (<1% of total sampled seedlings establishing by species; Fig. 3C, D, G, H). Specifically, establishment events coincided with greater snowpack (Mann–Whitney *U*: spruce $P < 0.05$, fir $P < 0.05$, Fig. 3C, D) and cooler and wetter summer conditions (positive SPEI) during the months of June (Mann–Whitney *U*: spruce $P < 0.01$, fir $P < 0.01$) and July (Mann–Whitney *U* spruce: $P < 0.01$, fir $P < 0.01$) (Fig. 3G, H).

As indicated by our logistic models of establishment events, Engelmann spruce and subalpine fir establishment events were strongly predicted by years of above-average snowpack (SWE) and cooler and wetter summer conditions (positive SPEI) during the year of germination (Fig. 4; Appendix S4). While SPEI better predicted establishment events (higher coefficient and lower *P*-value) than SWE, the combined explanatory power of SWE and SPEI was greater than their individual effect (AIC difference between multivariate and bivariate models >2, Bozdogan 1987; Appendix S4). Each climate variable captured a different component of favorable climate for establishment events [coefficients were relatively unchanged between the individual and multivariate models (Fig. 4), and SWE and SPEI for each year in the time series are not highly correlated (Appendix S3)]. Indeed, >60% of the establishment events occurred during years of above-average SWE, >70% of the establishment events coincided with years of above-average SPEI, and >90% of the events occurred during years with above-average SWE and/or SPEI (Fig. 2). Additionally, species was not a strong predictor of establishment events, indicating that Engelmann spruce and subalpine fir responded similarly to climate in years of abundant establishment (Fig. 4). Non-climate (e.g., topography, site moisture) related factors did not explain our observed patterns in establishment (Appendix S5).

DISCUSSION

Over the past 70 years, Engelmann spruce and subalpine fir established episodically with strong synchrony across the study area. Consistent with our hypothesis, broad-scale establishment events occurred during years of anomalously high soil moisture availability from above-average snowpack and/or cool and wet summer climatic conditions. A decrease in the number of fir and spruce establishment events from 1975 to 2010 coincided with declining snowpack (Clow 2010) and a multi-decadal trend of rising summer temperatures and increased moisture deficits (Andreadis and Lettenmaier 2006). In the context of increasing climate-driven tree mortality at or near our sample sites over the period from 1982 to 2013 (Smith et al. 2015), our results suggest that seedling establishment will also be negatively impacted by climate warming in systems with water-limited growing seasons across western North America. Collectively, these shifts in population dynamics of subalpine forests may reduce tree density or could result in a shift in vegetation type (e.g., forest to woodland) at some sites.

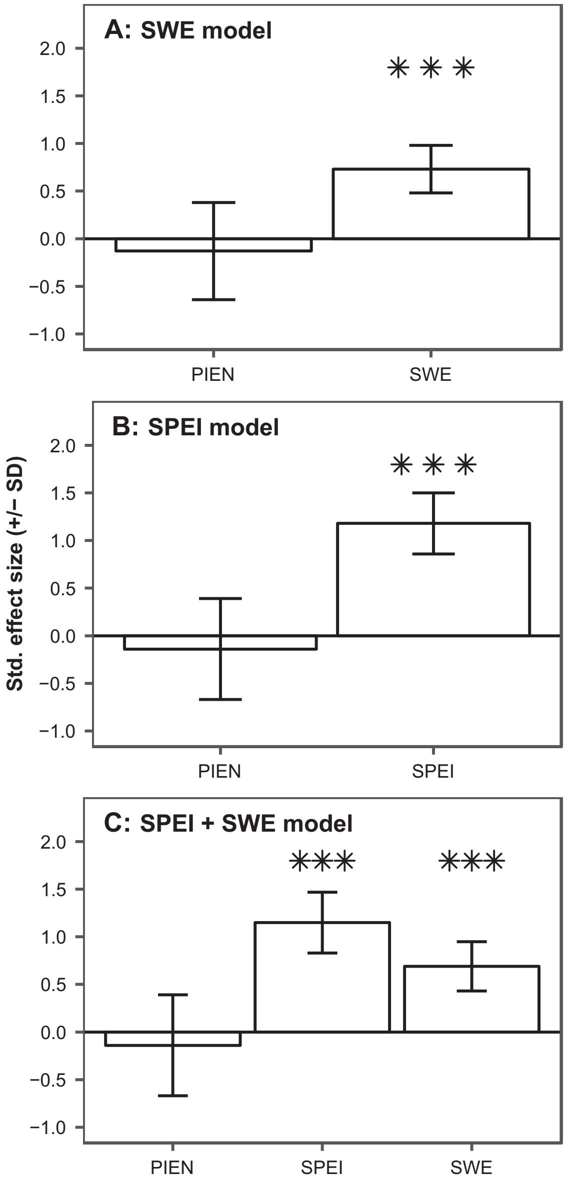

FIG. 4. Logistic model effects (i.e., coefficients) testing the influence of each predictor variable [snow water equivalent (SWE) on 1 May, summer standardized precipitation evaporation index (SPEI), species (PIEN, *Picea engelmannii*)], individually (A, B) and in combination (C), on establishment events. Predictor variables were standardized by standard deviation (SD) to allow comparison among predictor variables. Error bars show 95% confidence intervals. Significance levels are indicated by $^{***}P < 0.01$; $^{**}P < 0.05$; $^{*}P < 0.1$. See Appendix S4 for model results.

Synchrony in episodic establishment events

Both fir and spruce regenerated episodically at the plot-level (i.e., establishment peaks) and many of these episodes of establishment were synchronous across a majority of the ten plots (i.e., establishment events). In the absence of evidence of any disturbance-triggering establishment events, the coincidence of abundant seed production with suitable climate conditions is the likely explanation for synchronous establishment. Climate is a key driver of abundant spruce and fir seed crops every 2–6 yr (Woodward et al. 1994, Buechling et al. 2016), and abundant spruce seed production is commonly synchronous at distances >8 km in the CFR (Buechling et al. 2016). Infrequent years of high seed production typically yield much greater quantities of viable seed and greater densities of germinants (Noble and Ronco 1978, Woodward et al.

1994), suggesting that seed production serves as an initial filter for establishment. Though the lack of site-specific seed production data is a limitation of the present study, our analysis of the climate conditions that correlate with broad-scale seedling establishment provides important insight into the climatic influences on establishment.

Following seed dispersal, the influence of climate on soil moisture availability serves as a second filter for seedling establishment. Germination rates of Engelmann spruce are negatively affected by warmer and drier conditions (Kueppers et al. 2017), and seedling mortality of both species is typically very high (>85%) during the first year, particularly on dry south aspects (Noble and Alexander 1977). In the years following germination, seedling mortality remains high (typically >99% mortality after 4 yr) and in the southern Rocky Mountains is strongly influenced by soil moisture conditions (Noble and Ronco 1978, Kueppers et al. 2016). Our detection of a climate signal across complex topo-climatic gradients during the year of germination illustrates the importance of favorable climate conditions for broad-scale seedling establishment (Figs. 3, 4).

Moisture availability limits seedling establishment

Our findings demonstrate the importance of winter snowpack and summer moisture availability individually, and their alignment within the same year, for establishment of two common subalpine tree species occurring across western North America. The water content of snowpack (SWE) as well as climate conditions during the late spring and early summer determine the timing and rate of soil moisture loss (Harpold et al. 2015). Above-average SWE provides a greater contribution of water to soil moisture and typically results in a later melt out date (Trujillo and Molotch 2014), which may reduce the length of the summer drought and moisture stress on seedlings (Cui and Smith 1991, Brodersen et al. 2006). We found that the conditions created by an above-average snowpack were commonly a prerequisite for establishment events in a water-limited subalpine system. However, low snowpack in the CFR may be compensated for by cooler and wetter summer conditions.

Seedling moisture stress during the growing season is governed by the availability of soil moisture for physiological processes (Brodersen et al. 2006). Cooler and wetter conditions during the growing season likely reduce seedling moisture stress and increase survival rates (Noble and Alexander 1977, Gill et al. 2015, Kueppers et al. 2016). During years of below-average snowpack input to soil moisture, cooler and wetter summer conditions likely provide essential inputs to and reduce loss of soil moisture in the seedling root zone (top 5–10 cm of soil). In contrast, during years of above-average snowpack (greater input to soil moisture and a later melt out date), summer climate conditions may be less critical for survival. However, greater predictability of establishment events by summer conditions suggests that favorable summer conditions created by cool temperatures and precipitation in June and July are important for determining the length and magnitude of summer drought stress. While the favorable snowpack for seedling establishment appears to differ between maritime (low snowpack favors establishment) and continental (high snowpack favors establishment) subalpine forests, the importance of cooler and wetter summer climate conditions for seedling establishment has been highlighted in studies across the western US (Little et al. 1994, Gill et al. 2015, Johnson and Yeakley 2016, Kueppers et al. 2016).

Implications of climate change for seedling establishment

Strong links between moisture availability and tree regeneration suggest climate warming may decrease the frequency of seedling establishment events. Anthropogenic climate warming in combination with natural interannual to multi-decadal climate variability (i.e., ENSO and PDO) has led to a declining snowpack (lower April SWE) in Colorado since 1978 (Clow 2010) and a shift to earlier snow disappearance in the spring over the past 30 yr (Lukas et al. 2014). When compared to the first half of our study period (1940–1974), we found that climate conditions during the second half of the study period—a period indicative of future conditions – corresponded with the marked decline in the frequency of establishment events.

In the context of future climate scenarios, both medium-low emissions scenarios (RCP 4.5) and high emissions scenarios (RCP 8.5) suggest the timing of precipitation may shift, but neither scenario projects a reduction in annual precipitation for the eastern slope of the CFR (Lukas et al. 2014). However, climate models strongly agree that temperatures will warm, particularly in the summer (1°–2.7°C medium-low emissions scenarios [RCP 4.5] and 2°–3.6°C for high emissions scenarios [RCP 8.5], Lukas et al. 2014). Warming temperatures are anticipated to result in earlier snow melt out, which will further shift the timing of peak soil moisture to earlier in the growing season (Harpold et al. 2015). This will continue to increase the period of low soil moisture and seedling drought stress during the summer months. Additionally, warming temperatures are anticipated to increase summer moisture deficits (Andreadis and Lettenmaier 2006) with greater deficits and less favorable conditions for seedling establishment occurring under higher emissions scenarios. Under the medium-low emissions scenario, the hottest summer temperatures over the past 100 yr are projected to by typical summer temperatures by mid-century (Lukas et al. 2014). Such conditions present during a particularly sensitive time of year (as indicated by our study) were not correlated with any of our establishment events and illustrate the vulnerability of spruce and fir to regeneration failure.

The declining trend in establishment and the negative impacts of climate warming need to be considered in the context of the long lifespan of fir (~300 yr) and spruce (commonly exceeding 500 yr, Oosting and Reed 1952). Slightly longer intervals between establishment events could be insignificant for population persistence of long-lived species, and establishment events may still occur when strong seed years coincide with suitable climate conditions or seed disperses to favorable topo-climates (e.g., mesic, north aspects; Dobrowski 2011). However, recent increases in climate-driven tree mortality in combination with declining opportunities for new establishment events may drive novel changes in subalpine forest ecosystems.

Conclusion

To our knowledge this is the first annually resolved dataset of subalpine fir and Engelmann spruce establishment and survival in the southern Rocky Mountains. We documented the frequency and trends in broad-scale establishment events across complex topo-moisture gradients over the last 70 yr, and identified strong relationships between moisture availability and broad-scale establishment events. Future forest density and persistence of a forest cover will depend on the collective response of demographic processes (e.g., reproduction, growth, and mortality) to climate warming. In contrast to increasing trends in establishment associated with warming in more maritime subalpine forests (Dolanc et al. 2013), our results show that recruitment declines will likely occur across the core of subalpine tree ranges in systems with water-limited growing seasons, which expands upon similar findings for sites near alpine treeline (Gill et al. 2015, Kueppers et al. 2016). If management goals are to maintain ecosystem services provided by dense subalpine forests, declines in the frequency of establishment events are a notable and concerning trend that are likely to compound the effects of increasing forest mortality.

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Literature Cited

Adams, B. J., M. E. Mann, and C. M. Ammann. 2003. Proxy evidence for an El Niño-like response to volcanic forcing. Nature 426:274–278.

Anderson-Teixeira, K. J., A. D. Miller, J. E. Mohan, T. W. Hudiburg, B. D. Duval, and E. H. DeLucia. 2013. Altered dynamics of forest recovery under a changing climate. Global Change Biology 19:2001–2021.

Andreadis, K. M., and D. P. Lettenmaier. 2006. Trends in 20th century drought over the continental United States: US drought trends. Geophysical Research Letters 33:1–4.

Barnett, T. P., J. C. Adam, and D. P. Lettenmaier. 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438:303–309.

Bell, D. M., J. B. Bradford, and W. K. Lauenroth. 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States: Early indications of tree range shift. Global Ecology and Biogeography 23:168–180.

Bozdogan, H. 1987. Model selection and Akaike's information criterion (AIC): the general theory and its analytical extensions. Psychometrika 52:345–370.

Brodersen, C. R., M. J. Germino, and W. K. Smith. 2006. Photosynthesis during an Episodic Drought in *Abies lasiocarpa* and *Picea engelmannii* across an Alpine Treeline. Arctic, Antarctic, and Alpine Research 38:34–41.

Buechling, A., P. H. Martin, C. D. Canham, W. D. Shepperd, and M. A. Battaglia. 2016. Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains. Journal of Ecology 104:1051–1062.

Bunn, A. G. 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28:251–258.

Clow, D. W. 2010. Changes in the timing of snowmelt and Streamflow in Colorado: a response to recent warming. Journal of Climate 23:2293–2306.

Cui, M., and W. K. Smith. 1991. Photosynthesis, water relations and mortality in *Abies lasiocarpa* seedlings during natural establishment. Tree Physiology 8:37–46.

DesRochers, A., and R. Gagnon. 1997. Is ring count at ground level a good estimation of black spruce age? Canadian Journal of Forest Research 27:1263–1267.

Dobrowski, S. Z. 2011. A climatic basis for microrefugia: the influence of terrain on climate. Global Change Biology 17:1022–1035.

Dolanc, C. R., J. H. Thorne, and H. D. Safford. 2013. Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007: Shifting structure of subalpine forests in California. Global Ecology and Biogeography 22:264–276.

Elliott, G. P., and M. Cowell. 2015. Slope aspect mediates fine-scale tree establishment patterns at upper treeline during wet and dry periods of the 20th century. Arctic, Antarctic, and Alpine Research 47:681–692.

Gill, R. A., C. S. Campbell, and S. M. Karlinsey. 2015. Soil moisture controls Engelmann spruce (*Picea engelmannii*) seedling carbon balance and survivorship at timberline in Utah, USA. Canadian Journal of Forest Research 45:1845–1852.

Grissino-Mayer, H. D. 1995. Tree-ring reconstruction of climate and fire history at El Malpais National Monument, New Mexico. Ph.D. Dissertation. University of Arizona, Tucson, Arizona, USA.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Reviews 52:107–145.

Harpold, A. A., N. P. Molotch, K. N. Musselman, R. C. Bales, P. B. Kirchner, M. Litvak, and P. D. Brooks. 2015. Soil moisture response to snowmelt timing in mixed-conifer subalpine forests: soil moisture response to snowmelt. Hydrological Processes 29:2782–2798.

Hessl, A. E., and W. L. Baker. 1997. Spruce and fir regeneration and climate in the Forest-Tundra Ecotone of Rocky Mountain National Park, Colorado, USA. Arctic and Alpine Research 29:173.

Higuera, P. E. 2009. CharAnalysis 0.9: diagnostic and analytical tools for sediment-charcoal analysis. http://CharAnalysis.googlepages.com.

Johnson, A. C., and J. A. Yeakley. 2016. Seedling regeneration in the Alpine treeline ecotone: comparison of wood microsites and adjacent soil substrates. Mountain Research and Development 36:443–451.

Kittel, T., M. Williams, K. Chowanski, M. Hartman, T. Ackerman, M. Losleben, and P. Blanken. 2016. Contrasting long-term alpine and subalpine precipitation trends in a mid-latitude North American mountain system, Colorado Front Range, USA. Plant Ecology and Diversity 8:607–624.

Kroiss, S. J., and J. HilleRisLambers. 2015. Recruitment limitation of long-lived conifers: implications for climate change responses. Ecology 96:1286–1297.

Kueppers, L. M., E. Conlisk, C. Castanha, A. B. Moyes, M. J. Germino, P. de Valpine, M. S. Torn, and J. B. Mitton. 2016. Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. Global Change Biology 23:2383–2395.

Kueppers, L., A. Faist, S. Ferrenberg, C. Castanha, E. Conlisk, and J. Wolf. 2017. Lab and field warming similarly advance germination date and limit germination rate for high and low elevation provenances of two widespread subalpine conifers. Forests 8:433.

Langdon, J. G. R., and J. J. Lawler. 2015. Assessing the impacts of projected climate change on biodiversity in the protected areas of western North America. Ecosphere 6:1–14.

League, K., and T. Veblen. 2006. Climatic variability and episodic *Pinus ponderosa* establishment along the forest-grassland ecotones of Colorado. Forest Ecology and Management 228:98–107.

Little, R. L., D. L. Peterson, and L. L. Conquest. 1994. Regeneration of subalpine fir (*Abies lasiocarpa*) following fire: effects of climate and other factors. Canadian Journal of Forest Research 24:934–944.

Lukas, J., J. Barsugli, N. Doesken, I. Rangwala and K. Wolter. 2014. Climate change in Colorado: a synthesis to support water resources management and adaptation. Pages 1–114. In A Report for the Colorado Water Conservation Board, University of Colorado Boulder, Western Water Assessment, Cooperative Institute for Research in Environmental Sciences (CIRES).

Maher, E., and M. J. Germino. 2006. Microsite differentiation among conifer species during seedling establishment at alpine treeline. Ecoscience 13:334–341.

Malanson, G. P., et al. 2007. Alpine treeline of western North America: linking organism-to-landscape dynamics. Physical Geography 28:378–396.

van Mantgem, P. J., et al. 2009. Widespread increase of tree mortality rates in the western United States. Science 323:521–524.

McGuire, C. R., C. R. Nufio, M. D. Bowers, and R. P. Guralnick. 2012. Elevation-dependent temperature trends in the Rocky Mountain Front Range: changes over a 56- and 20-year record. PLoS ONE 7:1–12.

Moyes, A. B., M. J. Germino, and L. M. Kueppers. 2015. Moisture rivals temperature in limiting photosynthesis by trees establishing beyond their cold-edge range limit under ambient and warmed conditions. New Phytologist 207:1005–1014.

Noble, D., and R. Alexander. 1977. Environmental factors affecting natural regeneration of Engelmann spruce in the Central Rocky Mountains. Forest Science 23:420–429.

Noble, D., and F. Ronco Jr. 1978. Pages 1–12Seedfall and establishment of Engelmann spruce and subalpine FIr in clearcut openings in Colorado. Research Paper. USFS Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

NRCS. 2016, September 23. University Camp Snow Course. Government. https://wcc.sc.egov.usda.gov/nwcc/rgrpt?report=snowcourse&state=CO

NWT LTER. 2016, January 11. Data Access Home. http://niwot.colorado.edu/data

Oosting, H. J., and J. F. Reed. 1952. Virgin spruce-fir of the Medicine Bow Mountains, Wyoming. Ecological Monographs 22:69–91.

Peet, R. K. 1981. Forest vegetation of the Colorado Front Range. Vegetation 45:3–75.

Pepin, N., et al. 2015. Elevation-dependent warming in mountain regions of the world. Nature Climate Change 5:424–430.

Petrie, M. D., A. M. Wildeman, J. B. Bradford, R. M. Hubbard, and W. K. Lauenroth. 2016. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. Forest Ecology and Management 361:328–338.

PRISM. 2016, November. PRISM Climate Group. Oregon State University. http://prism.oregonstate.edu

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Smith, J. M., J. Paritsis, T. T. Veblen, and T. B. Chapman. 2015. Permanent forest plots show accelerating tree mortality in subalpine forests of the Colorado Front Range from 1982 to 2013. Forest Ecology and Management 341:8–17.

Speer, J. H. 2010. Fundamentals of tree-ring research. University of Arizona Press, Tucson, Arizona, USA.

Telewski, F. W. 1993. Determining the germination date of woody plants: a proposed method for locating the root/shoot interface. Tree-Ring Bulletin 53:13–16.

Tepley, A. J., and T. T. Veblen. 2015. Spatiotemporal fire dynamics in mixed-conifer and aspen forests in the San Juan Mountains of southwestern Colorado, USA. Ecological Monographs 85: 583–603.

Trujillo, E., and N. P. Molotch. 2014. Snowpack regimes of the Western United States. Water Resources Research 50:5611–5623.

Veblen, T. T. 1986. Age and size structure of subalpine forests in the Colorado Front Range. Bulletin of the Torrey Botanical Club 113:225.

Vicente-Serrano, S. M., S. Beguería, and J. I. López-Moreno. 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. Journal of Climate 23:1696–1718.

Villalba, R., T. T. Veblen, and J. Ogden. 1994. Climatic influences on the growth of subalpine trees in the Colorado Front Range. Ecology 75:1450.

Weisberg, P., and W. Baker. 1995. Spatial variation in tree regeneration in the forest-tundra ecotone, Rocky Mountain National Park, Colorado. Canadian Journal of Forest Research 25:1326–1339.

Woodward, A., D. G. Silsbee, E. G. Schreiner, and J. E. Means. 1994. Influence of climate on radial growth and cone production in subalpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*). Canadian Journal of Forest Research 24:1133–1143.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2134/suppinfo

DATA AVAILABILITY

Data associated with this study are available from the LTER Network Data Portal at: https://doi.org/10.6073/pasta/81dfd2bd8d47708f99479fd33b47fb00