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Forest Density Intensifies the Importance of Snowpack to Growth in Water-Limited Pine Forests

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Abstract

Warming climate and resulting declines in seasonal snowpack have been associated with drought stress and tree mortality in seasonally snow-covered watersheds worldwide. Meanwhile, increasing forest density has further exacerbated drought stress due to intensified tree-tree competition. Using a uniquely detailed dataset of population-level forest growth (n=2495 sampled trees), we examined how inter-annual variability in growth relates to snow volume across a range of forest densities (e.g., competitive environments) in sites spanning a broad aridity gradient across the United States. Forest growth was positively related to snowpack in water-limited forests located at low latitude, and this relationship was intensified by forest density. However, forest growth was negatively related to snowpack in a higher latitude more energy-limited forest, and this relationship did not interact with forest density. Future reductions in snowpack may have contrasting consequences, as growth may respond positively in energy-limited forests and negatively in water-limited forests; however, these declines may be mitigated by reducing stand density through forest thinning.

Key Words: Forest density, snowpack, snow, snow accumulation, forest growth, water-limited forests, energy-limited forests, pine forests, adaptive forest management, climate change resilience

Introduction

Projections for decreased snowpack in the 21st century will influence forest ecohydrology and patterns of soil moisture availability for trees. Rising temperatures are decreasing the proportion of precipitation falling as snow, which reduces the volume of snow water storage, increases rain-on-snow events, and accelerates spring snowmelt, effects that combine to reduce water availability in much of the US (Barnett et al. 2005, Ning and Bradley 2015). Looking forward, continued temperature increases are consistent features of climate projections, meaning that impacts to snowpack may only increase (Collins et al. 2013b, Knutti and Sedlacek 2013, Polade et al. 2014, Trenberth et al. 2015, Diffenbaugh et al. 2017, Prein et al. 2017). Although the impact of climate change on many aspects of the hydrologic cycle are still uncertain (Collins et al. 2013a, Padrón et al. 2019, Bradford et al. 2020), the close link between temperature and snowpack implies that declining snowpack is expected to continue, and loss will be relatively extreme in lower elevation and/or lower latitude forests, where snowpack is particularly vulnerable and also where drought dynamics are particularly important (Demaria et al. 2016, Scalzitti et al. 2016).

The volume of water stored as snowpack, or snow water equivalent (SWE), provides an important water subsidy for high elevation ecosystems (Trujillo et al. 2012), particularly in water-limited forests that experience frequent seasonal drought. Seasonal snowpack provides water storage capacity greater than what could be stored in the soil alone, and delays the release of winter precipitation into the soil until the spring growing season. In snow-dominated temperate ecosystems, soils tend to recharge during the cool season, and dry out following snowmelt. The timing of soil drying in early summer can be altered by several weeks due to heterogeneity of snowmelt across the landscape (Bales et al. 2011). Decreased snow water storage, earlier snowmelt, and earlier loss of soil moisture are associated with longer warm season droughts (Harpold 2016).

Enhanced drought resulting from declining snowpack will impact forest growth and demography, and these impacts may have unexpected interactions with tree basal area density (i.e. the cross-sectional area of tree stems per unit ground area). Low seasonal snowpack is strongly correlated with drought-induced tree mortality and reduced tree growth (Guarín and Taylor 2005, Parida and Buermann 2014). In recent decades, ecosystem productivity has declined due to widespread drought in water-limited forests, where annual precipitation is less than annual evapotranspiration, (Angert et al. 2005, Buermann et al. 2007), while in energy-limited forests, where annual precipitation is substantially greater than annual evapotranspiration, forest growth may be responding positively to recent warming (McKenzie et al. 2001, Littell et al. 2010). Simultaneously, forest density has increased primarily as a result of fire exclusion and land-use change in many regions of the US (Hanberry et al. 2014). Increased forest density directly influences soil water availability by increasing canopy interception and sublimation, which decreases the proportion of snowfall that eventually enters the soil profile (Pomeroy et al. 2002, Gelfan et al. 2004, Musselman et al. 2008), and by changing the snowpack energy balance, which alters spring snowmelt timing (Musselman et al. 2012, Lundquist et al. 2013). Increased forest density also indirectly influences soil water availability by amplifying the competitive intensity for water among trees (Westoby 1984, Andrews et al. 2020). Competition is a strong determinant of forest growth (Fraver et al. 2014, Bottero et al. 2017, Graham et al. 2019), and may interact with hydroclimate variability and change to influence forest growth response to current and future climate conditions (Clark et al. 2011, Ford et al. 2017, Gleason et al. 2017). The impacts of longer warm season droughts as a result of reduced snowpack and earlier snowmelt are likely to be exacerbated by increased forest density (i.e., increased competitive intensity), which may together have profound consequences for productivity in snow-dominated forested ecosystems.

Previous work suggests that in many locations high peak SWE promotes annual forest growth and reduces levels of tree mortality (see references in Figure 1a). However, in other locations excessive snow may limit annual growth, particularly in more energy-limited climates (see references in Figure 1a). Both the hydroclimate of the site and intensity of tree-to-tree resource competition influence forest growth; however, we still do not understand how these factors interact to influence the relationship of snow water resources to forest growth. As temperature increases are expected to continue across the globe, with non-linear warming inducing relatively greater warming at higher elevations (Pepin et al. 2015) and higher latitudes (Pithan and Mauritsen 2014), it is imperative to understand how future changes in seasonal snowpack will influence forest growth across a range of forest densities. Such information can inform potential adaptation strategies for reducing impacts of reduced snowpack through density management regimes. Our objective was to evaluate the combined effects of declining snowpack and increasing forest density on forest productivity across a broad aridity gradient spanning the continental US. Our primary research question was, how does forest density influence the sensitivity of forest growth to inter-annual variability in snowpack volume in water-limited vs. energy-limited pine forests?

Methods

For the observational period of 1960-2009, we evaluated the relationship between annual SWE accumulation and annual forest growth in three pine-dominated, long-term forest density experiments that span a broad aridity gradient across the US (Figure 1). Each research site has been maintained at a range of forest densities since approximately 1960 in multiple replicate plots (Figure 2), although the specific target densities and treatment schedules vary among sites. To represent inter-annual dynamics of snow abundance across spatial scales, we examined five related variables: in situ measurements of maximum SWE, modeled maximum SWE, modeled SWE / annual precipitation data, cumulative PRISM-derived cold season precipitation, and cumulative PRISM-derived cold season / annual precipitation. The latter variable was derived from a physically-based spatially distributed mass and energy balance snowmodel entitled SnowModel (Liston and Elder 2006), which was parameterized to represent forest structural attributes of the density treatments. We evaluated the relationships between these variables and forest growth, quantified by a uniquely robust dataset of stand-level dendrochronological measurements (n=2495 sampled trees) collected for all trees in high, medium, and low density forest treatments as well as un-thinned or "control" forest treatments.

Site Description

Research sites include the ponderosa pine (*Pinus ponderosa*) dominated Fort Valley Experimental Forest (FVEF) in northern Arizona, and Black Hills Experimental Forest (BHEF) in South Dakota, as well as the red pine (*Pinus resinosa*) dominated Birch Lake Experimental research area (BLE) in northern Minnesota, US (Figure 1). As an index of climatological aridity for each site, we used the Global Aridity Index by the United Nations Food and Agriculture Organization calculated as mean annual precipitation (PPT) / mean annual potential evapotranspiration (PET) (Zomer et al. 2008). PPT and PET were aggregated to mean annual values to represent the climatological aridity from 1950-2000. Fort Valley is the lowest latitude (35.28°N, 111.72°W), highest elevation (2266 m), and most water-limited forest where precipitation is typically only half of the potential evapotranspiration (PPT/PET = 0.51). Fort Valley is at the edge of climatological moisture limitations where ponderosa pine forests persist in the western US. The Black Hills is a mid-latitude (44.17°N, 103.63°W), high elevation (1687 m), and water-limited forest typically receiving less than 70% of the annual water demand as precipitation (PPT/PET = 0.68). Birch Lake is a high latitude (47.7°N, 91.93°W) and low elevation (453 m) site, and is nearly balanced in the water versus energy requirements of the forest site (PPT/PET = 0.92). These sites also span a gradient in the mean proportion of precipitation stored in maximum spring SWE (SWE/PPT: FVEF, 0.37; BHEF, 0.25; BLE, 0.19).

Analyses

In each of the three research sites, forest growth was calculated as the stand-level basal area increment (BAI), as derived from tree cores sampled at each site (FVEF, n=598; BHEF, n=420; BLE, n=1477). Cores were collected from 2009 to 2012 from each tree > 10 cm diameter at breast height (DBH) at Fort Valley and Black Hills and > 5 cm DBH at Birch Lake in 0.08 ha plots of low, medium, high, and control forest density treatments. The target forest density maintained for these treatments at each site include 9, 14, 34 m^2 ha^{-1} and an unthinned control (45 m^2 ha^{-1}) at Fort Valley (1962-2009), 5, 14, 28 m^2 ha^{-1} and an unthinned control (37 m^2 ha^{-1}) at Black Hills (1963-2009), and 7, 21, 35 m^2 ha^{-1} and an unthinned control (67 m^2 ha^{-1}) at Birch Lake (1960-2008). As the unthinned control site density values likely changed over time, these values are from the last measurement period. In each research site, treatment plots were located within an approximately 1 km^2 area and had similar soils, microclimate variability, and similar forest conditions prior to treatment (Gleason et al., 2017 & references therein). Three replicate subplots in each density treatment were sampled at Fort Valley and Black Hills, and nine replicate subplots in each density treatment were sampled at Birch Lake (Gleason et al. 2017). COFECHA software was used to check dating errors, improve the cross-dating of tree-ring series, and identify potential false rings, which were confirmed by visual inspection and corrected in the dataset (Grissino-Mayer 2001). We then estimated the diameter inside bark (DIB) using empirical equations to remove the bark thickness from the field-measured DBH (Bunn 2008, Keyser et al. 2008). Ring-width series were adjusted to account for off-center piths due to elliptical trunk shape (Frelich 2002). Using back reconstruction starting from inside the bark toward the pith, BAI values were obtained using the dplR package in R (Bunn 2008). Plot-level BAI values were calculated as the sum of all individual tree BAIs within a plot for each year since establishment. Stand-level BAI was calculated as the mean of the sample plots in a treatment.

The stand-level BAI values were developed from cores of living trees, and thus do not account for tree mortality or the trees that were harvested from treatment plots to maintain the target density throughout the experimental period. The greater the intensity of tree removal, the greater the underrepresentation of stand-scale BAI derived from tree cores due to sample size reduction over time, rather than hydro-climate influences on stand-scale BAI over time. To account for this underrepresentation, we increased the stand-level BAIs based on the proportion of trees historically measured prior to each treatment to trees cored at the time of tree core sampling (Gleason et al. 2017). This correction accounts for growth of trees that were harvested prior to our collection of increment cores, and is simplified by the relatively consistent tree sizes within each basal area treatment (Bottero et al. 2017). Stand-level forest growth (BAI) values were de-trended using a cubic spline over the study period for each plot to remove low frequency (long-term) variability and preserve the high frequency (inter-annual) variability in forest growth using the dplR package in R (Bunn 2008).

In order to evaluate relationships of forest growth to snow accumulation across spatial scales, we used three sources of snow accumulation data, including measured snow accumulation at the point scale, modeled snow accumulation at a 100-m gridded spatial resolution, and statistically-derived PRISM cold season precipitation at an 800-m gridded spatial resolution. Maximum measured snow accumulation data were obtained from the nearest snow pillow sensor to each research site with the longest possible record, which includes the Mormon Mountain National Resource Conservation Service Snow Telemetry station (SNOTEL) for Fort Valley (1981-2009), the North Rapid Creek SNOTEL station for Black Hills (1997-2009), and the Glacial Ridge Soil Climate Analysis Network (SCAN) site for Birch Lake (2000-2009). Because measured SWE data are spatially and temporally limited near Birch Lake, we augmented those data with the closest annual snow course transect data for the observational period (1962-2000) from the Marcell Experimental Forest to represent the interannual variability of snowpack in the region. Modeled annual maximum SWE data were derived for each site for the experimental period (1960-2009) using SnowModel (Liston and Elder 2006), a physically-based spatially distributed snow mass and energy balance model. Modeled SWE/PPT values were obtained using maximum modeled SWE / cumulative annual precipitation input data. Model inputs include spatially distributed fields of precipitation, air temperature, relative humidity, wind speed and direction, land cover, and topography. We used daily total precipitation, mean air temperature, and mean relative humidity gridded at 1/16° spatial resolution (Livneh et al. 2013), and average wind speed and direction gridded at 2.5° spatial resolution (Kalnay et al. 1996) and bilinearly interpolated to the 1/16° data grid, from the National Center for Environmental Prediction-National Center for Atmospheric Research. The daily gridded air temperature and precipitation data were bias corrected using monthly PRISM data at 800-m spatial resolution using the delta and ratio methods, respectively (Watanabe et al. 2012). Final model inputs were interpolated using the topography and land cover data resampled to 100 m during model setup using the MicroMet submodel within SnowModel. Topography data were obtained from the US National Elevation Dataset digital elevation model gridded at 30 m spatial resolution (Gesch et al. 2002). Land cover classification data were obtained from the 2011 National Land Cover Database (Homer et al. 2015).

The model was modified to include a function to partition precipitation into snow vs. rain using a linear function of temperature from -2 to 2º C, where all precipitation is defined as snow below -2º C, as rain above 2º C, and a combination of rain and snow between -2 to 2º C (US Army Corps of Engineers 1956). We also modified the forest structure parameters within the model to represent snow accumulation patterns between the density treatments. We altered the default leaf area index (LAI) values used in the model to those representing LAI values measured in the forest density treatments. At Fort Valley, LAI values of 0.77, 1.03, 1.43, and 1.84 were used to represent the low (9 m^2 ha^{-1}), medium (23 m^2 ha^{-1}), high (34 m^2 ha^{-1}), and unthinned (45 m^2 ha^{-1}) forest density treatments (Flathers et al. 2016). A linear model was developed from these measurements to define LAI values in the model according to the associated specific forest densities at Black Hills and Birch Lake (LAI = 0.018*(basal area (m^2 ha^{-1})) + 0.647). The sites have similar long-needle pine structure, although there is uncertainty associated with applying the linear model for LAI from a ponderosa pine dominated site to a red pine dominated site. Ponderosa pine dominated forest LAI values may underestimate red pine dominated forest LAI values (Deblonde, et al., 1994, Penner and Deblonde, 1996), and therefore overestimate snow accumulation differences between density treatments in the red pine dominated forests. However, modeled SWE was not different between sites at Birch Lake, demonstrating this uncertainty doesn't significantly influence model results. Measured SWE from all snow pillows within the modeling domain were used to validate modeled SWE results by evaluating the root mean square error (RMSE) between modeled and observed SWE at each validation site location. These validation stations include the Mormon Mountain (1981-2009), Snowslide Canyon (1997-2009), Fort Valley (2008-2009), and Fry (1971-2009) SNOTEL sites for Fort Valley, North Rapid Creek (1996-2009) and Blind Park (1990-2009) SNOTEL sites for Black Hills, and from the annual snow course data from the Marcell Experimental Forest for Birch Lake, which is approximately 8 m lower in elevation and 47 km linear distance from Birch Lake. Cumulative cool season precipitation data (October – April) were derived for each site for the entire experimental period (1960-2009) from monthly PRISM data gridded at 800-m spatial resolution (Daly et al. 2008). Cumulative cool season / annual precipitation data were obtained using monthly PRISM data from (October – April) / (October – September) for the experimental period.

Differences in measured forest growth and modeled SWE between density treatments were evaluated for each site using ANOVA followed by Tukey's Honestly Significant Difference analyses. Spearman-rank correlation tests were used to evaluate the initial relationships of seasonal hydroclimate variables and forest growth including measured SWE, modeled SWE, cool season PPT, warm season PPT, annual PPT, cool season temperature, warm season temperature, annual temperature, forest density, forest age, and years since treatment.

An optimal mixed effects model was developed for all sites to evaluate the overall relationship of forest growth to snow/winter precipitation parameters and interactions of density treatments. We explored the site-specific relationships of forest growth relative to snow/winter precipitation parameters using a number of statistical model iterations, and ultimately selected the best model based on model fit (AIC and R^2), normalized residuals, and interpretability of the results. The inter-annual variability of forest growth and snow accumulation was evaluated within each site using least-squares regression analysis for all treatment plots together, and each treatment plot individually. In order to normalize residuals, log-transformed snow/winter precipitation parameters were used throughout these site-specific analyses. All analyses were performed in R 3.1.3 (R Core Team 2016). Significance for statistical tests was determined using an alpha value of 0.05.

Results

Annual stand-level forest growth generally increased with stand density between all treatments in Fort Valley ($F = 78.7$, $P < 0.001$) and Black Hills ($F = 164.3$, $P < 0.001$), as higher density forests tend to have more trees contributing to overall forest growth, however this was not the case in Birch Lake (Figure 3). In Fort Valley and Black Hills, the control treatments were the exception, where the highest density forests were at the upper limits of maximum density levels for these species and were dominated more by self-thinning mortality than by growth. At Black Hills, mountain pine beetle epidemics in recent decades have caused widespread tree mortality in the highest density treatments (Graham et al. 2019), observable in the reduced growth in both the high-density and control treatment plots. Mean modeled SWE decreased with forest density, as lower density forests have greater below-canopy snow accumulation than the higher density forests due to reduction of canopy interception; however, these were not significant differences due to high interannual variability (Figure 3).

The Importance of Snow to Forest Growth

Across all sites, forest growth demonstrated significant correlations with snow accumulation across spatial scales, while summer precipitation and seasonal temperature were less important across all sites (Table 1). The relationship of snowpack to forest growth differed across these three climatically divergent sites (Figure 4). At Fort Valley, the most water-limited site, measured SWE, modeled SWE, and cool season precipitation were all positively related to forest growth. At Black Hills, the moderately water-limited site, measured SWE and cool season precipitation were positively related to forest growth. At Birch Lake, the cold energy-limited site, the opposite relationship was observed: measured SWE, modeled SWE, and cool season precipitation were negatively related to forest growth. The non-linearity of the logarithmic relationships between the inter-annual variability of measured SWE, modeled SWE, and cool season precipitation with forest growth suggests that the moisture subsidy provided by snow during low snow years has a more pronounced influence on forest growth than during high snow years (Figure 4).

The Influence of Forest Density on the Snow-Forest Growth Relationship

Across all sites, the optimal mixed effects model defined the relationship of forest growth to cold season precipitation, with random (variable slope) effects of treatment and fixed (variable intercept) effects of site (f(log cold season precipitation + treatment(within-site) | site), P = <0.001). The influence of forest density on the relationship of snowpack to forest growth also varied within sites (Figure 4). In Fort Valley, the higher density treatments displayed a stronger relationship (i.e., higher R^2, lower P, and a steeper slope) between forest growth and measured SWE, modeled SWE, and cool season precipitation, than did lower density treatments (Table 2).

In Black Hills, the highest density treatments had a stronger relationship between forest growth and cool season precipitation than did lower density treatments. Compared to lower density treatments, the high density forest stands in these water-limited sites displayed greater slopes and higher statistical significance in the relationships of snowpack to forest growth. There was no influence of forest density on the relationship of snowpack to forest growth in Birch Lake, the cold, more energy-limited site.

Discussion

We assessed how the relationship of snow to forest growth varies with both site aridity and forest density, and applied the results to identify locations where forest management may mitigate drought stress in trees resulting from a reduction in the seasonal snowpack. Our results indicate that forest growth can have divergent responses to both measured and modeled snow accumulation metrics. Specifically, snow promotes forest growth in water-limited sites, but may limit forest growth in energy-limited sites. In addition, the role of forest density in mediating the relationship between snowpack and growth varied among sites. Previous work in a suite of long-term forest management experiments that include these sites found that the impact of forest density on the drought–growth relationship was unrelated to site aridity (Gleason et al 2017). Here, we add detail to those previous results by demonstrating that density amplified the importance of snowpack to positive forest growth in water-limited sites, but not in energy-limited sites. Variation among sites in the influence of density and snowpack implies that these conditions may influence drought stress and forest growth in ways that are both distinct from other aspects of drought and important to recognize for managing forests in a changing climate. Also, different forest types may respond divergently to future change, and perhaps require different management approaches to promote resilience across forest ecosystems.

Specifically, our results suggest two key principles about the consequences of altered snowpack on forest growth that have implications for forest management. First, forest growth in water-limited, dryland areas is likely to be most dramatically impacted by snowpack reductions. In these semi-arid climates, future reductions in seasonal snowpack may negatively influence forest growth and may increase mortality by reducing the cool-season soil moisture subsidy. In contrast, in energy-limited forests, warmer winters (i.e., reduced snowpack) may positively influence forest growth, potentially by extending the growing season, although additional observations are required to confirm this mechanism. The vulnerability of dry forests to rising temperature is consistent with recent widespread drought-driven tree mortality (Williams et al. 2013, Allen et al. 2015).

Second, the negative impacts of declining snowpack on forest growth in water-limited forests will be exacerbated by high stand density. Forest density increases competition for water resources as well as the volume of SWE and timing of snowmelt under the forest canopy. Although climate change has uncertain long-term projections for many components of drought, other aspects, particularly seasonal moisture dynamics with high ecological relevance, display reasonably consistent responses because of a tight link to temperature (Bradford et al. in revision). In the context of rising temperature and declining snowpack in the 21st century, these results suggest that moderating forest density may be particularly important in hot-dry, water limited forests.

There are numerous micro- to macro-scale interactions influencing forest growth response to inter-annual variability of snow-associated water resources. Canopy interception of falling snow is positively related to forest canopy density and influences peak snow accumulation, where less snow volume accumulates under thick forest canopies than in open environments (Lundquist et al. 2013, Dickerson-Lange et al. 2017, Schneider et al. 2019). Snow intercepted by the forest canopy is typically lost to the water budget by 30-70%, as it blows away and/or is sublimated. Dark forest canopies absorb incoming shortwave radiation, and reradiate this absorbed energy as longwave heat energy contributing to snowpack energy balance. Denser forests warm snow, accelerating snowmelt, advancing snow disappearance, driving watershed-scale water resource availability, and in areas with dry summer periods, triggering the beginning of seasonal summer drought.

Many other processes affect growth in these forests, including soils, geology, and soil-water availability that are not quantified here (Fellows and Goulden 2017), but presumably contribute to the variability in forest growth not attributable to inter-annual variations in maximum snow accumulation. In particular, these study sites included two pine species. Ponderosa and red pine species are similar long-needle species, but there may be confounding factors introduced by interspecific differences between the water- vs. energy-limited sites. Nevertheless, previous studies have demonstrated some important aspects of functional similarity among these sites, notably that drought conditions can dramatically reduce forest growth across all sites (Bottero et al 2017, Gleason et al. 2017). Disentangling species differences from the influences of climate and aridity will require either long-term term observational studies as climates change, or similarly long-term common garden experiments. In addition, snowpack dynamics can be highly heterogeneous within a forest stand, a process that we were unable to evaluate here because the long-term experiments experienced repeated thinning treatments that reduced spatial heterogeneity in tree arrangements to maximize resource availability across remaining trees (Ashton and Kelty 2018).

Despite these uncertainties, our study is particularly unique and applicable to forest and water management, because resource managers are typically most interested in stand-level forest responses to climate and water stresses, but most dendrochronology research only evaluates averages of the most sensitive and vulnerable individuals (Carrer 2011, Nehrbass-Ahles et al. 2014, Foster et al. 2016). This work utilized an unusually rich dataset of annual stand-level forest growth data quantified across entire populations of trees maintained for decades at distinctly different forest densities and spanning an aridity gradient to examine the influence of snowpack and density on growth in pine-dominated forests.

Our research suggests that impacts of future loss of seasonal snowpack in water-limited forests can be mitigated by reducing stand density through forest management, but this will have less of an impact on the snowpack–growth relationship in energy-limited forests. Previous work has indicated that forest thinning reduces competition for water resources among trees in water-limited forests and energy-limited forests (D'Amato et al. 2013, Bottero et al. 2017, Gleason et al. 2017). Our examination of growth response to density and snowpack adds seasonal details to those results. Specifically, our results in water-limited forests support previously documented general patterns and indicate that thinning promotes resilience to snow droughts. By contrast, in energy-limited forests, we found that density and resilience to snow-droughts were unrelated, implying that the drought resilience benefits of lower density conditions previously demonstrated in these energy-limited forests likely relate to warm season precipitation. Thus, attention to density management may still be warranted in all forests despite the different relationship to snowpack. Additionally, forest thinning would increase the total volume of SWE in the snowpack, and potentially delay the timing of snowmelt and subsequent soil drying.

Our results also underscore the potential climate-adaptation benefits of forest restoration programs, which are widely utilized across forests to lower density and promote conditions more consistent with historical stand structures (Covington et al. 1997). The low to moderate density treatments included in our study are consistent with the target density for many restoration projects. These densities, which were prevalent prior to European settlement of the western US, as well as in fire-dependent systems in the eastern US (e.g., Hanberry et al. 2014), may enhance forest resilience to disturbances, including fire and drought (Churchill et al. 2013). Although the capability of these ecological restoration treatments to create forest systems that are adapted to future climate conditions remains unclear (Fulé 2008), our results suggest that restoration may have the additional benefit of partially mitigating snowpack losses. Furthermore, reducing stand density is the first step to resiliency, while incorporating other factors such as spatial pattern, multi-cohort structure, and mixed species composition may also support more resilient future forest communities. While supporting multiple management objectives, including snowpack retention (Stevens 2017), wildlife habitat (Wang et al. 2015), and microbial community diversity (Brooks et al. 1996), heterogeneous forest structure and composition contribute to resiliency and adaptability of forests to a future of changing climate (Levin 1992, Franklin et al. 2018, Hessburg et al. 2019).

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Data Availability

Data are publicly available from PDXScholar: https://doi.org/10.15760/esm-data.2

Tables

Table 1. Significant Spearman-rank correlation coefficients for forest growth (BAI) and measured snow water equivalent (SWE), measured SWE/precipitation (PPT), modeled SWE, modeled SWE/PPT, PRISM-derived cool season precipitation (Winter PPT), PRISM-based summer precipitation (Summer PPT), winter PPT/PPT, PRISM-based annual precipitation, winter temperature, summer temperature, annual mean temperature, and years since treatment. Significant correlations are shown for all densities together, and each density treatment individually at Fort Valley (FVEF), Black Hills (BHEF), and Birch Lake (BLE). Correlations not shown were not significant. P-values for Pearson correlation tests are shown as asterisks as follows, *** P < 0.001, ** P < 0.01, * P < 0.05.

Correlations w/ BAI (Scale)	FVEF All	FVEF Con	FVEF High	FVEF Mid	FVEF Low	BHEF All	BHEF Con	BHEF High	BHEF Mid	BLE All
Measured SWE (point)	0.3 **	0.4 *	0.38 *			0.46 ***				

Measured SWE/PPT (point)	0.47 ***	0.58 **	0.59 ***	0.4 *						
Modeled SWE (100 m^2)	0.3 ***	0.39 **	0.40 **	0.31 *						-0.16 *
Modeled SWE/PPT (100 m^2)	0.29 ***	0.36 *	0.35 *	0.29 *						
Winter PPT (800 m^2)	0.43 ***	0.55 ***	0.54 ***	0.38 **	0.31 *	0.40 ***	0.54 ***	0.47 ***	0.35 *	-0.16 *
Summer PPT (800 m^2)						0.20 **				
Winter PPT/PPT (800 m^2)	0.36 ***	0.46 ***	0.42 *							
Winter temperature (800 m^2)	0.48 ***	0.55 ***	0.59 ***	0.45 **	0.35 *	0.35 ***	0.56 ***	0.47 ***	0.34 **	-0.15 *
Summer temperature (800 m^2)	-0.15 *					-0.19 **				
Annual temperature (800 m^2)	-0.36 ***	-0.39 **	-0.44 **	-0.36 ***						
Years since treatment (Plot)	-0.25 ***	-0.29 *	-0.29 *							

Table 2. Significant regression model coefficients for forest growth (BAI) = f(log snow accumulation parameters) across spatial scales including measured snow water equivalent (SWE), modeled SWE, and PRISM-derived winter precipitation (PPT) for all densities together, and each density treatment individually (Con, control; High, high density; Mod, moderate density; Low, low density), at Fort Valley (FVEF), Black Hills (BHEF), and Birch Lake (BLE). The models are plotted in Figure 4. Model combinations not shown were not significant (P > 0.05).

Site	Snow parameter	Model	R^2	Slope	P	Error
FVEF All	Measured SWE	lm(BAI ~ log(SWE))	0.08	0.09	<0.001	0.28
FVEF All	Modeled SWE	lm(BAI ~ log(MSWE))	0.20	0.15	<0.001	0.26

FVEF Con	Modeled SWE	lm(BAI ~ log(MSWE))	0.29	0.19	<0.001	0.27
FVEF High	Modeled SWE	lm(BAI ~ log(MSWE))	0.28	0.18	<0.001	0.25
FVEF Mid	Modeled SWE	lm(BAI ~ log(MSWE))	0.19	0.15	<0.01	0.26
FVEF All	Winter PPT	lm(BAI ~ log(WPPT))	0.26	0.33	<0.001	0.25
FVEF Con	Winter PPT	lm(BAI ~ log(WPPT))	0.39	0.42	<0.001	0.25
FVEF High	Winter PPT	lm(BAI ~ log(WPPT))	0.34	0.37	<0.001	0.24
FVEF Mid	Winter PPT	lm(BAI ~ log(WPPT))	0.21	0.29	<0.001	0.26
FVEF Low	Winter PPT	lm(BAI ~ log(WPPT))	0.15	0.24	<0.01	0.26
BHEF All	Measured SWE	lm(BAI ~ log(SWE))	0.17	0.35	0.002	0.22
BHEF All	Winter PPT	lm(BAI ~ log(WPPT))	0.14	0.34	<0.001	0.21
BHEF C	Winter PPT	lm(BAI ~ log(WPPT))	0.32	0.57	<0.001	0.21
BHEF H	Winter PPT	lm(BAI ~ log(WPPT))	0.22	0.34	<0.001	0.16
BHEF M	Winter PPT	lm(BAI ~ log(WPPT))	0.09	0.25	0.04	0.20
BLE All	Measured SWE	lm(BAI ~ log(SWE))	0.31	-0.09	<0.01	0.15
BLE All	Modeled SWE	lm(BAI ~ log(MSWE))	0.03	-0.04	0.02	0.16
BLE All	Winter PPT	lm(BAI ~ log(WPPT))	0.02	-0.12	0.04	0.17

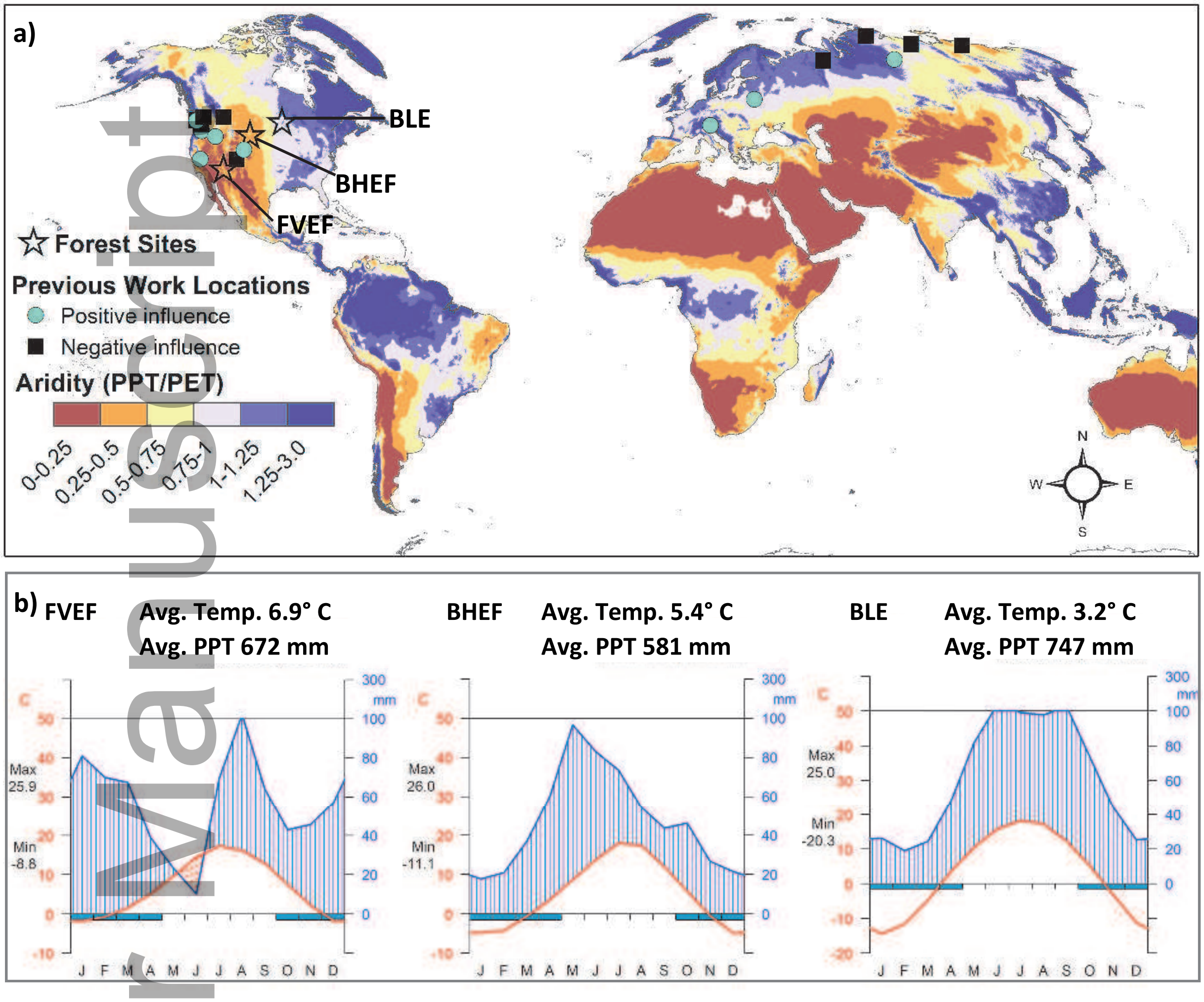
Figure Captions

Figure 1. (a) Previous work locations where researchers investigated the relationship of snow to forest growth, are shown in cyan circles where a positive influence was found (Kirdyanov et al. 2003, Guarín and Taylor 2005, Littell et al. 2008, Hu et al. 2010, Trujillo et al. 2012, Anderegg et al. 2013, Castagneri et al. 2015, Kharuk et al. 2015a), and in black squares where a negative influence was found (Peterson et al. 2002, Littell and Peterson 2005, Littell et al. 2008, Kharuk et al. 2015b). The three forest research sites included in this study (Fort Valley Experimental Forest (FVEF), Black Hills Experimental Forest (BHEF), and Birch Lake Experimental research area (BLE)) are shown as black stars. **(b)** Monthly ensemble mean values of PRISM-derived temperature and precipitation data are shown as Walter-Lieth diagrams, as well as average temperature (Avg. Temp.) and average precipitation (Avg. PPT) for the three forest research sites from the experimental period of 1960-2009.

Figure 2. Control (untreated) and high, mid, and low forest density treatments in ponderosa pine forests at the Fort Valley Experimental Forest site near Flagstaff, AZ. (Photos: K. Gleason)

Figure 3. Measured forest growth (or basal area increment, BAI) and modeled snow water equivalent (SWE) in low, mid, high density and control treatments for each site. Uncorrected forest growth (BAI) (m^2 ha^{-1}) for low, mid, high, and control density treatments from the experimental period of 1960-2009 in, (**a**) Fort Valley, (**b**) Black Hills, and (**c**) Birch Lake research sites. Modeled SWE in low, mid, high, and control density treatments from the experimental period of 1960-2009 in, (**d**) Fort Valley, (**e**) Black Hills, and (**f**) Birch Lake sites.

Figure 4. Forest growth and snow metrics for each density treatment at each site for all treatments (shown in black) and for low, mid, and high density and control treatment plots (shown as green gradient). (**a**) Relationship between forest growth (m^2 ha^{-1}) and measured SWE (mm) at the nearest SNOTEL/SCAN site to each research site (Fort Valley (FVEF, 1981-2009), Black Hills (BHEF, 1997-2009), Birch Lake (BLE, 2000-2009)), and black open circles in measured SWE at BLE are from Marcell Experimental Forest (1962-2009. (**b**) Relationship between forest growth (m^2 ha^{-1}) and modeled SWE (mm). **(c)** Relationship between forest growth (m^2 ha^{-1}) and PRISM-derived winter precipitation (mm; October to April). Linear models, P, and R^2 values are shown in Table 1 for each significant linear regression model. Linear models shown as solid lines indicate a $P < 0.05$, and as dashed lines indicate a $P < 0.1$). All modeled and PRISM-based snow accumulation parameters extended the full observed experimental period (FVEF, 1962-2009; BHEF, 1963-2009; BLE, 1960-2008).


a)
BLE
BHEF
FVEF
☆ Forest Sites
Previous Work Locations
● Positive influence
■ Negative influence
Aridity (PPT/PET)
0-0.25
0.25-0.5
0.5-0.75
0.75-1
1-1.25
1.25-3.0
N
W
E
S
b) FVEF
Avg. Temp. 6.9° C
Avg. PPT 672 mm
BHEF
Avg. Temp. 5.4° C
Avg. PPT 581 mm
BLE
Avg. Temp. 3.2° C
Avg. PPT 747 mm
C
mm
Max 25.9
Min -8.8
Max 26.0
Min -11.1
Max 25.0
Min -20.3
300
100
80
60
40
20
0
50
40
30
20
10
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-10
-20
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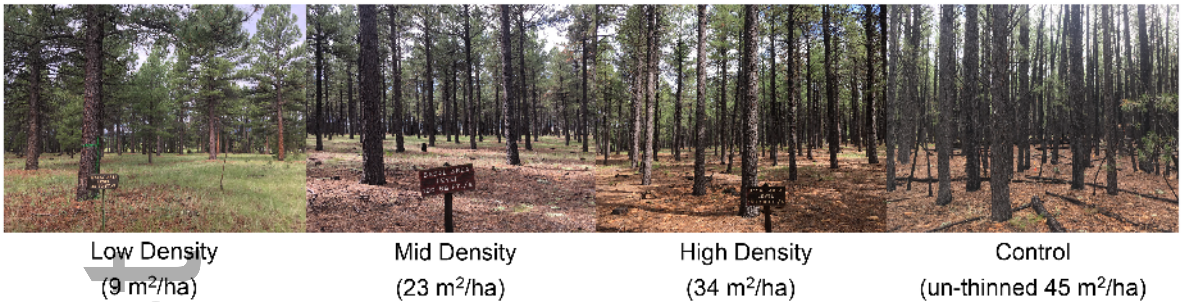

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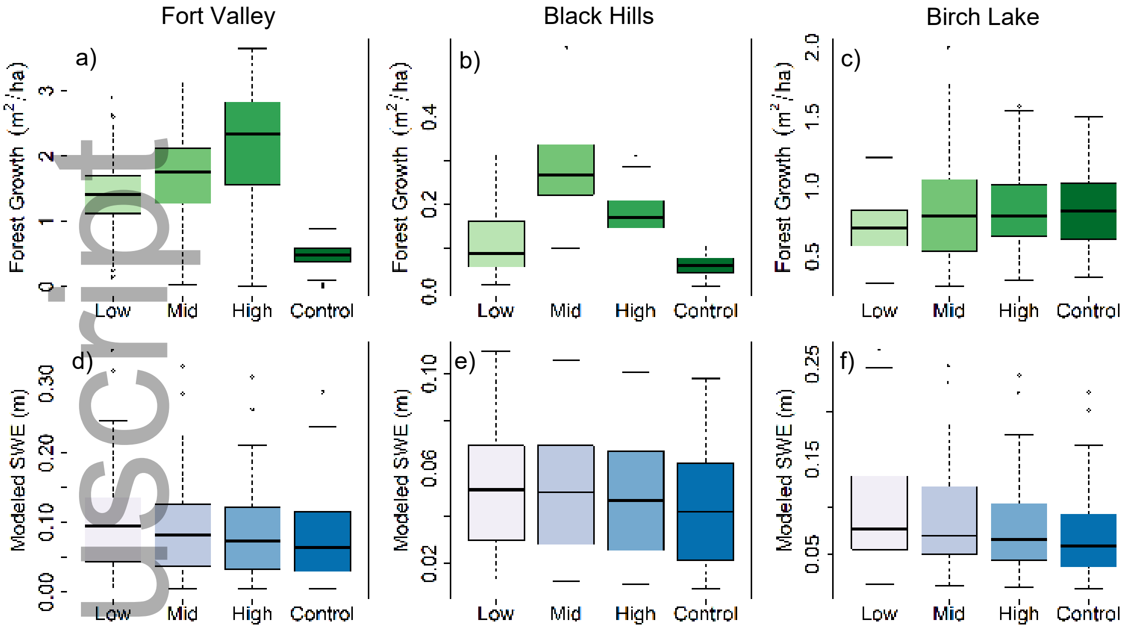

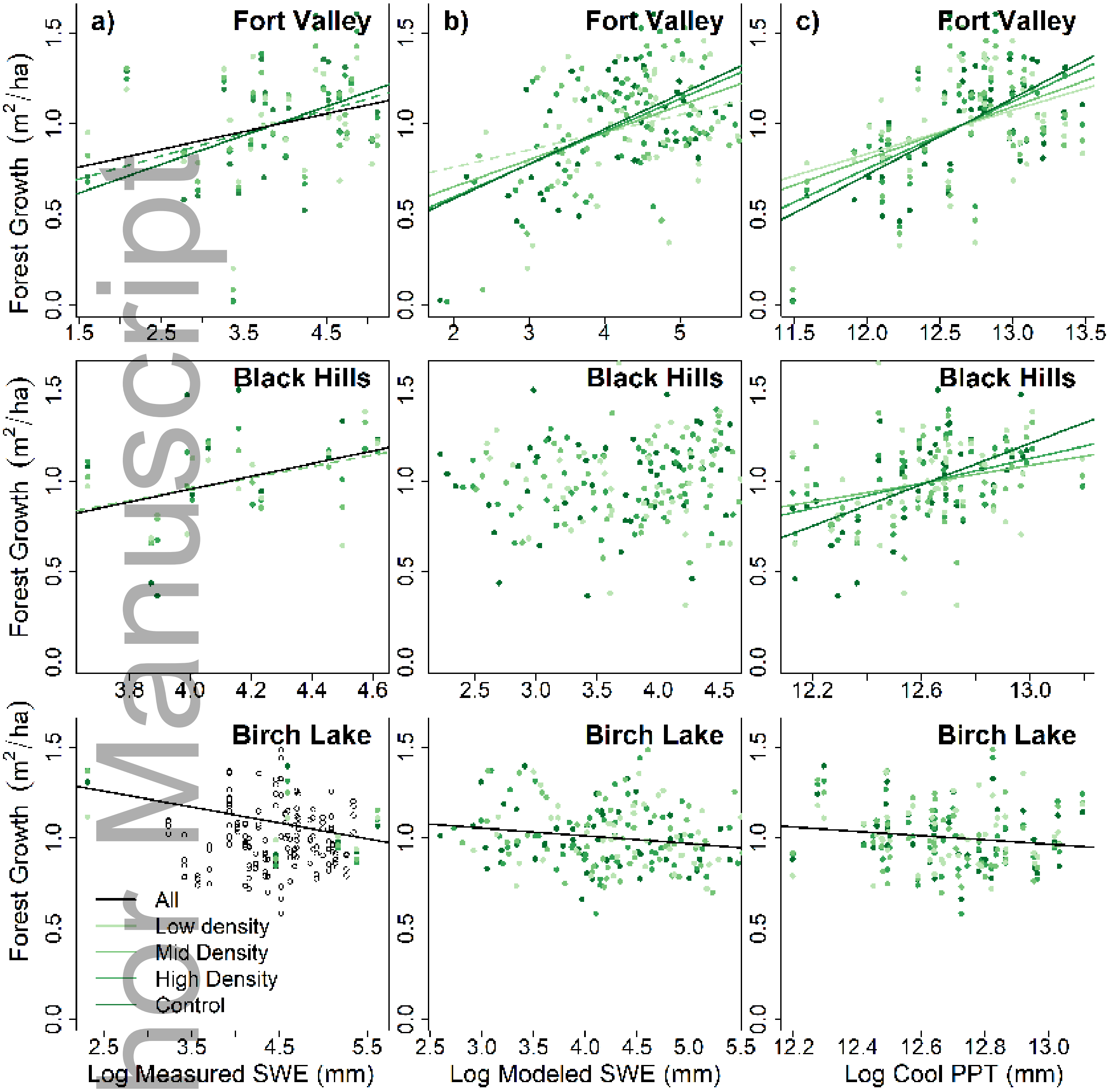
a)
Fort Valley
b)
Fort Valley
c)
Fort Valley
Black Hills
Black Hills
Black Hills
Birch Lake
Birch Lake
Birch Lake
Forest Growth (m²/ha)
Forest Growth (m²/ha)
Forest Growth (m²/ha)
0.0
0.5
1.0
1.5
1.5
2.5
3.5
4.5
2
3
4
5
11.5
12.0
12.5
13.0
13.5
3.8
4.0
4.2
4.4
4.6
2.5
3.0
3.5
4.0
4.5
12.2
12.6
13.0
2.5
3.5
4.5
5.5
2.5
3.0
3.5
4.0
4.5
5.0
5.5
12.2
12.4
12.6
12.8
13.0
All
Low density
Mid Density
High Density
Control
Log Measured SWE (mm)
Log Modeled SWE (mm)
Log Cool PPT (mm)