



Long term persistence of aspen in snowdrift-dependent ecosystems

Alec M. Kretchun^a, Robert M. Scheller^{b,*}, Douglas J. Shinneman^c, Benjamin Soderquist^d, Kaitlin Maguire^c, Timothy E. Link^e, Eva K. Strand^e

^a Quantum Spatial, 421 SW 6th Ave #800, Portland, OR 97204, United States

^b North Carolina State University, Dept. Forestry Env. Resources, Campus Box 7106, Raleigh, NC 27695, United States

^c U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 970 Lusk St., Boise, ID 83706, United States

^d United States Forest Service, Office of Sustainability and Climate, 240 West Prospect Road, Fort Collins, CO 80521, United States

^e University of Idaho, Dept of Forest, Rangeland, and Fire Science, 875 Perimeter Dr., MS 1133, Moscow, ID 83844, United States



ARTICLE INFO

Keywords:

Quaking aspen
Drought
Regeneration
Snowdrift zones

ABSTRACT

Quaking aspen (*Populus tremuloides*) forests throughout the western United States have experienced significant mortality in recent decades, which has been influenced by climate variability, especially drought. In the western portion of its range, where most precipitation arrives during winter as snowfall and summers are dry, snowdrifts that persist into the growing season provide soil moisture recharge that sustain aspen groves. Aspen groves are important locations of biodiversity within these landscapes. There is growing concern that reduced snowpack due to climate change may reduce the long-term persistence and productivity of aspen communities in these regions. In this study, we evaluated the potential for climate change and drought to reduce or eliminate isolated aspen communities in southwestern Idaho. We used a landscape simulation model integrated with inputs from an empirically derived biogeochemical model of growth, and a species distribution model of regeneration to forecast how changes in climate, declining snowpack, and competition with a conifer species is likely to affect aspen occupancy over the next 85-years. We found that simulated reductions in snowpack depth (and associated increases in climatic water deficit) caused a reduction in aspen persistence; aspen occupancy was reduced under all high emissions climate scenarios. Douglas-fir (*Pseudotsuga menziesii*) occupancy also declined under all future climates. Aspen regeneration declined over the course of all simulations, with an ensemble ratio of mortality/establishment increasing over the course of both low and high emissions climate scenarios. Climate-induced mortality of aspen clones increased in frequency under all climate scenarios and, under the most severe emissions scenarios, contributed to a substantial decline of aspen cover. Our research suggests that snowbanks will become an important determinant of long-term persistence of aspen under changing climate in the region.

1. Introduction

When viewed across the entirety of the western United States, forest vegetation patterns can largely be explained by the periodicity of precipitation and the interaction between temperature and precipitation (Rehfeldt, 2006). However, at finer spatial scales, topography and forest community dynamics become important determinants of how vegetation is distributed across the landscape (Coppenhaver-Parry and Cannon, 2016). These fine-scale dynamics will influence species response to climate variability over time. Shifts in species assemblages and distribution across the western U.S. are already occurring due to climate change. In California, for instance, large trees have declined with a shift towards more oak-dominated systems over the last ~80 years (McIntyre et al., 2015). Continued global climate change is

expected to further drive changes in species distributions, as temperatures rise and precipitation becomes more variable (e.g. Duveneck and Scheller, 2016). A meta-analysis by Hansen and Philips (2015) projected similar patterns for the Northern Rockies, specifically increased vulnerability of already sensitive species such as whitebark pine (*Pinus albicaulis*). However, regeneration success and persistence of a species do not always follow spatial patterns consistent with expected climate change effects on tree species distributions (i.e. poleward migration, elevational shifts) (e.g., Crimmins et al., 2011). For instance, Serra-Diaz et al. (2016) forecast that tree species regeneration under changing climate in California will be greatly influenced by topographic mediators.

The coarse-scale projections derived from statistical models of climate suitability do not adequately reflect the climate that an individual

* Corresponding author.

E-mail address: rschell@ncsu.edu (R.M. Scheller).

<https://doi.org/10.1016/j.foreco.2020.118005>

Received 12 September 2019; Received in revised form 20 January 2020; Accepted 15 February 2020

0378-1127/ © 2020 Elsevier B.V. All rights reserved.

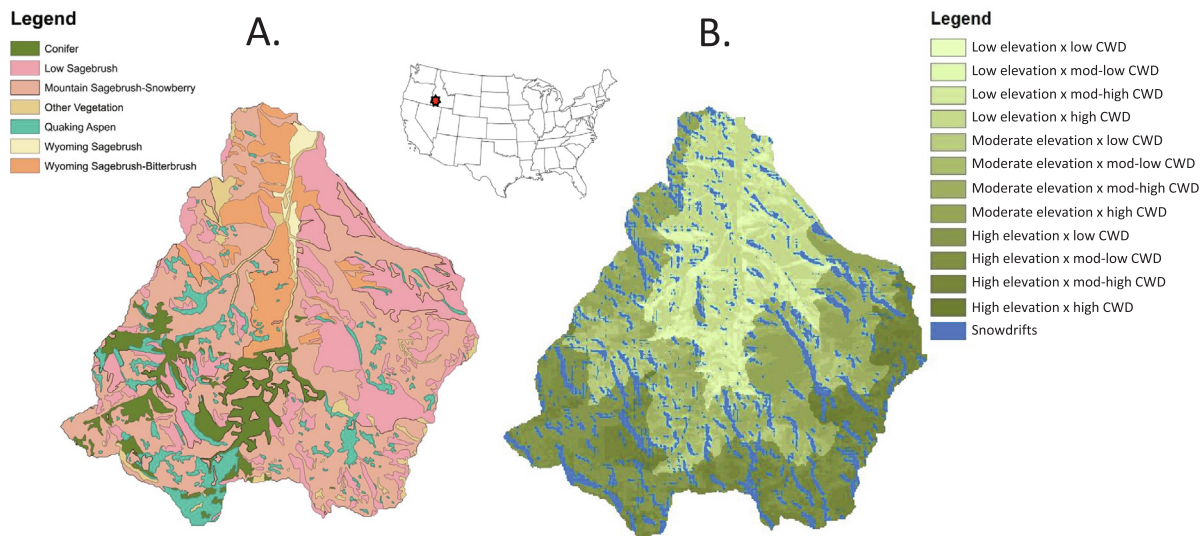


Fig. 1. (A) Current configuration of vegetation communities, derived from the Reynolds Creek Geographic Database (Seyfried et al., 2001). (B) The Reynolds Creek Experimental Watershed with LANDIS-II ecoregions. Ecoregions were developed using binned combinations of climatic water deficit and elevation; blue ecoregions represents spatially-consistent snowdrifts caused by topographically-mediated redistribution of snow.

tree experiences (Lo et al., 2010). This ‘lived climate’ is a combination of temperature, precipitation, available soil water, topography, and other factors that determine a tree’s ability to establish and persist on a site. The complex terrain of many mountainous landscapes creates diverse and highly localized growing conditions that provide opportunities for a species to persist in an area that could be considered outside of its climatically suitable niche when conditions are averaged over broad-scales. Such conditions may also create microrefugia (Hannah et al., 2014; McLaughlin et al., 2017) that result in lagged relationships between the current distribution of species and their climatically optimal ranges— what Dullinger et al. (2012) refer to as ‘extinction debt.’ Indeed, because many trees, or clonal root systems in the case of aspen, in the west are long-lived, theoretically such lags (or the ‘debt’) can extend for decades (Bell et al., 2014; Campbell and Shinneman, 2017; Shinneman and McIlroy, 2019).

1.1. Aspen, snow redistribution, and climate change

In the western U.S, quaking aspen (*Populus tremuloides*) is a widely distributed tree species that is already responding to climate change differentially among diverse topographic settings (e.g., Worrall et al., 2008). Aspen is a clonal species and quickly resprouts following disturbance (Shinneman et al., 2013). However, in the far western portion of its range where most precipitation occurs during winter months and summers are characterized by an extended dry period (McNamara et al., 2005), aspen are locally dependent on seasonal snowdrifts that accumulate due to topography and wind patterns (LaMalfa and Ryle, 2008) and are therefore key topographic mediators. As temperatures rise in the spring and summer, these snowdrifts melt and provide a soil moisture subsidy during the growing season to adjacent aspen stands (Winstral and Marks, 2002; Burke and Kasahara, 2010; Soderquist et al., 2018; Marshall et al., 2019a). Though the response can be lagged, a year or two of extremely low snow accumulation and high temperatures can cause high levels of aspen mortality and affected stands will be more susceptible to future drought (Huang and Anderegg, 2012; Anderegg et al., 2013). Such drought-induced mortality trends have been shown to affect high-density stands more often, with larger older trees exhibiting the highest levels of dieback (Worrall et al., 2008). Coupled field and remote sensing studies have identified a nonlinear positive relationship between cumulative climatic water deficit and widespread aspen mortality, which is linked to moisture deficit-related

xylem cavitation (Anderegg et al., 2015); this hydraulic threshold predicted with high accuracy (75%) regional patterns of mortality observed in Landsat imagery.

It is uncertain to what degree aspen will be able to persist within snow-based microrefugia as temperatures rise and precipitation patterns change, including predicting shifts from snow to rain in the fall and spring (Klos et al., 2014). Previous modeling studies have shown that temperature increases of 2–5 °C could cause a substantial reduction in aspen coverage, particularly at lower elevations (Yang et al., 2015; Rehfeldt et al., 2009). Areas currently experiencing high aspen mortality (e.g., lower elevation and/or southwest facing aspects; Worrall et al., 2008) are also those where the climatic niche of aspen is projected to disappear by the year 2060, suggesting that range shifts in response to climate change may already be occurring (Rehfeldt et al., 2009).

In this study we assessed the influence of both site- and landscape-scale climatic variability on aspen establishment, succession, and persistence over time, by evaluating the consequences of changing climate on quaking aspen in the Owyhee Mountains of southwestern Idaho. To achieve this, we employed a spatially-explicit process-based forest landscape change model (LANDIS-II) integrated with inputs from a biogeochemical model (Biome-BGC) and a species distribution model (MARS). We hypothesized that: (1) the relative occupancy and site persistence of aspen would decline over time under all climate change scenarios, (2) the response would be largest in snowdrifts due to reduced water resources; and (3) the response of aspen would be modified by competition with Douglas-fir .

2. Methods

2.1. Study area

We evaluated aspen persistence in two adjacent sub-watersheds of the Reynolds Creek Experimental Watershed (hereon, ‘RCEW’), in southwestern Idaho (Fig. 1). The RCEW is administered by the USDA-Agricultural Research Service (ARS) and is located within the larger Owyhee Plateau and Owyhee Mountain Range, which extends from Owyhee County, Idaho to Malheur County, Oregon. Soils throughout this upland region belong primarily to the Chestnut Great Soil Group (Kastanozems) with primarily rhyolitic parent material. At low- to mid-elevations, vegetation is dominated primarily by sagebrush-bunchgrass

communities, and common species include big sagebrush (*Artemisia tridentata*), low sagebrush (*A. arbuscula*), bitterbrush (*Purshia tridentata*), Idaho fescue (*Festuca idahoensis*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and small inclusions of western juniper (*Juniperus occidentalis*). At mid-to high elevations, forests consist almost entirely of aspen and Douglas-fir (*Pseudotsuga menziesii*) stands; Douglas-fir also benefits from snowdrift soil water subsidies. Subalpine fir (*Abies lasiocarpa*) is interspersed among mountain shrub communities (e.g., *Artemisia* spp, *Symphoricarpos oreophilus*, *Rosa woodsii*). The area has historically been grazed by cattle and sheep (Burkhardt and Tisdale, 1969). Our 5463 ha study area encompasses the most southerly headwater region of the RCEW, and sits at the highest elevation within the RCEW (1398–2244 m) which is the only portion of RCEW with any significant tree cover (discussed below). Over the last century, climate fluctuations around the RCEW has shown moderate change (velocity, measured as km decade^{-1}) in minimum temperature, evapotranspiration, and climatic water deficit (Dobrowski et al., 2013) with a concomitant decline in the proportion of snow to rain at all elevations (Nayak et al., 2010).

2.2. Simulation approach

We coupled several process- and statistically-based models to forecast landscape dynamics (Fig. 2). LANDIS-II (Scheller et al., 2007) is a process-based simulation model that projects forest change over time. LANDIS-II has been extensively used to estimate climate change effects on forested landscapes, including in the western U.S. (e.g., Loudermilk et al., 2013; Creutzburg et al., 2017; Scheller et al., 2018; Campbell and Shinneman, 2017). Species-specific productivity estimates are a required input of LANDIS-II, therefore the biogeochemical process model Biome-BGC (Thornton et al., 2002) was used to estimate site-specific net primary productivity for use within LANDIS-II. Finally, in order to estimate the probability of regeneration and establishment for each species over time, multivariate adaptive regression spline (MARS) models were developed, and the predicted occurrence probabilities for each species were provided to LANDIS-II. Both Biome-BGC and MARS models require climate inputs, which were synchronized to provide continuity of inputs for both.

We projected future aspen persistence in the study area using LANDIS-II, a spatially dynamic framework for estimating forest landscape change as a function of establishment, growth, and mortality. Tree species composition is spatially and temporally dynamic and represented as species-age cohorts; each species has unique life history

attributes that determine response to disturbance and seed dispersal capacity (Scheller et al., 2007). Dispersal allows for recruitment on suitable sites across the entire landscape, given appropriate site conditions and propagule pressure. For each modeled species, life history attributes influence growth, dispersal, shade tolerance and other physiological traits (Table 1). Given the limited establishment of aspen beyond existing clones, we limited aspen dispersal to areas immediately adjacent to existing clones. Succession is an emergent property of life history traits and stochastic disturbances, therefore each model scenario was replicated five times. The individual climate scenarios, model extensions used, and model parameterization process are described below, and all model inputs are available at <https://github.com/LANDIS-II-Foundation/Project-Idaho-Aspen>. Given the relatively fine spatial scale of snowdrifts (typically < 100 m in width), our simulations used a 10 m cell resolution. We simulated productivity and regeneration at an annual time step to capture year-to-year variations in hydrometeorological conditions. Competition primarily occurs via exclusion due to light limitations: higher biomass reduces forest-floor light and therefore limits aspen establishment.

2.3. Initial communities

LANDIS-II requires an estimate of the spatial distribution of current vegetation communities across the landscape, with each community defined by species and age cohorts. Current communities for our RCEW study area were created using Forest Inventory Analysis (FIA; most recent sampling years 2008–2013, <https://www.fia.fs.fed.us/>) plot data (U.S. Forest Service, 2018) within a radius of 50 km around the RCEW. This resulted in 1894 unique FIA plots, each of which contained 4 subplots (14.6 m diameter), for a total of 7576 unique subplots. FIA plots were used to provide tree attributes to a digitized map of forest types within the RCEW, that was derived from color aerial photographs (1:12,000 scale) and available from the Reynolds Creek Geographic Database (Seyfried et al., 2001) (Fig. 1). The analysis provided the following estimated cover percentages for major forest community types within our study area extent: Douglas-fir/big sagebrush 5.68%, Douglas-fir/quaking aspen/big sagebrush 0.6%, aspen/Douglas-fir 0.3%, and aspen dominated 8.57%. The unique subplots contained both mixed and single species communities, from which we extracted tree species, diameter at breast height (DBH), age (in years), and biomass (oven-dry weight). When tree ages were absent from the FIA data, they were estimated by regressing age against DBH (from the subplots above) for each species (aspen intercept = 17.486, slope = 5.6;

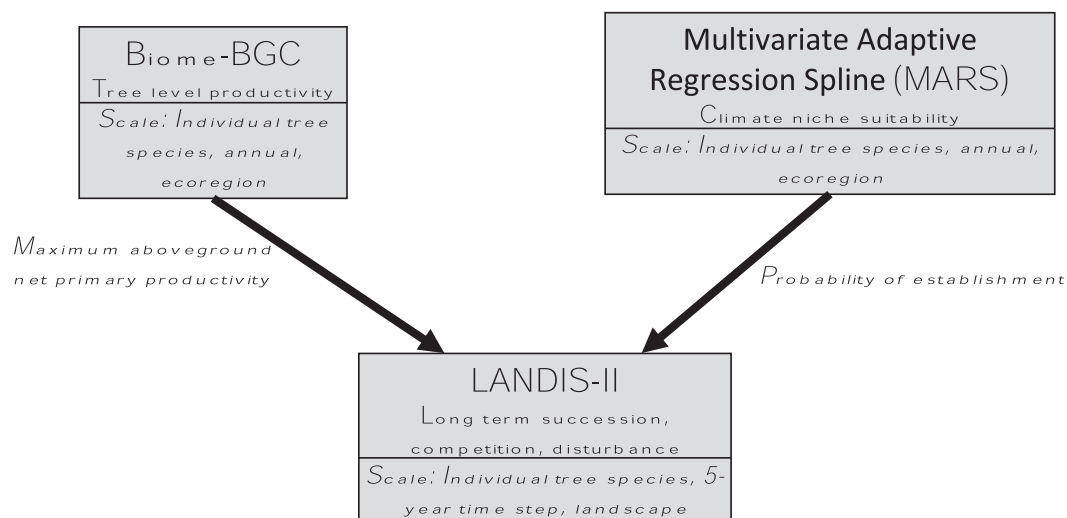


Fig. 2. Model architecture showing integration of three approaches: Biome-BGC, MARS, and LANDIS-II. Specific LANDIS-II input parameters provided by Biome-BGC and MARS are indicated by italics.

Table 1

Species life history life history attributes for the LANDIS-II modeling. *Shade and fire tolerance use a five-point scale from 1 (least tolerant) to 5 (most tolerant). Vegetative reproduction is contingent upon a probability of establishment > 0.0 .

Species	Longevity (years)	Sexual maturity (years)	Shade tolerance*	Fire tolerance*	Effective seed dispersal distance (m)	Max seed dispersal distance (m)	Vegetative reproductive probability	Minimum sprout age (years)	Maximum sprout age (years)	Post-fire regeneration (type)
<i>J. occidentalis</i>	800	20	2	2	75	500	0	0	0	None
<i>P. tremuloides</i>	120	10	1	2	5	10	0.95	10	120	Resprout
<i>P. menziesii</i>	600	12	4	3	75	800	0	0	0	None
Generic shrub	80	3	2	1	10	10	0.1	1	70	Resprout

Douglas fir intercept = 10.66, slope = 6.412; Western juniper intercept = 7.01, slope = 6.955) using the R statistical package (R Core Team, 2017). Initial communities were then created by imputing the FIA derived species-cohort data (above) across the RCEW landscape, based on FIA forest type and forest type data in the Reynolds Creek Geographic Database (full R code is provided in the GitHub repository: <https://github.com/LANDIS-II-Foundation/Project-Idaho-Aspen>). We grouped all shrub species into a generic shrub cover-type to simplify modeled competition among species, and because aspen-shrub competition dynamics are poorly understood (Harvey et al., 2016).

Species' establishment probabilities, mortality rates, and above-ground net primary productivity are assigned to unique 'ecoregions' in the LANDIS-II model, each of which represents similar soil and climate conditions. Following Yang et al. (2015), the study area was first divided into ecoregions using elevation zones and estimates of climatic water deficit (Fig. 1). Snowdrift adjustments to climatic water deficit has been shown to improve models of species distributions relative to either temperature or precipitation estimates alone (e.g., Lutz et al., 2010), and was obtained as 270-m resolution raster data from the Basin Characterization Model (Flint et al., 2013). To gauge the efficacy of climatic water deficit for determining patterns of vegetation productivity in our study area, we first analyzed the spatial correlation between monthly climatic water deficit estimates (averaged over a 20-year period) and satellite-based estimates of the relative density of green plant cover, which was derived from the soil adjusted vegetation index (SAVI) available for the RCEW from Seyfried et al. (2001). Correlation coefficients were calculated using the 'raster' package in R v2.6 (R Core Team, 2017); relationships for the study area were negative and seasonally variable, but were especially strong during peak summer months (averaged over the study area; the highest $R = -0.8$ for August). We then used Jenks natural breaks algorithm to delineate four climatic water deficit bins (9.45–41.45 mm, 41.58–58.8 mm, 58.8–73.52 mm, 73.52–96.47 mm) and three elevation bands (1398–1717 m, 1717–1934 m, 1923–2244 m derived from 30 m digital elevation models), resulting in twelve unique ecoregions when combined. Snowdrifts were geographically delineated as a single ecoregion and superimposed on these twelve ecoregions (Fig. 1). Snowdrift locations were previously modeled using Isnobal (Winstral et al., 2013), a mass and energy balance distributed model that estimates precipitation redistribution and accumulation. Isnobal has been previously applied to the RCEW to simulate wind-affected snow accumulations, matching field observations with a high degree of accuracy ($R^2 = 0.66$ – 0.70 ; Winstral et al., 2013). Because field observations have shown that year-to-year changes in precipitation and temperature affect depth of snowdrifts more than extent (Cooley, 1988), we held the locations of the snowdrift ecoregion constant over time.

2.4. Succession simulation

The Biomass Succession extension (v3.2) was used to simulate cohort establishment, growth, and mortality (Scheller and Mladenoff, 2004). Biomass Succession tracks aboveground net primary productivity (ANPP; $\text{g C m}^{-2} \text{ year}^{-1}$), as well as aboveground biomass (g C m^{-2}). Updates to cohort mortality functions within Biomass Succession

were made to accommodate the unique clonal biology of quaking aspen (described below).

Within the Biomass Succession extension, maximum ANPP (maxANPP) and maximum biomass (maxB) are species-specific parameters. Maximum ANPP values represent the maximum possible above-ground productivity (in $\text{g biomass m}^{-2} \text{ year}^{-1}$) for a species within a given ecoregion and for a given year. For this study, maximum ANPP was simulated using the biogeochemical process model Biome-BGC (v. 4.2). Biome-BGC simulates ecosystem processes for a single plant functional type (PFT) through daily fluxes of carbon, nitrogen, water, and radiation. Maximum annual ANPP for three species, aspen, Douglas-fir, and western juniper was simulated for the 13 ecoregions described above. Within each ecoregion, Biome-BGC was run using daily inputs of precipitation (P , cm), maximum air temperature (T_{max} , $^{\circ}\text{C}$), minimum air temperature (T_{min}), average daytime air temperature (T_{daytime}), average daytime vapor pressure deficit (VPD, Pa), incoming solar radiation (S_{in} , W m^{-2}), and daylight period (s) (Appendix A). Final historical climate datasets for each ecoregion spanned 1979–2009.

The Biomass Succession extension uses growth and mortality rates to calculate net productivity by species. The growth curve parameter dictates how quickly a species reaches maximum ANPP relative to its longevity. Conversely, the mortality curve parameter dictates how quickly age-related mortality begins, relative to a species' longevity. Biomass ~ age curves for each of the modeled tree species were constructed from available FIA subplot data, using data on individual trees to construct an empirical growth relationship for the RCEW. Growth and mortality parameters within Biomass Succession were then calibrated in order to best match the biomass ~ age relationships of individual cohorts with the curves derived from FIA. In addition, maximum aboveground biomass was calibrated such that simulated aboveground biomass captured FIA sub-plot total aboveground biomass. These calibrations generated accurate cohort-level biomass and site-scale stocking levels.

Within Biomass Succession, probability of establishment (P_{est}) for each species, ecoregion, and year defines how likely a species is to successfully establish given climate and soils conditions. For this study, we developed climate niche models to define P_{est} for each species. Multivariate adaptive regression spline (MARS) models for each species were developed using known presence and absence locations across the region to define important climate variables for species occupancy (Appendix A). The final MARS models were then applied to contemporary and future GCM climate inputs (Flint et al., 2013) to project species occurrence probabilities for each 100 m^2 cell in the study area under different climate scenarios. Species occupancy values were then re-scaled in order to reduce known model artifacts and resulting inflated species establishment probabilities. These probability estimates for each species were then spatially-averaged for each of the 13 ecoregions. This approach has been used in previous LANDIS-II studies in the region, which successfully predicted species presence (Campbell and Shinneman, 2017; a full explanation of the methodology and model results are available in Appendix A).

Because we sought to test hypotheses about how future climate change will affect both recruitment/establishment and mortality of

aspen in water-limited systems subsidized by snowdrifts (Shepperd et al., 2006), we needed to capture climate-related mortality of both individual aspen cohorts and entire clones that span multiple cells. Therefore, we created a probability of mortality (P_{mort}), defined for each ecoregion, species, and time step to induce climate-related mortality events not previously implemented within Biomass Succession. We created a threshold based on Anderegg et al. (2015), who modeled a climatic water deficit threshold for aspen mortality linked to moisture deficit-related xylem cavitation. We used an annual cumulative threshold of 700 mm climatic water deficit that, if exceeded, induced a 30% probability of aboveground mortality within a particular site (Anderegg et al., 2015). If a site experienced climate-induced mortality, aspen biomass was reduced by 50% (Anderegg et al., 2015) to approximate aboveground stem (i.e., cohort) mortality. This approach assumed that aboveground aspen mortality does not necessarily lead to clone mortality, but if conditions that cause stem mortality persist, clone mortality will eventually occur. More specifically, if all neighboring (adjacent) aspen cohorts also died over a given period of simulated time, then the larger, multi-cell clone effectively died (e.g., the cohort became incapable of resprouting) until the area was re-colonized via spreading from neighboring cells (aspens were restricted to spreading from neighboring sites). Future P_{mort} values were calculated based on projections of climatic water deficit (both within and outside of snowbanks) produced by the Basin Characterization Model for our selected GCM projections (discussed below). Therefore, P_{mort} reflects both climate change and the influence of topography and elevation on climate-related mortality.

2.5. Wildfire simulation

Wildfire is an important ecological process that influences long-term trends in relative dominance of aspen and conifer species at both stand and landscape-scales (Shinneman et al., 2013). For our model, fire was included as a forcing mechanism for both cohort mortality and regeneration (through fire-induced resprouting). We used the Base Fire extension (v3.1) to simulate stochastic wildfire events based on ignition and fire spread probabilities. A single contemporary fire regime scenario was used in our simulations, in order to focus on direct effects of climate change on tree establishment and mortality. To parameterize the contemporary fire regime, we obtained fire data for a recent 23-year period (1992–2014) from the Fire Program Analysis fire-occurrence database (FPA FOD; Short, 2017 <https://www.fs.usda.gov/rds/archive/Product/RDS-2013-0009.4/>). However, characterizing fire regimes requires either a large enough area or a long enough time period (or both) to adequately capture the range of fire sizes and fire intervals. Thus, in addition to our study area, we also included fire history data for other locations in south-central Idaho with similar vegetation, topography, and climate. Contemporary fire regime parameters were calibrated (within a targeted percentage range) for the entire study area using several metrics: mean and standard deviation of fire size ($\pm 25\%$), average number of fires per year adjusted for area ($\pm 50\%$), and mean rotation interval ($\pm 25\%$). Fire size was further parameterized to fit a log-normal distribution, allowing the model to stochastically generate more small than large fires, commensurate with historical distributions.

2.6. Climate data

Climate data were coordinated across models and used as direct inputs for Biome-BGC and MARS, which subsequently generated inputs for LANDIS-II. Downscaled climate data were obtained from the Basin Characterization Model (BCM). BCM calculates water balance (including runoff, recharge, and evapotranspiration) by modeling the interaction between climate and empirically measured biophysical landscape features (Flint et al., 2013). Climate data available from the BCM includes maximum/minimum temperature, precipitation, climatic water deficit, and actual evapotranspiration (AET), and is produced

monthly at a 270 m \times 270 m resolution (Flint et al., 2011). For this study, the BCM was applied to the RCEW for both a reference historical period (1979–2009), and for a future period (2016–2099) under projected climate regimes simulated by three different global circulation models (GCMs) and two Representative Concentration Pathways (RCPs) per GCM, resulting in six total climate scenarios. The suite of three GCMs (GFDL ESM2m, ACCESS, CanESM2) was chosen to capture a range of anticipated climatological outcomes and because locally calibrated BCM projections have been produced using these GCMs and emission scenarios. The RCPs represent greenhouse gas concentration trajectories developed for the Intergovernmental Panel on Climate Change (IPCC), identified by changes in total radiative forcing in 2100 compared to preindustrial conditions. The most optimistic or ‘low’ emissions scenario used in our analyses is RCP4.5, while the most pessimistic or ‘high’ emissions scenario is RCP8.5, which effectively represents a future with continued high growth in emissions. Each of the six climate scenarios were individually and directly used to derive estimates of P_{est} for each species and P_{mort} for aspen (described above), which in turn were used as yearly inputs for LANDIS-II, thereby integrating the effects of interannual variability of climate into simulated growth and succession of forest species.

2.7. Analysis

We examined output from LANDIS-II using two key metrics that track species-level change over space and time in response to dynamic climate conditions: occupancy and persistence. Occupancy is defined here as the percentage of the landscape occupied by a particular species at a given point in time, and persistence is defined as the amount of time a given site is occupied by a particular species. Within LANDIS-II, occupancy and persistence are determined by several processes and species attributes for which parameters remain unchanged over time, including frequency of disturbance (fire), species maximum longevity, and species dispersal (Table 1). Occupancy and persistence are also strongly influenced by changing probabilities of species establishment and mortality over time and space, which ultimately determine regeneration success and are directly influenced by dynamic climate conditions represented in our model (via changes in P_{est} and P_{mort}). Thus, to more efficiently assess these key drivers of aspen occupancy and persistence, we defined and analyzed an integrated indicator of local decline, defined as the ratio $P_{\text{mort}}:P_{\text{est}}$. We also performed a post-hoc analysis of the relative importance of establishment and mortality (by averaging of the sequential sum-of-squares using the R package ‘relaimpo’; Grömping, 2006).

3. Results

The indicator of local decline for aspen increased over the 100-year simulation period, both generally across the study area landscape and specifically within the snowdrift ecoregion (Fig. 3). For both emissions scenarios, individual years of high local decline (> 0.5) are largely predicted to be absent within the first 35–40 years simulated, but are then predicted to occur frequently and with increasingly greater magnitude after mid-century for both the broader landscape-scale and within snow drifts. Local aspen decline is more pronounced (i.e., with higher peak values) under the high versus low emissions scenario for the snowdrift ecoregion, but not across the entire study area landscape (Fig. 3). Via a sequential sum of squares analysis, the probability of mortality was estimated to be more influential on aspen occupancy (contributing to $\sim 12\%$ of the variance in both scenarios) than probability of establishment.

Projected occupancy trends over time differed among tree species, emissions scenarios, and location (inside or outside snowdrifts) (Fig. 4). For the low emissions (RCP4.5) scenarios, average initial occupancy of quaking aspen increased by more than a third by mid-century, followed by a slight decline. Under the high emissions (RCP8.5) scenario aspen

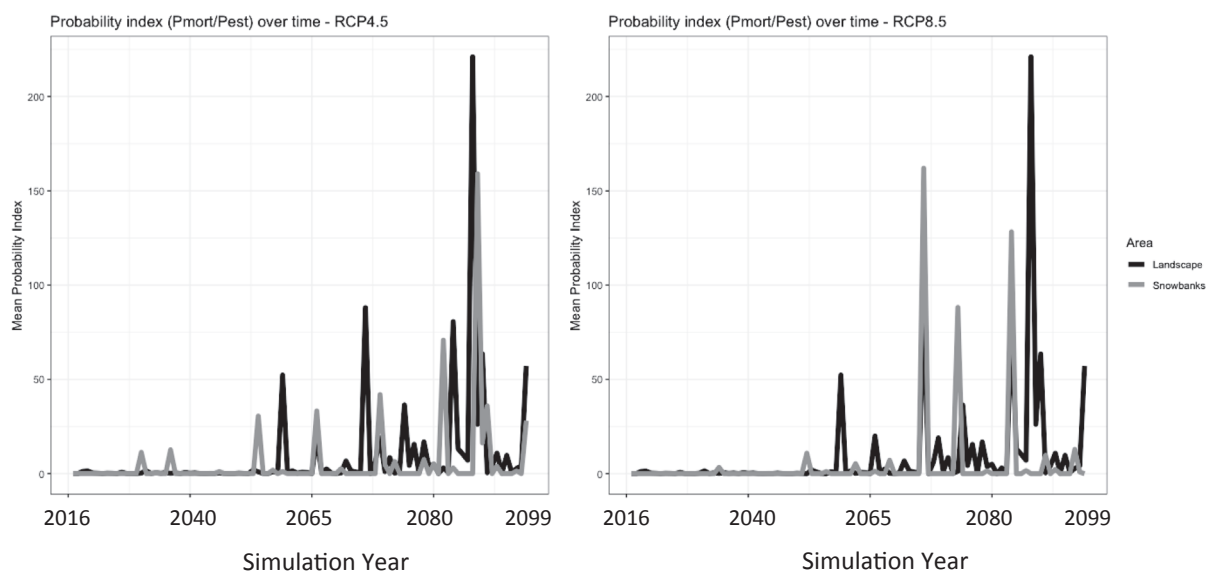


Fig. 3. Indicator of local aspen decline, defined as P_{mort}/P_{est} for each emissions scenarios (RCP4.5 and RCP8.5) at both the landscape-scale (black) and specifically for the snowpack ecoregion (gray).

peaked earlier, with less overall landscape cover, and then declined rapidly. Under the RCP4.5 emissions scenario, aspen occupancy until the end of the century was higher, although the variability around the mean was higher than the high emissions scenario climate characteristics (Fig. 4). Douglas-fir declined monotonically with a decline of nearly 60% by the end of the century. In general, both aspen and Douglas-fir saw the largest occupancy reductions at lower elevations, although Douglas-fir also declined noticeably in higher elevations of the

southeastern portions of the study area (results not shown). Western juniper occupied the smallest portion of the study area (< 0.5%) initially, but increased in occupancy during the entire RCP4.5 and RCP8.5 emissions scenarios, respectively. For all tree species, the general trends within and outside snowdrifts were similar although snowdrifts consistently had higher percent cover.

Aspen had a higher total area and higher percentage of sites with relatively brief persistence in the RCP 4.5 scenarios compared to the

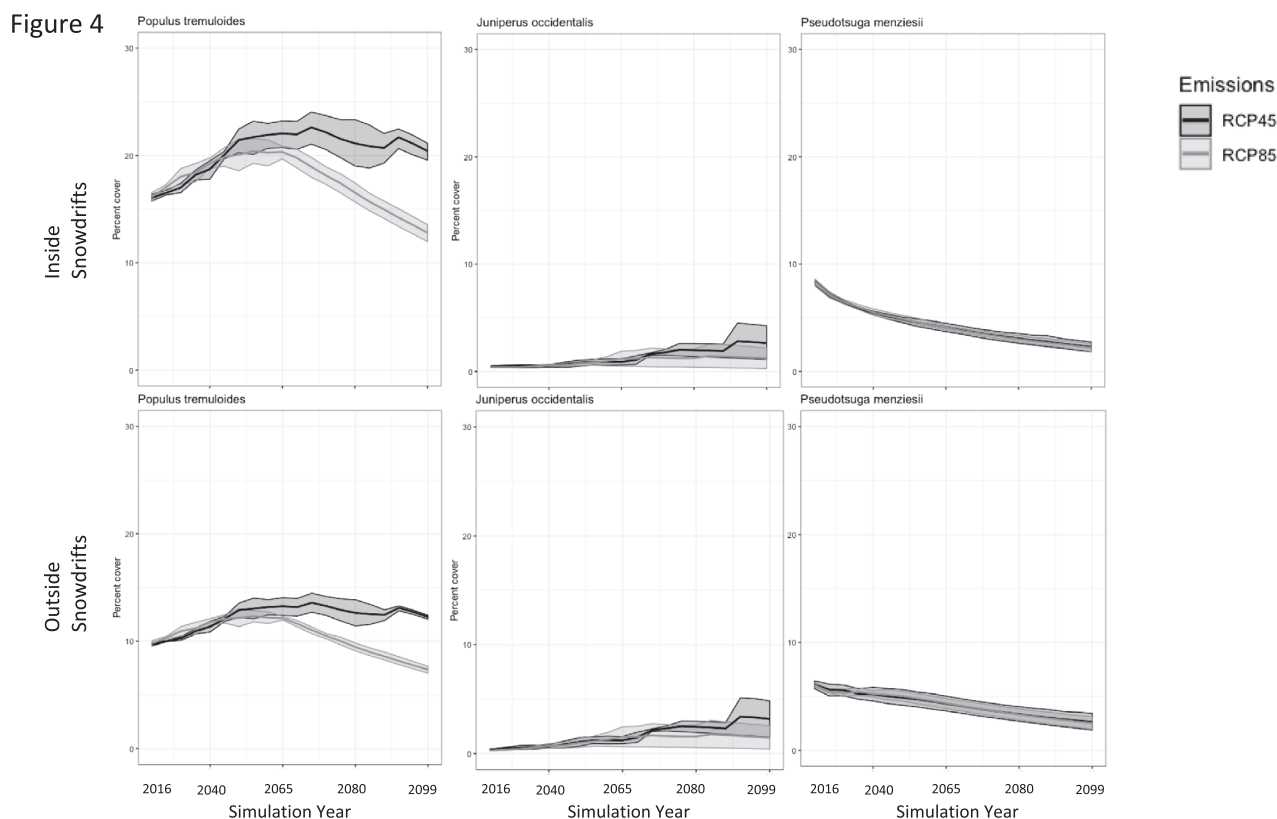


Fig. 4. Percent cover of each of the three modeled tree species. Mean across three GCMs of each emissions scenario, with ribbons representing minimum and maximum values at each time step.

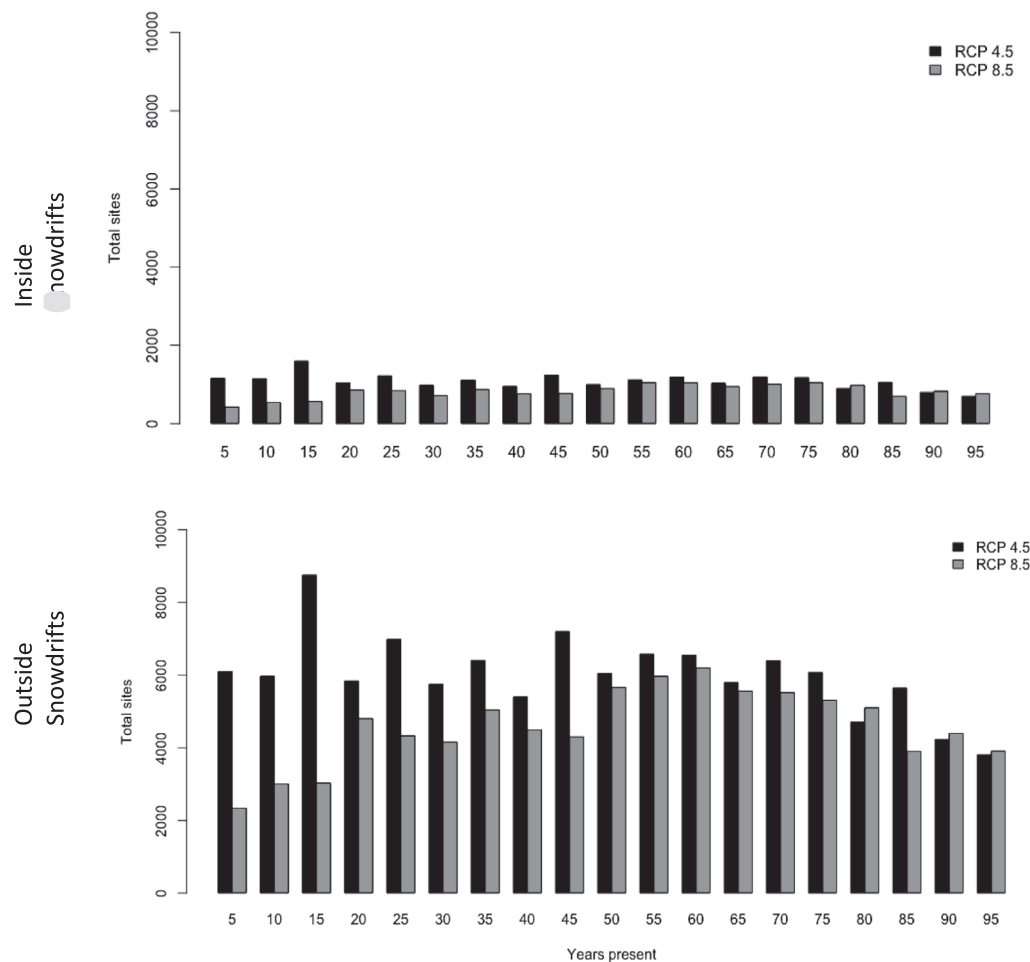


Fig. 5. Aspen persistence across the landscape as measured by length of presence on sites for both modeled climate emissions scenarios. Bars represent the amount of uninterrupted time aspen occupied a particular number of sites, averaged across all replicates.

RCP 8.5 scenarios (Fig. 5). Only when aspen persisted for 80 years or longer were there more sites in the high emissions compared to the low emissions scenario, and these absolute differences in area were minimal. These trends were similar for both inside and outside snowdrifts although percent cover was much higher inside snowbanks. Thus, our model generally predicted little differences between the two emissions scenarios in terms of the absolute area persistently occupied by aspen (i.e., sites that maintained aspen for > 50 years), but predicted more spatial-temporal fluctuation via short-duration sites for the low emissions scenario. This difference reflects the overall net loss of aspen in the high emissions scenario and the increase in aspen area over time in the low emissions scenario (Fig. 4), as the former would result in few if any sites gaining aspen after the first 50 years, while the latter reflects sites that gained aspen during the second half of the simulation time period and that would have < 50 modeled years remaining to “persist” before the end of the simulation, an artifact of model duration.

A sample of model output (one replicate of one RCP 8.5 GCM) is indicative of the spatial and temporal trends predicted for aspen under severe climate change (Fig. 6). At simulation year 2035, areas in and around snowdrifts had majority aspen coverage with both internal pockets of mortality (Fig. 6: white patches within the general area) and short-distance spread (indicated by aspen just outside the snowdrift, giving the drift zones a ‘fuzzy’ perimeter). By 2099, larger pockets of mortality are predicted to dominate within these aspen stands, which have also become older on average, with little or no regeneration contributing to either infilling mortality gaps or to expanding beyond the initial perimeter.

4. Discussion

Our results integrate various ecological processes, including competition, disturbance, mortality, and regeneration dynamics, and suggest that for the next 100 years aspen cover and persistence in RCEW area will vary over time and space, and among future climate scenarios. For both emissions scenarios, our models forecast an initial increase in aspen covered area over the first ~40–60 years, followed by sharp declines under higher emissions and a tapering decline under lower emissions (Fig. 4). These initial increases in aspen area might be explained in part by favorable growing conditions provided by milder and wetter winters (e.g., Brown et al., 2006) projected for the region initially, but later offset by steadily rising temperatures and increasing climatic water deficits (Marshall et al., 2019a). Despite its broad climatic tolerance, aspen is susceptible to drought stress; thus, reduced water availability during growing season, less snow pack, or earlier snowmelt could explain the mechanisms behind population declines and die-back events (e.g., Frey et al., 2004; Anderegg et al., 2013; Soderquist et al., 2018). However, our simulations suggest a less pessimistic estimate of future aspen distribution as compared to studies using species distribution modeling approaches alone. For instance, Rehfeldt et al. (2009) delineated aspen climate profiles using Random Forests classification trees and predicted a 6% to 41% loss in area for the aspen climate profile across the western U.S. by 2030, depending on GCM and emissions scenario, and as much as 94% loss by 2090. These contrasts likely stem in part from fundamentally different modeling approaches used. In this study, SDM-predicted occurrence probabilities

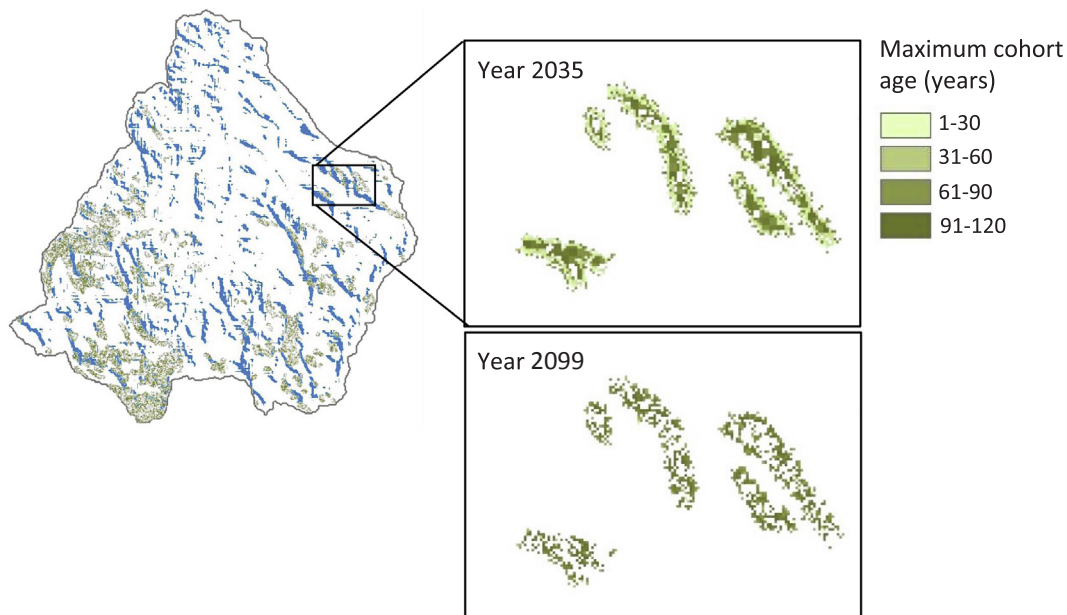


Fig. 6. Maximum age of aspen cohorts at simulation years 25 and 100 under the most extreme climate scenario (ACCESS RCP8.5); the larger map is year 25. Darker colors represent older cohorts. Areas in blue represent snowpack delineated ecoregions, where green shades represent age cohorts of quaking aspen.

were used to define future establishment probabilities for the LANDIS-II model (Appendix A), which in turn predicted aspen occurrence under simulated ecosystem dynamics. In contrast, SDMs typically delineate a threshold-derived climate profile that matches extant distributions, and then project the profile distribution under different climate scenarios. Other differences likely arise from the specific geographical areas analyzed and climate projections used.

Although our models suggest that aspen is more likely to persist under lower rather than higher anthropogenic greenhouse gas emissions, they also indicate the persistence of aspen under lower emissions may be more dynamic over time. There were much higher numbers of sites occupied for relatively short periods of time under RCP 4.5 emissions scenario compared to RCP 8.5 (< 45 years, Fig. 5). These short persistence times are a combination of two processes: (1) sites that are occupied and extirpated multiple times as establishment and mortality events alternate over time, and (2) sites that are occupied only once for a short period of time during a simulation. During the latter half of the century, increased probability of mortality relative to establishment was more substantial for the RCP 8.5 than the RCP 4.5 emissions scenario (Fig. 3). Thus, the frequency of both mortality and establishment events created a more dynamic aspen presence in the lower emissions scenario, while relatively few aspen sites reestablished after mortality events in the higher emissions scenario. This suggests the importance of mortality that drives localized extirpation and potentially facilitates recolonization (under favorable climates), similar to findings by Xu et al. (2012). Therefore although snowdrifts can create microrefugia (McLaughlin et al., 2017) and reduce extinction debt (Dullinger et al., 2012) under low emissions, they are highly spatially and temporally dynamic. Under high emissions, local extirpation occurs relatively quickly (Fig. 4) and there appears to be little ‘debt’.

Operating within these broad-scale dynamics for each emissions scenario, snowdrift-based microrefugia may help to maintain (i.e., in the RCP 4.5 scenarios) or at least slow the decline (in the RCP 8.5 scenarios) of aspen in the study area. Although the rate of mortality increased relative to establishment for both climate projections for snowdrift ecoregions, mortality increased less dramatically than for the landscape as a whole (Fig. 3). However, under the higher emission scenario, the loss of aspen combined with little to no regeneration over time (as indicated by model-year 100; Fig. 6) suggest such advantages

may not persist. Winter precipitation in the form of snowpack provides important soil moisture subsidies essential to aspen survival. Snowpack may also insulate root systems from exposure to freeze-thaw events (Frey et al., 2004) and inhibit winter ungulate browsing (Martin, 2007). Snowpack decline has been documented across much of the western United States over the past several decades (Mote et al., 2018) and the frequency of successive snow droughts is expected to continue into the 21st century (Klos et al., 2014; Marshall et al., 2019b). Concomitant with these changes is a shift from energy to water-limited conditions in the snowdrift ecoregions (e.g. Marshall et al., 2019). Our results suggest that, at least under more severe climates projected under high emissions scenarios, the loss of moisture provided by snow drifts in winter-dominated precipitation regimes could be detrimental to its persistence.

Other processes also influence aspen’s relative occupancy and persistence over time under climate change. In particular, conifer competition can negatively influence aspen regeneration through altered light, temperature, and soil conditions (Calder et al., 2011; St. Clair et al., 2013). Our simulations projected an increase in juniper cover, largely limited to lower elevations with little aspen cover, and a steady decline in Douglas-fir cover. Both conifer species have been shown to be competitive with aspen in the region; however, relatively slower rates of succession to conifer-dominated stands occur in wet microsites characteristic of our study area compared to drier sites (Strand et al., 2009). Douglas fir is a more direct competitor with aspen, given its broadly overlapping niche, but because of its decline, we conclude that competition with aspen also declined. Douglas fir is considered at the edge of its climatic range in our study area and growth declines are expected under future climates in areas where summer water deficits mediate productivity (Chen et al., 2010; Restaino et al., 2016). Thus, increasing growing season temperatures and altered precipitation under projected climate change will likely be unfavorable for continued Douglas-fir persistence at relatively low elevations in the northern and central Rocky Mountains (Rehfeldt et al., 2014). Other LANDIS-II simulations have shown that conifer species, including Douglas-fir, may not keep pace with mortality caused by wildfire under climate change, even if favorable climate persists at higher elevations, due to seed-dispersal limitations (Campbell and Shinneman, 2017). Similar to Yang et al. (2015), our results suggest that aspen may benefit, as fire and changing climate may reduce conifer competition at higher elevations.

4.1. Model limitations

Although we took steps to minimize data and model scale-discrepancies, the simulated dynamics were derived from data sources with different spatial scales. For example, the climate data, originally obtained at 800 m resolution to develop establishment probabilities, was projected to 270 m resolution under future climates, and modeled in LANDIS-II on a 10 m grid (and then averaged across ecoregions). Thus, although fine scale processes (e.g., seed dispersal) were occurring in our simulations, variability in P_{est} and P_{mort} was not represented at the 10 m resolution. Also, snowdrifts were simplified in our simulations; they were only modeled as a single, spatially-static ecoregion (with changing climate) over time, and represented simple redistribution of water to and from neighboring cells based on historical consistency in storm patterns and drift formation. Finally, we also chose not to simulate the fire regime as a function of climate change, as changes to the fire regime in this particular small watershed were not the main focus. However, increases in fire frequency or severity would increase mortality of conifers and could potentially increase establishment of aspen under favorable climates (e.g., Yang et al., 2015).

Although we were able to represent multiple sources of uncertainty, including seed dispersal and climatic uncertainty (exemplified by the broad range of percent cover forecast for juniper under three GCMs, Fig. 4), we were not able to represent all potential sources of uncertainty. We did not capture the potential uncertainty generated by non-drought mortality (insects, grazers) or a more active fire regime due to climate change. There is also likely additional uncertainty not captured by the limited selection of RCP and GCMs forecast. Ultimately, uncertainty informs the appropriate scale of forecasting: finer-scale modeling could add precision, although the accuracy would still be limited by larger sources of uncertainty including the response of localized soil water availability and landscape interactions among species and disturbance.

4.2. Conclusions and management implications

The long-term viability of regional restoration projects in the western U.S. may be increasingly in doubt as climate change unpredictably alters ecosystems and their disturbance regimes (e.g., Harris et al., 2006). Indeed, our results suggest that climate change effects on aspen occurrence and persistence will vary spatially and temporally in our study area, and the utilization of restoration efforts may need to vary accordingly. Thus, monitoring both managed and unmanaged aspen stands may help to develop adaptive management approaches, by learning from ongoing restoration efforts and adjusting to accommodate newly available information on climate-induced ecological change (Millar et al., 2007). Our simulations also suggest that environmental stress caused by climate change, rather than competitive stress from conifers, is likely to be a dominant threat to aspen persistence. Given that climate change cannot be locally mitigated, management techniques that actively promote aspen regeneration are the logical focus for management, including reducing the effects of ungulate browsing on young aspen, or utilizing fire to promote environments conducive to aspen colonization at higher elevations. However, given the limited elevation range in the RCEW (maximum elevation of ~ 2,561 m), as well as the potential for declining snowpack in the future, even these strategies may provide only temporary refugia.

CRedit authorship contribution statement

Alec M. Kretchun: Conceptualization, Data curation, Formal analysis, Methodology, Writing - original draft, Writing - review & editing. **Robert M. Scheller:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing - original draft, Writing - review & editing. **Douglas J. Shinneman:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing - original draft,

Writing - review & editing. **Benjamin Soderquist:** Data curation, Formal analysis, Methodology. **Kaitlin Maguire:** Data curation, Formal analysis, Methodology. **Timothy E. Link:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing - original draft, Writing - review & editing. **Eva K. Strand:** Data curation, Formal analysis, Methodology.

Acknowledgments

Funding was provided by the U.S. Geological Survey, Northwest Climate Adaptation Science Center. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118005>.

References

- Anderegg, W.R.L., Plavcova, L., Anderreg, L.D., Hacke, U.G., Berry, J.A., Field, C.B., 2013. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. *Global Change Biol.* 19 (4), 1188–1196.
- Anderegg, W.R., Flint, A., Huang, C.Y., Flint, L., Berry, J.A., Davis, F.W., Sperry, J.S., Field, C.B., 2015. Tree mortality predicted from drought-induced vascular damage. *Nat. Geosci.* 8, 367–371.
- Bell, D.M., Bradford, J., Lauenroth, W.K., 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Glob. Ecol. Biogeogr.* 23 (2), 168–180.
- Brown, K., Hansen, A.J., Keane, R.E., Graumlich, L.J., 2006. Complex interactions shaping aspen dynamics in the Greater Yellowstone Ecosystem. *Landscape Ecol.* 21, 933–951.
- Burke, A.R., Kasahara, T., 2011. Subsurface lateral flow generation in aspen and conifer-dominated hillslopes of a first order catchment in northern Utah. *Hydrol. Process.* 25, 1407–1417.
- Burkhardt, J.W., Tisdale, E.W., 1969. Nature and successional status of Western Juniper vegetation in Idaho. *J. Range Manag.* 22 (4), 264–270.
- Calder, W.J., Horn, K.J., St. Clair, S.B., 2011. Conifer expansion reduces the competitive ability and herbivore defense of aspen by modifying light and soil chemistry. *Tree Physiol.* 31, 582–591.
- Campbell, J.L., Shinneman, D.J., 2017. Potential influence of wildfire in modulating climate-induced forest redistribution in a central Rocky Mountain landscape. *Ecol. Process.* 6, 7. <https://doi.org/10.1186/s13717-017-0073-9>.
- Chen, P.Y., Welsh, C., Hamann, A., 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change. *Global Change Biology* 16 (12), 3374–3385.
- Cooley, K.R., 1988. Snowpack variability on western rangeland. In: Kalispell, M.T. (Ed.), *Proceeding of the Western Snow Conference, 56th Annual Meeting, April 19–21*. Colorado State University, Fort Collins, CO, pp. 1–12.
- Coppenhaver-Parry, P.E., Cannon, E., 2016. The relative influences of climate and competition on tree growth along montane ecotones in the Rocky Mountains. *Oecologia* 182, 13.
- Creutzburg, M.K., Scheller, R.M., Lucash, M.S., LeDuc, S.D., Johnson, M.G., 2017. Forest management scenarios in a changing climate: trade-offs between carbon, timber, and old forest. *Ecol. Appl.* 27 (2), 503–518.
- Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T., Mynsberge, A.R., 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* 331, 324–327.
- Dobrowski, S.Z., Abatzoglou, J.A., Swanson, A.K., Greenberg, J.A., Mynsberge, A.R., Holden, Z.A., Schwartz, M.K., 2013. The climate velocity of the contiguous United States during the 20th century. *Glob. Change Biol.* 19, 241–251.
- Dullinger, Stefan, Gattringer, Andreas, Thuiller, Wilfried, Moser, Dietmar, Zimmermann, Niklaus E., Guisan, Antoine, Willner, Wolfgang, Plutzar, Christoph, Leitner, Michael, Mang, Thomas, Caccianiga, Marco, Dirnböck, Thomas, Ertl, Siegrun, Fischer, Anton, Lenoir, Jonathan, Svenning, Jens-Christian, Psomas, Achilleas, Schmatz, Dirk R., Silc, Urban, Vittoz, Pascal, Hülber, Karl, 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. *Nat. Clim. Change* 2 (8), 619–622. <https://doi.org/10.1038/nclimate1514>.
- Duveneck, M.J., Scheller, R.M., 2016. Measuring and managing resistance and resilience under climate change in northern Great Lake forests (USA). *Landscape Ecol.* 31, 1933–1947.
- Flint, A.L., Flint, L.E., Masbruch, M.D., 2011. Input, calibration, uncertainty, and limitations of the basin characterization model: appendix three. In: Heilweil, Victor M., Brooks, L.E. (Eds.), *Conceptual model of the Great Basic Carbonate and Alluvial Aquifer System*. USGS.
- Flint, L., Flint, A.L., Thorne, J.H., Boynton, R., 2013. Fine-scale hydrologic modeling for regional landscape applications: the California Basin Characterization Model

- development and performance. *Ecol. Process.* 2, 25.
- Frey, B.R., Lieffers, V.J., (Ted) Hogg, E.H., Landhäusser, S.M., 2004. Predicting landscapes patterns of aspen dieback: mechanisms and knowledge gaps. *Can. J. For. Res.* 34.
- Grömping, U., 2006. Relative importance for linear regression in R: the package relaimpo. *J. Stat. Softw.* 17 (1).
- Hannah, L., Flint, L., Syphard, A.D., Moritz, M.A., Buckley, L.B., McCullough, I.M., 2014. Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. *TREE* 29, 390–397.
- Hansen, A.J., Phillips, L.B., 2015. Which tree species and biome types are most vulnerable to climate change in the US Northern Rocky Mountains? *For. Ecol. Manage.* 338, 68–83.
- Harvey, B.J., Donato, D.C., Turner, M.G., 2016. High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. *Global Ecol. Biogeogr.* 25 (6), 655–669.
- Huang, C.Y., Anderegg, W.R.L., 2012. Large drought-induced aboveground live biomass losses in southern Rocky Mountain aspen forests. *Glob. Change Biol.* 18 (3), 1016–1027.
- Harris, J.A., Hobbs, R.J., Higgs, E., Aronson, J., 2006. Ecological restoration and global climate change. *Restor. Ecol.* 14 (2), 170–176.
- Klos, P.Z., Link, T.E., Abatzoglou, J.T., 2014. Extent of the rain-snow transition zone in the western US under historic and projected climate. *Geophys. Res. Lett.* 41, 4560–4568.
- LaMalfa, E.M., Ryle, R., 2008. Differential snowpack accumulation and water dynamics in aspen and conifer communities: Implications for water yield and ecosystem function. *Ecosystems* 11 (4), 569–581.
- Lo, Y.H., Blanco, J.A., Kimmins, J.P., 2010. A word of caution when planning forest management using projections of tree species range shifts. *Forest. Chronicle* 86 (3), 312–316.
- Loudermilk, E.L., Scheller, R.M., Weisberg, P.J., Yang, J., Dilts, T.E., Karam, S.L., Skinner, C., 2013. Carbon dynamics in the future forest: the importance of long-term successional legacy and climate–fire interactions. *Global Change Biol.* 19 (11), 3502–3515.
- Lutz, J.A., van Wagtenonk, J.W., Franklin, J.F., 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. *J. Biogeogr.* 37, 936–950.
- Marshall, A.M., Abatzoglou, J.T., Link, T.E., Tennant, C.J., 2019b. Projected changes in interannual variability of peak snowpack amount and timing in the western United States. *Geophys. Res. Lett.* 46 (15), 8882–8892.
- Marshall, A.M., Link, T.E., Abatzoglou, J.T., Flerchinger, G.N., Marks, D.G., Tedrow, L., 2019a. Warming alters hydrologic heterogeneity: simulated climate sensitivity of hydrology-based microrefugia in the snow-to-rain transition zone. *Water Resour. Res.* 55. <https://doi.org/10.1029/2018WR023063>.
- Martin, T.E., 2007. Climate correlates of 20 years of trophic changes in a high-elevation riparian system. *Ecology* 88 (2), 367–380.
- McIntyre, P.J., Thorne, J.H., Dolanc, C.R., Flint, A.L., Flint, L.E., Kelly, M., Ackerly, D.D., 2015. Twentieth-century shifts in forest structure in California: denser forests, smaller trees, and increased dominance of oaks. *Proc. Natl. Acad. Sci.* 112 (5), 1458–1463.
- McLaughlin, B.C., Ackerly, D.D., Klos, P.Z., Natali, J., Dawson, T.E., Thompson, S.E., 2017. Hydrologic refugia, plants, and climate change. *Glob. Change Biol.* 23, 2941–2961.
- McNamara, J.P., Chandler, D., Seyfried, M., Achet, S., 2005. Soil moisture states, lateral flow, and streamflow generation in a semi-arid, snowmelt-driven catchment. *Hydrol. Process.* 19 (20), 4023–4038.
- Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. *Ecol. Appl.* 17, 2145–2151.
- Mote, P.W., Li, S., Lettenmaier, D.P., Xiao, M., Engel, R., 2018. Dramatic declines in snowpack in the western US. *Npj Climate and Atmospheric Science* 1 (1), 1–6.
- Nayak, A., Marks, D., Chandler, D.G., Seyfried, M., 2010. Long-term snow, climate, and streamflow trends at the Reynolds Creek experimental watershed, Owyhee Mountains, Idaho, United States. *Water Resour. Res.* 46 (6).
- Restaino, C.M., Peterson, D.L., Littell, J., 2016. Increased water deficit decreases Douglas fir growth throughout western US forests. *Proc. Natl. Acad. Sci.* 113, 9557–9562.
- Rehfeldt, G.E., 2006. A spline model of climate for the Western United States. Rocky Mountain Research Station. General Technical Report RMRS-GTR-165. January 2006.
- Rehfeldt, G.E., Ferguson, D.E., Crookston, N.L., 2009. Aspen, climate, and sudden decline in western USA. *For. Ecol. Manage.* 258, 2353–2364.
- Rehfeldt, G.E., Jaquish, B.C., Lopez-Upton, J., Saenz-Romero, C., St Clair, J.B., Leites, L.P., Joyce, D.G., 2014. Comparative genetic responses to climate for the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: Realized climate niches. *For. Ecol. Manage.* 324, 126–137.
- Seyfried, M., Harris, R., Marks, D., Jacob, B., 2001. Geographic database, Reynolds Creek Experimental Watershed, Idaho, United States. *Water Resour. Res.* 37 (11), 2825–2829.
- Serra-Diaz, J.M., Franklin, J., Dillon, W.W., Syphard, A.D., Davis, F.W., Meentemeyer, R.K., 2016. California forests show early indications of both range shifts and local persistence under climate change. *Glob. Ecol. Biogeogr.* 25, 164–175.
- Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Mladenoff, D.J., Gustafson, E.J., 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial scales. *Ecol. Model.* 201, 409–419.
- Scheller, R.M., Kretchun, A.M., Loudermilk, E.L., Hurteau, M.D., Weisberg, P.J., Skinner, C., 2018. Interactions among fuel management, species composition, bark beetles, and climate change and the potential effects on forests of the Lake Tahoe Basin. *Ecosystems* 21 (4), 643–656.
- Shepperd, W.D., Rogers, P.C., Burton, D., Bartos, D.L., 2006. Ecology, biodiversity, management, and restoration of aspen in the Sierra Nevada. Gen. Tech. Rep. RMRS-GTR-178. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station 122 p., 178.
- Shinneman, D.J., Baker, W.L., Rogers, P.C., Kulakowski, D., 2013. Fire regimes of quaking aspen in the Mountain West. *For. Ecol. Manage.* 299, 22–34.
- Shinneman, D.J., McIlroy, S.K., 2019. Climate and disturbance influence self-sustaining stand dynamics of aspen (*Populus tremuloides*) near its range margin. *Ecol. Appl.* 29, 1187–1201.
- Short, K.C., 2017. Spatial wildfire occurrence data for the United States, 1992–2015. 4th Edition. Fort Collins, CO: Forest Service Research Data Archive. <https://doi.org/10.2737/RDS-2013-0009.4>.
- Soderquist, B.S., Kavanagh, K.L., Link, T.E., Seyfried, M.S., Winstral, A.H., 2018. Simulating the dependence of aspen (*Populus tremuloides*) on redistributed snow in a semi-arid watershed. *Ecosphere* 9 (1).
- St. Clair, S.B., Cavard, X., Bergeron, Y., 2013. The role of facilitation and competition in the development and resilience of aspen forests. *For. Ecol. Manage.* 299, 91–99.
- Strand, E.K., Vierling, L.E., Bunting, S.C., Gessler, P.E., 2009. Quantifying successional rates in western aspen woodlands: Current conditions, future predictions. *For. Ecol. Manage.* 257 (8), 1705–1715.
- Thornton, P.E., Law, B.E., Gholz, H.L., Clark, K.L., Falge, E., Ellsworth, D.S., Goldstein, A.H., Monson, R.K., Hollinger, D., Falk, M., Chen, J., 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agric. For. Meteorol.* 113, 185–222.
- U.S. Forest Service, 2018. Forest Inventory and Analysis National Program. <https://www.fia.fs.fed.us/>.
- Winstral, A., Marks, D., 2002. Simulating wind fields and snow redistribution using terrain-based parameters to model snow accumulation and melt over a semi-arid mountain catchment. *Hydrol. Process.* 16 (18), 3585–3603.
- Winstral, A., Marks, D., Gurney, R., 2013. Simulating wind-affected snow accumulations at catchment to basin scales. *Adv. Water Resour.* 55, 64–79.
- Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. *For. Ecol. Manage.* 255, 686–696.
- Xu, C., Gertner, G.Z., Scheller, R.M., 2012. Importance of colonization and competition in forest landscape response to global climatic change. *Climatic Change* 110 (1&2), 53–83.
- Yang, J., Weisberg, P.W., Shinneman, D.J., Dilts, T.E., Earnst, S.L., Scheller, R.M., 2015. Fire modulates climate change response of simulated aspen across topographic gradients in a semi-arid landscape. *Landscape Ecol.* 30 (6), 1055–1073.