Long term persistence of aspen in snowpack-dependent ecosystems.

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**Abstract**

**Introduction**

*Vegetation distribution patterns in sagebrush landscapes at different scales/climate change vegetation shifts. Local vs global*

When viewed across the entirety of the Western United States, vegetation patterns can largely be explained by the periodicity of precipitation and the interaction between temperature and precipitation (Rehfeldt et al 2006). However, at finer spatial scales topography and forest community dynamics become increasingly important determinants of how vegetation is distributed across the landscape (Coppenhaver-Parry and Cannon 2016).

Wide spread shifts in species assemblages and distribution across the western US 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 2014). 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 Phillips (2015) project similar patterns for the Northern Rockies: reduced conifer cover, increased climate suitability for montane tree species, and increased vulnerability of already sensitive species such as whitebark pine. However, regenerative success does not always follow spatial patterns consistent with expected climate change effects on tree species distributions (i.e. poleward migration); Serra-Diaz et al (2016) showed that tree species regeneration in California is influenced greatly by topographic mediators, and that past disturbances are linked to regeneration hotspots.

*Competition/Regeneration/Microrefugia*

Though they are useful from a generalized perspective, statistical models of climate suitability do not reflect the climate that an individual tree experiences. This ‘lived climate’ is a combination of temperature, precipitation, topography, daily wind patterns, etc.; it determines a tree species’ ability to regenerate on a site. The complex terrain of many western landscapes creates endless site-specific growing conditions and opportunities for species to persist on sites that have moved out of their climatically suitable niche. Such microrefugia (Hannah et al. 2014) can cause lags in the relationship between where a species is and where it ‘ought’ to occur, climatically speaking – what Dullinger et al (2012) refers to as ‘extinction debt’. Many trees in the west are very long-lived, which can extend such lags for decades (Bell et al 2014). This ‘lived climate’ is further complicated by the fact that within a single species, climatic tolerance and competitive ability differs greatly depending on age (Dobrowski et al 2015, REF). For instance, Dobrowski et al (2015), showed that climatic niches for a given species were different across demographic groups, and that those differences were most significant at a species’ range margin and in species with high drought and shade tolerance. Forest canopies mitigate this effect somewhat, supporting other work which has shown microclimate moderation and stability as a function of canopy cover (REF).

*Aspen/snowbank connection/climate change*

Quaking aspen (*Populus tremuloides*) is the most widespread tree species in North America. Contrary to many coniferous species in the interior West, aspen is a clonal species, and establishes quickly in recently disturbed areas (Shinneman et al 2013). In many areas, aspen are locally dependent on seasonal snowdrifts that accumulate due to topography and wind patterns (REF). As temperatures rise in the spring and summer, these snow drifts melt and provide a soil moisture subsidy during the growing season of the adjacent aspen stands (REFS). Though the response can be lagged, a year or two of extremely low snow accumulation and high temperatures can cause high levels of mortality and make affected stands more susceptible to future drought (Huang and Anderegg 2011, Anderegg et al 2013). Such drought-induced mortality tends to affect high-density stands more often, with larger older trees showing the highest levels of dieback (Bell et al 2014, Worrall et al 2007). Coupled field and remote sensing studies have identified a nonlinear positive relationship between cumulative climatic water deficit (CWD) and widespread aspen mortality, which is linked to moisture deficit-related xylem cavitation (Anderegg et al 2015). Though derived from field measurements and partially based on previous physiologically-based studies of aspen mortality, 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 on western landscapes as temperatures rise and precipitation patterns change. Previous modeling studies have shown temperature increases of 2-5oC could cause a substantial reduction in aspen coverage, particularly as lower elevations (Yang et al 2015, Rehfeldt et al 2009, Worral et al 2008). Additionally, many of these studies also show that areas currently experiencing high levels of aspen mortality are those where the climatic niche of aspen has completely disappeared by the year 2060, which suggests that range shifts in response to climate change may already be occurring (Rehfeldt et al 2009, Worral et al 2008).

**Objective**

In this study we evaluated the long-term future consequences of changing climate and conifer competition on quaking aspen (*Populus tremuloides*) in a small well-instrumented watershed in southwest Idaho, focusing specifically on aspen’s regenerative success over time. To address the influence of site-level climate, succession, and competition, we are employing a well-vetted spatially-explicit process-based forest succession model (LANDIS-II).

**Methods**

**Study Extent**

We evaluated aspen persistence in the Tollgate and Dobson Creek subwatersheds of Reynolds Creek Experimental Watershed (hereon, ‘RCEW’), in southwestern Idaho. These are the two most southerly sub-watersheds of the RCEW, and sit at the highest elevation within the RCEW (1298m - 2244m). They are also the only two subwatersheds with any significant tree cover. The RCEW study extent is approximately 5500ha.

Over the last century, climate velocity around the RCEW has shown moderate to high increases in minimum temperature, evapotranspiration, and climatic water deficit (Dobrowski et al 2012).

**Simulation Approach**

We projected future aspen persistence in the RCEW 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). LANDIS-II has been extensively used to estimate climate change effects in the western US (Loudermilk, Creutzberg, Kretchun), including Idaho (Yang). Model inputs are detailed below.

**Climate data**

Downscaled climate data was 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 (CWD), snowpack, and actual evapotranspiration (AET), and is produced monthly at a 270mx270m resolution.

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 three different climate projections (GFDL ESM2m, ACCESS, CanESM2). A low (RCP4.5) and high (RCP8.5) emissions scenario were modeled for each chosen GCM to examine the effects of climate change. Each climate scenario is run individually within LANDIS-II rather than averaged a priori, in order to preserve individual years of extreme weather present in each GCM. The suite of GCM climate projections was chosen to capture a range of anticipated climatological outcomes and for their generally high hind-casted performance in the West, and because locally calibrated BCM projections have been produced using these GCMs and emission scenarios.

**Initial Communities**

*FIA*

An initial community must be created that defines that spatial distribution and ages of each tree or shrub species present on the landscape. Initial communities were created by sampling US Forest Service FIA subplots from a radius of 50km around RCEW, and randomly assigning those plots to a digitized map of forest types within the RCEW. Because of our small cell size, we will be using the FIA subplots (14.6m diameter) as our pool of potential initial communities. FIA sampling from around the RCEW resulted in 1894 unique FIA plots, which each contained 4 subplots – a total of 7576 unique subplots. From these subplots, tree species, DBH, age, and biomass were extracted. 3 tree species were modeled in this study: Douglas fir (*Pseudotsuga menziesi*), Quaking aspen (*Populus tremuloides*), and Western juniper (*Juniperus occidentalis*). Shrubs were grouped into a generic shrub type. Where ages were absent from the FIA data, infilling was performed based on species-specific age ~ DBH relationships.

*Forest type assignment*

FIA sites were randomly assigned to matching forest type cells based on ranked species biomass dominance. FIA/forest type matching was based on a map of specific vegetation types and percent cover for Reynolds Creek Experimental Watershed (RCEW), administered by the USDA-Agricultural Research Service Northwest Watershed Research Center (ARS NWRC). Field mapping for this map was done on color aerial photographs at 1:12,000 and transferred to 1:24000 base maps. These were then hand digitized by the NWRC. The NWRC maps created ninety unique forest types, each a combination of present tree species and relative dominance. Initial communities for the LANDIS-II simulations were created by randomly assigning FIA plots to matching forest types within the ARS-NWRC maps, based on tree species and dominance.

**Ecoregions**

The RCEW landscape was divided in ecoregions which describe areas with similar soils, climate, and snowbank accumulation. Ecoregions are assigned establishment and mortality rates that vary through time. Ecoregion delineation was based on the approach used by Yang et al (2015) which created ecoregions based on elevation bands and climatic water deficit (CWD) bins. For ecoregion creation, historical CWD (1979-1999) was obtained from BCM model outputs. This approach was justified in part by running spatial correlations between remotely sensed productivity maps (soil adjusted vegetation index) of the RCEW with average monthly CWD estimates. The relationship was inverse, with reasonably supportive correlation coefficients (seasonally variable, around -0.7 at lowest). We chose a 10mx10m cell resolution with an annual time step in order to analyze competition and regeneration at a relatively fine-scale and to incorporate fine-scale snow pack dynamics, which fundamentally influence those processes.

Within the RCEW, elevation ranged from 1298m-2244m, while average monthly CWD ranged from 0.9mm-.94mm. Four CWD bins were created using a Jenks natural breaks algorithm, three equivalent elevation bands were created, which were combined to create twelve unique ecoregions.

A thirteenth ecoregion was created to represent snowbank accumulation, an ecologically meaningful feature of the RCEW. Snowbanks were geographically delineated using Isnobal (Winstral et al 2013), a mass and energy balance distributed model which can estimate precipitation redistribution and accumulation. This model has been previously applied to the RCEW to simulate wind-affected snow accumulations, matching field observations with a high degree of accuracy (R2 = 0.66-0.7). Because ecoregions within LANDIS-II are static through time, snowbank ecoregions will not be spatially dynamic. This assumption is supported by field observations which show that depth, rather than extent, of snowbanks are affected most by year-to-year changes in precipitation and temperature. Below are the ecoregions constructed for the RCEW. Values represent ecoregion codes within LANDIS-II.

**Biomass Succession extension**

The Biomass Succession extension (modified v3.2) was used to model cohort growth and mortality (Scheller and Mladenoff 2004). Biomass Succession tracks aboveground net primary productivity (ANPP; g C/m2/year) as well as aboveground biomass (g C/m2). Updates to cohort mortality functions within Biomass Succession were made to accommodate the unique clonal biology of quaking aspen (described below). All Biomass Succession input files, including species life history parameters, are available via GitHub.

*Maximum ANPP and biomass*

Within Biomass Succession, maximum ANPP (maxANPP) and maximum Biomass (maxB) are species-specific parameters. Maximum ANPP values represent the maximum possible above ground productivity (in g biomass/m2/year) for a species within a given ecoregion and timestep. For this study, maximum annual aboveground net primary productivity (ANPP, g C m-2 yr-1) was simulated using the biogeochemical process model Biome-BGC (v. 4.2, Thornton et al., 2002). Biome-BGC simulates ecosystem processes for a single plant functional type (PFT) through daily fluxes of carbon, nitrogen, water, and radiation. Maximum ANPP for three species, aspen (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii*), and western juniper (*Juniperus occidentalis*) was simulated for 13 ecoregions located in southern region of the Reynolds Creek Critical Zone Observatory and Experimental Watershed (RCEW). Within each ecoregion, Biome-BGC was run using daily inputs of precipitation (cm), maximum air temperature (*Tmax*), minimum air temperature (*Tmin*), average daytime air temperature (*Tdaytime*), average daytime vapor pressure deficit (VPD), incoming solar radiation (W m-2), and daylight period (s). Daily values of precipitation, *Tmax*, and *Tmin* were downscaled from the Basin Climate Model (BCM). The remaining inputs of *Tdaytime*, VPD, incoming solar radiation, and daylight period were simulated using the microclimate simulation model MTCLIM (v. 4.3, Thornton et al., 2000). Final historical climate datasets for each ecoregion spanned 1979-2009.

Biome-BGC is further parameterized by site conditions and species specific ecophysiological data. Site conditions for each ecoregion, including soil depth and texture parameters were obtained from the Soil Survey Geographic Database (SSURGO, http://soildatamart.nrcs.usda.gov). For each species, key ecophysiological parameters including carbon to nitrogen ratios (C:Nleaf, C:Nroot), and specific leaf area (SLA) were measured in the field. Values of C:Nleaf, C:Nroot, and SLA for co-occurring aspen and juniper were measured at three sites at mid and high elevations in the RCEW during the summers of 2012-2014. Values of C:Nleaf, C:Nroot, and SLA for Douglas fir were previously measured in the Boise National Forest in 2009 (A. Noble-Stuen, unpublished data). Average measured values of C:Nleaf, C:Nroot, and SLA for each species were used to parameterize Biome-BGC. The remaining species or PFT specific ecophysiological parameters were obtained from previously published values (e.g. White et al., 2000). Following Biome-BGC simulations, annual ANPP for each species was calculated from daily sums of carbon accumulated and stored in vegetation foliage and stem pools. Average ANPP values simulated from 1979-2009 were used to parameterize values of maximum ANPP for LANDIS II.

*Growth and Mortality curves*

Biomass Succession extension for LANDIS-II uses two slope parameters (growth and mortality) to define productivity patterns by species. The growth curve parameter dictates how quickly a species reaches maxANPP, 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 LANDIS-II cohorts at year zero of the model simulations with the curves derived from FIA.

In addition to the biomass ~ age calibrations, total biomass calibrations were done at the site level. This was done to ensure a realistic representation of cohort-level biomass, but also site-scale stocking levels. The below figure shows comparisons between FIA species biomass, and LANDIS-II at year zero of our simulations, used to calibrate species and site level biomass.

**Probabilities of establishment and mortality**

*Probability of establishment*

Within Biomass Succession, probability of establishment (Pest) is a species specific parameter, defined by ecoregion and time step which defines how likely a species is to successfully establish given climate and soils conditions. For this study, HyperNiche (REF) was implemented to define Pest for each species. HyperNiche uses non-parametric regressions to create ecologically reasonable habitat models. Monthly climate data for RCEW was used to estimate species presence/absence, which is then used as Pest values within LANDIS-II. This approach has been used in previous LANDIS-II studies in the region, which successfully predicted species presence. Full explanation of HyperNiche results is available in the Supplement.

*Probability of mortality*

A central question for this study is understanding how future climate change will affect both recruitment/establishment and mortality of aspen in water-limited systems. Aspen is a unique species for many reasons, but one of the primary dynamics of interest is capturing climate-related mortality of both individuals (‘stems’) and an entire clone. The challenges in modeling stem and clone mortality within LANDIS-II are:

1. Biomass Succession extension lacks a mechanism for inducing climate-related mortality.
2. LANDIS-II uses species-age cohorts, so directly simulating the death of individual trees is impossible.

Therefore, we implemented a simple threshold approach for inducing aspen cohort mortality, which can be used to simulate both partial clone (i.e. ‘stem’) mortality, and clone mortality. An underlying assumption is that stem mortality does not necessarily lead to clone mortality, but if conditions that cause stem mortality persist, clone mortality will eventually occur.

Anderegg et al (2015) identified a cumulative modeled CWD threshold for aspen mortality, linked to moisture deficit-related xylem cavitation. Though derived from field measurements and partially based on previous physiologically-based studies of aspen mortality, this hydraulic threshold predicted regional patterns of tree mortality with 75% accuracy, as found in field plots and mortality maps derived from Landsat imagery.

So in order to create the necessary behavior, we have created the following function within Biomass Succession:

Probability of mortality (Pmort) – Probability that a cohort will experience a significant climate-related reduction (50%) in biomass. Within Biomass Succession this probability is defined for each ecoregion/species/time step, as a parameter ranging from 0-1.0.

This probability is calculated externally, and is based on projections of climatic water deficit (CWD) produced by BCM for our selected GCM model projections. Pmort within our simulations is temporally and spatially dynamic to reflect the influence of topography and elevation on climate-related mortality. Aspen mortality induced by this function within our simulations peaks at 30%, which corresponds to the cavitation-mediated increase in mortality levels observed at the individual and landscape level. Once cumulative CWD has exceeded the pre-defined threshold, mortality increases exponentially until it reaches 30%.

In years of high CWD, Pmort will be higher and Pest will likely be lower. This means the likelihood of climate-induced mortality will be higher, and the likelihood of aspen resrouting at that site will be lower. If a site experiences climate-induced mortality, this is approximating ‘individual’ mortality, because the cells adjacent to it do not necessarily see the same levels of mortality. Adjacent cells could reestablish aspen cohorts via vegetative reproduction, if soil moisture conditions were amenable. If conditions continue to be poor for growth and establishment (i.e., high CWD), then aspen may never resprout at that site and would be effectively extirpated due to inhospitable growing conditions. If such conditions persist and Pmort eventually kills all aspen cells in an area, then the clone is effectively dead.

**Base Fire**

**Results**

* *Prob of establishment/mortality*
* *Area occupied by species*
* *Aspen persistence*
  + *Permanent*
  + *Episodic*

**Discussion**

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