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UNIVERSITY OF CALIFORNIA MERCED

EXTENT AND CAUSES OF CONIFER ENCROACHMENT INTO SUBALPINE
MEADOWS IN THE CENTRAL SIERRA NEVADA

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor
of Philosophy

in

Environmental Systems

by

Kaitlin Lubetkin

Committee in charge:
Dr. A. Leroy Westerling, chair
Dr. Stephen C. Hart
Dr. Lara M. Kueppers
Dr. Jason P. Sexton

2015

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- 2015 **Lubetkin, K. C.**, A. L. Westerling, and L. M. Kueppers. 2015. Adult survival drives population growth while seedling responses to microsite drive spatial distribution of conifers encroaching into subalpine meadows. In prep.
- 2015 **Lubetkin, K. C.**, A. L. Westerling, and L. M. Kueppers. 2015. Spatial and temporal patterns of conifer encroachment into subalpine meadows of the central Sierra Nevada, CA. In prep.
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ABSTRACT

EXTENT AND CAUSES OF CONIFER ENCROACHMENT INTO SUBALPINE MEADOWS IN THE CENTRAL SIERRA NEVADA, CALIFORNIA

by

Kaitlin Lubetkin

Doctor of Philosophy

University of California, Merced

Dr. A. Leroy Westerling, Chair

Mountain meadows provide a number of ecosystem services, including sequestering carbon, storing and regulating the release of water, and maintaining biodiversity. However, as with other grassland systems, many meadows are currently experiencing woody plant encroachment. In my first chapter, I used a landscape scale survey of mountain meadows in the central Sierra Nevada to quantify the extent of conifer encroachment, the density of encroaching conifers, and determine if synchronous temporal patterns of encroachment existed. By examining overall encroachment density among 310 meadows in the central Sierra Nevada, I found that essentially all high elevation meadows, up to the krummholz vegetation zone near treeline, have some degree of encroachment. Using natural variation in physical parameters among meadows, as well as variation in climatic conditions since the early 1900s, I was able to identify conditions conducive to conifer recruitment and/or survival. When I correlated annual recruitment with climatic conditions since 1930, conditions during the year of germination were unimportant with success instead depending on conditions during a 3-year seed production period and a 6-year seedling establishment period. Applying a temporal model based on climate during both seed production and seedling establishment periods to downscaled output from four global climate models indicates that the average meadow will convert to forest by the end of the 21st century. Given the ubiquitous nature of conifer encroachment in the central Sierra Nevada, in my second chapter I explored important life stages driving encroachment and the environmental factors influencing each. Using a 4-year study of 30 meadows in Yosemite National Park, I examined seed availability, germination, establishment, and adult survival. I found that seed was abundant throughout most of the interior of the meadows. Germination and seedling emergence showed high interannual variability, and locations with new germinants tended to be those that melted later and experienced more gradual summer dry-down than locations without new germinants. The mortality curve showed that mortality levels off around age 10, leading me to define establishment as survival to 10 years of age. During this establishment phase, most trees occurred in locations where soils reached relatively dry levels by the end of the summer, as opposed to locations that did not dry down as strongly, which had no establishing trees. Adult trees (>10 years) were also found in locations that experienced strong dry down. However, matrix population models built for *Pinus contorta* in these meadows showed that the asymptotic growth rate of tree numbers in meadows was more sensitive to adult survival than to germination or establishment. Thus, it appears that adult survival drives overall population growth, while microsite

constraints on germinants and young seedlings drive the spatial distribution of encroaching trees. Having determined that adult survival has a strong influence on population growth rate of conifers in meadows, and assuming that years of poor adult tree growth indicate years of increased mortality, my third chapter focused on adult growth rates and the influence of climate. Using tree cores from 80 trees in 12 different meadows and from 144 trees in the forest immediately surrounding those 12 meadows, I was able to show that growth patterns of trees in meadows are more similar to each other than they are to growth patterns of trees in the adjacent forest. Thus, there appears to be a distinct topoclimate shared by geographically separate meadows. Meadow tree growth was sensitive to interannual climate variability both during the winter and during the growing season, with growing season effects dependent on the phase of the Pacific Decadal Oscillation. My work shows that conifer encroachment into subalpine meadows is common throughout the central Sierra Nevada. Both recruitment and adult growth are likely to increase with anthropogenic climate change, assuming that responses to climate are stationary. Even if these assumptions are violated, meadows are likely to change toward forest habitat in the short term. This reduction in meadows has management implications, and may result in the loss of important ecosystem services that meadows provide.

INTRODUCTION

Mountain meadows provide a number of important ecosystem services, including carbon sequestration, water storage/release regulation, and biodiversity maintenance. Wet mountain meadows store disproportionately large amounts of soil organic carbon (Mitra et al. 2005, Kayranli et al. 2010, Norton et al. 2011, Norton et al. 2014), making them a valuable carbon sink. This is partially due to high soil moisture, which creates anaerobic conditions that slow decomposition (Budge et al. 2010) and partially due to high primary productivity in wet meadows. Mountain meadows also provide important water storage, and regulate the release of stored water. Acting as secondary reservoirs following snowmelt, meadows can attenuate flood peaks and increase the duration of high downstream flows (Hammersmark et al. 2008). Additionally, mountain meadows provide habitat for many species, including some that are threatened or endangered (Kayranli et al. 2010, Roche et al. 2012).

Many mountain meadows are experiencing woody plant encroachment, which has the potential to change a meadow's ability to provide ecosystem services. Encroachment by either shrubs (e.g. Chambers and Linnerooth 2001, Bauer et al. 2002, Bork and Burkinshaw 2009, Brandt et al. 2013) or by trees (e.g. Ratliff 1985, Moore and Huffman 2004, Halpern et al. 2010, Haugo et al. 2011) can alter a meadow's functioning by changing its carbon cycling, the hydrologic regime, and the species it is able to support. This in turn can impact the meadow's ability to provide ecosystem services.

Changing from a meadow to a forest can affect abiotic meadow characteristics such as soil. The transition from mesic grassland to shrubland has been shown to decrease soil organic carbon stocks (O'Donnell and Caylor 2012). The dependence of carbon on high soil moisture content means that changes in the hydrologic regime may also affect soil carbon stocks. Woody plant encroachment can increase vegetation water use in meadows (Darrouzet-Nardi et al. 2006, 2008). Comparison of soil pedons across a subalpine forest – meadow ecotone showed that forest soils had lower clay content as well as lower soil organic carbon (Munroe 2012), both of which would decrease a soil's water holding capacity (Brady and Weil 2008). With increased water use by woody plants and decreased soil water holding capacity, a meadow's ability to store water could be strongly diminished.

In addition to physical soil parameters, woody plant encroachment can affect biotic interactions. Loss of meadows could result in loss of species that rely on meadow habitat, such as the Yosemite toad (Mullally 1953) and willow flycatcher (Bombay et al. 2003). Also, a forest – meadow mosaic provides varied habitat for both flora and fauna, further increasing biodiversity. Some species, such as the great gray owl, even rely specifically on the forest – meadow ecotone (Van Riper and Van Wagendonk 2006). The conversion of meadow to forest through encroachment has the potential to eliminate valuable habitat for species dependent on a meadow environment.

Meadows are among many grassland ecosystems being encroached by woody plants (e.g., Humphrey and Mehrhoff 1958; Brown and Archer 1989; Archer 1994; Higgins and Richardson 1998; Van Auken 2000, Van Auken 2009). Studies have implicated a number of factors, including fire suppression (e.g., Van Auken and Bush 1997, Takaoka and Swanson 2008, Van Auken 2009), grazing (e.g., Brown and Archer 1989; Miller and Halpern 1998), climate change (e.g., Archer et al. 1995; Miller and Halpern 1998; Bauer et al. 2002), increased CO₂ levels (Archer et al. 1995; Bond and Midgley 2000), and local factors such as rodent activity (e.g., Tilman 1983; Berlow et al. 2002). Additionally, many of these factors have been shown to co vary with local topography (e.g., Takaoka and Swanson 2008). In meadows, encroachment could be caused by any of the factors listed above, or could be the result of a natural succession process following the traditional series from lake to meadow to forest (Benedict 1982).

Meadows of the Sierra Nevada, California, have a long history of conifer encroachment (Vale 1981, Ratliff 1985, Helms and Ratliff 1987, Vale 1987, Cooper et al. 2006). Encroachment into a few individual Sierran meadows has been intensively studied through field observations (Vale 1981; Helms and Ratliff 1987; Cunha 1992, Millar et al 2004, Cooper et al 2006) and through photo re visitation (Vale 1987). However, no landscape scale study of conifer encroachment into Sierran meadows and broadly influential factors has been conducted. This limits our understanding of more general spatial and temporal patterns of Sierran meadow encroachment, thus preventing identification of drivers.

The aim of this work is to provide observations of mountain meadows in the central Sierra Nevada on a landscape scale, and to assess climatic factors influencing encroaching conifers. In the first chapter, I report a broad-scale survey of meadows to examine patterns in space and time. This provides a basis for understanding encroachment by quantifying the extent and severity of encroachment and determining the onset of encroachment and its synchronicity across meadows. The second and third chapters explore potential causes of encroachment. In the second chapter I consider different life stages of encroaching conifers (seed production, germination, establishment, and adult survival) to examine the factors influencing each life stage and their relative importance to the overall growth of populations of trees in meadows. Finally, in the third chapter I evaluate adult growth patterns and the influence of historical climate. By examining common growth rates from trees established across multiple meadows, I explore the potential for a shared meadow topoclimate.

CHAPTER 1

Spatial and temporal patterns of conifer encroachment into subalpine meadows in the central Sierra Nevada, California

Introduction

Mountain meadows provide a number of essential ecosystem services, including regulating release of snow meltwater into streams and maintaining biodiversity. Mountains of the world play critical roles as “water towers” with snowmelt acting as a natural reservoir that provides water to downstream lowlands (Messerli et al. 2004), and meadows with proper hydrologic functioning may serve as a secondary reservoir extending water release past the primary snowmelt pulse. For example, models of a northern California montane meadow following plug-and-pond restoration showed that a restored meadow increased duration of high downstream flows and attenuated downstream flood peaks (Hammersmark et al. 2008). Mountain meadows are also locations of high biodiversity, with wet meadows heavily utilized by unique flora and fauna (Patton and Judd 1970, Allen-Diaz 1991, Highland and Jones 2014).

In many locations, the continued existence of mountain meadows is threatened by woody plant encroachment (Dyer and Moffett 1999, Lepofsky et al. 2003, Takoaka and Swanson 2008, Haugo et al. 2011). Encroachment into similar systems has been attributed to a number of factors, including changes in climate (Archer 1995, Miller and Halpern 1998, Bond and Midgley 2000, Bauer et al 2002). An understanding of historic trends of encroachment could allow us to predict how woody plant encroachment is likely to respond to climate change. Meadows in the Sierra Nevada mountain range of California provide an opportunity to examine such historic trends, having a long history of conifer encroachment (Vale 1981, Ratliff 1985, Helms and Ratliff 1987, Vale 1987, Cooper et al. 2006). Encroachment into a few individual Sierran meadows has been intensively studied through field observations (Vale 1981; Helms and Ratliff 1987; Cunha 1992, Millar et al 2004, Cooper et al 2006) and through photo re-visitation (Vale 1987). However, no broad, landscape scale study of conifer encroachment into Sierran meadows has been conducted, limiting understanding of broad spatial and temporal patterns of Sierran meadow encroachment and potential drivers.

Storage and regulation of water release is of particular importance for meadows in the Sierra Nevada, but conversion of herbaceous meadows into forest could impact this hydrologic service by altering soil properties important to water retention and by altering vegetation water use. Along a forest-meadow ecotone, meadow soils were found to have higher soil organic carbon and clay contents than forest soils (Munroe 2012), both of which enhance soil water holding capacity (Brady and Weil 2002). Griffiths et al. (2005) further found changes in soil biogeochemical transformations across a forest-meadow ecotone. Encroaching woody plants can also alter depth of vegetation water use

(Darrouzet-Nardi et al. 2006) as well as altering biogeochemical cycling (Darrouzet-Nardi et al. 2008).

Even as encroachment of woody species may alter meadow hydrology, meadow encroachment may itself be determined by the hydrologic regime as well as by growing season length. Meadow hydrology is affected by fluxes from the surrounding hillslope and catchment as well as snowmelt within the meadow (Lowry et al. 2010). The snowpack depth can also affect soil hydrology (e.g., Hardy et al. 2001, Dunne et al. 2003), and affect growing season lengths in high elevation meadows that are seasonally covered in snow (e.g., Dunne et al. 2003). Aside from spatial variation in average hydrologic and growing season conditions, interannual variability in climate can influence hydrologic regime and growing season length. Meadows or years with early melt provide a longer snow-free period for plant growth and have the potential for earlier conifer germination, resulting in greater seedling growth and therefore enhancing over-winter survival (Ronco 1967). However, conifer seedlings in early melting meadows may experience earlier drought stress.

We hypothesize that meadow hydrologic regime and length of the growing season play co-dominant and interacting roles in determining encroachment intensity by influencing success of encroaching conifers. Here, we examine spatial and temporal patterns of encroachment into subalpine meadows in the central Sierra Nevada. Specifically, we test the following hypotheses: 1) the majority of meadows across the Central Sierran landscape are encroached, 2) encroachment intensity is highly variable among meadows and is related to hydrologic properties and the length of the growing season, 3) meadows with similar physical parameters show synchronous timing of encroachment, and 4) past encroachment occurred in periods of climatic conditions conducive to both seed production and seedling germination and establishment.

Methods

We conducted a landscape-scale survey of conifer encroachment into subalpine (2700-3350 m elevation) meadows in the Sierra Nevada between 2009 and 2013, defining the edge of a meadow based on herbaceous vegetation shifts. We considered only those trees >0.1 m tall and/or older than approximately 10 years (“adult” trees), both for reliability of observation in the field and to eliminate the large number of trees still in the establishment phase. Considering only adult trees allowed us to compare our measurements of recent encroachment abundance with those of historic encroachment abundance. We conducted the majority of the fieldwork in Yosemite National Park (YNP), which provides an ideal natural laboratory that has been more protected than surrounding National Forests. Protection provides sites with the least anthropogenic impacts and fewest confounding factors such as recent grazing and woodcutting, facilitating interpretation of numerous causal factors of encroachment. All meadows were in remote locations to further minimize direct anthropogenic influences such as trail building, trampling, stock use, or direct management of encroaching conifers. We

surveyed a total of 84 meadows in YNP, including 30 at a detailed level, an additional 243 meadows in Kings Canyon National Park (KNP), and 11 meadows along the Pacific Crest Trail from YNP to Lake Tahoe (PCT; Figure 1). We correlated intensity of meadow encroachment with physical meadow properties. We then used the ages of trees within the meadows to construct a regional meadow encroachment time series, correlating this with climate variables.

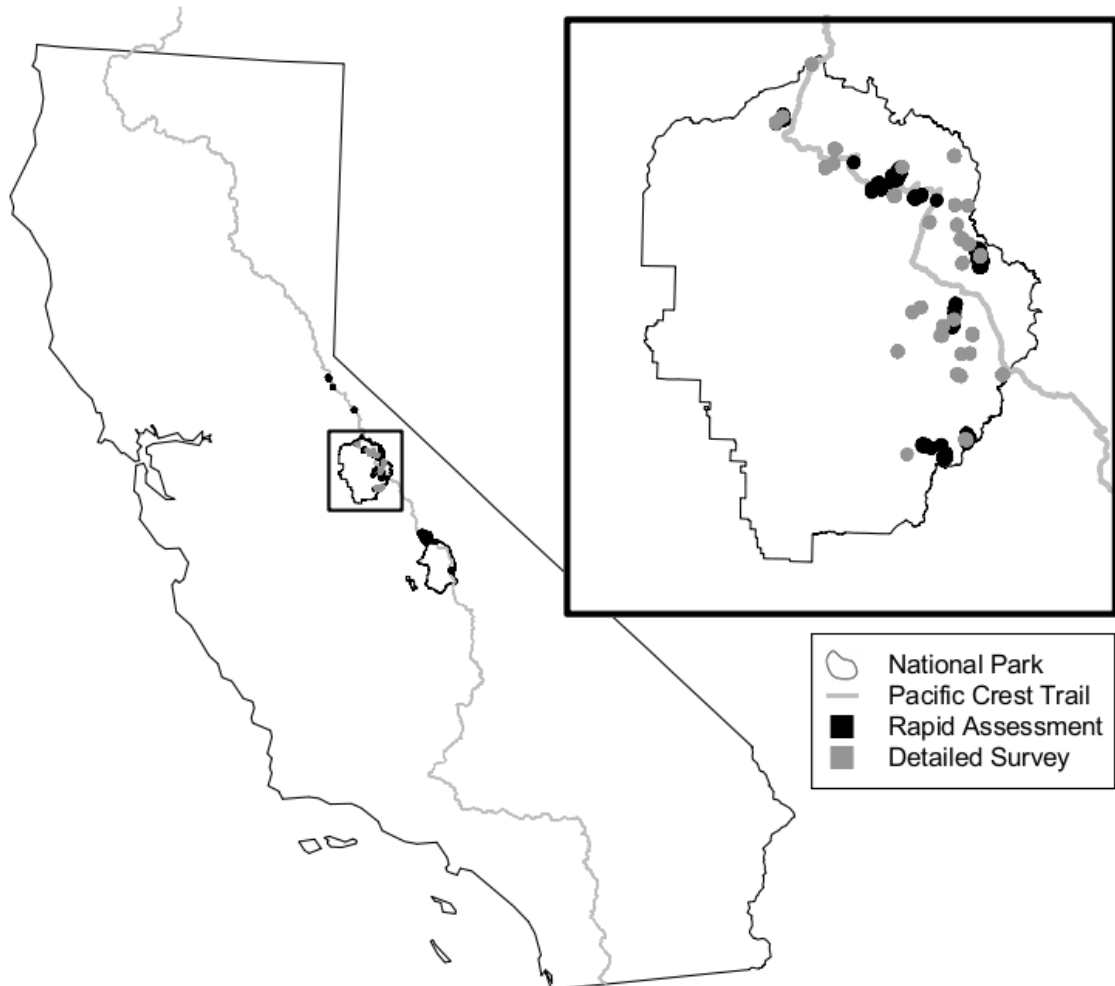


Figure 1. Study location. Study meadows were located along the western side of the Sierra Nevada crest, ranging from Kings Canyon National Park north to Lake Tahoe. The study included 11 rapid assessment meadows along the Pacific Crest Trail between Yosemite National Park and Lake Tahoe, 30 detailed survey and 56 rapid assessment meadows in Yosemite National Park, and 243 rapid assessment meadows in Kings Canyon National Park.

Detailed surveys

We selected detailed survey meadows using the 1997 digital vegetation map for YNP (Aerial Information Systems 2007), eliminating meadows with extreme areas ($> 200,000 \text{ m}^2$ or $< 2,000 \text{ m}^2$, in order to focus on “average” meadows and exclude the most extreme 5%), below the subalpine zone (below 2700 m), outside of designated wildernesses, within 2.4 km of a paved road, or inaccessible ($> 2.5 \text{ km}$) from the nearest trail. From the remaining 1,351 meadows, we chose 30 meadows using a stratified random design based on surrounding vegetation and winter 2004-2005 average snowmelt date. After grouping snowmelt dates into quartiles, within each quartile we chose 7-8 meadows—5-6 with conifers adjacent to the meadow, and 1-2 with no conifers within a 50 m buffer around the meadow. The combination of meadows with and without adjacent conifers enabled us to examine meadows experiencing different biotic pressures.

We conducted detailed surveys of 22 meadows in 2009, and visited these and an additional 8 meadows in 2010. In 2009-2010, we established two to six (depending on size and homogeneity of the meadow) 3 m wide belt transects (Figure 2). We placed each transect to be representative of a region in the meadow with a homogeneous encroachment pattern. To test the dependability of our subjective transect placement, we also recorded conifers in two meadows with a full grid of transects located every 20 m. For both meadows, the estimated overall conifer abundance based on our subjective transects fell within the 95% confidence interval of all possible combinations of transects from the full grid.

Transects ran along cardinal directions and spanned the meadow/forest transition zone, extending either 50 m into the meadow where the meadow diameter was $> 100 \text{ m}$, or across the width of the meadow where the meadow diameter was $< 100 \text{ m}$. Along each transect, we recorded the distance from meadow edge (to the nearest 0.1 m), species, height, diameter, and age of all conifers with bases in a 1 m belt, and the same information for all “adult” trees larger than 0.2 m tall within a 3 m belt centered around the 1 m belt (Figure 2).

We estimated age of younger trees based on nodes/branch whorls for trees up to $\sim 2 \text{ m}$ tall and ~ 40 years old. We collected basal cross-sections from fourteen trees up to $\sim 1.5 \text{ m}$ tall scattered across five meadows, and made cross sectional cuts higher along the same fourteen trees at different node-count intervals. These ring counts corroborated that Sierra lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *murrayana* (Balf.) Engelm.) in these meadows are uni-nodal (producing only a single whorl of branches per year), confirming the validity of our node counts. For all trees, basal ring count was within one year of the node count, and all cross sections taken higher along the trees were identical to their node counts.

We estimated ages of larger trees in the lab using a height/age regression, which provided a stronger fit than an age regression based on diameter at breast height ($R^2=0.53$ and $R^2=0.43$, respectively). To calibrate this regression, we cored and aged, using standard

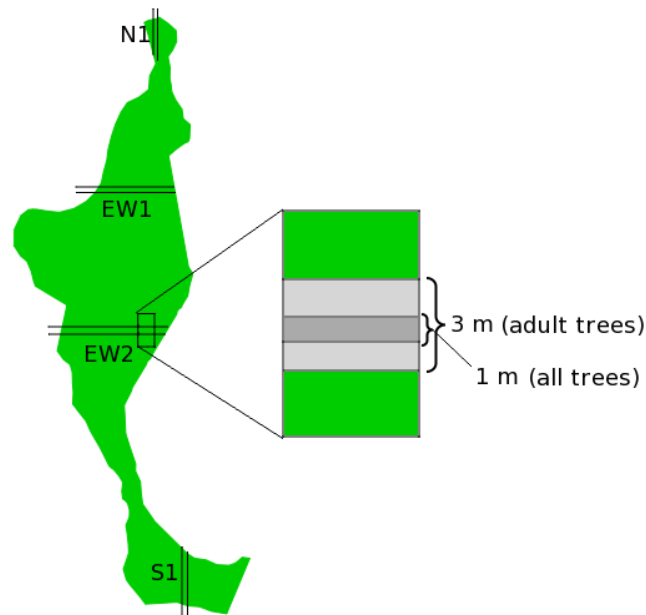


Figure 2. Sampling design. An example meadow with one “north” transect, two “east-west” transects, and one “south” transect. This meadow is bordered by a lake on the west side, and transects extend into the surrounding forests on the east side. Each transect had a three m belt transect in which adult trees (>0.2 m tall, approximately 10 years old) were recorded. At the center of the three m belt was a one m belt in which all trees, adults and seedlings, were recorded.

cross-dating techniques (see Fritts 1976), 5 to 10 *P. contorta* per meadow. We preferentially chose to core trees along transects except when no trees of sufficient size were present along the transects, and cored trees were chosen to span the size range of larger *P. contorta* (>2m tall).

Rapid assessments

To expand the spatial extent of the study, we developed a rapid assessment protocol based on characteristics of data collected in 2009. We classified the degree of encroachment, the height classes of conifers present (as a proxy for age classes), and the conifer species composition in 56 meadows within YNP, 11 north of Yosemite toward Lake Tahoe, and 243 south in Kings Canyon National Park. Meadows were chosen using the same selection criteria used for the detailed surveys, concerning size, elevation, location in a wilderness, and distances from trails and paved roads. In order to use size classes as a proxy for age classes, we examined the data to find size class breaks that would result in classes with minimal age spread while remaining easily distinguishable in the field. Our rapid assessment protocol involved visually estimating the number of trees of each species within each height class (<0.5 m, 0.5-1.5 m, 1.5-5 m, and >5 m), and also visually estimating the conifer species composition of the immediately surrounding mature forest. We also conducted rapid assessments for all detailed survey meadows to calibrate the two methods. While abundance of trees >1.5 m tall was similar between

detailed and rapid surveys, rapid assessments underestimated the abundance of smaller trees (data not shown). Thus, we used linear regressions to adjust rapid assessment estimates of smaller trees with estimates from the detailed surveys.

Meadow physical parameters

We used the topographic wetness index developed by Beven and Kirkby (1979) as a proxy for meadow hydrologic regime. We used slope and catchment size (obtained from the USGS National Elevation Dataset, with 30-m resolution) to calculate a hydrologic index (HI) based on

$$HI = \ln\left(\frac{\text{catchment}}{\tan(\text{slope})}\right) \quad \text{Equation 1}$$

where *catchment* is the catchment area in m², and *slope* is the slope in degrees. A high hydrologic index would indicate a meadow that gathers more water, which could be the result of a large catchment area and/or very shallow slope. Conversely, a meadow receiving less water would have a lower hydrologic index, indicating a small catchment and/or steep slope. We computed a spatial index to indicate the edge:area ratio as

$$SI = \frac{\text{perimeter}}{\text{area}} \quad \text{Equation 2}$$

where *perimeter* is the length of the meadow perimeter in m, and *area* is the total meadow area in m². Both *perimeter* and *area* were obtained by GPSing the perimeter of the meadow. A high spatial index results from meadows where most of the meadow interior is close to the edge (more elongated and convoluted shapes of meadows) while a low spatial index results from meadows where much of the interior is far from an edge (rounder meadows). We also created a solar radiation raster from the ArcGIS solar radiation tool (using ArcGIS version 9.3) and USGS National Elevation Dataset, with monthly totals of incoming solar insolation. We considered the cumulative solar radiation during the melt period (May-June), which would affect the rate of snow melt and thus length of growing season, and the cumulative solar radiation late in the growing season (Sep-Oct), which would affect soil evaporation and plant water stress. We obtained cumulative annual precipitation and annual mean of average monthly maximum temperature from PRISM data at 800 m resolution, averaged over the period from 1960 to 1990.

Analysis of spatial patterns of encroachment

We used generalized additive models (GAMs; Hastie and Tibshirani, 1986) to create mathematical models of encroachment density as a function of physical and climatic parameters described above. The GAM is a data driven model useful for analyzing non-parametric data with non-linear relationships, and does not require prior assumptions about the shape of the relationship between explanatory and response variables. The GAM works by fitting a link-function between the mean of the response variable and

smoothed function of the explanatory variables. For our study, we created GAMs using Gaussian distributions with a logit link function.

We selected predictor variables from an initial set using gradient boosting. Gradient boosting is a machine learning technique that can be used to fit parametric and nonparametric models, and is especially useful for choosing the most informative explanatory variables while avoiding overfitting (Buhlmann & Hothorn 2007). Using the `mboost` (Hothorn et al. 2013) package in R, we considered 21 predictor variables (Table 1) with both linear (baselearner “bols”) and spline smoothed (baselearner “bbs”) potential relationships, along with an additional spatial predictor (baselearner “bspatial”). We ran a boosted GAM analysis on the full dataset, running 500 iterations and using 5-fold cross-validation risk assessment to choose the optimal stopping point. We chose six predictors identified as significant at the optimal stopping point for use in a conventional GAM (i.e. a GAM not created using gradient boosting; Hastie and Tibshirani, 1986).

We created the conventional GAMs using the `mgcv` (Wood 2012) package in R in order to obtain more explicit statistics of the importance of each predictor. We ran 1000 bootstrapped iterations, randomly splitting the data into 80% training and 20% validation for each run. We used bootstrapped iterations to determine the standard error, though we based all qualitative analyses on the model using the full data set in a conventional GAM. We further tested predictive capability of the models using independent rapid assessments conducted in 2013. To do this, we predicted encroachment density in all subalpine meadows of Yosemite National Park that fit the criteria used to select our detailed and rapid assessment meadows. We then surveyed 13 accessible meadows that spanned a range of predicted encroachment densities, focusing especially on meadows in which we predicted very low or very high encroachment.

Analysis of temporal patterns of encroachment

We used ages of conifers to create time series of encroachment for each of 19 meadows containing at least 100 conifers (≥ 0.1 m tall, ~ 6 years old). We created these time series using 5-year running averages, to account for uncertainty in observations of tree ages resulting from the age-height regression, and percent of conifers in each meadow that germinated in a given year. We averaged percentages across all 20 encroached meadows to obtain a composite regional time series of meadow encroachment. We used the `e1071` package in R (Meyer et al. 2012) to cluster the meadows based on date of encroachment onset. We identified onset as the year when 99% of the encroaching trees were established in that year or more recently. This allowed us to look at the main onset rather than the year in which single older individuals established. We compared physical parameters of meadows in different onset clusters using ANOVA and Tukey HSD post hoc tests.

We then correlated the composite regional encroachment signal with historical climate variables using the same GAM methods above. This method allowed us to reduce 12 predictor variables (Table 2) to a set of 4 and create a conventional GAM. We obtained

historical snow water equivalence from the Tioga Pass Entry Station snow course (CA Dept. of Water Resources, manual measurements taken monthly, available from 1926 to present), which is within our elevational band and between 4 and 41 km from our meadows. We obtained historical precipitation and temperature measurements from the Yosemite Park Headquarters station (United States Historical Climatology Network (USHCN) v2.5, Menne et al. 2014), which is below our elevation but the nearest station in the USHCN. We chose to use the USHCN data rather than raw meteorological station data since it has been corrected for inhomogeneities and missing data. We correlated the composite regional encroachment time series with historical climate conditions for the year of germination as well as climate conditions averaged across the prior three years and averaged across the six following years using a GAM. We chose the three year period before germination (“seed” period) based on the time of cone development and seed release (Owens 2006). We then chose the six year period after germination (“estab” period) based on four years of data on young conifer mortality, which showed that 58% of mortality occurred within the first six years following germination. As with the spatial data, we tested the strength of our temporal GAM using 1000 bootstrapped iterations, splitting the data into 80% training and 20% validation.

To examine potential future encroachment, we used statistically downscaled (~12 km x 12 km grid) output from four global climate models (GCMs) included in the Intergovernmental Panel on Climate Change (IPCC)’s Fourth Assessment report: National Center for Atmospheric Research (NCAR) CCSM 3.0, NCAR PCM1, Centre National de Recherches Meteorologiques (CNRM) CM 3.0, and Geophysical Fluid Dynamics Laboratory (GFDL) CM 2.1. We forced each GCM with both a medium-high emissions pathway (SRES A2) and a low emissions pathway (SRES B1; IPCC 2000, Metsaranta et al. 2010). We used these outputs to drive the variable infiltration capacity (VIC) hydrologic model (Liang et al. 1994), chosen for its ability to simulate water and energy balances. This enabled us to obtain future projections of precipitation, temperature, and April 1st snow water equivalent that we then used to project encroachment. We tested that using the downscaled VIC output in our GAM was reasonable by applying the GAM to historical VIC model output. This historical output uses the same downscaling method as the forecasted data.

Table 1. Twenty-one predictor variables considered in the gradient boosted generalized additive model (GAM) for spatial patterns of conifer encroachment, with p-values obtained from the conventional GAM. GAM p-values are only shown for those predictor variables that were identified as significant by the gradient boosted GAM.

Predictor Variable	GAM p-value	Description
<u>Abiotic</u>		
<u>Physical</u>		
Elevation	0.002	Elevation of the meadow centroid (meters above sea level)
Area		Meadow area (square meters)
Slope		Average slope of the meadow (degrees)
Aspect	0.040	Direction in which the meadow is facing (degrees)
Aspect - N		North- component of aspect, computed as $\cos(\text{aspect})$
Aspect - E		East- component of aspect, computed as $\sin(\text{aspect})$
Hydrologic Index		Hydrologic index based on slope and catchment size, computed as $\ln(\text{catchment/slope})$
Spatial Index		Spatial index indicating the ratio of interior to perimeter, computed as area/perimeter
<u>Climate</u>		
Maximum		
Temperature	0.009	Annual average of the monthly average maximum temperatures (oC)
Annual Precipitation	0.016	Cumulative annual precipitation (m)
SoiRad_melt	0.067	Cumulative solar radiation a meadow receives during the melt season (May-June)
SoiRad_lateGS		Cumulative solar radiation a meadow receives late in the growing season (Sept-Oct)
Melt 50% 2004		Date when 50% or less surface area of a meadow remained under snow in 2004 (Julian day)
Melt 25% 2004		Date when 25% or less surface area of a meadow remained under snow in 2004 (Julian day)
Melt 50% 2005		Date when 50% or less surface area of a meadow remained under snow in 2005 (Julian day)
Melt 25% 2005		Date when 25% or less surface area of a meadow remained under snow in 2005 (Julian day)
Melt Length 2004		Length of time it took for a meadow to melt from 50% to 25% snow remaining in 2004 (Julian day)
Melt Length 2005		Length of time it took for a meadow to melt from 50% to 25% snow remaining in 2005 (Julian day)
<u>Biotic</u>		
<u>Conifers</u>		
Surrounding %		% of a 100m buffer immediately surrounding a meadow that was classified as a conifer vegetation type
Surrounding Density		Average density of surrounding conifers
LP Dominance	<0.001	Dominance of Lodgepole Pine in the surrounding buffer, a weighted average using $\text{absent}=0$, $\text{subdominant}=1$, $\text{dominant}=2$

Table 2. Four main predictor variables, each averaged over three time periods¹, considered in the gradient boosted generalized additive model (GAM) for temporal patterns of conifer encroachment, with p-values obtained from the conventional GAM. GAM p-values are only shown for those predictor variables that were identified as significant by the gradient boosted GAM.

Predictor Variable	p-value	Description
SWE		April 1 st snow water equivalent at the Snow Flat snow course in Yosemite National Park
SWE: current		
SWE: seed	<0.001	
SWE: establish	<0.001	
PCP late gs		Late growing season (July, August, September, October) precipitation
PCP late gs: current		
PCP late gs: seed		
PCP late gs: establish	0.01	
maxT late gs		Late growing season (July, August, September, October) average maximum temperature
maxT late gs: current		
maxT late gs: seed	0.014	
maxT late gs: establish	0.015	
minT melt		Melt period (April, May, June) average minimum temperature
minT melt: current		
minT melt: seed		
minT melt: establish		

¹ The three time periods included “current”: the year of germination, “seed”: 3-year seed production period prior to germination, and “establish”: 6-year establishment period following germination.

Results

Spatial Patterns

Consistent with our expectations, encroachment was common across the landscape. Both detailed surveys and rapid assessments showed that encroachment was nearly ubiquitous up to 3200 m (Figure 3). Of 30 detailed survey meadows, 23 were considered encroached (≥ 0.002 trees/m², ages >10), and the 7 un-encroached meadows were all in the krummholtz vegetation zone >3200 m. This pattern was consistent across meadows surveyed in Yosemite National Park (YNP), Kings Canyon National Park (KNP), and along the Pacific Crest Trail (PCT) from Yosemite to Tahoe (Table 3). Encroaching conifers were predominantly *Pinus contorta* (lodgepole pine; 94% of encroachers) even when *P. contorta* was not a large component of the surrounding forest. Conversely, the second and third most common encroachers, *Pinus albicaulis* (whitebark pine; 3.4% of encroachers) and *Tsuga mertensiana* (mountain hemlock; 1.1% of encroachers), were only a noticeable percentage of the encroaching conifer community when trees of those species were present as a sizable percentage of the surrounding forest (>40% of surrounding trees).

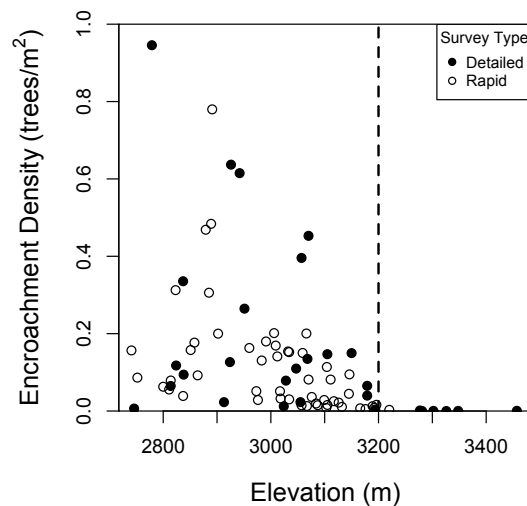


Figure 3. Density of encroaching conifers in 86 subalpine meadows in Yosemite National Park as a function of elevation. Encroachment intensity was highly variable up to the krummholtz vegetation zone at 3200 m, after which elevation meadows remained un-encroached (below our threshold of 0.002 trees/m², determined by Jenks natural breaks). This trend was true both of detailed survey and rapid assessment meadows.

Table 3. Median and interquartile range of encroachment densities of conifers within subalpine meadows below the krummholtz vegetation zone (~3200 m) in three locations across the central Sierra Nevada.

Location	Type	Number	Encroachment Density (trees/m ²)		
			1 st quartile	Median	3 rd quartile
YNP	Detailed	23	0.010	0.068	0.178
YNP	Rapid	54	0.020	0.071	0.178
PCT	Rapid	11	0.032	0.096	0.176
KNP	Rapid	186	0.007	0.025	0.086

We further hypothesized that the density of encroachment would be highly variable and related to biotic and abiotic factors affecting meadow hydrology and length of growing season. Indeed, of those meadows that were encroached, there was a wide range of encroachment densities, defined as total number of trees per m² in a meadow. The gradient boosted GAM identified six variables (Table 1) that explained variation in encroachment density. When used in the conventional GAM, these six predictors explained 81% of the variation in encroachment density, with presence of *P. contorta* in vegetation surrounding the meadow the strongest predictor. In meadows that had sufficient surrounding *P. contorta*, encroachment was most dense in lower elevation meadows, meadows with mean monthly maximum temperatures above or below average of values for meadows in this study, low precipitation, high solar radiation during the melt period (May-July), and south to east facing aspects (Figure 4). Additional interactive effects were apparent. For example, cumulative annual precipitation played a smaller role in meadows with *P. contorta* dominating the vegetation in the surrounding buffer (where encroachment was heavy regardless of precipitation) than it did in meadows surrounded by less *P. contorta* (where encroachment was heavy only when precipitation was low; Figure 4c). Similarly, cumulative annual precipitation was largely unimportant at lower elevations (where encroachment was heavy across the precipitation spectrum) than at higher elevation meadows (where encroachment was heavy only at low precipitation values; Figure 4g).

When 1,000 bootstrap iterations of the conventional GAM were run, the relationship between the actual and modeled encroachment densities for the training data had a mean $R^2 = 0.921 \pm 0.046$ SD, while the validation data had a mean $R^2 = 0.568 \pm 0.249$ SD. Fully independent rapid assessments not included in the initial model training and validation showed that the GAM was robust within YNP as well as within KNP and along the PCT (Figure 5).

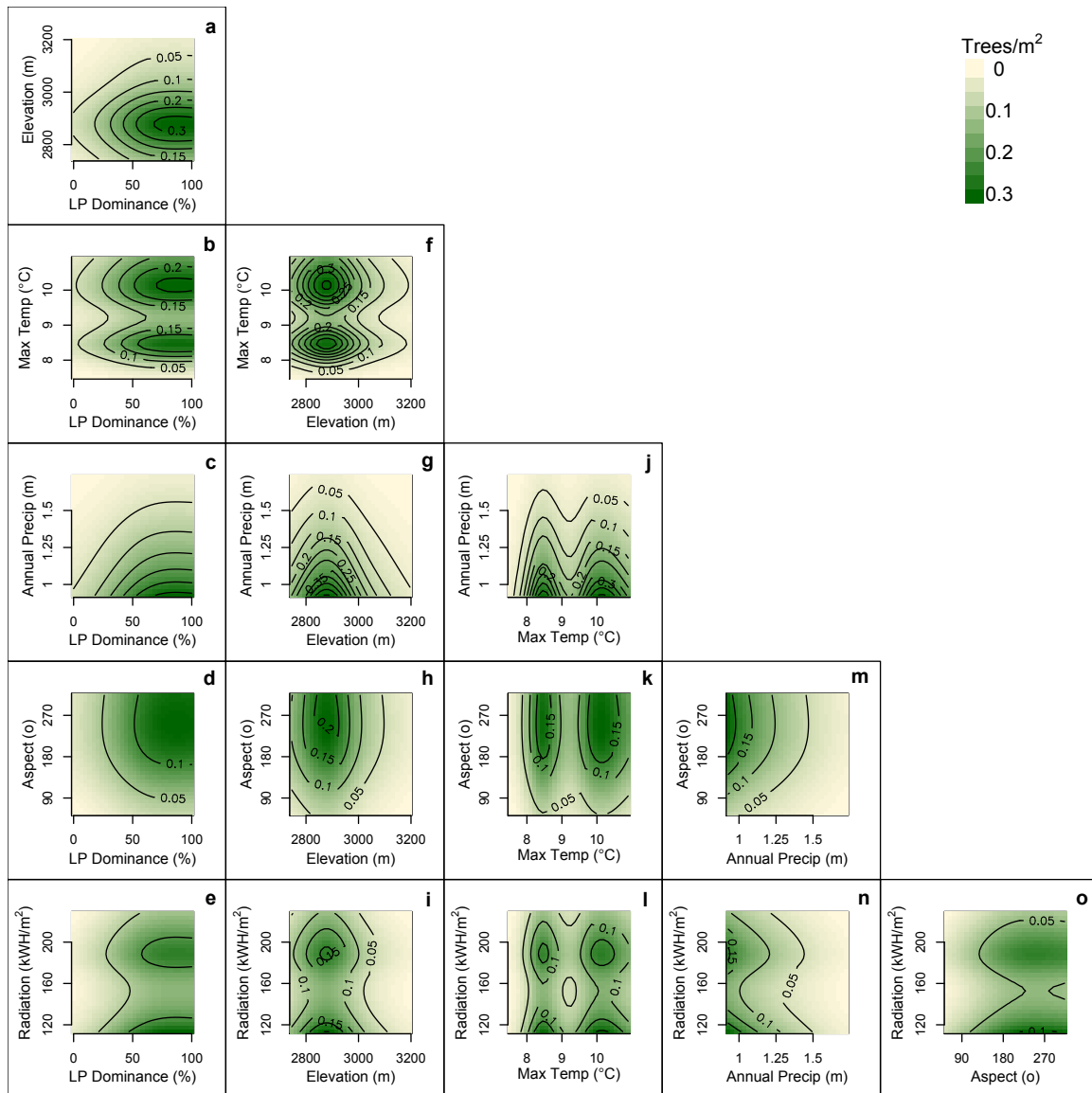


Figure 4. Encroachment density in 86 meadows in Yosemite National Park as it relates to six predictor variables in the spatial GAM. Color corresponds to encroachment density, with darker green colors indicating dense encroachment, shown with contour lines indicating the number of trees per m^2 . **a)** Elevation of the meadow versus the dominance of lodgepole pine in a 50 m buffer around the meadow. **b)** Annual average of mean monthly maximum temperature versus dominance of lodgepole pine in 50 m buffer around the meadow. **c)** Cumulative annual precipitation versus the dominance of lodgepole pine in a 50 m buffer around the meadow. **d)** Meadow aspect versus dominance of lodgepole pine in a 50 m buffer around the meadow. **e)** Cumulative solar radiation received by the meadow during the late growing season (September-October) versus dominance of lodgepole pine in a 50 m buffer around the meadow. **f)** Annual average of mean monthly maximum temperature versus meadow elevation. **g)** Cumulative annual precipitation versus meadow elevation. **h)** Meadow aspect versus

elevation. **i)** Cumulative solar radiation received by the meadow during the late growing season (September-October) versus meadow elevation. **j)** Cumulative annual precipitation versus annual average of mean monthly maximum temperature. **k)** Meadow aspect versus annual average of mean monthly maximum temperature. **l)** Cumulative solar radiation received by the meadow during the late growing season (September-October) versus annual average of mean monthly maximum temperature. **m)** Meadow aspect versus cumulative annual precipitation. **n)** Cumulative solar radiation received by the meadow during the late growing season (September-October) versus cumulative annual precipitation. **o)** Cumulative solar radiation received by the meadow during the late growing season (September-October) versus meadow aspect.

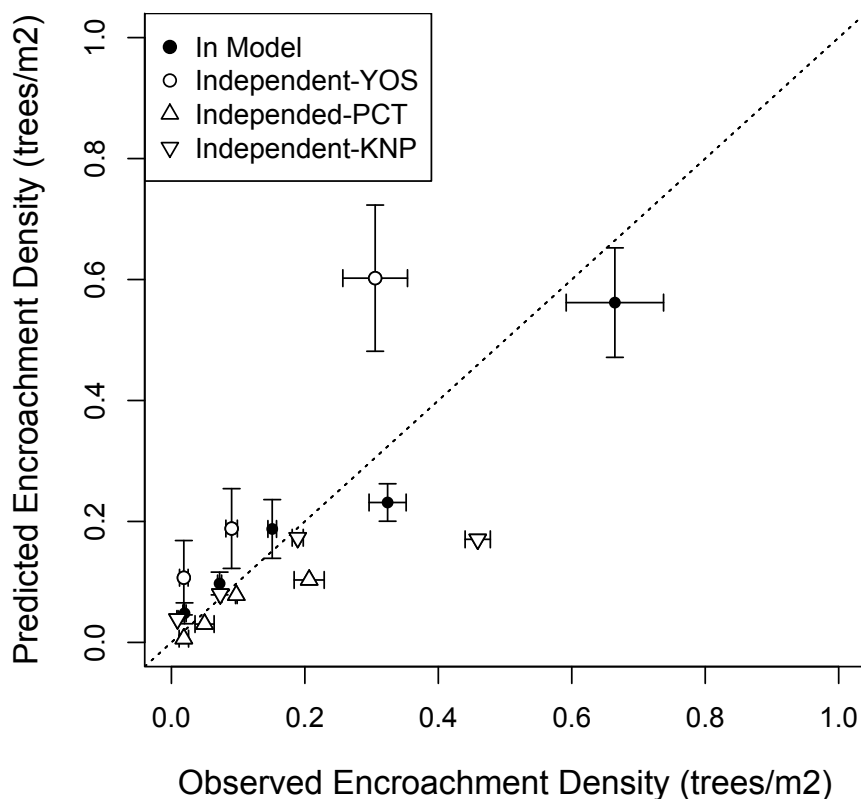


Figure 5. Predicted versus observed encroachment density. Mean \pm 1 SE encroachment. Meadows are binned by observed encroachment density (Jenks natural breaks, Jenks and Caspall 1971). 86 meadows from Yosemite National Park (YNP) were used to train the model, which was then applied to fully independent meadows for secondary validation (13 in Yosemite National Park (YOS), 11 north of Yosemite National Park toward Lake Tahoe along the Pacific Crest Trail (PCT), and 243 in Kings Canyon National Park (KNP)).

Temporal Patterns

Encroachment onset varied among meadows, although most existing encroachment began after 1920. Ninety-eight percent of established conifers older than 10 years and still present in the meadows germinated after 1920. Variation in timing among meadows fit into three general patterns, with encroachment beginning either around 1904 (5 meadows), 1945 (8 meadows), or 1978 (5 meadows; Figure 6). While we hypothesized that meadows with similar timing would display similarity in physical parameters, we found little evidence of this. Encroachment density was higher among meadows with mid-century encroachment onset than those with earlier or later onset ($F=4.9$, $p=0.02$, $df=2$), though the groups did not differ in climate and site factors that proved important in the spatial GAM (surrounding *P. contorta*, $F=2.2$, $p=0.14$, $df=2$; elevation, $F=1.1$, $p=0.36$, $df=2$; maximum temperature, $F=0.49$, $p=0.62$, $df=2$; annual precipitation, $F=2.55$, $p=0.11$, $df=2$; solar radiation in melt period, $F=3.54$, $p=0.06$, $df=2$; aspect, $F=2.88$, $p=0.09$, $df=2$).

The composite regional encroachment time series showed a strong peak in the early 1950s, followed by a dip, after which encroachment increased fairly steadily until approximately 1980, followed by another dip after which encroachment again increased steadily (Figure 7). We were able to model the regional time series with a GAM based on 4 climatic drivers (Figure 8, Table 2), which had high predictive power (78.7% of deviance explained, $AIC=552.6$, $n=71$). Encroachment was high in years preceded by a 3-year seed production period characterized by high April 1st snow water equivalent (SWE), and in years followed by a 6-year seedling establishment period characterized by high summer maximum temperatures, high summer precipitation, and high April 1st SWE. Conditions during the year of germination showed little effect on recruitment (Table 2).

Seed production period alone produced a model that explained 26.1% of the deviance ($AIC=625.4$, $n=71$) while seedling establishment period alone produced a model that explained 61.3% of the deviance ($AIC=612.8$, $n=74$). When we examined conditions during the seed production years only, the model captured the recent peaks in number of young recruits (Pearson's correlation coefficient=0.70; Figure 7a). Predicting encroachment with seedling establishment years only was more predictive, picking up the long term trend of increasing recruitment (Pearson's correlation coefficient=0.82; Figure 7b). When combined, the lead and lag model not only captured the longer timescale trend but also tracked more of the decadal variability (Pearson's correlation coefficient=0.95; Figure 7c).

When we ran 1000 bootstrapped iterations, the model explained on average 88.9% of the deviance (mean $AIC=412.0$, $n=53$). A linear regression of the predicted recruitment as a function of the observed recruitment had a mean $R^2=0.89$ for the training data (mean $p<0.001$, $n=53$) and a mean $R^2=0.72$ for the validation data (mean $p=0.013$, $n=14$). When we applied the temporal GAM to historical VIC-generated data, it predicted the observed time series with an $R^2=0.75$ ($p<0.001$, $n=42$; Figure 9). When applied to future predicted

climate, the average across the four downscaled GCMs predicts an increase in annual conifer recruitment under the A2 emission and B1 emission scenarios (Figure 10).

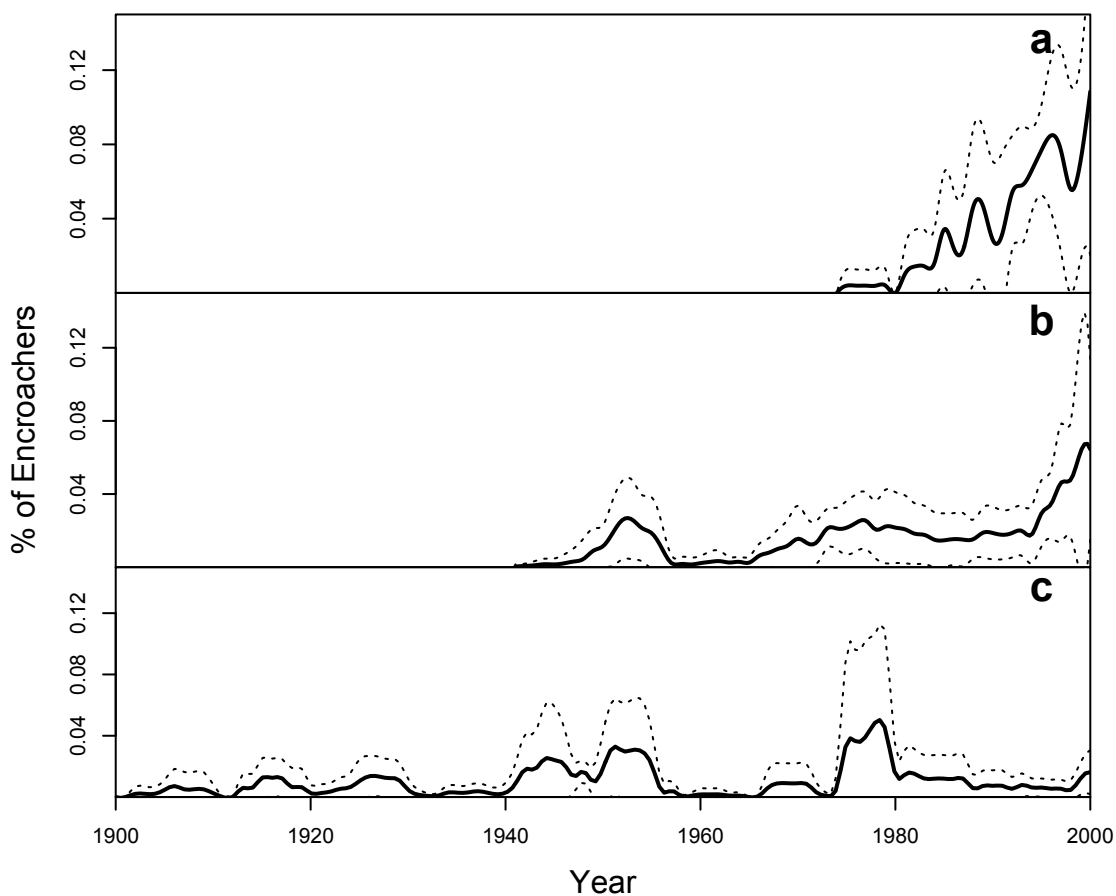


Figure 6. Percent of total adult encroachers that recruited in a given year (mean \pm 1 SD) for three groupings of meadows among 19 encroached meadows in Yosemite National Park. Meadows fit three general trends of encroachment timing, with the onset of encroachment occurring in approximately **a)** 1978, 5 meadows, **b)** 1945, 8 meadows, and **c)** 1904, 5 meadows. Meadows were clustered based on the date of encroachment onset, which we defined as the year in which 99% of the encroachment occurred during that year or more recently, using the R package e1071 (Meyer et al. 2012).

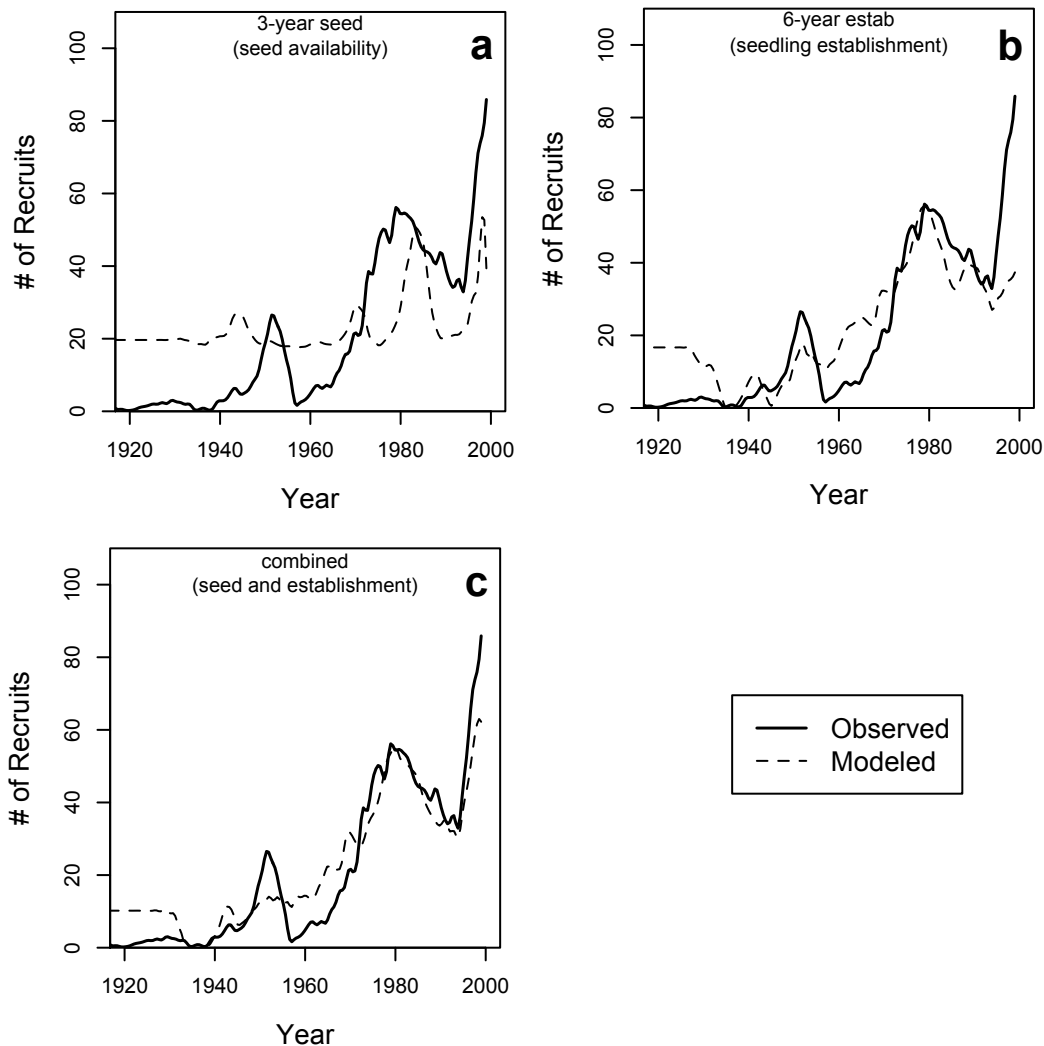


Figure 7. Actual encroachment time series versus that modeled using climate conditions averaged over the seed production and/or seedling establishment period. The actual data presented is a regional composite time series with 20 meadows containing at least 100 trees each. Encroachment was modeled using four climatic variables. Models were created with **a)** only those during the three-year period prior to germination, **b)** only those during the six-year period following germination, or **c)** all four variables during periods prior to and following germination.

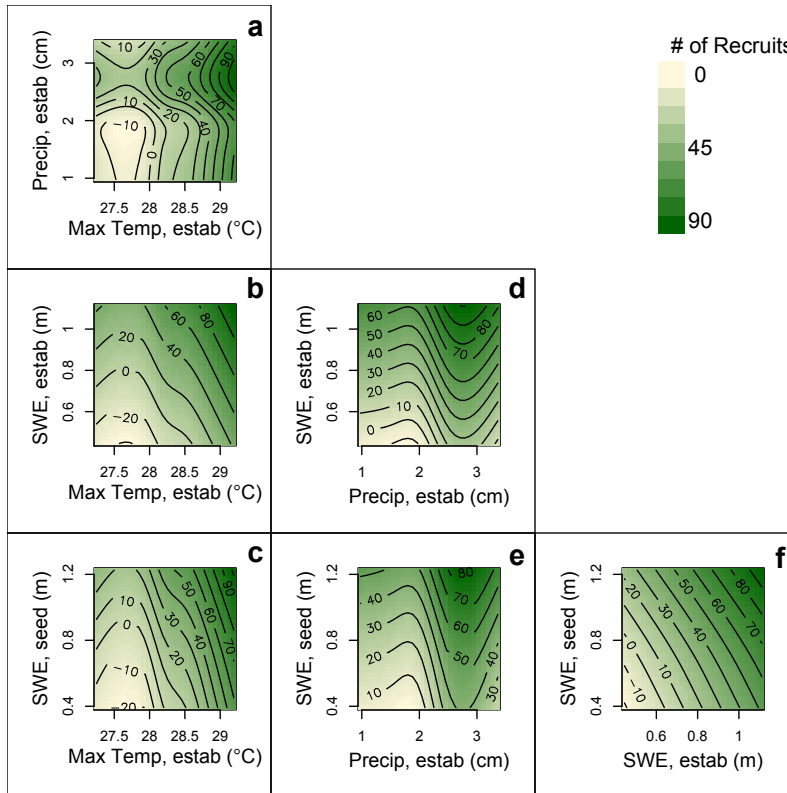


Figure 8. Recruitment intensity in 30 meadows in Yosemite National Park as it relates to four predictor variables in the temporal generalized additive model. Color corresponds to recruitment abundance, with darker greens indicating more abundant recruits, shown with contour lines indicating the number of new recruits per year. **a)** Cumulative growing season (July-October) precipitation averaged over a three year period prior to germination versus average mean monthly spring (March-May) minimum temperature averaged over the same three year period prior to germination. **b)** Mean monthly spring (March-May) minimum temperature averaged over a six year period following germination versus average mean monthly spring (March-May) minimum temperature averaged over a three year period prior to germination. **c)** April 1st snow water equivalent averaged over a six year period following germination versus average mean monthly spring (March-May) minimum temperature averaged over a three year period prior to germination. **d)** Mean monthly spring (March-May) minimum temperature averaged over a six year period following germination versus cumulative growing season (July-October) precipitation averaged over a three year period prior to germination. **e)** April 1st snow water equivalent averaged over a six year period following germination versus cumulative growing season (July-October) precipitation averaged over a three year period prior to germination. **f)** April 1st snow water equivalent averaged over a six year period following germination versus mean monthly spring (March-May) minimum temperature averaged over a six year period following germination.

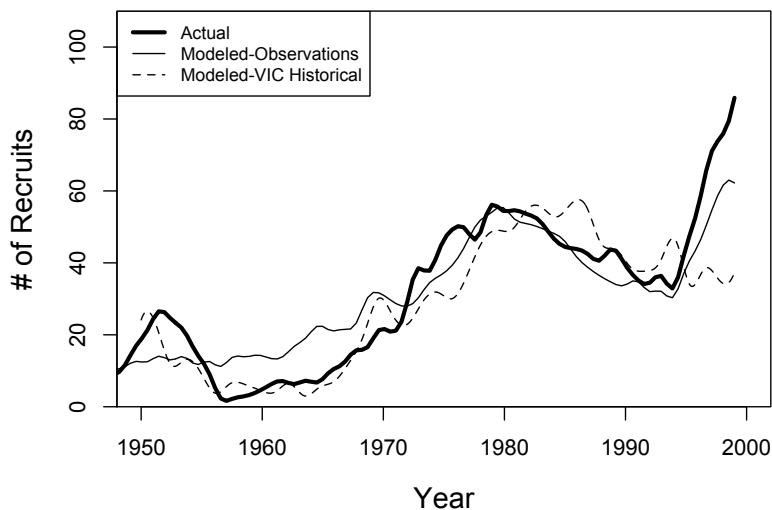


Figure 9. Actual encroachment time series versus that modeled using climate conditions obtained from the US historical climate network (USHCN v2.5) meteorological observations and the variable infiltration capacity (VIC) hydrologic model. The actual data presented is a regional composite time series across 20 meadows containing at least 100 trees each. Encroachment was modeled using four climatic variables. The resultant generalized additive model was then applied to an independent climate data set generated from the VIC hydrologic model.

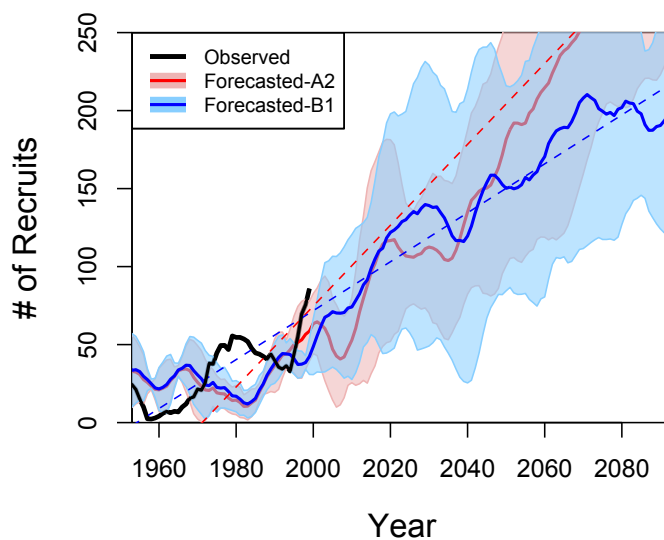


Figure 10. Encroachment forecasting using data averaged across four downscaled global climate models (GCMs), under two emission scenarios. The average amongst the four models is indicated in the solid line, with the shaded region showing the range of values across all models.

Discussion

Spatial Patterns

As predicted, encroachment was common across the central Sierra Nevada and encroachment was most commonly by Sierra lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *murrayana* (Balf.) Engelm.). Widespread Sierra Nevada encroachment is consistent with a landscape scale decrease in mountain meadow area in Oregon between 1946 and 2000 (Takaoka and Swanson 2008), as well as broad trends of woody plant encroachment into other grassland ecosystems (e.g., Van Auken 2000, Naito and Cairns 2011, Liu et al. 2013). However, Sierra Nevada meadows present different challenges to encroaching conifers than those experienced in semi-arid grassland systems. Sierra Nevada meadows are groundwater dependent systems with high water table levels (Allen-Diaz 1991). *P. contorta* is well adapted to establishing into wet Sierra Nevada meadows, being shade intolerant with seedlings germinating best in full sunlight (Lotan and Critchfield 1990), and being tolerant of high water tables (Minore 1970; Cochran 1972).

High density of encroaching conifers depended primarily on the presence of *P. contorta* in the surrounding area, though not on the density of those surrounding *P. contorta*, suggesting that seed supply is sufficient even with few *P. contorta* in proximity to the meadow. Indeed, mature *P. contorta* are able to produce $59,409 \pm 68,806$ SD seeds (Vander Wall 2008), and the wind-dispersed *P. contorta* seeds often travel 30-60 m from the parent tree (Schmidt and Alexander 1985). On average amongst our 30 meadows, less than 2% of a meadow's area is more than 40 m from the nearest forest edge. Thus, the majority of the area of these meadows is well within range of seed produced by surrounding forest trees.

Encroachment density was also enhanced at higher temperatures, lower precipitation, and under conditions conducive to drier soils, which suggests that meadows may become increasingly vulnerable to heavy encroachment with climate change. Predictions for the Sierra Nevada region estimate that temperature will increase 3.3 °C over the 1985-1994 period by 2060-2069 while winter precipitation will rise only 5% over the same period (Pierce et al. 2013). This is likely to contribute to warmer, drier meadows more susceptible to encroachment.

High density of conifer encroachment depended to a lesser extent on lower elevation, which could also increase vulnerability to encroachment with climate change. Because we explicitly included temperature and precipitation in the models, it is unlikely that these are the mechanisms by which elevation affects encroachment intensity. Instead, there are biotic changes such as shifts in the herbaceous meadow vegetation (e.g., Potter 2005) that elevation could be a proxy for, and different meadow species could be more or less successful at excluding pine seedlings. With evidence that many plant species are moving upward with climate change (e.g., Lenoir 2008), movement of lower elevation

species into higher elevation meadows could remove limits on encroachment provided by existing meadow vegetation or even facilitate encroachment.

With melt date not a significant driver of encroachment intensity, the length of the growing season appears not to play a strong role in the success of encroaching conifers. Indeed, cold adapted conifers can quickly recover full photosynthetic capacity in spring – some pine species can recover in as little as 1-3 days following emergence above the snow level (e.g., Ottander and Oquist 1991, Ottander et al. 1995, Suni et al. 2003) and *P. contorta* can recover in 4-7 days (Monson et al. 2005). These short recovery periods would allow conifers to take advantage of even short growing seasons, minimizing their sensitivity to growing season length.

Temporal Patterns

The composite regional encroachment time series showed encroachment starting around 1900 with a number of peaks throughout the twentieth century. Various peaks match those found in a number of other central Sierra Nevada studies (Cunha 1985, in 1 meadow; Helms 1987, in two meadows; Millar et al. 2004, in 10 meadows; Nelson 2008, in 1 meadow). This indicates a synchrony of encroachment beyond our study meadows. Additionally, the fact that peaks in our study match with those found in studies conducted nearly thirty years ago (Cunha 1985, Helms 1987) helps to show that evidence of older peaks is not being lost due to tree mortality.

Both seed supply and seedling survival/establishment were important in predicting the timing of encroachment, with seedling survival having a stronger impact on the overall number of successful recruits. In contrast, no conditions during the year of germination showed as significant drivers of recruitment. This emphasizes the importance of examining periods prior to and following germination rather than focusing simply on the year of germination.

During the three year seed production period, times of high snowpack led to high recruitment while during the establishment period, high recruitment was correlated with years with high summer temperatures, increased summer precipitation, and high winter snowpack. Results from the seedling establishment period are consistent with findings from Hessler and Baker (1997) who also found that tree establishment occurred during periods of high snowpack. Warm summer temperatures, combined with summer precipitation, could provide favorable growing season conditions. Insulation by spring snowpack could protect delicate seedlings from early season frost events. Years with high winter snowpack could also increase water availability in subalpine Sierran meadows that are highly dependent on snowmelt derived soil water storage and groundwater fluxes (e.g., Ratliff 1985, Lowry et al. 2010). Conifer recruitment into meadows could respond to climate change in several ways depending on the relative importance of warmer temperatures, which would increase establishment, versus lower snowpack, which would decrease both seed production and establishment.

Despite the uncertainty in individual mechanisms of recruitment response to climate change, our models predict that these meadows will fully convert from meadow to forest by the end of the century. By 2100, the mean stand density index (Reineke 1933) is forecasted to increase dramatically from the 2000 level and move well above the *Pinus contorta* forest density index determined by Cochran and Dahms (2000) under both A2 and B1 emission scenarios. Thus, it appears that the benefits of warmer temperatures and increased summer precipitation will overwhelm the negative impact of lower snowpack over the twenty-first century.

Limitations of our approach

The strength of our inferences is necessarily limited by the observational and correlative nature of our study. For the spatial analysis, we were also constrained by the coarse scale at which we were working. We have only a single value of the total number of trees in a meadow despite the fact that meadows are most often heterogeneous features with regions of very different vegetation and topography.

Similarly, there are caveats to our temporal analysis. Without a manipulative experiment we cannot test the validity of our models of conifer recruitment response to climate. Additionally, our model only predicted recruitment with trees surviving to age six and did not take into account mortality events affecting older trees. Our model is also applying a historical relationship to future climate conditions outside the historical range. There is the possibility of thresholds being crossed beyond which conifers will respond differently to climate drivers.

Conclusion

Our findings indicate that conifer encroachment is prevalent throughout the central Sierra Nevada, with recruitment increasing since approximately 1900. In order for encroachment to occur, meadows need some surrounding *P. contorta* to supply seed, after which encroachment is highest in meadows with parameters conducive to early season soil drying. However, while even a few trees may provide sufficient seed supply over a long timescale, there is annual variation in seed availability that partially drives the timing of encroachment. In order for high abundances of new recruits, periods of high snowpack need to be followed by periods of high summer maximum temperatures, high summer precipitation, and high snowpack for seedling establishment. We want to emphasize the importance of examining periods prior to and following germination rather than looking only at the year of germination.

Our study helps to predict the likelihood of future meadow persistence in the Sierra Nevada. It appears that encroachment is likely to continue to increase during the twenty-first century, with the average meadow experiencing a full type conversion from meadow to forest by the end of the century. Such a loss of meadow ecosystems would result in a

loss of the ecosystem services that they provide, including their capacity to store and regulate the release of snowmelt into streams. Without meadows to help regulate snowmelt release, winter flooding could worsen while periods of decreased summer stream flow could lengthen.

Key Life Stage Filters on Conifer Encroachment into Subalpine Meadows in the Central Sierra Nevada, California

Introduction

During the past 150 years, woody species have been encroaching into grassland ecosystems worldwide (e.g., Humphrey and Mehrhoff 1958; Brown and Archer 1989; Higgins and Richardson 1998; Van Auken 2000, Van Auken 2009, Lunt et al. 2010, Liu et al 2013). Both land management (Brown and Archer 1989, Shlesinger et al. 1990, Van Auken and Bush 1997, Miller and Halpern 1998, Takoaka and Swanson 2008) and climate change (Archer et al. 1995, Miller and Halpern 1998, Bauer et al. 2002) have been proposed as potential causes. Meadow ecosystems have experienced both shrub and tree encroachment (e.g., Moore and Huffman 2004, Bork and Burkinshaw 2009, Haugo et al. 2011, Brandt et al. 2013). In particular, meadows in the Sierra Nevada mountain range in California have a long history of conifer encroachment (Vale 1981, Ratliff 1985, Helms and Ratliff 1987, Vale 1987, Millar et al. 2004, Cooper et al. 2006).

Demographic matrix models provide a useful tool for examining the effects of different life stages on the overall growth rate of a population (Caswell 2001). Through sensitivity analysis, we can consider both the effects of changes in vital rates and the effects of small inaccuracies in our estimates of vital rates (Morris and Doak 2002). Population matrix models are widely used for evaluating the impact of management strategies on a target species (Menges 1986, Schemske et al. 1994). For example, in the classic case study of loggerhead sea turtles (Crouse et al. 1987), population matrix modeling allowed researchers to identify which life stages should be targeted for management strategies to protect the species.

We can use population matrix models to examine the importance of various life stages on conifer species encroaching into meadows. In order for conifers to successfully encroach into a meadow, they must pass through several life stages: seed production, germination, establishment, and survival of established individuals. Each successive life stage provides a juncture for potential limitation of encroachment, through either natural sources or management intervention.

Understanding the relative importance of each life stage can inform management decisions regarding meadow conservation. Here, we use field observations and demography modeling to examine the roles of seed production, germination, establishment, and survival of established trees as they relate to conifer encroachment in the central Sierra Nevada. We use stage-based matrix population models to identify the stage(s) that have the strongest impact on meadow conifer population size, and determine environmental drivers influencing each stage. Seed availability is likely a product of distance from the mature, cone-bearing forest trees. However, in the small or sinuous meadows we studied, we expected seed to be available throughout the meadow. We expected survival of established trees to be high, driven largely by regional climate

conditions. Therefore, we hypothesized that germination and establishment likely play the most limiting role to conifer population sizes in meadows, and that these stages would be most strongly impacted by microhabitat conditions rather than macroclimate.

Methods

We conducted repeat surveys of conifer abundance and age in 30 subalpine (>2700 m elevation) meadows in Yosemite National Park (YNP) from 2009-2012. Meadows were chosen in remote locations to minimize direct anthropogenic impacts. We used our repeat survey data to create population transition matrices for demographic modeling. These models allowed us to explore the importance of different life stages. In order to examine drivers of spatial patterning within a meadow, we collected microclimate data and installed seed traps in a subset of 5 meadows.

Lubetkin et al (in prep) found that encroachment into subalpine meadows in the central Sierra Nevada is predominantly by Sierra lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *murrayana* (Balf.) Engelm.). *P. contorta* is well adapted to encroach into meadows, being shade intolerant with seedlings germinating best in full sunlight (Lotan and Critchfield 1990), while being tolerant of high water tables (Minore 1970, Cochran 1972). For *P. contorta*, cones initiate in late summer with seeds dispersing in fall two years later (Owens 2006). While *P. contorta* varieties in other locations are often serotinous, those in our study location within the Sierra Nevada, *P. contorta* var. *murrayana*, produce primarily non-serotinous cones (Lotan and Critchfield 1990). The majority of seedlings (75 – 90%) germinate within two weeks of snowmelt the following spring (Lotan 1964). The designation of what constitutes the establishment period varies; here, we define establishment as beginning immediately after germination, and use a mortality curve to define the end of establishment as the age at which the mortality rate drops below 10%. Established adult *P. contorta* commonly live up to 300 years (Kaufmann 1996), though individual trees can live up to 600 years (Keeley 1981).

Conifer Surveys

We chose potential survey meadows using the 1997 digital vegetation map for YNP (Aerial Information Systems 2007). From the subset of meadows in designated wilderness with intermediate areas (< 200,000 m² and > 2,000 m²), in the subalpine/alpine zone (above 2700 m), over 2.4 km from a paved road, and accessible (< 2.4 km from the nearest trail), we chose 40 meadows using a stratified random design based on surrounding vegetation and the 2004/2005 winter average snowmelt date calculated from daily MODIS imagery (see Berlow et al. 2013 for discussion of snowmelt date calculations). Snowmelt dates were grouped into quartiles within each of which 10 meadows were chosen at random—8 with conifers adjacent to the meadow, and 2 with no conifers within a 50 m buffer around the meadow. Of these 40 meadows, we were able to visit 30. The final meadows included 5-6 meadows with surrounding conifers and 1-2 without surrounding conifers in each snowmelt quartile.

We conducted surveys of 22 meadows in 2009, and visited 20 of these and 8 new meadows in 2010. We continued to survey these 30 meadows in 2011 and 2012, focusing on young (1-10 year old) trees. Initial surveys were conducted using two to six (depending on size and homogeneity of the meadow) three m wide belt transects, each selected to be representative of a region of the meadow characterized by a shared encroachment pattern. Transects ran along cardinal directions and spanned the meadow/forest transition zone. These transects began in the surrounding mature vegetation and extended either 50 m into the meadow where the meadow diameter was >100 m, or across the width of the meadow where the meadow diameter was <100 m. Along each transect, we recorded the location, species, height, diameter (basal for trees <1.3 m tall or diameter at breast height for taller trees), and age (based on node counts, tree cores, or a size/age regression equation) of all conifers whose bases are located within the 3 m belt. We reoccupied transects using GPS and photo documentation in 2010-2012, focusing on young seedlings and recording tree mortality.

We estimated age of younger trees based on nodes/branch whorls for trees up to ~2 m tall and ~40 years old. Taking cross-sections from fourteen trees up to ~1.5 meters tall, we were able to corroborate that all fourteen of these Sierra lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *murrayana* (Balf.) Engelm.) meadows were uni-nodal (producing only a single whorl of branches per year), confirming the validity of our node counts. We estimated ages of larger trees using a size/age regression. To calibrate this regression, for each meadow up to 10 *P. contorta* spanning the size range of larger (>2 m tall) trees were cored and aged using standard tree-ring cross-dating techniques (see Fritts 1976). This allowed us to examine conifer age structure.

We outfitted a subset of five meadows with seed traps, which were placed in three meadows in 2010 to capture seeds from the 2010-2011 season, and in all five meadows in 2011 to capture the 2011-2012 season. *P. contorta* seeds are dispersed in fall and early winter, so seed traps were deployed in late summer. In each meadow, we placed seed traps at regular intervals offset five m from the conifer transects. Seed traps were 0.5 x 0.5 m wooden frames with fine wire mesh bottoms, screening to capture the seeds, and 0.64 cm hardware-cloth on top to exclude seed predators. We collected seeds from the traps in early summer of the year following deployment.

Microsite Measurements

In the same five meadows where seeds were collected, we measured soil moisture using a PR2-Profile Probe (Delta-T Devices Ltd) at monthly intervals throughout the 2012 and 2013 field seasons. We installed access tubes for the probe at 10 m intervals along the center of each transect in each meadow in 2011 and collected soil moisture measurements at 10, 20, 30, and 40 cm depth. We used a calibration for organic soil to convert from voltage to volumetric water content. Each tube was accompanied by an iButton thermochron to obtain measurements of soil temperature every four hours. iButtons were buried at 5 cm depth to match rooting depth of new conifer germinants (Balisky and

Burton 1997). The iButtons further allowed us to determine the day snowmelt occurred within each instrumented meadow based on a rapid rise in soil temperature. This gave us more exact melt dates, including within-meadow variation, as opposed to the average melt dates used to stratify meadows for selection.

Data analysis

We conducted all statistical analyses using R 3.0.1 (R Core Team 2013). Using transect as the unit of replication, we used Pearson's correlation tests to compare the distribution along transects of new germinants among years, as well as the percent of new germinants establishing to their second year. Using each square meter along a transect as the unit of replication in order to characterize microsites with versus without new germinants, we used Kolmogorov-Smirnov (K-S) tests to compare the distribution of melt dates, absolute shallow soil moisture (<10 cm) at four times across the growing season, and the change in soil moisture between measurement dates. Similarly, we used K-S tests to compare the distribution of fates (survived, died, disappeared) of two-year-old seedlings based on their developmental stage at the time of the prior year's survey. We also used K-S tests to compare microsite conditions with no, low, or high abundances of establishing trees (up to the age when mortality leveled off) and adult trees. For the older trees we used an average soil moisture across the four depths (10, 20, 30, and 40 cm) since their roots extend deeper.

Life stage modeling

We used matrix population modeling to test the importance of the various life stage transitions to overall conifer population sizes in meadows. Given that we were interested in seed production, germination, establishment, and survival of adult trees, we used deterministic stage-specific (Lefkovich) transition matrices created from field-based vital rates for each of the three year-to-year transitions surveyed (see Caswell 2001, Morris and Doak 2002). We divided the stages into one germination phase, three establishment phases, and six adult survival phases (Table 3). Using separate deterministic matrices for each year-to-year transition allowed us to examine interannual variability in the key life stages identified depending on the parameters used to create the matrix.

We used a simple metapopulation model following Caswell (2001), where the external forest trees providing seed were treated as a much-reduced second population with 100% survival and constant annual seed production of 41,825 seeds per year (fertility). Fertility was based on average seed production by *P. contorta* var. *murryana*, as measured over 5 years by Vander Wall (2008). To model early stages of encroachment when the seed source is solely external to a meadow, we set our model to allow no meadow trees to become sexually mature. To model later stages of encroachment, once encroaching meadow trees have reached sexual maturity, we added fertility for meadow trees above 40 years old (based on the ages of the youngest observed cone bearing meadow trees) to the metapopulation model described above. Fertility for meadow trees was set as 50% of

the forest tree seed production based on cone counts conducted in 2013. This assumed equal numbers of viable seeds per cone in meadow trees and forest trees.

We examined the relative sensitivity of the asymptotic-growth rate (λ) to changes in each vital rate using elasticities (Kroon et al. 1986). Elasticities are proportional to each matrix element, allowing us to directly compare responsiveness of λ to fertility and survival rates despite the large difference in their magnitudes. We calculated elasticities using the popbio package (Stubben and Milligan 2007) in the statistical environment R (version 3.0.1).

Results

Seed Availability

While seed was more abundant nearer the forest-meadow transition zone, there was still seed available up to 40 meters from the nearest cone-bearing tree (Figure 11). In the small and/or sinuous meadows in our study, only an average of two percent of each meadow was further than 40 meters from the nearest forest edge. Seed availability was generally higher in 2011 than in 2012 (mean seeds/m² \pm 1 SE for 2011 17.2 ± 1.2 , 2012 4.8 ± 0.4) and the number of seeds in a given seed trap in 2011 and 2012 were independent ($R^2 = 0.007$, $n = 24$, $p = 0.69$).

Germination

Germination was highly variable from year to year and was more successful in drier areas. Abundance of new germinants was nearly an order of magnitude greater in 2009 than in any of the following three years (total across 30 meadows 2255 in 2009 vs. 273 in 2010, 280 in 2011, and 274 in 2012). Germination showed moderate spatial consistency, with new germinants abundant in the same positions along the same transects across all four years (Table 4). Locations with and without 2012 germinants differed in microsite conditions: locations with new germinants melted on average 3.8 days later in 2012 than did locations without germinants (day 139.6 with versus day 135.8 without 2012 germinants, $p=0.065$). Locations with germinants also experienced continuous soil drying throughout the summer, while most locations without germinants stopped drying after the initial two months following snowmelt.

There appears to be a flush of germination soon after snowmelt, followed by diminishing germination over the growing season. At an average survey date of 114 \pm 12.7 days after snowmelt in 2012 (determined as the number of days past the average snowmelt date for a given meadow that the meadow was surveyed), we found only 3.2% of new germinants still in their seed coats with cotyledons visible (CV), 12.5% of new germinants with their seed coats shed and only cotyledons (SS), and 84.2 % of new germinants already showing growth of primary leaves (PL).

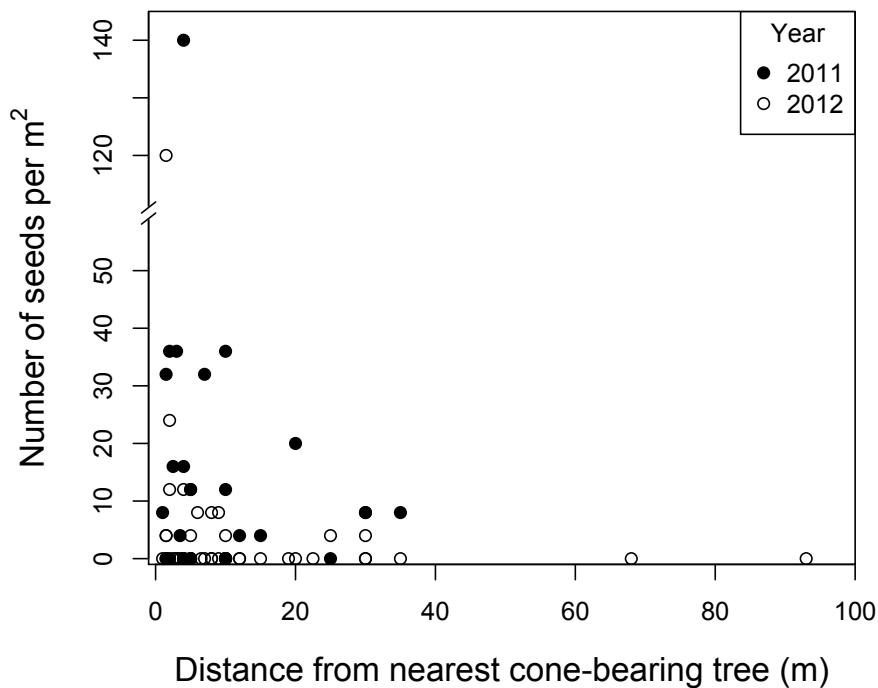


Figure 11. Seed abundance as a function of distance from the nearest cone-bearing tree. Seed was collected in traps from a subset of three meadows in 2011 to capture the 2010 seed rain, and from a subset of five meadows in 2012 to capture the 2011 seed rain.

Table 4. Pearson correlation coefficient for spatial distribution of germinant abundance. Correlations were computed for each transect in 30 meadows, including only transects that had at least five germinants in both years.

	2009	2010	2011
2010	0.33 ± 0.02^1 (15) ²	---	---
2011	0.27 ± 0.02 (15)	0.39 ± 0.09 (10)	---
2012	0.39 ± 0.04 (11)	0.30 ± 0.05 (7)	0.42 ± 0.11 (9)

¹ Average Pearson's correlation coefficient \pm 1 SD

² Number of transects with at least five new germinants in each year

Establishment

New germinants surviving to their second year showed little interannual spatial consistency, with locations along the transects showing high establishment in one year having little relation to establishment in other years (Table 5). As expected given the lack of spatial consistency, early establishment success did not vary with seedling microsite melt date ($p=0.25$) or any of the four soil moisture measurements during the summer ($p=0.53$ one month following snowmelt, 0.10 two months following snowmelt, 0.33 three months following snowmelt, and 0.29 four months following snowmelt).

The developmental stage at the time of survey, and thus timing of germination, was not a significant factor explaining seedling establishment from one year to two years. Of those with only cotyledons visible (stage CV), 100% of seedlings went missing by the following season. Of those with their seed coat shed (stage SS), 9% survived, 9% were visibly dead, and 82% went missing by the following season. Of those already producing primary leaves (stage PL), 16% survived, 12% were visibly dead, and 72% went missing by the following season. However, there was no significant difference in the fate distribution between any of the stages (chi-squared test showed CV:SS $p=0.52$; CV:PL $p=0.10$, SS:PL $p=0.52$).

Mortality remained substantial until trees reached 10 years old (Figure 12), a period we inferred to be the establishment phase. Unlike during the initial establishment from age one to age two, microsite snowmelt timing and soil moisture did explain some differences in 10-year establishment (Figure 13). Locations with low abundance (0.1-1 trees per m^2) of trees 10 years and younger had wetter soil early in the season than did locations with either no establishing trees or a high abundance of establishing trees. Toward the end of the season, locations with many establishing trees became significantly drier than locations with few or no establishing trees. Finally, there was no consistent pattern of melt date among locations with different abundances of establishing trees.

Survival of Established Trees

Table 5. Pearson correlation coefficient for spatial distribution of survivorship of new germinants establishing to their second year. Correlations were computed for each transect, including only locations that had at least 5 initial germinants in both years.

	2009	2010
2010	0.16 ± 0.04^1 (13) ²	---
2011	0.12 ± 0.03 (16)	-0.16 ± 0.06 (7)

Most mortality occurred in the first 10 years following germination (Figure 12a), leaving older trees with nearly 100% survival over the four years of the study. However, the 2011-2012 winter season, with unusually low snowpack, resulted in mortality among trees up to 30 years old (Figure 12b). Locations with many adult trees were those that dried to significantly lower soil moisture levels by 3 months after snowmelt when compared to locations with few or no adult trees, and locations with both high or low abundances of adult trees dried to significantly lower soil moisture levels by 4 months after snowmelt when compared to locations with no adult trees. Locations with high abundances of adult trees showed a very complex distribution of melt dates that differed significantly from locations with few or no adult trees (Figure 14). Locations where adult trees died over the course of the survey did not differ in terms of microsites from the locations where adult trees survived (melt $p=0.18$, soil moisture at 1 $p=0.63$, 2 $p=0.99$, 3 $p=0.66$, and 4 months $p=0.37$).

Life Stage Modeling

Population dynamics of conifers in high elevation meadows were modeled using vital rates of seed production, survival, and growth determined from field observations. For seed production, we counted cones on both forest and meadow trees in 2013. Sixty-eight cone-bearing meadow trees produced 31.2 ± 1.2 SE cones per tree, while 181 cone-bearing forest trees produced 67.1 ± 0.8 SE cones per tree. Using the assumption that there were equal numbers of seeds per cone for meadow and forest trees, for the model we set fertility of younger meadow trees to half that of forest trees for a rough approximation of internal seed availability. We then gradually scaled up fertility of meadow trees with increasing age so that the oldest stage classes of meadow trees had fertility equal to that of trees in the surrounding forest. Both seedlings' and adult trees' survival and growth to the next larger stage were calculated using the three year-to-year transitions between 2009 and 2012 (Table 6).

We ran two simulations within the computer model, each representative of a different stage of meadow encroachment. The first scenario was equivalent to early encroachment when seed supply was external to the meadow, coming from the surrounding forest. This was the case until recently for most meadows, when interior meadow trees had not yet reached sexual maturity. To maintain this scenario, our model allowed no meadow trees to become mature, cone bearing trees. The second scenario was equivalent to later stages of encroachment once meadow trees have reached sexual maturity. In this scenario, our model allowed meadow trees to become sexually mature at age 40 (based on personal field observations of cone bearing tree ages in our study meadows).

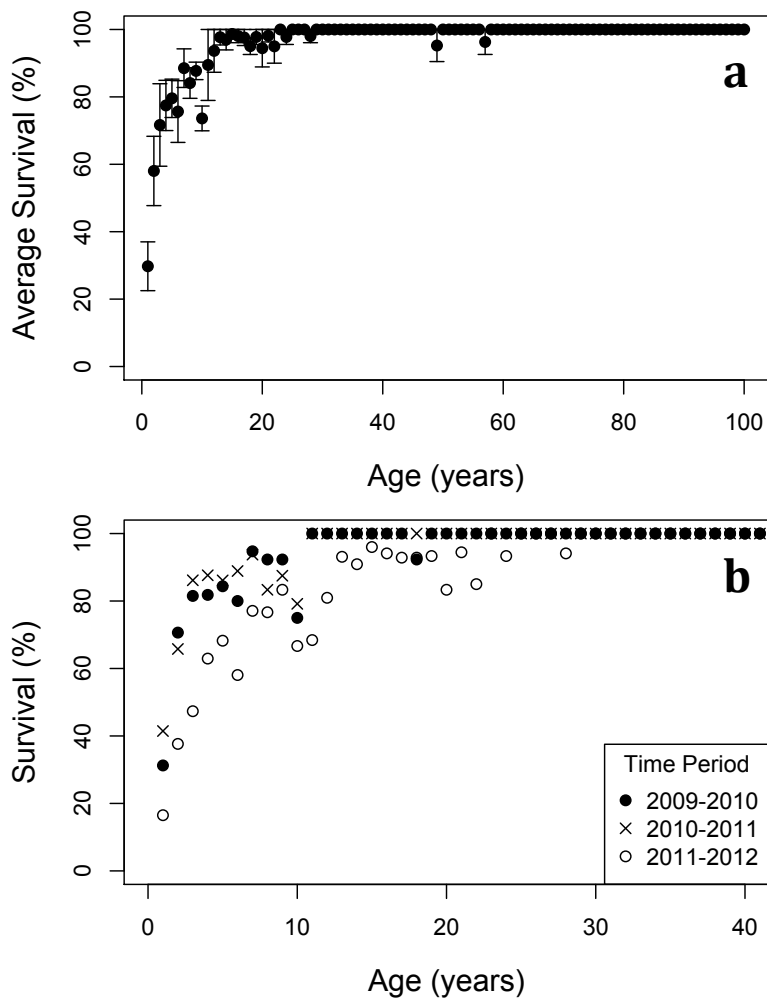


Figure 12. Average and yearly survival as a function of conifer age. Survival rates were determined from four years of repeat surveys across 30 meadows. **a)** Survival averaged across all three year-to-year transitions. **b)** Annual survival.

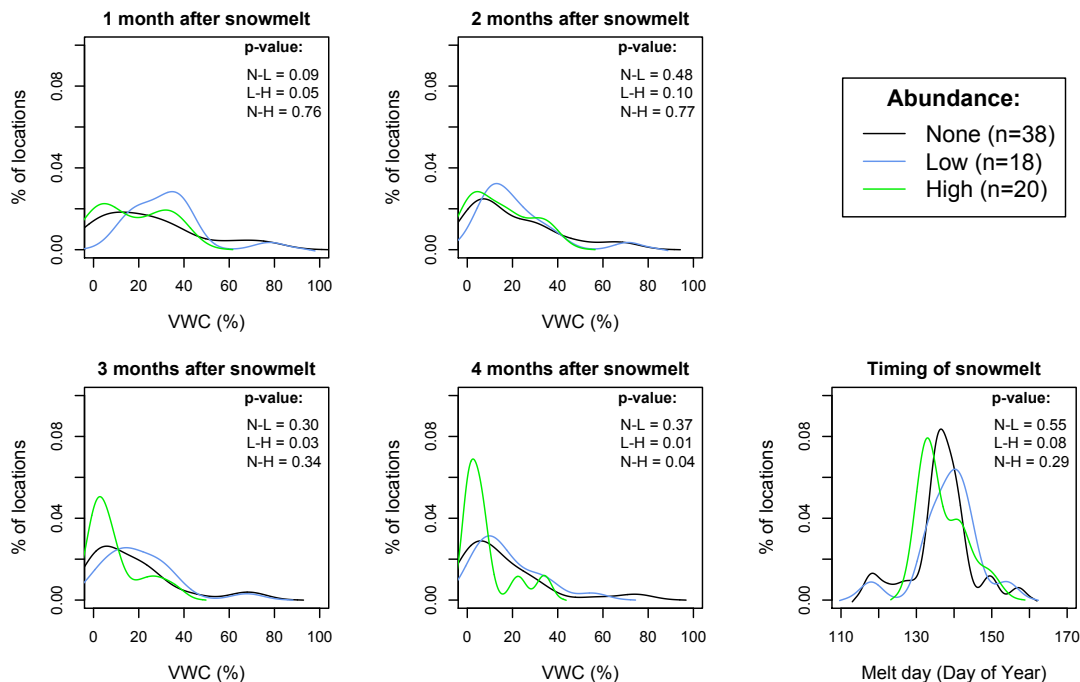


Figure 13. Microsite conditions of locations with varying abundances of establishing trees. Trees were considered to still be in the establishment phase up until 10 years of age. Volumetric water content (VWC) is averaged across all soil depths (10, 20, 30, and 40 cm). Locations with low abundance of establishing trees were those with 0.1-1 trees per m^2 , while those with high abundance of establishing trees were those with more than 1 tree per m^2 .

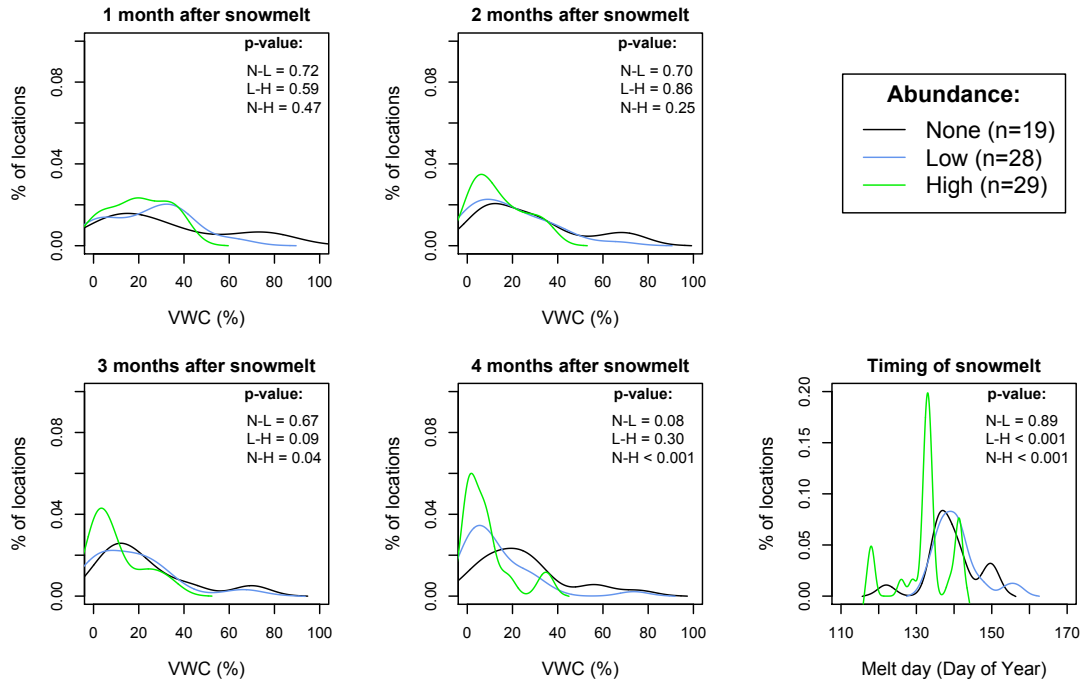


Figure 14. Microsite conditions of locations with varying abundances of adult trees. Adult trees were those older than 10 years of age. Volumetric water content (VWC) is averaged across all soil depths (10, 20, 30, and 40 cm). Locations with low abundance of adult trees were those with 0.1-1 trees per m^2 , while those with high abundance of adult trees were those with more than 1 tree per m^2 .

The asymptotic growth rate (λ), which indicates the long-term growth rate of the population, varied in its sensitivity to vital rates of survival and growth under the two modeled scenarios. Under the scenario with external seed only (early in the encroachment sequence), λ was insensitive to germination and establishment rates, and most sensitive to adult survival and fertility. Thus, even small changes in adult survival and fertility caused large changes in λ , while equivalent changes in germination and establishment rates caused little change in λ . This pattern was similar across all three seasons (Figure 15), with fertility playing a smaller role in 2009 than in either of the following years. Under the scenario with internal as well as external seed (later in the encroachment sequence), λ was more sensitive to germination and establishment than in the scenario without internal seed, but the strongest influence on λ continued to come from adult survival. However, this must be viewed in the context of the likelihood of interannual variation in different vital rates. During our four survey years, adult growth and survival were nearly constant while germination and establishment were highly variable. Thus, germination and establishment rates may change enough on an interannual scale to have a large influence on the population growth rate λ .

Table 6. Vital rates determined from four years of field surveys in Yosemite National Park.

Vital Rate	Estimated Value		
	2009-2010	2010-2011	2011-2012
G, % of seeds successfully germinating	0.060	0.007	0.008
E ₁ , establishment for ages 1-3 years	0.58	0.81	0.67
E ₂ , establishment for ages 4-6 years	0.80	0.90	0.74
E ₃ , establishment for ages 7-10 years	0.93	0.96	0.82
S ₁ , survival for ages 11-20 years	0.99	0.99	0.99
S ₂ , survival for ages 21-40 years	1.00	1.00	1.00
S ₃ , survival for ages 41-80 years	1.00	1.00	1.00
S ₄ , survival for ages 81-150 years	1.00	1.00	1.00
S ₅ , survival for ages 151-300 years	0.99	0.99	0.99
S _M , survival for mature forest trees	1.00	1.00	1.00
G _{S1} , growth for seedlings ages 1-3 years	0.33	0.33	0.33
G _{S2} , growth for seedlings ages 4-6 years	0.33	0.33	0.33
G _{S3} , growth for seedlings ages 7-10 years	0.25	0.25	0.25
G _{A1} , growth for adults ages 11-20 years	0.10	0.10	0.10
G _{A2} , growth for adults ages 21-40 years	0.05	0.05	0.05
G _{A3} , growth for adults ages 41-80 years	0.025	0.025	0.025
G _{A4} , growth for adults ages 81-150 years	0.014	0.014	0.014
G _{A5} , growth for adults ages 151-300 years	0.00	0.00	0.00
F _M , fertility of mature forest trees	41825	41825	41825

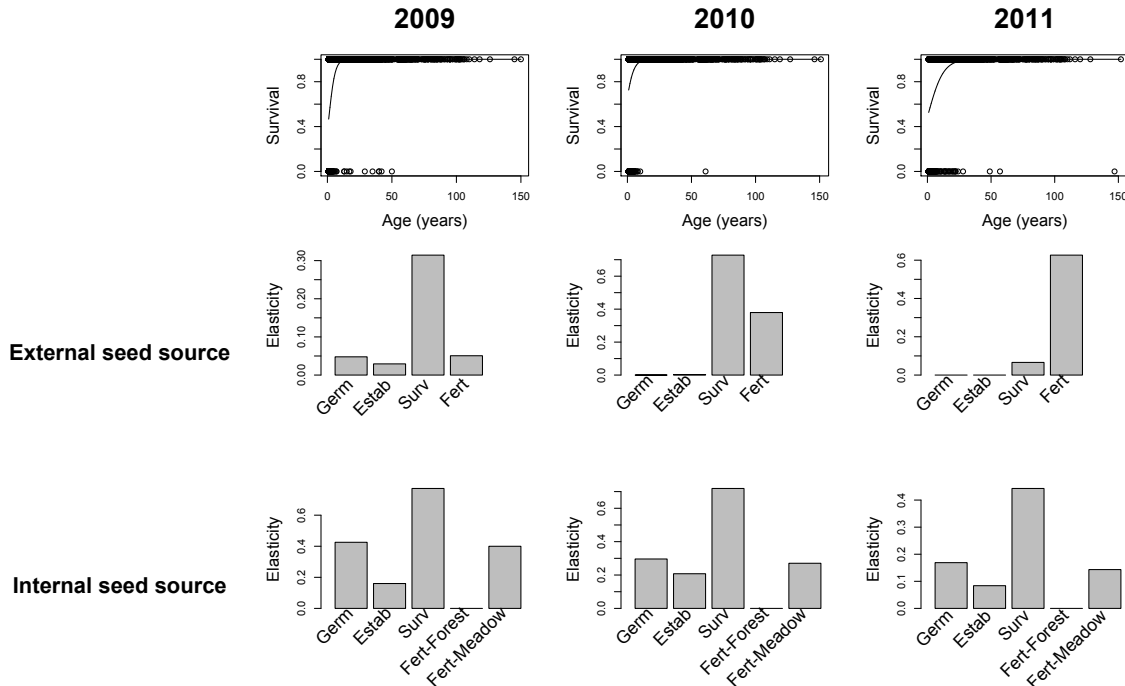


Figure 15. Logistic regressions used in the matrix models, and resultant elasticities over 3 year-to-year transitions based on populations with either external or internal seed sources. “External seed” indicates the period early in the encroachment history when all seed comes from the surrounding forest trees. “Internal seed” indicates later periods of encroachment, once meadow trees reach cone-bearing age around 40 years old. “2009” indicates the 2009-2010 transition, etc. “Germ” indicates germination, “Estab” indicates the establishment phase, “Surv” indicates the survival of adult trees, and “Fert” indicates fertility, or seed production.

Discussion

We considered four stages necessary for successful encroachment: seed production, germination, establishment, and survival of established individuals. Of these four stages, the only stage that had no consistent spatial pattern was seed production. Seed was available up to 40 m from the nearest cone-bearing tree, and on average only two percent of a meadow’s area is further than 40 m from the nearest meadow edge. Over a 5-year study, Vander Wall (2008) estimated that *P. contorta* var. *murryana* in the Carson Range, CA, produced $59,409 \pm 68,806$ SD seeds per year of which 70.4% dispersed to the ground (the remaining 29.6% experienced pre-dispersal mortality). Thus, even a modest number of forest trees could disperse a substantial number of seeds into a nearby meadow. Trees in the current wave of encroachers, which are nearing cone-bearing age of 40 years (while some *P. contorta* have been shown to begin producing cones even before 10 years of age (Owens 2006), in central Sierra meadows, conifers do not begin to produce cones

until approximately 30-40 years of age, personal observation) could soon provide yet another source of seed. Thus, overall seed input could soon dramatically increase.

Unlike seed, which was available throughout most meadows, trees were spatially patchy within meadows. This appears to be linked to microsite conditions, which differed between locations with new germinants, establishing trees, and adult trees, and locations without trees of each life stage. While our study is correlative, it is consistent with other experimental studies. For example, Drescher and Thomas (2013) found that various tree species with fall seed dispersal, similar to *P. contorta*, experienced decreased seed germination after a snow removal manipulation. This finding supports our observation that new germinants occurred more often in locations with later snow melt. Snow can provide thermal insulation for germinating seeds, protecting seeds and new seedlings from early season frost events.

Soil moisture patterns were correlated with presence of trees of all three stages beyond the initial seed stage. While studies have indicated that *P. contorta* seedlings germinate very soon after snowmelt (Lotan 1964), it takes time for seedlings to fully emerge. At survey dates as late as four to five months after snowmelt some seedlings were still in their seed coats, and many had only recently shed their seed coats. Thus, soil moisture content two to three months after snowmelt could easily affect seedling emergence. Our finding that new germinants occurred in locations that retained high soil moisture levels up to three months after snowmelt is consistent with findings that drought is a common cause of mortality among first year *P. contorta* seedlings (Lotan 1964) with very shallow root systems (Noble 1979).

For both establishing and adult trees, locations with trees reached drier soil moisture levels than locations without trees. It appears that the stronger the summer dry-down of a location, the greater the chance of successful establishment and the greater the chance of adult tree presence. Adult tree spatial patterns could be following the pattern of establishing trees because adult trees can only exist where they have successfully established. These two stages are likely interacting, since there was no effect of microsite conditions on likelihood of mortality when we examined locations where adult trees died.

There are several important caveats to our microsite-tree correlations. One is the possibility of spurious correlations. Another main caveat is the difficulty of teasing apart cause and effect. Although the new germinants have such small root systems and low transpiration rates that they are unlikely to affect the soil in which they are growing, older trees could be drawing down the water table. Thus, establishing and adult individuals could be capable of growing primarily in locations that reach very dry late-season soil moisture levels, or those trees could be exhausting available soil moisture and causing dry late-season soil moisture.

Having explored the effects of microsite conditions on different life stages, and the role that this plays in spatial patterning, we then used matrix modeling to identify key life stages influencing population viability. Using a metapopulation matrix modeling

approach, we were able to explore the relative importance of each vital rate to the overall population growth term (λ) when the seed source was external to the meadow and compare this to later in the encroachment progression once trees grew old enough to provide an internal seed source. Across the three year-to-year transitions (2009 to 2010, 2010 to 2011, and 2011 to 2012), λ was initially much more sensitive to survival among adult trees than to germination or any portion of the establishment phase. When we calculated elasticities for a model later in encroachment, now incorporating internal seed sources, λ became more sensitive to germination and establishment phases. However, survival of adult trees continued to have the strongest effect on λ . This follows the general pattern that a plant population's λ is increasingly sensitive to survival and decreasingly sensitive to fecundity as life span increases (Silvertown et al. 1996, Ramula et al. 2008). For the long-lived *P. contorta*, a given population's growth rate should thus be highly sensitive to adult survival.

One reason for examining the effects of life stages on λ is to inform management decisions. Given that λ was mostly insensitive to germination and establishment, management actions aimed at young encroachers are likely to be ineffective. Germination and establishment rates are already very low, so drastic management actions would be needed to further decrease them. Instead, it would be more effective to allow trees to go through the naturally limiting process of establishment and focus on older trees.

Adult survival showed no correlation with microsite conditions while adult abundance did vary with microsite. Thus, there may be different factors influencing the population growth and the spatial distribution. It appears that the overall growth rate of an encroaching conifer population is dependent on adult survival, while the spatial distribution of that population may depend more strongly on microsite conditions that drive seedling germination and establishment. Soil dry-down, especially late in the summer, is likely conducive to seedling germination and establishment, causing a spatial pattern in which adult trees are located in areas where soils reach dry late-season levels.

Lodgepole pine (*Pinus contorta*) established in meadows respond to a common topoclimate distinct from that in the adjacent forest

Introduction

Woody plants are sensitive to a number of climate factors, causing years with varying climate to result in growth rings of different widths (Fritts 1976). Studies often assume that woody plants will respond to a regional climate signal, or macroclimate, on a scale of 10s to 100s of kilometers (e.g., Fritts 1976, Briffa 2000). However, studies have recognized the importance of fine scale topoclimate, climate dependent on terrain at a local scale of topography and microhabitat (Geiger 1969, Slavich et al. 2014). Indeed, topographic position can decouple tree growth from the macroclimate (e.g., Oberhuber and Kofler 2000). While some species of woody shrubs have been shown to respond strongly to a regional signal with minimal influence of topoclimate (Baer et al. 2008), Knutson et al. (2008) found trees to be more sensitive to drought when they were growing on steeper slopes. Similarly, Duethorn et al. (2013) showed trees along lakeshores to be more sensitive to temperature than were trees that were only several meters further inland, though lakeshore and inland trees were equally sensitive to precipitation. Thus, it appears that topography and location on the landscape can influence the strength of a tree's response to climate, and that the macroclimate-topoclimate interactions can differ depending on the climate variable. This would indicate that predictions of tree growth under climate change conditions need to take topographic position into account.

One landscape feature likely to result in a different topoclimate than the surrounding area is mountain meadows, which are often areas with local high water tables. Mountains in general have varied terrain that results in a complex climate signal (Barry 1992, Pape and Loeffler 2004, Loeffler et al. 2006). Along with the climate heterogeneity associated with complex mountain terrain and the higher soil moisture levels associated with meadows, trees established in mountain meadows would not be under the overstory trees present in the forest. Thus, they would likely experience higher solar radiation, colder minimum temperatures, and less interception of precipitation than would trees in a nearby forest. Lodgepole pine, *Pinus contorta*, encroaching into meadows (Vale 1981, Ratliff 1985, Helms and Ratliff 1987, Vale 1987, Millar et al. 2004, Cooper et al. 2006) provides an opportunity to explore the way in which trees in varied landscape positions respond to climate variability.

Examining the role of meadow topoclimate in modifying the response of trees to historical climate variability can also provide a case study in how incorporating topoclimate might enable us to adjust predictions of landscape change. The continued persistence of mountain meadows is uncertain given ongoing woody plant encroachment (e.g., Takaoka and Swanson 2008). Under climate change conditions, many meadows are predicted to experience a full conversion to forest by the end of the twenty-first century (Lubetkin et al., in prep). However, this prediction of meadows transitioning to forest

fails to take into account potential topoclimate impacts on growth of conifers established in meadows.

We present a study based on growth of trees established in subalpine meadows of the Sierra Nevada, paired with growth of trees in the immediately surrounding forest, to consider whether a meadow environment modifies the response of adult trees to climate. We ask: 1) do meadow trees show a coherent signal across locations, and 2) do meadow and forest trees respond equally to the same climate variables? If topoclimate is a driving factor, we would expect the shared meadow environment to result in a strongly coherent signal across meadow locations. Similarly, we would expect to see a difference in the climate variables meadow trees versus forest trees respond to, or a difference in direction or magnitude of growth response between the meadow and forest trees.

Methods

We collected 80 cores from trees established in 12 subalpine (~2750-3400 m elevation) meadows in Yosemite National Park from 2009 to 2012. We also collected 144 cores from trees in the forest immediately surrounding each meadow. We correlated tree ring-width patterns with regional climate signals for the Yosemite National Park area obtained from meteorological stations and snow courses.

Tree Cores

We collected one core each from 224 lodgepole pines (*Pinus contorta* var. *murrayana*) within or adjacent to 12 meadows, all of which were chosen to minimize direct anthropogenic impact (in wilderness areas, more than 2.4 km from a paved road) and were located in the subalpine zone at elevations ranging from 2750 to 3350 m. Eighty cores were from trees established in meadows, while the remaining 144 were from forest trees within 200 m of a meadow. Of the 12 meadows, we took 10 meadow and 20 forest trees from four meadows, and took 5 meadow and 8 forest trees from an additional eight meadows. Cores were taken at a height of 0.5 to 1.0 m depending on the geometry of the tree, and were taken perpendicular to the slope for forest trees.

We visually cross-dated all cores with a dissecting microscope and measured them to 0.01 mm resolution using a Velmex sliding stage apparatus. We used COFECHA for further cross-dating, then used the dplR package (Bunn et al. 2012) in R (R Core Team 2013) to calculate basic statistics of ring width means, standard deviations, and first order autocorrelations. We detrended each series (using a modified negative exponential curve) and calculated various rbar and expressed population signal (EPS) values. The rbar values are average correlations (see Briffa 1995), and EPS indicates how well an individual chronology represents the hypothetical “true” chronology. We then built site residual, mean-value chronologies using Tukey’s biweight robust mean separately for the meadow trees and the forest trees, as well as individually for each meadow.

Climate Data

We obtained historical April 1st snow water equivalent (SWE) from the Tioga Pass Entry Station snow course (CA Dept. of Water Resources, manual measurements taken monthly 1926 to present), and temperature and precipitation from the Yosemite Park Headquarters meteorological station (United States Historical Climatology Network v2.5, Menne et al. 2014).

Data analysis

All statistical analyses were conducted using R 3.0.1 (R Core Team 2013). We compared the tree ring width means, standard deviations, and first order autocorrelations between the forest and meadow trees using Student's T-tests. We then correlated our meadow and forest chronologies with each other using moving 10-year, 20-year, and 30-year windows with Pearson's correlation coefficients. This range of window lengths allowed us to consider both decadal and longer term trends. We also correlated the individual meadow chronologies with the chronology from trees in the immediately surrounding forest as well as chronologies from all other meadows.

In order to establish that the forest trees' chronology was consistent with that of other trees in the region, we obtained two tree ring width lists from the International Tree-Ring Data Bank (ITRDB, National Climatic Data Center) for *P. contorta* in Yosemite National Park (King and Graumlich, ITRDB CA580; Briffa and Schweingruber, ITRDB CA560). Both locations were in the subalpine zone (King and Graumlich, at Kuna Crest, 3065 m; Briffa and Schweingruber, at E. Eingang, 3000 m) matching our sites. We subjected the ITRDB tree rings to the same detrending and chronology building methods used with our tree rings.

To examine the reaction of the trees to climate variability, we used the bootRes package (Zhang and Biondi 2012) in R. The bootRes package is based on DENDROCLIM2002 (Biondi and Waikul 2004), which is designed to calculate bootstrapped response and correlation functions for tree ring chronologies. We used a moving 30-year window to examine how the tree growth response to climate has changed during the 20th century, in order to assess the climate drivers of *P. contorta* growth under varying climatic conditions. We set our dendroclimatic year as the previous September through the current August based on studies that have shown that the growing period ends around August in the Sierra Nevada (Royce and Barbour 2001), and used a 95% confidence interval.

Results

General Growth Patterns

We used Welch two sample t-tests to compare meadow and forest tree ring widths. For the period 1900-2010, the meadow trees had ring widths significantly larger than those of

the forest trees ($t=3.3$, $df=235.3$, $p=0.001$). The meadow trees also had more interannual variation in ring width than did forest trees ($t=5.5$, $df=211.4$, $p<0.001$), and less first order autocorrelation ($t=-3.0$, $df=236.8$, $p=0.003$).

Correlation of ring width indices for the meadow trees with each other within a meadow had $r_{\text{bar within}} = 0.404$ ($n=599$), and correlation amongst trees in all meadows was weaker with $r_{\text{bar between}} = 0.224$ ($n=7139$). Correlation of forest tree ring width indices with other trees surrounding the same meadow had $r_{\text{bar within}} = 0.243$ ($n=1946$), with correlation amongst trees surrounding all meadows resulting in $r_{\text{bar between}} = 0.094$ ($n=21890$). The effective r_{bar} for the forest (0.266) was in line with those from the ITRDB tree ring datasets (Eingang $r_{\text{bar}}=0.381$; Kuna $r_{\text{bar}}=0.481$). All tree ring sets had strong expressed population signals (EPS; Table 7). We also looked at ring width index statistics for meadows and the surrounding forest locations individually by meadow (Table 8). Each location showed stronger correlations among trees within the same meadow than among trees from different meadows. However, locations also showed stronger correlations among trees from different meadows than among trees in a meadow and trees in the immediately surrounding forest.

Chronologies

Pearson's correlation showed that meadow and forest trees were moderately correlated ($r=0.48$, $n=109$, $p<0.001$), and the forest trees were moderately correlated with the ITRDB chronologies (Kuna $r=0.47$, $n=89$; Eingang $r=0.53$, $n=82$). However, the strength of the correlation between meadow and forest trees varied over time (Figure 16). There appears to be a step change in the degree of correlation between the meadow tree chronology and that of the trees in the surrounding forests around 1950, at which point they go from weakly correlated to very strongly correlated. The correlation remains high through the mid 1980s, after which it shows a slowly decreasing degree of correlation (Figure 16). When we examined individual meadows, meadow chronologies were generally more strongly correlated with chronologies of other meadows than with the chronology from the immediately surrounding forest (Table 9).

Response to Climate Variability

Meadow and forest tree growth responded similarly to winter temperature, precipitation, and April 1st snow water equivalent (SWE) across the 1900-2010 period. Tree growth was negatively correlated with greater winter and spring precipitation and greater SWE, and positively correlated with higher spring temperature (Figure 17). Meadow trees' ring width indices were more strongly correlated with SWE ($r = -0.58$) than were forest trees ($r = -0.39$).

Unlike growth response to winter climate, response to temperature and precipitation during the growing season varied across the 1900-2010 period. Mid-century, both meadow and forest tree growth were positively correlated with previous September precipitation and negatively correlated with current year July precipitation. Toward the end of the century, both meadow and forest tree growth were positively correlated with

previous October and current June temperature. Forest tree growth was positively correlated with July temperature mid-century, while meadow tree growth was positively correlated with July temperature toward the end of the century (Figure 18).

Over the 1900=2010 period, total precipitation increased slightly, as did year-to-year variability (Figure 19a). Precipitation also began to be concentrated earlier in the year, with the fraction of precipitation falling in November increasing while the fraction of precipitation falling in April decreased (Figure 19b). Thus, toward the mid and end of century, when precipitation came earlier in the year, trees general responded more strongly to summer temperatures.

Table 7 Ring width statistics by site. Mean, stdev, and ar1 refer to the raw ring width data. They indicate the mean, standard deviation, and first-order autocorrelation, respectively. Rbar and EPS refer to detrended ring width indices. Rbar within is the mean correlation between trees in/near the same meadow location for meadow and forest, or within the same tree for Kuna and Eingang. Rbar between is the mean correlation between trees in/near different meadow locations for meadow and forest, or between different trees in Kuna and Eingang. Rbar effective is the overall effective correlation. EPS is the expressed population signal, indicating the strength of the composite signal.

	no. trees	mean	stdev	ar1	rbar within	rbar between	rbar effective	EPS
Meadow (this study)	80	1.85	0.85	0.64	0.404	0.224	0.439	0.899
Forest (this study)	144	1.55	0.59	0.69	0.243	0.094	0.266	0.848
Kuna (ITRDB)	35	0.76	0.23	0.60	0.380	0.260	0.381	0.913
Eingang (ITRDB)	22	0.81	0.25	0.55	0.485	0.357	0.481	0.911

Table 8 Ring width index statistics for individual meadow sites. Rbar effective indicates the effective correlation amongst all of the trees in that location. EPS is the expressed population signal, indicating the strength of the resultant chronology.

Meadow ID	meadow			forest		
	no. trees	rbar effective	EPS	no. trees	rbar effective	EPS
437	10	0.246	0.521	20	0.088	0.640
910	10	0.349	0.766	20	0.298	0.884
1024	5	0.571	0.727	8	0.135	0.507
1104	5	0.559	0.677	8	0.244	0.706
1490	5	0.166	0.370	8	0.280	0.725
1776	10	0.595	0.866	20	0.446	0.941
1830	10	0.519	0.821	20	0.242	0.809
1934	5	0.630	0.793	8	0.197	0.609
1977	5	0.475	0.648	8	0.252	0.702
2392	5	0.335	0.685	8	0.179	0.585
2398	5	0.166	0.286	8	0.365	0.805
2755	5	0.206	0.474	8	0.428	0.836

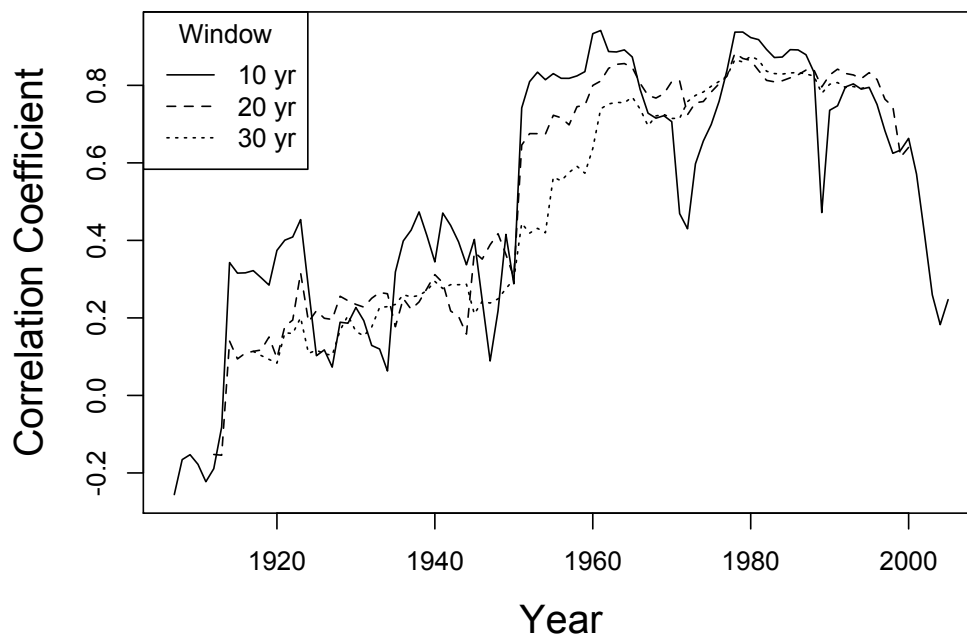


Figure 16. Strength of the correlations between forest and meadow trees. We calculated Pearson's correlation coefficients over a moving 10-year window, 20-year window, and 30-year window. Values are graphed at the mid point of each window.

Table 9. Correlations between meadow chronologies and the chronology from their surrounding forest and chronologies from all other meadow sites. Correlations were calculated for the residual chronologies for the period 1900-2010. Values shown in parentheses are the p-values for each Pearson's correlation.

Meadow ID	437	910	1024	1104	1490	1776	1830	1934	1977	2392	2398	2755
forest	0.36 (0.004)	0.14 (0.117)	0.05 (0.675)	0.14 (0.294)	0.53 (<0.001)	0.05 (0.644)	0.67 (<0.001)	0.38 (0.002)	0.36 (0.001)	0.57 (<0.001)	0.59 (<0.001)	0.06 (0.360)
437												
910	0.35 (0.005)											
1024	0.09 (0.499)	0.34 (0.002)										
1104	0.29 (0.029)	0.49 (<0.001)	0.52 (<0.001)									
1490	0.29 (0.022)	0.43 (<0.001)	0.28 (0.016)	0.38 (0.004)								
1776	0.36 (0.004)	0.08 (0.477)	0.41 (<0.001)	0.48 (<0.001)	0.31 (0.008)							
1830	0.21 (0.105)	0.64 (<0.001)	0.62 (<0.001)	0.63 (<0.001)	0.54 (<0.001)	0.47 (<0.001)						
1934	0.17 (0.189)	0.39 (0.001)	0.42 (<0.001)	0.57 (<0.001)	0.42 (<0.001)	0.55 (<0.001)	0.68 (<0.001)					
1977	0.21 (0.11)	0.31 (0.005)	0.42 (<0.001)	0.45 (0.001)	0.49 (<0.001)	0.36 (0.001)	0.68 (<0.001)	0.64 (<0.001)				
2392	0.12 (0.351)	0.56 (<0.001)	0.20 (0.095)	0.35 (0.008)	0.41 (<0.001)	0.10 (0.394)	0.59 (<0.001)	0.33 (0.007)	0.38 (0.001)			
2398	0.28 (0.030)	0.74 (<0.001)	0.40 (0.001)	0.60 (<0.001)	0.62 (<0.001)	0.30 (0.016)	0.68 (<0.001)	0.58 (<0.001)	0.65 (<0.001)	0.62 (<0.001)		
2755	0.31 (0.014)	0.13 (0.162)	0.29 (0.010)	0.49 (<0.001)	0.66 (<0.001)	0.27 (0.025)	0.42 (0.001)	0.44 (<0.001)	0.45 (<0.001)	0.30 (0.014)	0.57 (<0.001)	

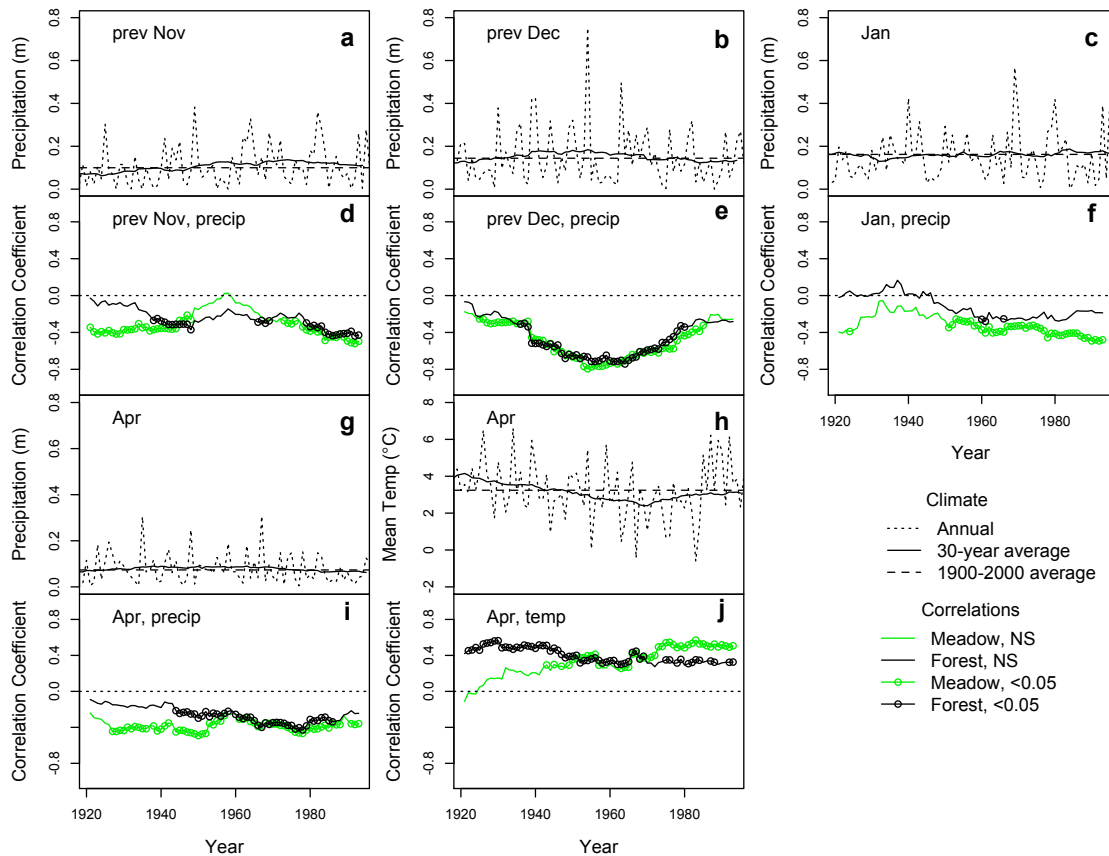


Figure 17. Annual winter climate conditions and response functions with tree ring chronologies. Response function correlations were calculated for a 30-year moving window, with values plotted at the mid point of each 30-year window. Open circles indicate significance at the 95% confidence level. Only those months for which there were periods of significant correlation are shown. Cumulative monthly precipitation is shown for **a**) November during the year prior to the year of growth, **b**) December during the year prior to the year of growth, and **c**) January during the year of growth. Response function correlations are shown between tree ring growth chronologies for forest (black) and meadow (green) trees and **d**) cumulative November precipitation during the year prior to the year of growth, **e**) cumulative December precipitation during the year prior to the year of growth, and **f**) cumulative January precipitation during the year of growth. Cumulative monthly precipitation is shown for **g**) April during the year of growth. Mean monthly temperature is shown for **h**) April during the year of growth. Response function correlations are shown between tree ring growth chronologies for forest (black) and meadow (green) trees and **i**) cumulative April precipitation during the year of growth, and **j**) mean April temperature during the year of growth.

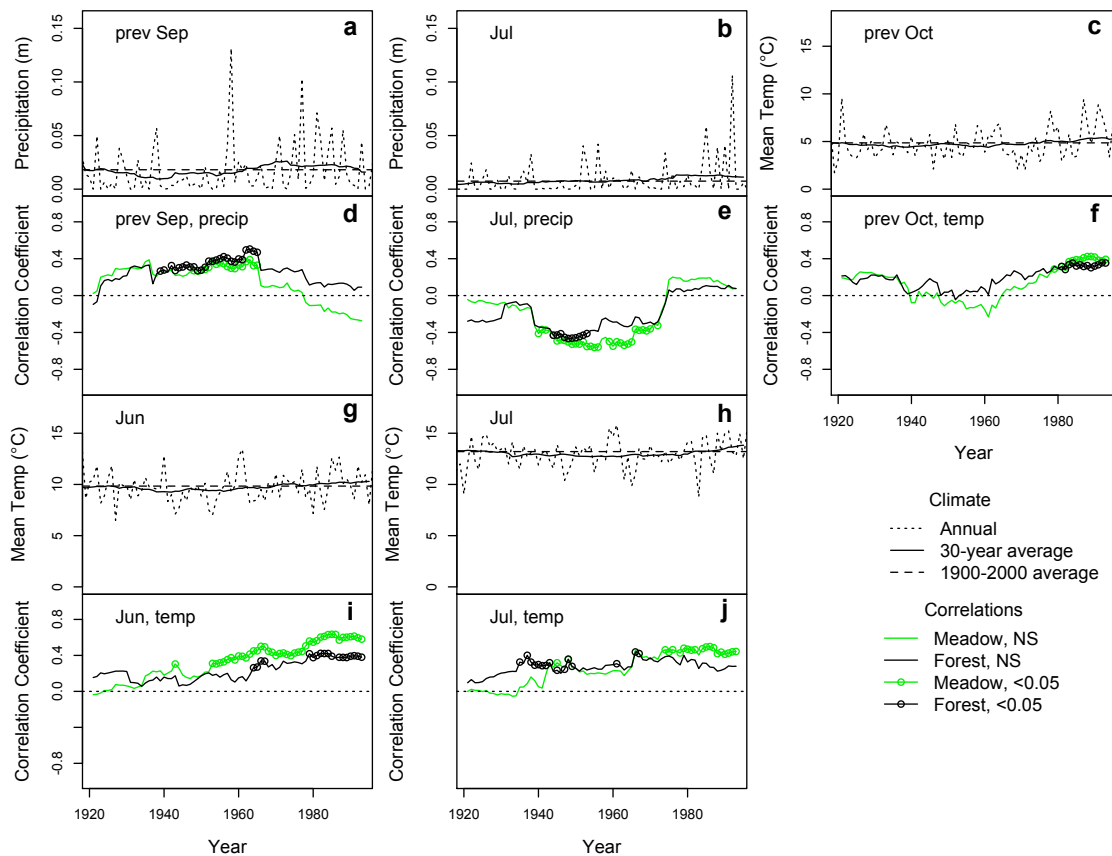


Figure 18. Annual summer climate conditions and response functions with tree ring chronologies. Response function correlations were calculated for a 30-year moving window, with values plotted at the mid point of each 30-year window. Open circles indicate significance at the 95% confidence level. Only those months for which there were periods of significant correlation are shown. Cumulative monthly precipitation is shown for **a**) September during the year prior to the year of growth and **b**) July during the year of growth. Mean monthly temperature is shown for **c**) October during the year prior to the year of growth. Response function correlations are shown between tree ring growth chronologies for forest (black) and meadow (green) trees and **d**) cumulative September precipitation prior to the year of growth, **e**) cumulative July precipitation during the year of growth, **f**) mean October temperature during the year prior to the year of growth. Mean monthly temperature is shown for **g**) June during the year of growth, and **h**) July during the year of growth. Response function correlations are shown between tree ring growth chronologies for forest (black) and meadow (green) trees and **i**) mean June temperature during the year of growth, and **j**) mean July temperature during the year of growth.

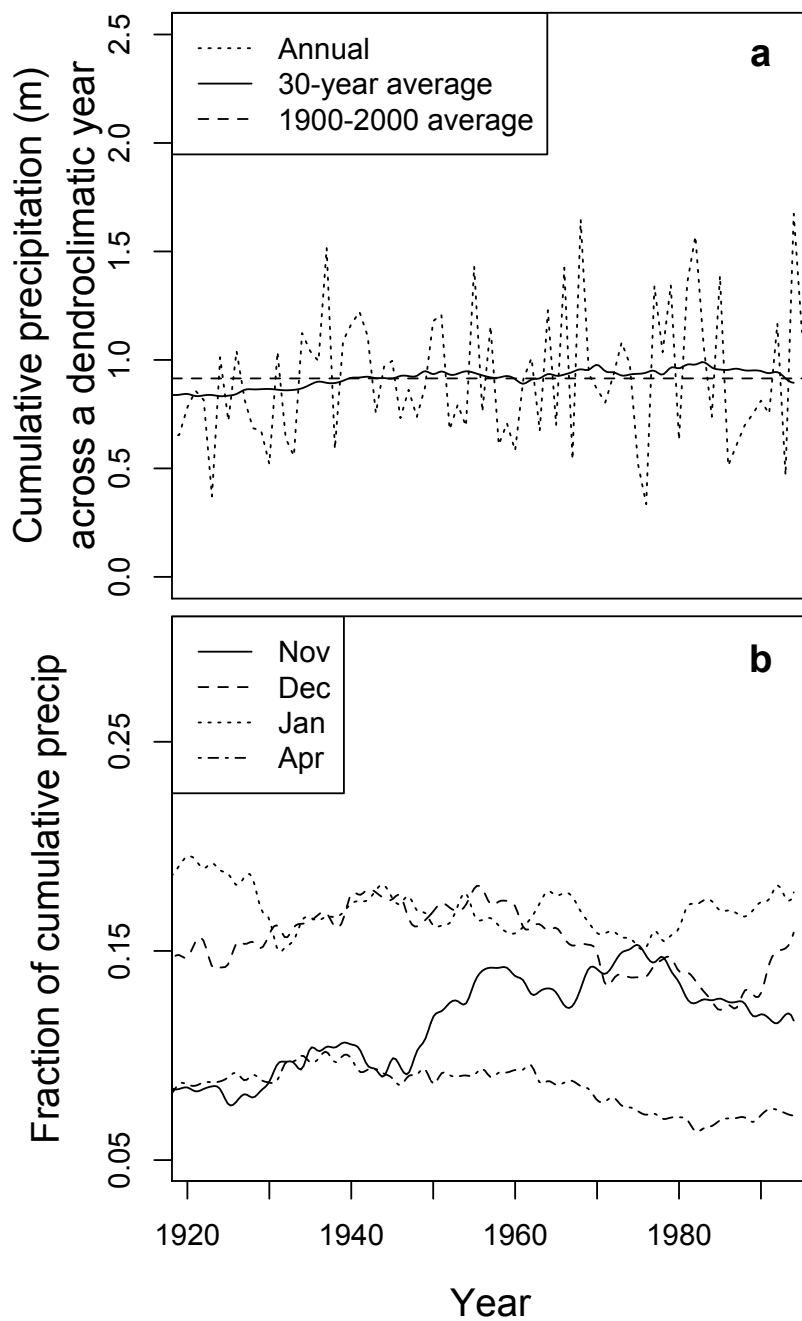


Figure 19. Cumulative dendroclimatic year precipitation and the fraction falling in different months over the 20th century. a) Cumulative precipitation over the dendroclimatic year (September-August). **b)** The fraction of the cumulative dendroclimatic year precipitation that fell in a given month.

Discussion

If the topoclimate of a meadow environment were a driving factor of tree growth rate, we would expect to see a coherent signal across all meadows and strong correlations between meadow chronologies. Indeed, growth patterns of trees were strongly correlated amongst the 12 meadows, with annual growth of trees in a meadow more similar to that of trees in other meadows than even that of trees in the immediately surrounding forest. As with meadow trees, forest trees show a coherent composite chronology. However, the strength of the composite forest tree chronology was weaker than that of the composite meadow tree chronology. Thus, it appears that meadows share a topoclimate regime that differs from the topoclimate of the adjacent forest while forest trees experience topoclimate unique to their location more so than a general forest topoclimate. Forest locations surrounding different meadows varied widely in terms of slope and aspect, lessening our ability to generalize forest into a single topographic feature. This was in contrast to the more uniform meadow topography, leading meadows to share a similar topoclimate regime.

P. contorta individuals in meadows are surprisingly sensitive to climate variation, which is unusual given that trees in more hydric locations are commonly more complacent to climate (Webb et al. 1993, Copenheaver et al. 2007, Anning et al. 2013). However, given that meadow trees' annual growth rings show a coherent pattern across all twelve sites, we can examine the common signal for evidence of how trees in a meadow environment respond to climate variability and predict how they might respond to future climate change. Winter precipitation in the Sierra Nevada is predicted to increase by 5% from the 1985-1994 period to the 2060-2069 period (Pierce et al. 2013), and precipitation in the subalpine zone is expected to continue to fall as snow (Klos et al. 2014). Because meadow trees respond negatively to winter precipitation and SWE, wetter winters with deeper snowpack are likely to decrease meadow tree growth.

The response of meadow tree growth to summer climate variability depends on the overall climatic conditions and appears to be closely linked to the Pacific Decadal Oscillation (PDO). Both forest and meadow trees respond to growing season precipitation (negative correlation with previous summer precipitation, positive correlation with current summer precipitation) only during periods of negative PDO, when the climate is cooler and wetter in this region (Benson et al. 2003). Conversely, both meadow and forest trees respond to growing season temperature (positive correlation to previous and current summer temperature) during periods of positive PDO, when the climate is warmer and drier (Benson et al. 2003). During the growing season, the Sierra Nevada region is predicted to have a 14% decrease in precipitation and a 3.3 °C increase in temperature between the 1985-1994 period and the 2060-2069 period (Pierce et al. 2013). The warmer, drier conditions will be similar to historical periods of positive PDO, during which times meadow trees responded positively to growing season temperature and were insensitive to precipitation. Thus, in a warmer environment meadow trees are likely to show enhanced annual growth due to the higher growing season temperatures.

However, predictions of meadow tree growth response to future climate based on historical responses to climate variability are inherently uncertain. Future climate conditions fall outside the range of historic variability (Pierce et al. 2013). As we move into conditions with no historical analog, responses to climate may no longer follow observed patterns. For example, while current conditions appear to increase meadow tree growth with longer growing seasons and warmer growing season temperatures, trees experiencing increased temperatures may become more sensitive to moisture availability. This could reverse the decreased growth with high precipitation and SWE based on shorter growing season length to increased growth based on higher soil water availability.

Previous studies based only on conifer recruitment have suggested that encroachment is likely to increase over the 21st century, with tree density in the average meadow reaching levels comparable to a forest by the end of the century (Lubetkin et al., in prep). However, including the response of adult trees to climate variability may give us a more complete picture of how encroaching trees are likely to respond to climate change. While years of high SWE have been shown to enhance germination in meadows at a regional scale, and locations within a meadow that have late snowmelt have more new germinants than locations with earlier snowmelt (Lubetkin et al., in prep), adult trees responded negatively to high SWE. If the same large snowpack that enhances recruitment causes a strong decrease in adult tree growth, there may be less of an increase in encroachment than previously predicted. Under a climate change scenario with wetter winters, new germination and establishment may be greater while adult growth may decrease.

In terms of temperature, both recruitment and adult tree growth show increases with warm growing season temperatures. Because temperature is predicted to increase, especially during the growing season (Pierce et al. 2013), the temperature effect on adults and seedlings may act synergistically, resulting in an even stronger increase in encroachment. Currently, trees successfully establish in locations that reach dry late-season soil moisture levels. The fact that growing season precipitation is likely to decrease while temperature is likely to increase (Pierce et al. 2013) may mean that trees are able to encroach further into the wet center of meadows. Thus, while adult responses to increased winter precipitation may counteract the enhancement of germination and establishment related to high SWE, the drying and warming of the growing season is likely to offset any such mitigation. Indeed, encroachment effects on meadows may increase more dramatically than expected based solely on increasing recruitment, because adult trees are likely to grow more rapidly and may establish further into meadows.

CONCLUSION

My work indicated that conifer encroachment is essentially ubiquitous across the central Sierra Nevada, with future climate conditions likely to increase encroachment in most meadows. Not only can recruitment be expected to rise, adult trees are likely to experience enhanced growth. Indeed, if *Pinus contorta* continue to respond to climate in the same manner that they have historically, most meadows can be expected to undergo a full conversion from meadow to forest by the end of the 21st century. The loss of meadows could result in loss of those ecosystem services meadows provide, such as water storage and regulation of release, carbon sequestration, and maintenance of biodiversity.

In my first chapter, I showed that the majority of high elevation meadows in the central Sierra Nevada have experienced some degree of encroachment. I was able to identify six physical meadow characteristics that correlated with high encroachment. While characteristics such as elevation, aspect, and solar radiation will remain constant, other predictive factors such as maximum temperature and the amount of precipitation are likely to be altered under climate change conditions. Increasing maximum temperatures (Pierce et al. 2013) could cause meadows that are currently experiencing low encroachment pressure to become more susceptible to encroachment. Because predictions of the direction of precipitation change are less certain, we can consider how encroachment might respond to changes in either direction. If precipitation were to decrease, it could also increase encroachment susceptibility because meadows with low precipitation tended to have denser encroachment. However, if precipitation were to increase, it could offset the rise in susceptibility due to higher temperatures.

The strongest factor affecting the density of encroaching conifers in a meadow was the presence of surrounding *P. contorta*. Currently, meadows near treeline remain un-encroached, perhaps in large part because these meadows have very few *P. contorta* in the vicinity. Treeline meadows are unlikely to experience strong encroachment pressure in the near future. However, an upward shift in *P. contorta* such as that seen for many plant species (Lenoir et al. 2008) could threaten the persistence of meadows near treeline in the long term.

Given that the majority of meadows were encroached to some degree and that encroachment can be expected to continue, in my second chapter I explored factors influencing the rate of encroaching conifer population growth. Population growth rates were more sensitive to small changes in adult mortality than to small changes in germination and establishment. If land managers are interested in preventing or slowing meadow loss through active management, it may be most effective to focus on older trees. The establishment phase already provides a strong natural thinning of encroachment, and management actions aimed at trees less than 10 years old would have to be drastic to further affect overall population growth. Trees establishing in meadows

do not reach cone bearing age until approximately 40 years of age, so it may be most effective to concentrate on removing trees between 10 and 40 years old.

Given the importance of adult tree survival to population growth rate, and making the assumption that years of poor growth indicate years of increased mortality, in my third chapter I focused on adult tree growth rates and their response to climate. Unlike seedlings, for which high snowpack enhanced recruitment, high snowpack limited adult tree growth. Similarly, growing season precipitation increased conifer establishment but had a negative effect on adult growth. However, both seedlings and adult trees responded favorably to warmer temperatures. Thus, the cumulative affect of climate change on encroaching conifers may depend on the strength of the response among different life stages.

Though adult trees' survival appears to dominate the population growth rates, in my second chapter I showed that the within-meadow spatial distribution of encroachment is driven by seedling dynamics. Encroaching trees are most successful in locations that remain wet for several months following snowmelt, enhancing germination, and then reach very dry soil moisture levels by the end of the season, enhancing establishment. Future scenarios indicate that precipitation is likely to decrease while temperature is likely to increase (Pierce et al. 2013). This may mean that trees are able to establish further into the wet portions of meadows as the meadows dry.

My work indicates that encroachment is likely to increase during the 21st century, both through conditions conducive to recruitment and to adult growth. However, this assumes that conifers will continue to respond to climate in the same manner that they have historically. As climate conditions move past historical analogs, there is the potential for non-stationary relationships. For example, while lower snowfall has enhanced tree growth historically, the low snow during the 2011-2012 winter resulted in high mortality amongst trees up to 30 years old. Thus, while low snow may enhance growth to a point, extremely low snow levels may be detrimental to survival. Similarly, warm growing season temperatures have enhanced both recruitment and adult growth. However, higher temperatures above those experienced during the 20th century may result in trees changing from being temperature limited to being moisture limited. Similarly, my predictions of future increases in conifer encroachment do not take into account disturbances. Disturbances such as landslides, fire, or tree throw resulting from high winds could kill entire cohorts of encroaching conifers, temporarily decreasing encroachment.

Regardless of future rates of encroachment, most meadows are already experiencing encroachment to some degree and are likely to experience higher encroachment pressure at least in the near term given high seed availability and survival rates in most subalpine meadows. The potential loss of mountain meadows as they transition to forest presents a number of management implications. Meadow restoration via burning or cutting down encroaching trees is a popular management technique. However, this may be a futile effort given my findings that encroachment is largely tied to climate. If restoration

measures are to be attempted, it would likely be most effective to target trees 10 – 40 years old (approximately 0.3 – 2 m tall). This would target trees after the natural winnowing process during establishment but before trees become sexually mature.

Aside from direct restoration of meadows, we can also think about managing to compensate for the ecosystem services they provide. Meadows are able to attenuate flood peaks and to store water that they then release later in the season, maintaining stream flow longer into the summer dry period. With meadow loss, we may need to increase reservoir capacity to help prevent floods and to ensure summer stream flow. There are also implications for wildlife. Many flora and fauna rely on meadow habitats, and their populations may be at risk with loss of habitat. It would be helpful to begin monitoring meadow-dependent species now to obtain baseline data, and to continue monitoring efforts into the future to watch for signs of extinction risk.

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