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Climate and landscape drive the pace and pattern of conifer encroachment into subalpine meadows

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Abstract

Mountain meadows have high biodiversity and help regulate stream water release following the snowmelt pulse. However, many meadows are experiencing woody plant encroachment, threatening these ecosystem services. While there have been field surveys of individual meadows and remote sensing-based landscape-scale studies of encroachment, what is missing is a broad-scale, ground-based study to understand common regional drivers, especially at high elevations, where land management has often played a less direct role. With this study, we ask: What are the climate and landscape conditions conducive to woody plant encroachment at the landscape scale, and how has historical climate variation affected tree recruitment in subalpine meadows over time? We measured density of encroaching trees across 340 subalpine meadows in the central Sierra Nevada, California, USA, and used generalized additive models (GAMs) to determine the relationship between landscape-scale patterns of encroachment and meadow environmental properties. We determined ages of trees in 30 survey meadows, used observed climate and GAMs to model the relationship between timing of recruitment and climate since the early 1900s, and extrapolated recruitment patterns into the future using downscaled climate scenarios. Encroachment was high among meadows with lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *murrayana* (Balf.) Engelm.) in the immediate vicinity, at lower elevations, with physical conditions favoring strong soil drying, and with maximum temperatures above or below average. Climatic conditions during the year of germination were unimportant, with tree recruitment instead depending on a 3-yr seed production period prior to germination and a 6-yr seedling establishment period following germination. Recruitment was high when the seed production period had high snowpack, and when the seedling establishment period had warm summer maximum temperatures, high summer precipitation, and high snowpack. Applying our temporal model to downscaled output from four global climate models indicated that the average meadow will shift to forest by the end of the 21st century. Sierra Nevada meadow encroachment by conifers is ubiquitous and associated with

climate conditions increasingly favorable for tree recruitment, which will lead to substantial changes in subalpine meadows and the ecosystem services they provide.

Key words: climate variation; lodgepole pine; *Pinus contorta*; recruitment; Sierra Nevada, California; subalpine meadow; tree establishment; woody encroachment; Yosemite National Park

Introduction

Mountain meadows provide essential ecosystem services, including maintaining biodiversity and regulating release of snow meltwater into streams. Mountain meadows are locations of high biodiversity, with wet meadows utilized by unique flora and fauna (Patton and Judd 1970, Allen-Diaz 1991, Wang 2012, Highland and Jones 2014). Some species even rely specifically on the forest-meadow edge, such as elk and deer (Patton and Judd 1970) or the Great Gray Owl (*Strix nebulosa*; van Riper and van Wagtendonk 2006). In addition, mountains of the world play critical roles as “water towers” with snow acting as a natural reservoir that provides water to downstream lowlands (Messerli et al. 2004). Undisturbed meadows serve as secondary reservoirs, 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).

In many locations, mountain meadows are being transformed by woody plant encroachment (Woodward et al. 1995, Dyer and Moffett 1999, Berlow et al. 2002, Lepofsky et al. 2003, Takaoka and Swanson 2008, Haugo et al. 2011, Brandt et al. 2013, Durak et al. 2015). Conversion of herbaceous meadows into forest could impact hydrologic services 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). This is opposite expectations for arid grasslands, which see increases in soil carbon with woody encroachment (e.g., Neff et al. 2009). Encroached locations also showed decreased soil water and downstream flow duration within a mesic grassland catchment (Zou et al. 2014) and showed increased aquifer water extraction (Scott et al. 2014). Encroaching woody plants can alter depth of vegetation water use (Darrouzet-Nardi et al. 2006), as well as biogeochemical cycling (Darrouzet-Nardi et al. 2008). Griffiths et al. (2005) similarly found changes in soil biogeochemical transformations across a forest-meadow ecotone in the central Cascade Mountains of Oregon.

While encroachment by woody species may alter meadow hydrology, the rate and intensity of encroachment may itself largely be determined by the hydrologic regime. Where direct human land use has been intense, woody encroachment at high elevations is driven by release from logging and

intensive grazing (as in Carlson et al. 2014). However, where land use history has been less intense, such as in subalpine meadows in the western United States, drivers are less well understood and may be more closely related to climate variability and change (Miller and Halpern 1998). Subalpine meadows in the Sierra Nevada Mountains are persistent (over millennia) features that occur in landscape positions with shallow water tables due to flooding of nearby streams, collection of snow meltwater in topographic basins, and/or groundwater seeps (Benedict 1982, Ratliff 1985). At lower elevations, fire may have been historically more prevalent due to burning by Native Americans, but in the subalpine, fire is not thought to maintain herbaceous meadow vegetation (Ratliff 1985). The floristic composition of meadows is most closely related to soil water dynamics (Benedict 1983, Lowry et al. 2011), and paleoenvironmental studies indicate that many wet meadows were established during the cooler, wetter late Holocene, with sagebrush pollen more abundant in earlier, drier periods (Anderson and Smith 1994).

Meadow hydrology is affected by fluxes from the surrounding hillslope and catchment, as well as snowmelt within the meadow (Lowry et al. 2010). Snowpack depth can affect soil hydrology (e.g., Hardy et al. 2001) and 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 temperature, hydrologic regime and growing season length. A literature review and synthesis indicates that temperature and hydroclimate variables influence lodgepole and ponderosa pine seedling emergence and establishment rates (Petrie et al. 2016). Early melt provides a longer snow-free period for plant growth and enables earlier conifer germination, resulting in greater seedling growth and therefore enhancing over-winter survival (Ronco 1967). However, conifers establishing in early melting meadows (or years) may experience earlier drought stress if summer rain is low or inconsistent (Moyes et al. 2013).

Meadows in the Sierra Nevada mountain range of California provide an opportunity to examine spatial variation and historic trends, due to their long history of conifer encroachment (Vale 1981, 1987, Ratliff 1985, Helms and Ratliff 1987, Cooper et al. 2006). However, no broad, ground-based, landscape-scale study of conifer encroachment into Sierran meadows has been conducted, from which to assess patterns of meadow encroachment and potential regional drivers. Here, we quantify spatial and temporal patterns of encroachment into subalpine meadows in the central Sierra Nevada through field surveys. We hypothesized that meadow hydrologic regime and length of the growing season play codominant and interacting roles in determining encroachment density by influencing success of encroaching conifers. Specifically, we tested the following hypotheses: (1) the majority of meadows across the Central Sierran landscape are recently (approximately last 100 yr) encroached, (2) encroachment density is driven

by a drier hydrologic regime and longer growing season, (3) meadows with similar physical parameters show synchronous timing of encroachment, and (4) past encroachment pulses were driven by increased temperature and decreased precipitation during periods of seed production and seedling germination and establishment. Finally, we used our understanding of historic trends of encroachment to project the future extent of woody plant encroachment using regional scenarios of climate change, a critical first step to managing its ecosystem consequences.

Methods

We conducted a field survey in subalpine (2,700–3,350 m elevation) meadows in the Sierra Nevada, California, between 2009 and 2013, defining the edge of a meadow based on herbaceous vegetation. We conducted the majority of fieldwork in Yosemite National Park (YNP), which provides an ideal natural laboratory with more protection from grazing and woodcutting than surrounding National Forests. All meadows were in remote locations to further minimize direct anthropogenic influences.

Detailed surveys

We selected YNP meadows for detailed surveys using the 1997 digital vegetation map for YNP (Aerial Information Systems 2007, see Berlow et al. 2013), eliminating meadows with extreme areas ($>200,000$ m² or $<2,000$ m²), below the subalpine zone (below 2,700 m), outside of designated wildernesses, within 2.4 km of a paved road, or inaccessible (>2.5 km from the nearest trail). From the remaining 1,351 meadows, we chose 30 using a stratified random design based on surrounding vegetation and winter 2004–2005 average snowmelt date. We chose seven to eight meadows within each snowmelt date quartile, five or six with conifers adjacent to the meadow, and one or two with no conifers within a 50-m buffer around the meadow, to examine meadows experiencing different biotic pressures.

In 2009–2010, we established two to six (depending on size and homogeneity of the meadow) 3 m wide belt transects (Fig. 1) to be representative of a region in the meadow with a homogeneous encroachment pattern. Along each transect, we recorded the distance from meadow edge, 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 (Fig. 1; Appendix S1: *Positioning of transects*).

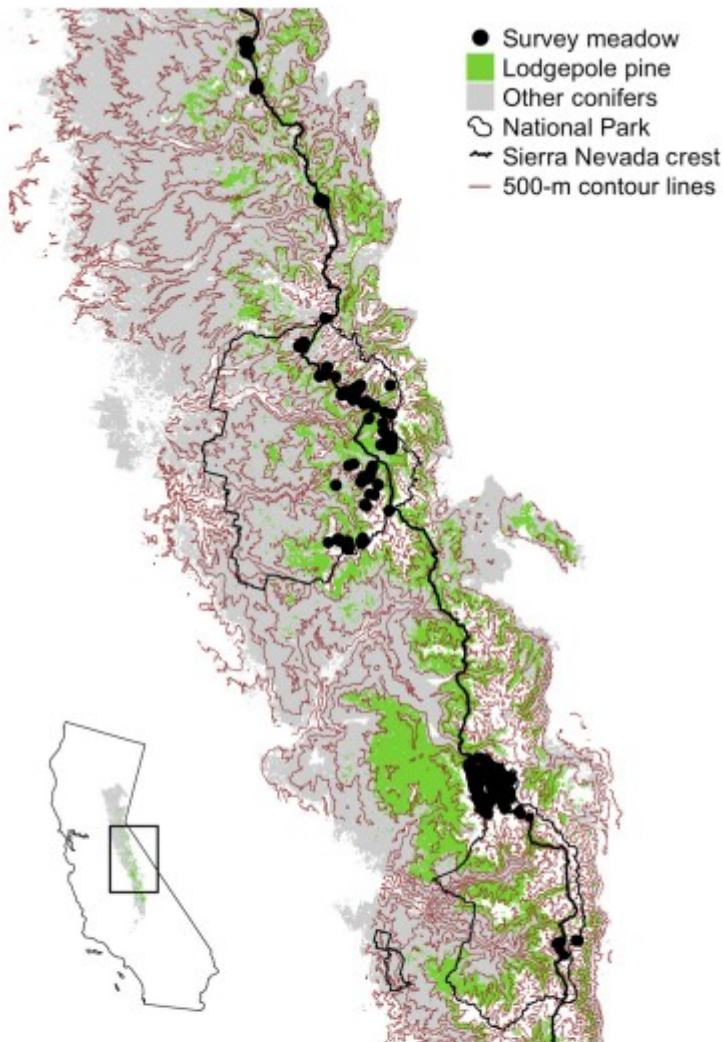


FIG. 1. Study locations within California's Central Sierra Nevada Mountains. Study meadows were located along the western side of the Sierra Nevada crest, ranging from Kings Canyon National Park north to Lake Tahoe. Rapid assessments were conducted in, as well as north and south, of Yosemite National Park, while detailed surveys were conducted in Yosemite National Park. Forest type maps were derived from the USDA Forest Service Forest Inventory and Analysis Program and Remote Sensing Applications Center (Ruefenacht et al. 2008).

We estimated ages of trees up to ~2 m tall and ~40 yr old based on nodes/branch whorls, since the 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; Appendix S1: *Tree node count validation*). We estimated ages of larger trees using a height/age regression ($R^2 = 0.53$). To calibrate this regression, we cored and aged, using standard cross-dating techniques (see Fritts 1976), 5–10 *P. contorta* per

meadow. We preferentially cored trees along transects and spanning the size range of larger (>2 m tall) *P. contorta*.

Rapid assessments

We classified degree of encroachment, height classes of conifers present (as a proxy for age classes), and conifer species composition in 56 additional meadows within YNP, 11 north of Yosemite toward Lake Tahoe, and 243 south in Kings Canyon National Park (KNP). Meadows were chosen using the same criteria described in *Detailed surveys*. Our rapid assessment protocol involved visually estimating the number of trees of each species within four height classes (<0.5, 0.5–1.5, 1.5–5.0, and >5.0 m) as proxies for age classes, and visually estimating conifer species composition of the immediately surrounding mature forest. We conducted rapid assessments for all detailed survey meadows to calibrate between detailed and rapid methods. While abundance of trees >1.5 m tall was similar between detailed and rapid surveys, rapid assessments underestimated the abundance of smaller trees. Thus, we used linear regressions to correct upward rapid assessment estimates of smaller trees.

Meadow physical parameters

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

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

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 (SI) to indicate the edge:area ratio as

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

where perimeter is the length of the meadow perimeter in m, and area is the total meadow area in m². Meadows with a high spatial index have most of the meadow interior close to the edge (elongated and convoluted meadows) while meadows with a low spatial index have mostly interior far from an edge (rounder meadows). We also created a solar radiation raster from the ArcGIS solar radiation tool (ArcGIS 9.3, Environmental Systems Research Institute, Redlands, CA, USA) 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 (September–October), which would affect soil evaporation and plant water stress. We obtained cumulative annual precipitation and annual mean of monthly maximum temperature from PRISM data at 800-m resolution, averaged over 1960–1990.

Analysis of spatial patterns of encroachment

We created generalized additive models (GAMs; Hastie and Tibshirani 1986) of encroachment density as a function of physical and climatic parameters. GAMs are data-driven models useful for analyzing nonparametric data with nonlinear relationships, and do not require prior assumptions about the shape of the relationship between explanatory and response variables. GAMs work by fitting a link-function between the mean of the response variable and a smoothed function of the explanatory variables. 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 and Hothorn 2007). Using the *mboost* (Hothorn et al. 2013) package in R, we considered 21 predictor variables, including abiotic physical and climatic predictors as well as biotic predictors relating to surrounding conifers (Appendix S1: Table S1). We chose six predictors identified as significant at the optimal stopping point (Appendix S1: *Gradient boosting details*) for use in a conventional GAM (i.e., a GAM without gradient boosting; Hastie and Tibshirani 1986).

We created the conventional GAMs using the *mgcv* (Wood 2012) package in R. We ran 1,000 bootstrapped iterations to determine the standard error, randomly splitting the data into 80% training and 20% validation for each run. 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 YNP that fit the above meadow selection criteria. We then surveyed 13 accessible meadows that spanned a range of predicted encroachment densities, focusing on meadows predicted to have very low or high encroachment.

Analysis of temporal patterns of encroachment

We created a 5-yr running average time series of encroachment (number of new trees per 5 yr) for each of 19 meadows containing at least 100 conifers (≥ 0.1 m tall, ~ 10 yr old). We then created a composite regional time series as the average percentage of trees across all 20 encroached meadows. We used the *e1071* (Meyer et al. 2012) package in R to cluster the meadows based on the year when 99% of the encroaching trees were established in or after a given year. This allowed us to look at the onset of encroachment 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 also correlated the composite regional encroachment signal with historical climate variables using the same GAM methods already described. This allowed us to reduce 12 predictor variables, including 1 April snow water equivalent (SWE), late growing-season precipitation, late growing-season maximum temperature, and melt season minimum temperature (Appendix S1: Table S2) to a set of four for a conventional GAM. We obtained historical snow water equivalent from the Tioga Pass Entry Station snow course (California Department of Water Resources, monthly manual measurements, 1926–present), which is at a similar elevation and between 4 and 41 km from the 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 is the nearest station in the USHCN and 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, the prior three years (“seed” period) based on the time required for cone development and seed release (Owens 2006), and the six following years (“establishment” period) based on four years of conifer mortality data, which showed that 58% of mortality occurred within the first six years following germination (K.C. Lubetkin, A. L. Westerling and L M. Kueppers, *unpublished data*). As above, we tested the robustness of our temporal GAM using 1,000 bootstrapped iterations, splitting the data into 80% training and 20% validation.

To examine potential future encroachment, we used 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, downscaled to a one-eighth-degree latitude–longitude grid using the Bias-Corrected Constructed Analogues statistical downscaling method (Maurer et al. 2010). We used downscaled projections of precipitation and temperature, and variable infiltration capacity (VIC) hydrologic model (Liang et al. 1994) projections of 1 April snow water equivalent to project encroachment using the regional GAM. These downscaled projections were generated for both a medium-high emissions scenario (SRES A2) and a low emissions scenario (SRES B1; Metsaranta et al. 2010). We tested our ability to reproduce historical encroachment patterns using downscaled historical GCM simulations of temperature and precipitation and historical VIC model output of snow water equivalent.

Results

Spatial patterns

Consistent with our expectations, encroachment was common across the landscape. Both detailed surveys and rapid assessments showed that encroachment is nearly ubiquitous up to 3,200 m (Fig. 2). Of 30 detailed survey meadows, 23 were considered encroached (≥ 0.002 trees/m², ages >10), and the seven un-encroached meadows were all in the krummholtz vegetation zone above treeline, >3,200 m. This pattern is consistent across meadows surveyed in YNP, KNP, and along the Pacific Crest Trail (PCT) from Yosemite to Lake Tahoe (Table 1). Encroaching conifers were predominantly *Pinus contorta* Douglas ex Loudon (lodgepole pine; 94% of trees) even when *P. contorta* was not a large component of the surrounding forest. Conversely, the second and third most common species, *Pinus albicaulis* Engelm. (whitebark pine; 3.4% of trees) and *Tsuga mertensiana* (Bong.) Carrière (mountain hemlock; 1.1% of trees), 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).

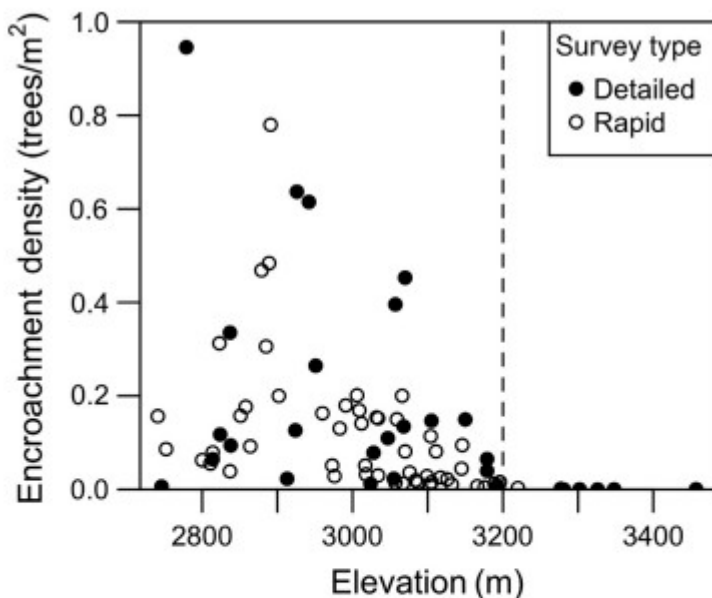


FIG. 2. Density of encroaching conifers in 86 subalpine meadows in Yosemite National Park as a function of elevation. Encroachment intensity was highly variable up to the krummholtz vegetation zone at 3,200 m, after which elevation meadows remained un-encroached (below our threshold of 0.002 trees/m², determined by Jenks natural breaks; Jenks and Caspall 1971). This trend was true both of detailed survey and rapid assessment meadows.

TABLE 1. Median and interquartile range of encroachment densities of conifers within subalpine meadows below the krummholtz vegetation zone (~3,200 m) in three locations across the central Sierra Nevada: Yosemite National Park (YNP), along the Pacific Crest Trail (PCT), and Kings Canyon National Park (KNP).

Location	Type	Number	Encroachment density (trees/m ²)		
			First quartile	Median	Third quartile
YNP	detailed	23	0.010	0.068	0.178
YNP	rapid	53	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 related to biotic and abiotic factors affecting meadow hydrology and growing-season length. Indeed, the gradient-boosted GAM identified six variables that explained 81% of the variation in encroachment density, with presence of *P. contorta* in vegetation surrounding the meadow the strongest predictor ($P < 0.001$). In meadows that had sufficient surrounding *P. contorta*, encroachment was most dense in lower elevation meadows ($P = 0.002$), meadows with mean monthly maximum temperatures above or below average of values for meadows in this study ($P = 0.009$), low annual precipitation ($P = 0.016$), high solar radiation during the melt period (May–July; $P = 0.067$), and south to east facing aspects ($P = 0.040$; Appendix S1: Fig. S1). 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 dense regardless of precipitation) than it did in meadows surrounded by less *P. contorta* (where encroachment was dense only when precipitation was low; Appendix S1: Fig. S1c). Similarly, cumulative annual precipitation was largely unimportant at lower elevations (where encroachment was dense across the precipitation spectrum), unlike higher elevation meadows (where encroachment was dense only at low precipitation values; Appendix S1: Fig. S1g).

When we ran 1,000 bootstrap iterations of the conventional GAM, the relationship between actual and modeled encroachment densities for the training data had a mean $R^2 = 0.921 \pm 0.046$ (mean \pm SD), while the validation data had a mean $R^2 = 0.568 \pm 0.249$. 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 (Fig. 3).

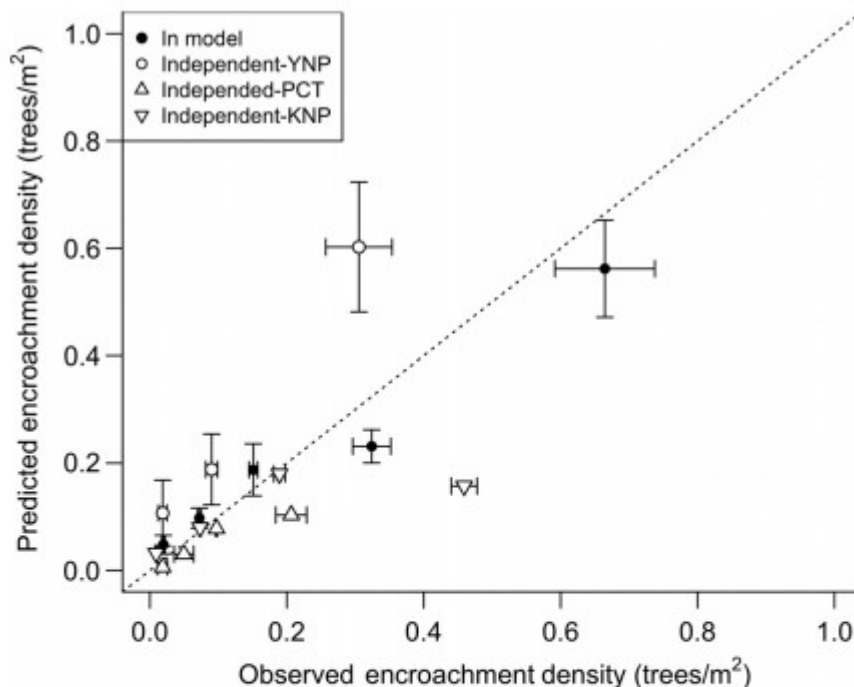


FIG. 3. Predicted vs. observed encroachment density (mean \pm SE encroachment). Meadows are binned by observed encroachment density (Jenks natural breaks; Jenks and Caspall 1971). Eighty-six meadows from Yosemite National Park (YNP) were used to train the model, which was then applied to fully independent meadows for secondary validation (13 in Yosemite National Park, 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 98% of established conifers older than 10 yr 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 (five meadows), 1945 (eight meadows), or 1978 (five meadows). 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 ($F = 4.9$, $P = 0.02$, $df1 = 2$, $df2 = 15$), though the groups did not differ in climate or site factors that proved important in the spatial GAM (surrounding *P. contorta*, $F = 2.2$, $P = 0.14$, $df1 = 2$, $df2 = 15$; elevation, $F = 1.1$, $P = 0.36$, $df1 = 2$, $df2 = 15$; maximum temperature, $F = 0.49$, $P = 0.62$,

df1 = 2, df2 = 15; annual precipitation, $F = 2.55$, $P = 0.11$, df1 = 2, df2 = 15; solar radiation in melt period, $F = 3.54$, $P = 0.06$, df1 = 2, df2 = 15; aspect, $F = 2.88$, $P = 0.09$, df1 = 2, df2 = 15).

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 (Fig. 4). We were able to model the regional time series with a GAM based on four climatic drivers (Appendix S1: Fig. S2), which had high predictive power (78.7% of deviance explained, AIC = 552.6, $n = 71$). Encroachment was high in years preceded by a 3-yr seed production period with high April 1st snow water equivalent (SWE; $P < 0.001$), and in years followed by a 6-yr seedling establishment period with high summer maximum temperatures ($P < 0.001$), high summer precipitation ($P < 0.001$), and high 1 April SWE ($P < 0.001$). 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, $n = 74$). Conditions during the year of germination showed little effect on recruitment.

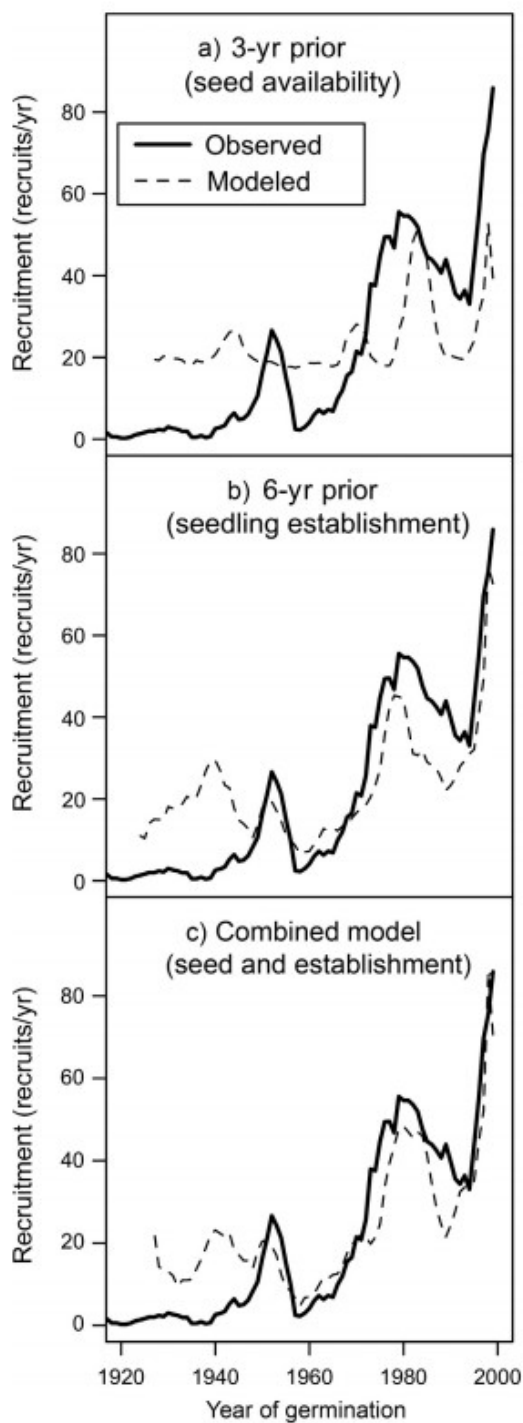


FIG. 4. Actual encroachment time series vs. that modeled using climate conditions averaged over the seed production and/or seedling establishment period. The actual data presented is a regional composite time series with 20 meadows containing at least 100 trees each. Encroachment was modeled using four climatic variables. Models were created with (a) only those during the 3-yr period prior to germination, (b) only those during the 6-yr period following germination, or (c) all four variables prior to and following germination.

When we ran 1,000 bootstrapped iterations, the model explained on average 88.9% of the deviance (mean AIC = 412.0, $n = 53$). A linear regression of predicted recruitment as a function of 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 climate and snow model output, it predicted the observed time series with an $R^2 = 0.75$ ($P < 0.001$, $n = 42$; Appendix S1: Fig. S3). When applied to future projected climate, the average across the four downscaled GCMs shows an increase in annual conifer recruitment under both the A2 emissions and B1 emissions scenarios (Fig. 5).

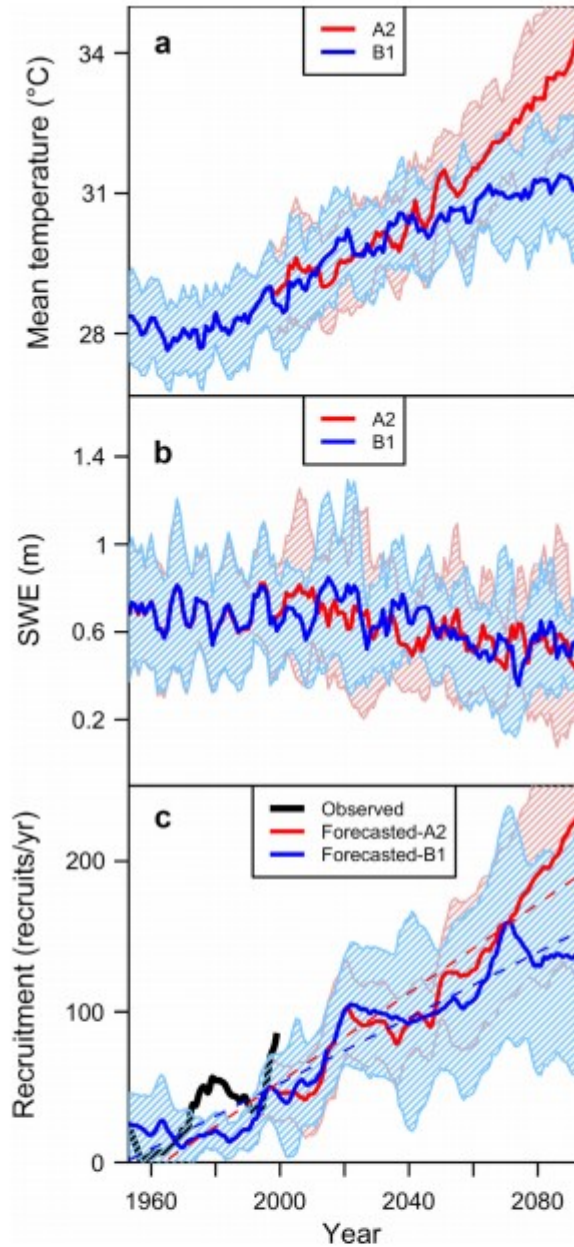


FIG. 5. Encroachment forecasting using climate data averaged across four downscaled global climate models (GCMs), under two emission scenarios. Solid lines indicate the averages among the four GCMs, with the shaded regions showing the range of values across all models. (a) July–October maximum temperature, (b) 1 April snow water equivalent (SWE), and (c) estimated number of tree recruits per year were calculated for high (A2) and low (B1) emissions scenarios. Historical values are from hindcasted GCM simulations, with average and range of encroachment similar to that of the observed historical encroachment (unforced, internal GCM climate variation would not be expected to match year-to-year observed historical climate variation).

Discussion

Spatial patterns

As expected, tree encroachment into subalpine meadows is common across the central Sierra Nevada and is most commonly by Sierra lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *murrayana* (Balf.) Engelm.).

Widespread encroachment in the Sierra Nevada is consistent with landscape-scale decreases in mountain meadow area in Oregon between 1946 and 2000 (Takaoka and Swanson 2008), as well as with broad trends of woody plant encroachment into other grassland ecosystems (e.g., Van Auken 2000, Naito and Cairns 2011, Liu et al. 2013, Formica et al. 2014). However, Sierra Nevada meadows present different challenges to encroaching conifers than do semiarid grasslands. Sierra Nevada meadows are groundwater-dependent systems with high water tables (Allen-Diaz 1991). *Pinus contorta* has a life history strategy well suited to invasion in general (Richardson and Rejmánek 2004), and is particularly adapted to establishing in wet meadows. *Pinus contorta* is shade intolerant with seedlings germinating best in full sunlight (Lotan and Critchfield 1990), and is tolerant of high water tables (Minore 1970, Cochran 1972).

The primary driver of encroachment density was neither hydrologic regime nor growing season length as expected, but instead the biotic pressure exerted by surrounding *P. contorta*. There was a threshold effect, with meadows with at least 50% of their perimeter surrounded by *P. contorta* experiencing dense encroachment. Indeed, mature *P. contorta* are able to produce $59,409 \pm 68,806$ (mean \pm 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 among subalpine meadows in YNP, <2% of a meadow's area is more than 40 m from the nearest forest edge. Thus, most of the area of these meadows is within range of seed produced by surrounding forest trees, resulting in dense encroachment among meadows with as little as one-half their surrounding buffer occupied by *P. contorta*.

Following *P. contorta* presence, factors contributing to a drier hydrologic regime, including low precipitation and high solar radiation, also increased encroachment density. While *P. contorta* can tolerate high water tables (Minore 1970, Cochran 1972), and *P. contorta* emergence in the field appears to increase unimodally with precipitation (Petrie et al. 2016), meadows with relatively less precipitation and greater insolation may provide a better environment for establishing seedlings to compete against herbaceous meadow vegetation. Further, while the seedlings and saplings may tolerate saturated conditions, they may be less likely to thrive and persist. If we infer from this spatial analysis the potential impacts of climate change, we expect meadows may become increasingly vulnerable to encroachment. Predictions for the Sierra Nevada region estimate that temperature will increase 3.3°C by 2060–2069 relative to the 1985–1994

period, while winter precipitation will rise only 5% over the same period (Pierce et al. 2013). This will likely result in drier meadows as a consequence of greater summer climatic water deficit (Stephenson 1990), making meadows more susceptible to encroachment. However, meadows are heterogeneous features with regions of different vegetation and topography. Spatial heterogeneity within meadows may contribute to increased encroachment, since drying of meadows may make areas of meadows that are currently wet refugia resisting encroachment susceptible to encroachment. Alternatively, those refugia may persist into the future, maintaining some level of meadow habitat and regulation of snowmelt release.

Density of conifer encroachment depends to a lesser extent on elevation. Because we included temperature and precipitation in the models, it may be that there are other mechanisms by which elevation affects encroachment density. For example, there are shifts in the herbaceous meadow vegetation (e.g., Potter 2005) for which elevation could be a proxy, and meadow species could either exclude or facilitate pine seedlings. For example, within alpine treeline ecotones, herbaceous cover actually facilitated conifer seedling photosynthesis and survival (Germino et al. 2002, Maher et al. 2005, Maher and Germino 2006). With evidence that many plant species are moving upward with climate change (e.g., Lenoir et al. 2008), movement of lower elevation species into higher elevation meadows could have removed prior limits on encroachment provided by historical meadow vegetation and could have introduced vegetation that is more effective at facilitating seedling survival.

With melt date not a significant driver of encroachment density, length of growing season appears to play a limited role in the success of encroaching conifers. Indeed, cold-adapted conifers quickly recover photosynthetic capacity in spring; some pine species can recover in as few as 1–3 d following emergence from the snow (e.g., Ottander and Öquist 1991, Ottander et al. 1995, Suni et al. 2003) and *P. contorta* can recover in 4–7 d (Monson et al. 2005). Short recovery periods allow conifers to take advantage of short growing seasons, minimizing their sensitivity to growing season length. Thus, longer growing seasons with earlier snowmelt expected as a consequence of climate change may not promote greater encroachment.

Temporal patterns

Surprisingly, while some meadows showed synchronous timing, these meadows did not share similar physical parameters. Thus, we combined all meadows into a regional time series that showed encroachment starting around 1900 with a number of peaks throughout the 20th century. Various peaks match those found in other, more spatially limited central Sierra Nevada studies (Cunha 1992; Helms 1987; Millar et al. 2004, Nelson 2008), indicating synchrony of encroachment beyond our study meadows.

Additionally, peaks in our study match those found in studies conducted nearly 30 years ago (Cunha 1992, Helms 1987), providing evidence that older peaks are not being lost due to tree mortality. Similarly, the age structure of trees in our study meadows, and the lack of dead wood, suggests low mature tree mortality.

Climate conditions during seed production and seedling survival/establishment were important in predicting timing of encroachment, with seedling survival having a stronger impact on the number of successful recruits. In contrast, conditions during the year of germination were not 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 when assessing climate drivers of vegetation change. One limitation to our approach was that our model only predicted recruitment with trees surviving to age six without taking into account mortality events affecting older trees. However, the success of our model at projecting historic encroachment using conditions only during the earliest life history stages indicates that dynamics of later life stages have less of an impact on encroachment success. That said, our model over-predicts recruitment early in the 20th century and after the 1950s. This suggests that while conditions were favorable for recruitment, more recent periods may not have been favorable for growth and survival.

During the seed production period, high snowpack contributed to high recruitment, while during the establishment period, recruitment was greater in 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 temperatures and high snowpack. Warm summer temperatures, combined with summer precipitation, could provide favorable growing season conditions. Insulation by a deeper snowpack could protect delicate seedlings from early spring and late fall frost events. Years with high winter snowpack could also increase water availability in forests, enhancing seed production, and 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, vs. lower snowpack, which would decrease both seed production and establishment. A more complete picture requires experimental manipulation of temperature and winter snowpack.

Despite uncertainty in recruitment response to individual variables affected by climate change, when taken together, our models predict that these meadows will fully convert to forest by the end of the century. By 2100, the mean stand density index (Reineke 1933) is forecast to increase dramatically from the 2000 level and move well above the *P. contorta* forest density index determined by Cochran and Dahms (2000) under both A2 and B1 emissions

scenarios. Thus, it appears that the benefits of warmer temperatures and increased summer precipitation will overwhelm the negative impact of lower snowpack over the 21st century. Indeed, while current recruitment is enhanced by high snowpack, a sensitivity analysis including or removing the projected future decrease in snowpack revealed that models including snowpack project greater encroachment than models without snowpack. This occurs because encroachment becomes even more tightly linked to temperature in the future, perhaps because warming could reduce damage from spring or fall frost, typically associated with decreased snowpack.

Integration

Both spatial and temporal patterns show that encroachment is largely driven by climate. In combination with seed availability, climate was sufficient to explain most variation in encroachment density among meadows, while climate during early life stages was able to explain nearly all historic variation in recruitment timing. This mirrors findings that climate was the most likely driver of woody plant encroachment into other meadow systems (Woodward et al. 1995, Dyer and Moffett 1999, Lepofsky et al. 2003, Brandt et al. 2013, Durak et al. 2015), although Takaoka and Swanson (2008) found fire to be of greater importance while Haugo et al. (2011) found little evidence of climate influencing recent meadow encroachment.

Despite the importance of climate to both spatial and temporal patterns, factors explaining variation in encroachment across the landscape were not always the same as those explaining temporal variation in encroachment over the 20th century. While apparently at odds, our temporal analysis only captured variation in encroachment into meadows with at least 100 adult trees. Thus, we were only able to determine temporal trends in encroachment into meadows already susceptible to encroachment, which tended to occur in drier landscape positions. As a result, the importance of wet years may be exaggerated in the temporal analysis.

Conclusion

Conifer encroachment is prevalent throughout the central Sierra Nevada, with recruitment increasing since approximately 1920. For encroachment to occur, meadows need surrounding *P. contorta* to supply seed, after which encroachment is highest with parameters conducive to early season soil drying. However, while even a few trees may provide sufficient seed supply over a century, there is annual variation in seed availability and seedling establishment that partially drive the timing of encroachment. High recruitment requires periods of high snowpack for seed production, followed by periods of high snowpack and high summer temperature and precipitation for seedling establishment.

In the Sierra Nevada, encroachment is likely to continue during the twenty-first century as a consequence of ongoing climate change, with the meadows in vulnerable landscape positions experiencing a type conversion to forest by

the end of the century. This loss of meadows would result in a loss of ecosystem services they provide, including their capacity to store and regulate release of snowmelt into streams and to provide animal habitat.

In light of ongoing encroachment into many grassland ecosystems, managers must consider restoration to maintain current ecosystem function. However, regardless of the initial degree of success of such projects, long-term requirements need to be considered. Encroachment is unlikely to be reversed through a single intervention as climate becomes increasingly conducive to recruitment. Sites should be chosen with care to focus on meadows with especial importance or on meadows that may be less susceptible to encroachment. For example, focusing on meadows containing patches of wet refugia where trees grow and recruit more slowly may be more effective than focusing on drier meadows where more intensive, ongoing efforts will be needed.

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