

ECOGRAPHY

Research

Post-fire vegetation and climate dynamics in low-elevation forests over the last three millennia in Yellowstone National Park

M. Allison Stegner, Monica G. Turner, Virginia Iglesias and Cathy Whitlock

M. A. Stegner (<https://orcid.org/0000-0002-1412-8203>) ✉ (astegner@stanford.edu), Gilbert Building, Stanford, CA, USA. – M. G. Turner (<https://orcid.org/0000-0003-1903-2822>) and MAS, Dept of Integrative Biology, Univ. of Wisconsin-Madison, Madison, WI, USA. – V. Iglesias (<https://orcid.org/0000-0001-5732-3714>), Earth Lab, Univ. of Colorado, Boulder, CO, USA. – C. Whitlock (<https://orcid.org/0000-0002-1585-1209>), Dept of Earth Sciences and Montana Inst. on Ecosystems, Montana State Univ., Bozeman, MT, USA.

Ecography

42: 1226–1236, 2019

doi: 10.1111/ecog.04445

Subject Editor: Kate Lyons

Editor-in-Chief: Miguel Araújo

Accepted 25 February 2019

Conifer forests of the western US are historically well adapted to wildfires, but current warming is creating novel disturbance regimes that may fundamentally change future forest dynamics. Stand-replacing fires can catalyze forest reorganization by providing periodic opportunities for establishment of new tree cohorts that set the stage for stand development for centuries to come. Extensive research on modern and past fires in the Northern Rockies reveals how variations in climate and fire have led to large changes in forest distribution and composition. Unclear, however, is the importance of individual fire episodes in catalyzing change. We used high-resolution paleoecologic and paleoclimatic data from Crevice Lake (Yellowstone National Park, Wyoming, USA), to explore the role of fire in driving low-elevation forest dynamics over the last 2820 yr. We addressed two questions: 1) did low-elevation forests at Crevice Lake experience abrupt community-level vegetation changes in response to past fire events? 2) Did the interaction of short-term disturbance events (fire) and long-term climate change catalyze past shifts in forest composition? Over the last 2820 yr, we found no evidence for abrupt community-level vegetation transitions at Crevice Lake, and no evidence that an interaction of climate and fire produced changes in the relative abundance of dominant plant taxa. In part, this result reflects limitations of the datasets to detect past event-specific responses and their causes. Nonetheless, the relative stability of the vegetation to fires over the last 2820 yr provides a local baseline for assessing current and future ecological change. Observations of climate–fire–vegetation dynamics in recent decades suggest that this multi-millennial-scale baseline may soon be exceeded.

Keywords: abrupt change, fire history, Holocene, low-elevation montane forest, paleoecology, pollen

Introduction

The consequences of future climate change in Rocky Mountain forests are highly uncertain, especially as climate conditions are projected to exceed historical ranges of variability in this century (Jiang et al. 2013). Biotic communities are well adapted to exist within a particular climate space, but novel disturbance regimes interacting



www.ecography.org

© 2019 The Authors. Ecography © 2019 Nordic Society Oikos

with altered climate have the capacity to alter ecosystems fundamentally (Paine et al. 1998, Williams and Jackson 2007, Littell et al. 2010, Westerling et al. 2011, Johnstone et al. 2016). In montane, subalpine and boreal conifer forests, recent fires have interacted with rising temperatures to trigger abrupt changes favoring species better suited to new conditions (Johnstone and Chapin 2003, Wirth et al. 2008, Johnstone et al. 2010a, Savage et al. 2013, Hansen et al. 2016). Slow-growing forests often require large, high-severity disturbance events to evoke an ecological state change (Turner et al. 1998, Johnstone et al. 2010b, Landhäusser et al. 2010, Hughes et al. 2013), and climate conditions during the post-fire regeneration window are particularly critical because they influence establishment and seedling success (Harvey et al. 2016, Kueppers et al. 2017, Liang et al. 2017, Hansen and Turner 2019). The early decades of post-fire regeneration can set the stage for stand development for centuries (Kashian et al. 2005, Brown and Johnstone 2012). Changes in dominant tree species, once they occur, influence a suite of ecosystem functions, including biodiversity, carbon storage, and water availability, and services like timber production. Anticipating how projected fires will alter forests has become a priority for conservation and management (Stephens et al. 2013).

Research following recent stand-replacing fires in the Greater Yellowstone Area (GYA; Wyoming, Montana and Idaho, USA) has shed light on mechanisms by which forests respond to high-severity fire and traits that lead to success of species in particular settings (Turner et al. 1997, Donato et al. 2016, Harvey et al. 2016). In the last few decades, considerable effort also has been directed towards understanding the long-term vegetation, fire and climate history of the GYA using a combination of pollen, charcoal and geochemical data from the sediments of lakes and wetlands (Whitlock 1993, Whitlock et al. 2008, 2012, Krause and Whitlock 2017, Iglesias et al. 2018). These records document vegetation dynamics since the last glaciation under a greater range of climate conditions than can be observed at present. Here, we combined paleoecological data and ecological information from the low-elevation montane forests of northern Yellowstone National Park with the goal of better understanding the response of moisture-stressed forests to interactions of climate and fires.

Extensive research in the US Northern Rockies, particularly in the aftermath of large fires, reveals the varied response of conifer species under different climate and fire conditions (Tepley et al. 2017, Stevens-Rumann et al. 2018). In the GYA, lodgepole pine *Pinus contorta* var. *latifolia* and Douglas-fir *Pseudotsuga menziesii* var. *glauca* are well adapted to fire, but their fire adaptations and patterns of post-fire recruitment are different. Post-fire regeneration of lodgepole pine, which dominates many subalpine forests, is rapid and prolific, especially where high levels of serotiny in the pre-fire population assure an abundant canopy seedbank (Turner et al. 1997, 1999, 2003, Turner 2010, Romme et al. 2011). Lodgepole pine can produce cones within 5–15 yr of

establishment (Turner et al. 2007) and maintain dominance through sequential high-severity fires via prolific regeneration. Douglas-fir dominates many montane forests at lower elevation, but it lacks a canopy seedbank and grows in less dense stands than lodgepole pine. As a result, post-fire regeneration takes longer than for lodgepole pine (Donato et al. 2016). Douglas-fir trees are slow to mature (30–50 yr), but once established, they can maintain dominance because their thick bark allows older trees to survive low-severity fires. Observations following past fires have shown that recruitment is lower for both Douglas-fir and lodgepole pine when conditions are dry (e.g. during dry years, on south-facing slopes, and/or at low-elevation sites; Harvey et al. 2016, Hansen and Turner 2019). However, Douglas-fir occupies drier areas (e.g. lower montane positions, south-facing slopes; Donato et al. 2016) and thus may have higher recruitment success than lodgepole pine when the post-fire recruitment period is dry (Heyerdahl et al. 2006).

At lower elevations where conditions are warmer and drier, sagebrush steppe, limber pine *Pinus flexilis* and Rocky Mountain juniper *Juniperus scopulorum* dominate the vegetation of northern Yellowstone National Park. Limber pine, in particular, is restricted to xeric or rocky soils and ridges where tree seedlings have little competition (Baker 2009, Knight et al. 2014), although moisture deficit is limiting (Moyes et al. 2013). Limber pines often withstand fires because they grow in low-density stands where fuels are limited (Baker 2009), whereas sagebrush *Artemisia tridentata* and *A. cana* is readily eliminated by fire but re-establishes within 10–30 yr (Wagner 2006).

Crevice Lake (lat. 45.000°N, long. 110.578°W, elev. 1713 m, 31 m water depth) is a closed-basin, alkaline lake in the canyon of the Yellowstone River (Fig. 1). The surrounding vegetation consists of forests of Douglas-fir, Rocky Mountain juniper, limber pine and steppe dominated by big sagebrush *Artemisia tridentata*, and bunchgrasses (Whitlock et al. 2008). We used high-resolution pollen, charcoal and geochemical records taken in 2001 (Whitlock et al. 2008) to explore changes in vegetation, fire and climate dynamics over the last 2820 yr near Crevice Lake. This time span was selected because the large-scale drivers of climate change (e.g. variations in the seasonal cycle of insolation and in the strength and location of dominant circulation features) were generally similar to modern climate drivers (Bartlein et al. 1986). Specifically, we asked: 1) did low-elevation forests at Crevice Lake experience abrupt changes across the plant community? And, 2) did interactions between climate and fire catalyze changes in species dominance? Based on previous research (Iglesias et al. 2018), we expected Douglas-fir to have been favored over lodgepole pine when fires were followed by dry periods. We also expected limber pine, juniper and/or sagebrush to have been favored over Douglas-fir when post-fire drought was severe. Question 1 addressed whether there was major vegetation change at Crevice Lake on a multi-millennial time scale. Question 2, in contrast, addressed potential mechanisms driving fluctuations in

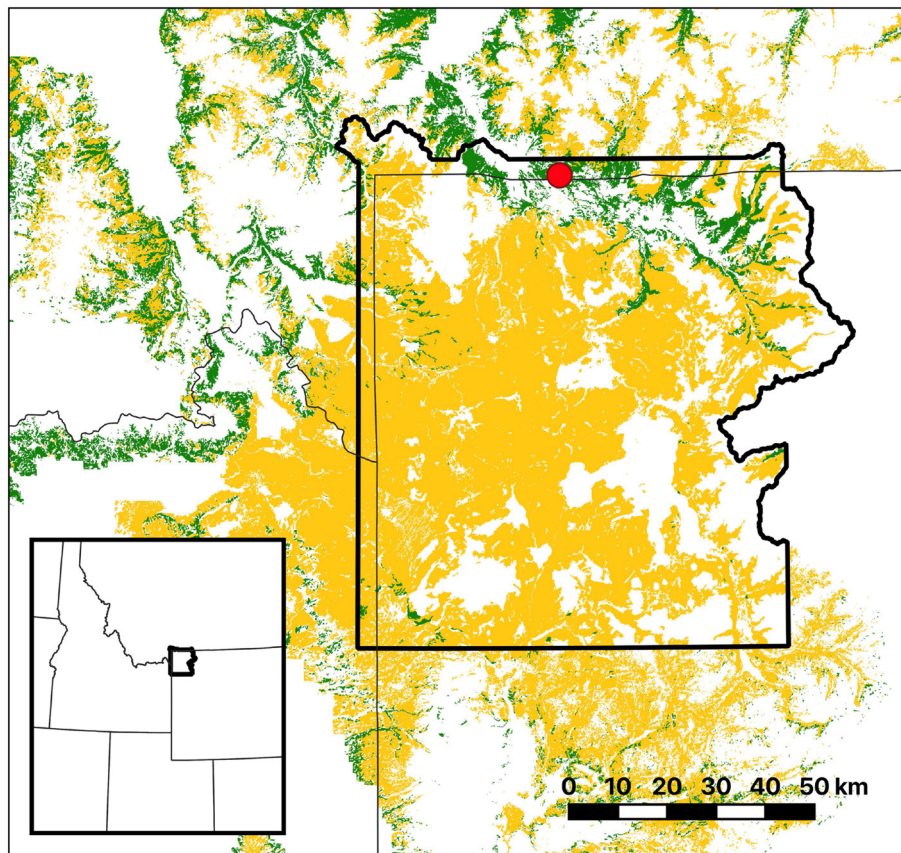


Figure 1. Map of the study region. Red point = Crevice Lake; yellow shading = regions dominated by lodgepole-pine; green shading = regions dominated by Douglas-fir; thick black line = border of Yellowstone National Park.

the abundance of the dominant tree species on the scale of decades to centuries. Understanding past climate–fire–vegetation relationships is important because projected warming and altered fire regimes are expected to alter forest composition and potentially convert forests to nonforested vegetation (Westerling et al. 2011).

Material and methods

Crevice Lake datasets

Cores collected from Crevice Lake in 2001 were analyzed for pollen, charcoal, diatoms and geochemical data (see Whitlock et al. (2008) for details). Although the Crevice Lake record extends back to 9300 calyr BP (Whitlock et al. 2012), our study focused on the high-resolution portion of the dataset from ~40 to 2820 calyr BP (calyear BP = years before AD 1950), where the sediments were annually laminated (varved). Accelerator Mass Spectrometer (AMS) radiocarbon dates and varve counts were used to develop the chronology. For this study, we updated the chronology using a Bayesian age-depth model with the IntCal13 calibration curve (Reimer et al. 2013) and the R Bchron package (Parnell 2018, R Core Team) (Fig. 2, Supplementary material Appendix 1). This revised age-depth model changed

the basal age of the pollen data described in the original papers (Stevens and Dean 2008, Whitlock et al. 2008) from 2650 calyr BP to 2820 calyr BP.

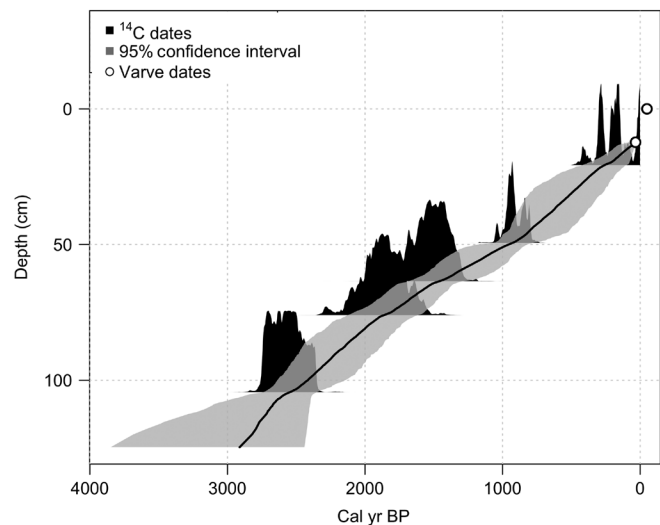


Figure 2. Bayesian age-depth model for Crevice Lake. Gray shading indicates the 95% quantiles for the Bayesian age-depth model, and the thick black line is the 50% quantile. Black distributions show the calendar age probabilities for each radiocarbon date; open circles are varve dates.

Changes in vegetation were inferred from pollen percentage as reported in Whitlock et al. (2008). The four species of interest (*Pinus contorta*, *Pseudotsuga menziesii*, *Pinus flexilis* and *Artemisia tridentata*) are identified as pollen types *Pinus contorta*-type, *Pseudotsuga*-type, *Pinus flexilis*/*P. albicaulis*-type and *Artemisia*. Sixty pollen samples were analyzed, with a median sampling interval of 43 yr, and pollen percentages were calculated based on total terrestrial pollen.

Macroscopic charcoal (i.e. charcoal particles > 125 μm), a proxy of past local fire activity, was tallied in continuous 1–5 mm core intervals (Whitlock and Larsen 2001). Charcoal counts were converted to charcoal accumulation rates (CHAR; particles $\text{cm}^2\text{yr}^{-1}$) and interpolated to the median sampling resolution (5.14 yr) to account for changes in sedimentation rates and sampling variability. Following Higuera et al. (2009), a locally weighted scatterplot smoother (LOWESS; 200-yr window) was employed to separate the high frequency component of the time series (i.e. residuals of the model) from the long-term trends in CHAR (i.e. 'background CHAR'). The positive residuals of the model that exceeded the 95th percentile of a locally fit Gaussian distribution (i.e. 'charcoal peaks') were interpreted as local fire episodes (one or more fires in the time span of the sample). We assumed that these charcoal peaks represent largely stand-replacing fires, given that much of the charcoal is wood and needle fragments. Crevice Lake charcoal data are available from the Global Charcoal Database (site code #540; <www.paleofire.org/>).

Endogenic calcium carbonate (CaCO_3) and $\delta^{18}\text{O}$ are discussed by Stevens and Dean (2008) and Whitlock et al. (2008) (Fig. 3). CaCO_3 at Crevice Lake is a proxy for seasonal organic productivity broadly related to summer temperature, with high values indicating warm conditions (Stevens and Dean 2008, Whitlock et al. 2008). $\delta^{18}\text{O}$ at Crevice Lake is interpreted as a proxy for hydrologic variability. Given the lake's subsurface connection with the nearby Yellowstone River, high values indicate low winter precipitation at high elevations, as reflected in Yellowstone River water composition (Stevens and Dean 2008, Whitlock et al. 2008).

We also analyzed reconstructed Palmer Drought Severity Index (PDSI) data for the last ~1600 yr from the North American Drought Atlas (Cook et al. 2010). These PDSI data were reconstructed from 1845 tree ring records from across North America and are available at a spatial resolution of $0.5 \times 0.5^\circ$ (Cook et al. 2010) (Fig. 3). We accessed PDSI data for the grid cell (centered on 45.00°N , 110.58°W) containing Crevice Lake which included data for 40–1581 cal yr BP.

Pollen abundance distributions are typically skewed, and variances scale with the means (Jackson and Williams 2004, Iglesias et al. 2018). To prevent variables with the largest values from dominating the analyses, we scaled the pollen data using a square-root transformation (Legendre and Gallagher 2001, Legendre and Birks 2012) and standardized the CaCO_3 , $\delta^{18}\text{O}$ and PDSI means and variances using a z-transformation. For autoregressive lag-1 models in particular (Assessment of

climate–fire–vegetation interactions' section), the magnitude of the coefficients can be compared among the predictor variables when variables have been z-transformed (a linear transformation where resulting variables have mean = 0 and standard deviation = 1).

Abrupt change detection

Before testing for abrupt vegetation changes in the past (question 1), we first tested for significant trends in the abundance of each pollen type using Kendall's tests. To identify abrupt vegetation changes, we used stratigraphically constrained cluster analysis, known as CONISS and implemented in the rioja package in R (Juggins 2017). CONISS is a multivariate clustering method which uses Euclidean distances and in which only temporally-neighboring samples may be grouped together (Grimm 1987). We tested the significance of each hierarchical cluster using a broken stick test, which compares the 'dispersion', a measure of variance, of the observed hierarchical classifications to that of a broken stick model: for each cluster, when dispersion in the observed model was greater than in the broken stick model, the cluster was considered statistically significant (see Bennett 1996 for details).

Assessment of climate–fire–vegetation interactions

Before examining the past interaction of fire and climate (question 2), we evaluated relationships between abundance of the pollen types, charcoal peaks and climate proxies on centennial time scales. Associations between CaCO_3 , $\delta^{18}\text{O}$ and PDSI values and the pollen abundance of each taxon were evaluated using Spearman's rank order correlation tests with Holm p-value adjustments. Specifically, we found the median value of each climate proxy (CaCO_3 , $\delta^{18}\text{O}$ and PDSI) in the 100 yr preceding each pollen sample, then correlated percent pollen abundance of each taxon with each climate proxy. CaCO_3 , $\delta^{18}\text{O}$ and PDSI had different sampling resolutions, and thus, the number of proxy samples per 100-yr window necessarily varied. Furthermore, the temporal coverage of each climate proxy differed (Fig. 3), so a different but overlapping subset of pollen samples was used for each proxy. This approach allowed comparison of pollen types when correlated with the same proxy, but did not allow comparisons across proxies.

Because we expected vegetation composition to shift only after stand-replacing fires, we evaluated the relationship between pollen abundance and climate proxies during a 20-yr window after each charcoal peak (i.e. the inferred fire episode). First, we determined the pollen percentage for each taxon 40 years before and after a charcoal peak. The 40-yr window was selected because the span is long enough for post-fire seed recruitment, sapling growth and pollen production for Douglas-fir, which is the slowest species to mature. We then determined the median CaCO_3 , $\delta^{18}\text{O}$ and PDSI values within a 20-yr period after each charcoal peak. For each pollen type and climate proxy pair, we used Spearman's rank

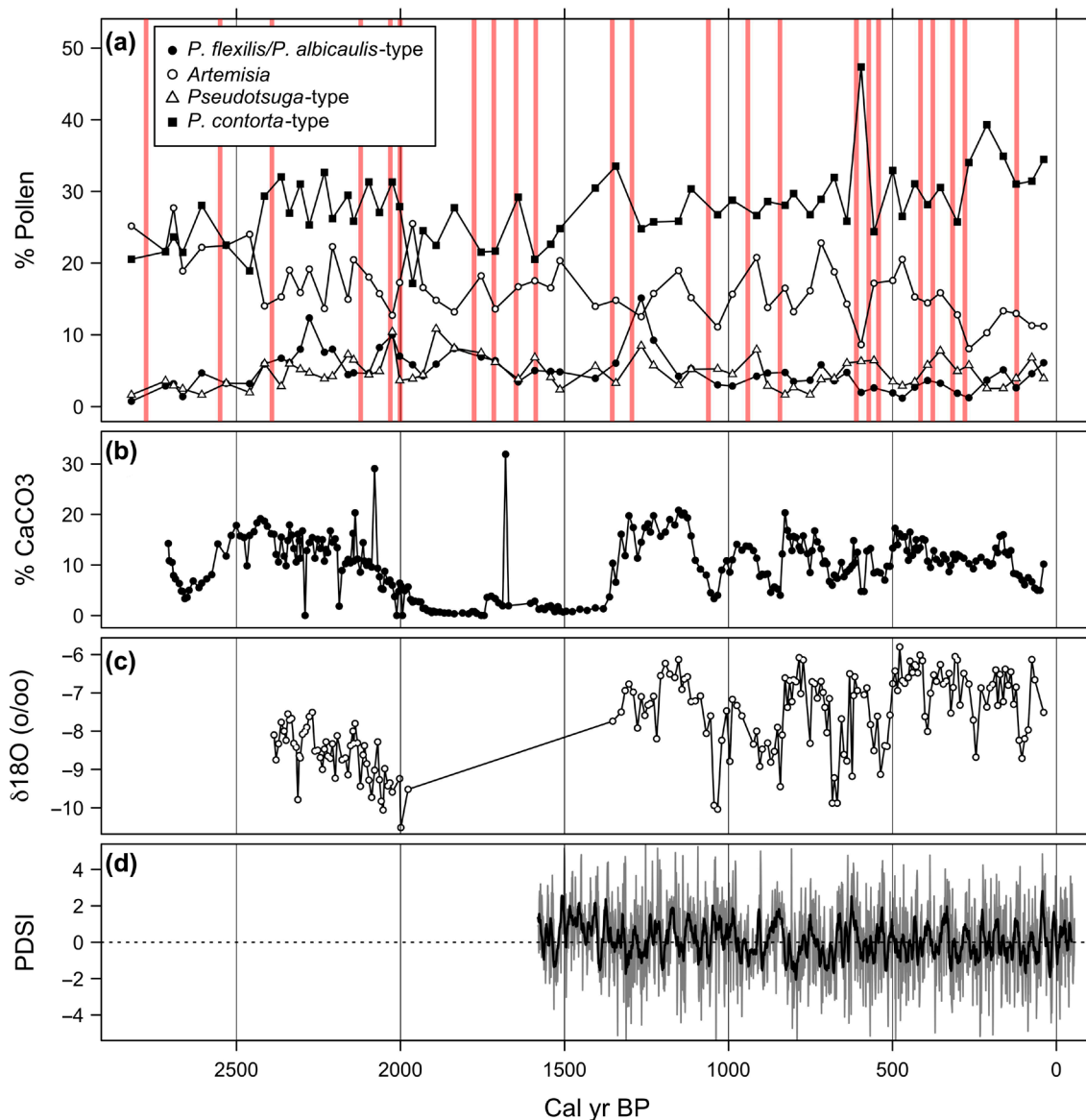


Figure 3. Crevice Lake pollen abundance and climate proxies. (a) Pollen percentages of *Pinus flexilis/albicaulis*-type (limber pine), *Artemisia* (sagebrush), *Pseudotsuga*-type (Douglas-fir) and *Pinus contorta*-type (lodgepole pine); red vertical lines = fire events inferred from charcoal peaks; (b) % calcium carbonate (CaCO₃); (c) δ¹⁸O (o/oo Vienna Pee Dee Belemnite carbonate standard) (data from Stevens and Dean (2008)); (d) annual (gray line) and 10-yr moving average (black line) Palmer drought severity index (PDSI) (data from Cook et al. (2010)).

correlations with Holm p-value adjustments to determine if there was a correlation between post-fire pollen abundance and the climate proxy. To determine if there was a significant difference in climate when a taxon decreased versus increased, we classified fire events according to whether a taxon increased or decreased after the fire, then compared the post-fire climate proxies for these two groups using Mann-Whitney tests with Holm p-value adjustments.

As an alternative, synthetic approach to examining correlations among climate, fire and vegetation, we used first-order autoregressive, or AR(1), models to test whether post-fire recruitment conditions drove pollen abundance. Autoregressive models are simple linear models that include

lagged effects in both the response variable and environmental noise (Ives et al. 2010). AR models and similar autoregressive moving average (ARMA) and autoregressive integrated moving average (ARIMA) models have been widely used to model the dynamical characteristics of ecological time series (Williams et al. 2003, Ives et al 2010, Einarsson et al. 2016). To assess the conditions during the recruitment window, we first determined if a charcoal peak took place within the 40–100 yr prior to a pollen sample. Across all pollen samples, the median amount of time to the preceding charcoal peak was 56 yr (minimum = 1.5, maximum = 172). For samples where a charcoal peak occurred during the 40–100-yr window, we quantified median CaCO₃, δ¹⁸O and PDSI

for a 20-yr window after the peak. For pollen samples not preceded by a charcoal peak in the 40–100-yr window, we quantified median climate proxy values for the 20-yr window beginning 56 yr prior to the pollen sample. We selected 100 yr as the maximum time window for a fire-related vegetation response because chronosequence studies (Kashian et al. 2005) and simulations have shown that postfire regeneration densities drive stand composition for at least ~100 yr in this system (Braziunas et al 2018). Consequently, we conservatively assumed that pollen samples taken within 100 yr post-fire would reflect the relative abundance of the dominant tree species following fire.

We created two sets of AR(1) models of pollen abundance for each taxon and climate proxy pair. Because CaCO_3 , $\delta^{18}\text{O}$ and PDSI data cover partially but not completely over-lapping time periods, we generated models for each taxon/climate proxy pair rather than combining proxies in a single model. The first set of models included the climate proxy and presence/absence of charcoal peaks as external drivers. These models represent the situation where pollen-inferred vegetation changes were driven by climate conditions in the long-term, but not by conditions during the recruitment period specifically. The second set of models included the climate proxy, presence/absence of a charcoal peak, and a charcoal peak \times climate proxy interaction term. The interaction term in the models accounts for the possible role of post-fire recruitment conditions in determining taxon abundance. We generated all AR(1) models with missing values to account for differences in sampling resolution. To do this, we rounded each sample time to the nearest decade, then entered missing values for unobserved decades. For each taxon/climate proxy pair, we compared the two models using log-likelihood ratio tests.

Results

Broad ecological changes over the last 2820 years

On multi-centennial time scales, the Crevice Lake record shows a gradual increase in *Pinus contorta*-type pollen (Kendall's tau = 0.33; $p < 0.001$) through time at the expense of *Artemisia* pollen (Kendall's tau = -0.38; $p < 0.0001$) (Fig. 3a), suggesting more lodgepole pine, probably on rhyolite substrates (Whitlock et al. 2008). Trends in *Pseudotsuga*-type and *P. flexilis*/*P. albicaulis*-type pollen were non-significant (Kendall's tau = 0.06 and -0.22, respectively), but both increased slightly from ca 2820 to 2400 calyr BP and had somewhat higher values from ca 2400 to 1850 calyr BP and after 300 calyr BP. These data suggest variations in Douglas-fir and limber pine cover in low-elevation forests. A total of 23 charcoal peaks were identified at Crevice Lake, indicating fires throughout the last 2820 yr at a median interval of 94 yr.

Endogenic CaCO_3 values were relatively high before 2000 calyr BP, and percentages dropped between ca 2000 and 1350 calyr BP (Fig. 3b). Values were again elevated from ca 1350 calyr BP to present, with a notable drop from

1100 to 800 calyr BP. These data suggest variations in limnic productivity, which was related to summer temperature, including a cooler, less productive period from 2000 to 1350 calyr BP. The $\delta^{18}\text{O}$ record has a significant gap where carbonates were not preserved (1950–1350 calyr BP), but the general trend suggests increasing values to the present (Fig. 3c) that are interpreted as a trend towards declining winter precipitation at high elevations (Stevens and Dean 2008).

Abrupt change

CONISS identified no statistically significant abrupt changes in vegetation composition at Crevice Lake over the last 2820 yr, irrespective of fire occurrence (Supplementary material Appendix 2).

Climate–fire–vegetation interactions

Counter to expectation, there were no significant correlations (with or without p-value adjustments) between the pollen abundance of the four focal taxa – *Pinus contorta*, *Pseudotsuga menziesii*, *Pinus flexilis* and *Artemisia tridentata* – and the climate conditions in the century preceding each pollen sample (Supplementary material Appendix 3), with one exception: *Pinus flexilis*/*P. albicaulis*-type pollen was negatively correlated with $\delta^{18}\text{O}$ (Fig. 4), suggesting that *Pinus flexilis* (or possibly *P. albicaulis* at high elevations) was more abundant when winter precipitation was high. Moreover, post-fire pollen abundances were not significantly correlated with post-fire climate proxies (with or without a Holm p-value correction) (Fig. 5). This result means that, across all taxa, differences in climate during the recruitment period were not significant, regardless of whether a taxon's abundance increased or decreased after a fire.

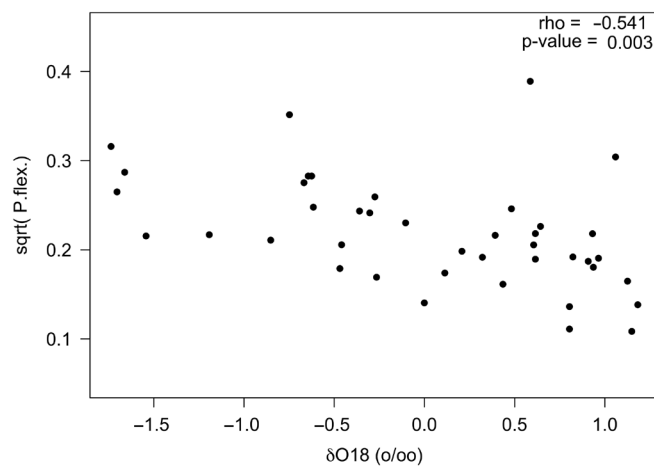


Figure 4. *Pinus flexilis*/*P. albicaulis*-type pollen abundance versus median $\delta^{18}\text{O}$ in the 100 yr preceding pollen samples. Pollen abundance is square-root-transformed proportion; $\delta^{18}\text{O}$ units are o/oo Vienna Pee Dee Belemnite carbonate standard (VPDB); *P.flex.* = *Pinus flexilis*/*P. albicaulis*-type; rho = Spearman's rho.

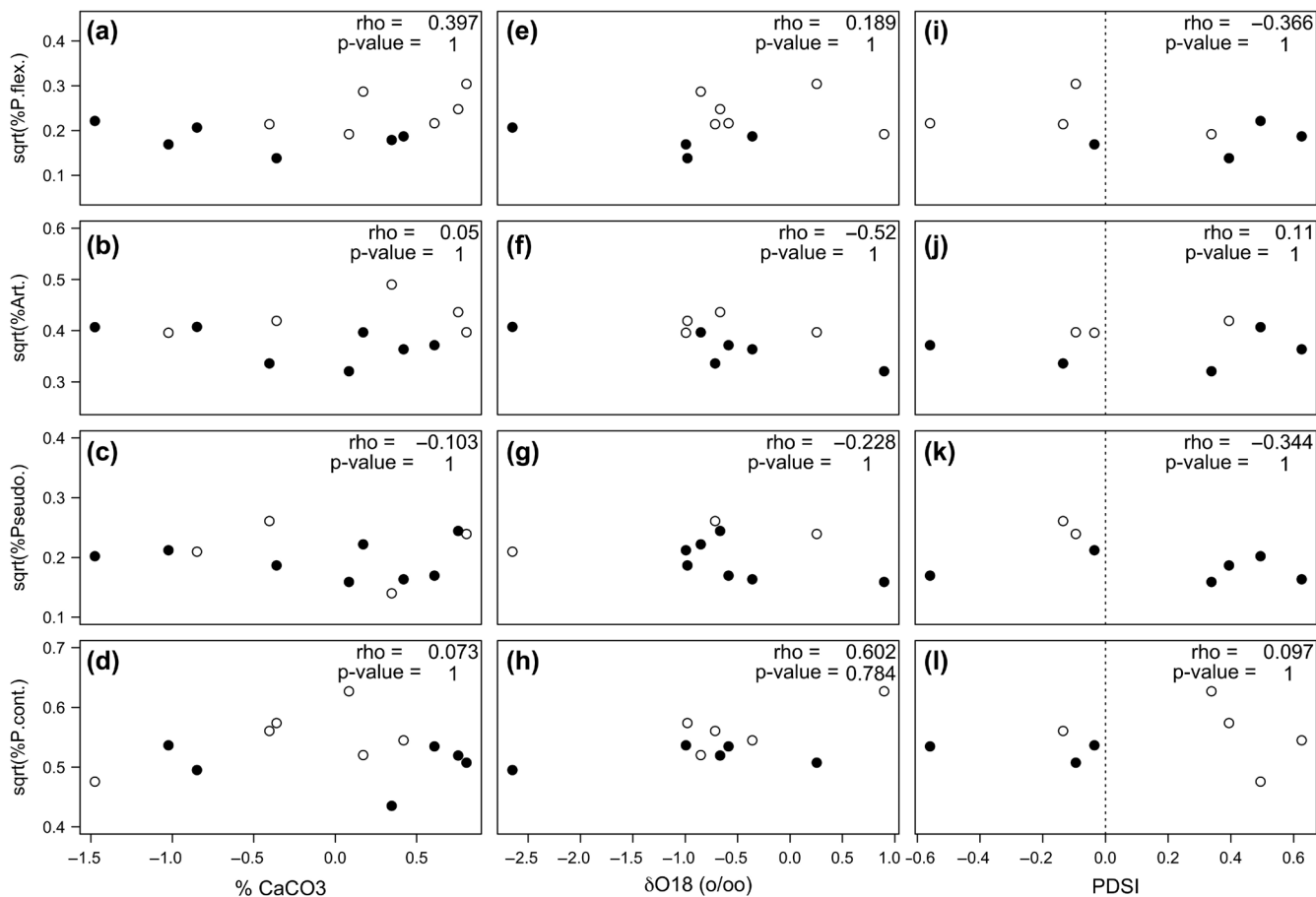


Figure 5. Post-fire pollen abundance versus post-fire climate conditions. Filled points indicate instances when pollen abundance increased from before to after the fire; open points are times when pollen abundance decreased from before to after the fire. CaCO_3 = calcium carbonate; PDSI = Palmer drought severity index; P.flex. = *Pinus flexilis*/*P. albicaulis*-type; Art. = *Artemisia*; Pseudo = *Pseudotsuga*-type; P.cont. = *Pinus contorta*-type; rho = Spearman's rho. $\delta^{18}\text{O}$ units are o/oo Vienna Pee Dee Belemnite carbonate standard (VPDB). Dashed vertical line in panels (i-l) are PDSI = 0 (normal conditions).

In all cases, the AR(1) model that included a charcoal peak \times climate interaction had higher log-likelihood values than the models without interaction, but no significant differences were evident between models for any pollen/climate proxy pair (Supplementary material Appendix 4). The interaction of charcoal peak and climate was no more predictive of species abundance than climate alone.

Discussion

We did not find evidence of abrupt community-level vegetation change following individual fires at Crevice Lake, and this result was surprising in light of recent observations of forest change following high-severity fires in parts of the GYA and Rocky Mountains (Stevens-Rumann et al. 2018). Shifts in both forest composition and structure have been substantial in recent decades when post-fire years have been warm and dry or fires have occurred in dry settings at lower treeline or on south-facing aspects (Rother et al. 2015, Donato et al.

2016, Harvey et al. 2016, Stevens-Rumann et al. 2018). Over the last 2820 yr at Crevice Lake, we found no evidence that the interaction of climate and fire produced statistically significant and predictable changes in the relative abundance of dominant taxa.

Four plausible reasons may contribute to the observed absence of a relationship between post-fire climate and the abundance of lodgepole pine, Douglas-fir, limber pine and sagebrush. First, climate changes over the last 2820 yr may not have been of sufficient magnitude to cause vegetation turnover in northern Yellowstone National Park, at least at the elevation of Crevice Lake. Put another way, the post-fire climate did not exceed temperature or moisture thresholds that would have allowed a different trajectory of regeneration. For example, experimental evidence found a nonlinear decline in post-fire establishment of lodgepole pine and Douglas-fir when mean soil temperature during the growing season exceeded 16°C (Hansen and Turner 2019); such conditions may have been infrequent over the last 2820 yr. The relative stability of Crevice Lake vegetation during the last three

millennia implies that climate conditions and disturbance over that time span remained within the tolerance limits for species at this site.

The remaining three explanations relate to factors that may obscure the driver-state relationships and mechanisms we sought to detect at Crevice Lake. First, while temperature and precipitation are critical drivers of vegetation change, large-scale climate variations are mediated by local non-climatic factors, such as slope, aspect, and soil type. The climate proxies that were analyzed at Crevice Lake do not directly measure the local climate conditions that would have been important in post-fire regeneration. The $\delta^{18}\text{O}$ record at Crevice Lake, for example, is a measure of high-elevation snowpack in winter and not a record of precipitation levels at the study site, which are highest in spring and early summer (Whitlock and Bartlein 1993). Similarly, the PDSI index is an interpolated data set that describes summer drought at a broad scale ($0.5 \times 0.5^\circ$) (Cook et al. 2010) and necessarily an incomplete description of effective moisture in the canyon of the Yellowstone River. CaCO_3 is a measure of limnic productivity and, indirectly, summer water temperature, but the interpretation is complicated by the carbon pump that balances production of organic matter and CaCO_3 in the epilimnion and decomposition and dissolution of these constituents in the anoxic, low pH hypolimnion and sediments (Dean 1999).

Second, the temporal resolution of the Crevice Lake dataset may be too coarse to detect subtle or short-term vegetation changes that may have occurred on the scale of decades to centuries. The median amount of time between pollen samples at Crevice Lake is 43 yr, and the median amount of time between fires is 93 yr. The number of pollen samples following charcoal peaks was probably too small to statistically identify short-term changes in vegetation, unless those pollen shifts were step-like, dramatic and persistent. Also, the temporal resolution of the climate proxies, as noted above, does not capture year-to-year variations in local growing-season conditions that determine success or failure of post-fire tree establishment: interannual variation in climate could have buffered trees from occasional, severe drought.

A third factor relates to the limitations of pollen and charcoal data to resolve local responses in vegetation and fire. For example, *Pinus contorta*-type pollen comes from a large source area spanning the watershed or beyond, and *Pseudotsuga*-type pollen is large and heavy and likely comes from trees growing near the lake (Iglesias et al. 2018). Similarly, the macroscopic charcoal peaks likely represent fire episodes that occurred within a few kilometers around the lake, irrespective of fire size (Higuera et al. 2011). The abundance of wood charcoal at Crevice Lake indicates the presence of high-severity fire, but low-severity burns may also have left areas of living trees. Different severities would have created a range of post-fire recruitment conditions and opportunities. In addition, the source area for the macroscopic charcoal peaks may be similar to that of *Pseudotsuga*-type pollen but it is probably much smaller than that of *Pinus contorta*-type pollen. Different

source regions of the pollen taxa and charcoal data means that the vegetation reconstruction is probably of larger scale than the fire information. This spatial mismatch necessarily limits our ability to detect clear relationships among climate, fires and vegetation (Calder et al. 2019).

Long-term baselines are important for contextualizing modern ecosystems and determining when ecosystems have departed from the range of variability that has shaped them for thousands of years (Whitlock et al. 2010, 2015). Already, climate change has increased disturbance frequency and extent in the western U.S. relative to 20th century baselines (Westerling et al. 2006, Kurz et al. 2008, Parks et al. 2012, Abatzoglou and Williams 2016, Westerling 2016), and warming temperatures and aridity are altering the environmental conditions that constrain post-fire recovery (Harvey et al. 2016, Petrie et al. 2016, Kueppers et al. 2017, Liang et al. 2017, Andrus et al. 2018). The GYA has warmed by $1\text{--}1.5^\circ\text{C}$ in the last 50 yr and an additional warming of $2.2\text{--}3.3^\circ\text{C}$ is projected by mid-century (Al-Chokhachy et al. 2013). Although there have been no discernible trends in precipitation in the region in recent decades (Hansen et al. 2016), moisture deficits in the west have been increasing (Westerling 2016). As a result of these changes, total burned area of forest across the West has increased $\sim 890\%$ from the 1970s to the early 2000s (Westerling 2016).

Paleoecological records across the GYA suggest that lower treeline has shifted upslope in the last millennium in response to drought and fire (Iglesias et al. 2018), and modern ecological studies predict that this shift will continue in the future with increasing stand-replacing fires and aridity. After the 1988 Yellowstone fires, Douglas-fir has so far failed to recruit on south-facing slopes at lower elevations, and steppe shrubland has replaced over 4000 hectares of lower montane forest (Donato et al. 2016). Recruitment of lodgepole pine also has been lower when fires were followed by warm, dry years (Harvey et al. 2016). Post-fire recruitment of lodgepole pine and Douglas-fir will likely continue to decline in lower montane forests as temperatures increase (Hansen and Turner 2019). Sedimentary records like that of Crevice Lake offer long-term baselines against which future ecological change can be assessed (Whitlock et al. 2018). The relatively small variations in vegetation, climate and fire activity in recent millennia highlight the challenges of reconciling past dynamics with recent and incipient changes in the contemporary landscape.

Conclusion

Paleoecological data from GYA show dramatic shifts in vegetation during the warming that occurred at the close of the last glaciation from 16 000 to 9000 cal yr BP. This transition included the abrupt appearance of new plant communities and fire regimes at ca 12 000 cal yr BP at all elevations of GYA (Iglesias et al. 2018). In contrast, our study shows relative stability in forest composition and fire conditions during the last 2820 yr, and individual fires did not trigger significant

vegetation change at Crevice Lake. In the Yellowstone region, the climate variations of the late Holocene were not as great as those of the late-glacial-to-Holocene transition, and as a result, the vegetation response to disturbance in recent millennia was similarly muted (Iglesias et al. 2018), a situation which seems to be changing in recent decades (Donato et al. 2016). With projected temperatures continuing to rise in the coming decades, the forest dynamics described over the last 2820 yr at Crevice Lake will soon be exceeded. Projected warming will be associated with a lengthened fire season, more stand-replacing fires, and ultimately, changes in forest composition (Westerling et al. 2011, Vose et al. 2018). The paleoecological record provides information on long-term ecological change to a range of climate conditions, and modern observations reveal ecological responses to individual disturbances and short-term climate events. Despite the challenges of their different spatial, temporal and taxonomic resolution, drawing on the two sources of information remains the best opportunity to examine change over a broad range of temporal scales.

Acknowledgements – We thank J. W. Williams, A. R. Ives, and the Univ. of Wisconsin-Madison Abrupt Change in Ecological Systems group for valuable discussions. Z. Ratajczak provided species distribution data for Fig. 1.

Funding – Funding for this study was provided by the Wisconsin Alumni Research Foundation (UW2020 initiative) (MAS and MGT), the Univ. of Wisconsin-Madison Vilas Research Trust (MGT) and the National Science Foundation (grant no. 0966472 and no. 1515353; CW).

Conflicts of interest – The authors declare no conflicts of interest.

References

- Abatzoglou, J. T. and Williams, A. P. 2016. Impact of anthropogenic climate change on wildfire across western US forests. – *Proc. Natl Acad. Sci. USA* 113: 11770–11775.
- Al-Chokhachy, R. et al. 2013. Thermal controls of Yellowstone cutthroat trout and invasive fishes under climate change. – *Global Change Biol.* 19: 2069–3081.
- Andrus, R. A. et al. 2018. Moisture availability limits subalpine tree establishment. – *Ecology* 99: 567–575.
- Baker, W. L. 2009. *Fire ecology in Rocky Mountain landscapes*. – Island Press.
- Bartlein, P. J. et al. 1986. Climate response surfaces from pollen data from some eastern North American taxa. – *J. Biogeogr.* 13: 35–57.
- Bennett, K. D. 1996. Determination of the number of zones in a biostratigraphical sequence. – *New Phytol.* 132: 155–170.
- Braziunas, K. H. et al. 2018. Looking beyond the mean: drivers of variability in postfire stand development of conifers in Greater Yellowstone. – *For. Ecol. Manage.* 430: 460–471.
- Brown, C. D. and Johnstone, J. F. 2012. Once burned, twice shy: repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. – *For. Ecol. Manage.* 266: 34–41.
- Calder, W. J. et al. 2019. Climate–fire–vegetation interactions and the rise of novel landscape patterns in subalpine ecosystems, Colorado. – *J. Ecol.* doi:10.1111/1365-2745.13138
- Cook, E. R. et al. 2010. Megadroughts in North America: placing IPCC projections of hydroclimatic change in a long-term palaeoclimate context. – *J. Q. Sci.* 25: 48–61.
- Dean, W. E. 1999. The carbon cycle and biogeochemical dynamics in lake sediments. – *J. Paleolimnol.* 21: 375–393.
- Donato, D. C. et al. 2016. Regeneration of montane forests 24 years after the 1988 Yellowstone fires: a fire-catalyzed shift in lower treelines? – *Ecosphere* 7: e01410.
- Einarsson, Á. et al. 2016. Identifying consumer–resource population dynamics using paleoecological data. – *Ecology* 97: 361–371.
- Grimm, E. C. 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. – *Comput. Geosci.* 13: 13–35.
- Hansen, W. and Turner, M. G. 2019. Origins of abrupt change? Postfire subalpine conifer regeneration declines non-linearly with warming and drying. – *Ecol. Monogr.* 89: e01340.
- Hansen, W. D. et al. 2016. Shifting ecological filters mediate postfire expansion of seedling aspen (*Populus tremuloides*) in Yellowstone. – *For. Ecol. Manage.* 362: 218–230.
- Harvey, B. J. et al. 2016. High and dry: post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches. – *Global Ecol. Biogeogr.* 25: 655–669.
- Heyerdahl, E. K. et al. 2006. History of fire and Douglas-fir establishment in a savanna and sagebrush-grassland mosaic, southwestern Montana, USA. – *For. Ecol. Manage.* 230: 107–118.
- Higuera, P. E. et al. 2009. Vegetation mediated the impacts of postglacial climatic change on fire regimes in the south central Brooks Range, Alaska. – *Ecol. Monogr.* 79: 201–219.
- Higuera, P. et al. 2011. Linking tree-ring and sediment-charcoal records to reconstruct fire occurrence and area burned in sub-alpine forests of Yellowstone National Park, USA. – *Holocene* 21: 327–341.
- Hughes, T. P. et al. 2013. Living dangerously on borrowed time during slow, unrecognized regime shifts. – *Trends Ecol. Evol.* 28: 149–155.
- Iglesias, V. et al. 2018. Past vegetation dynamics in the Yellowstone region highlight the vulnerability of mountain systems to climate change. – *J. Biogeogr.* 45: 1768–1780.
- Ives, A. R. et al. 2010. Analysis of ecological time series with ARMA (p,q) models. – *Ecology* 91: 858–871.
- Jackson, S. T. and Williams, J. W. 2004. Modern analogs in quaternary paleoecology: here today, gone yesterday, gone tomorrow? – *Annu. Rev. Earth Planet. Sci.* 32: 495–537.
- Jiang, X. et al. 2013. Projected future changes in vegetation in western North America in the 21st century. – *J. Clim.* 2013: 3671–3687.
- Johnstone, J. F. and Chapin, F. S. 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. – *Global Change Biol.* 9: 1401–1409.
- Johnstone, J. F. et al. 2010a. Fire, climate change and forest resilience in interior Alaska. – *Can. J. For. Res.* 40: 1302–1312.
- Johnstone, J. F. et al. 2010b. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. – *Global Change Biol.* 16: 1281–1295.
- Johnstone, J. F. et al. 2016. Changing disturbance regimes, ecological memory and forest resilience. – *Front. Ecol. Environ.* 14: 369–378.
- Juggins, S. 2017. rioja: analysis of quaternary science data. – R package ver. 0.9-15.1, <<http://cran.r-project.org/package=rioja>>.

- Kashian, D. M. et al. 2005. Variability and convergence in stand structural development on a fire-dominated subalpine landscape. – *Ecology* 86: 643–654.
- Knight, D. H. et al. 2014. Mountains and plains: the ecology of Wyoming landscapes. – Yale Univ. Press.
- Krause, T. R. and Whitlock, C. 2017. Climatic and non-climatic controls shaping postglacial conifer history in the northern Greater Yellowstone Ecosystem, USA. – *J. Q. Sci.* 32: 1022–1036.
- Kueppers, L. M. et al. 2017. Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. – *Global Change Biol.* 23: 2383–2395.
- Kurz, W. A. et al. 2008. Mountain pine beetle and forest carbon feedback to climate change. – *Nature* 452: 987–990.
- Landhäusser, S. M. et al. 2010. Disturbance facilitates rapid range expansion of aspen into higher elevations of the Rocky Mountains under a warming climate. – *J. Biogeogr.* 37: 68–76.
- Legendre, P. and Gallagher, E. D. 2001. Ecologically meaningful transformations for ordination of species data. – *Oecologia* 129: 271–280.
- Legendre, P. and Birks, H. J. B. 2012. Clustering and partitioning. – In: Birks, H. J. B. et al. (eds), *Tracking environmental change using lake sediments, volume 5: data handling and numerical techniques*. Springer, pp. 123–141.
- Liang, S. et al. 2017. Response of Sierra Nevada forests to projected climate-wildfire interactions. – *Global Change Biol.* 23: 2016–2030.
- Littell, J. S. et al. 2010. Forest ecosystems, disturbance and climate change in Washington State, USA. – *Clim. Change* 102: 129–158.
- Moyes, A. B. et al. 2013. Warming and the dependence of limber pine (*Pinus flexilis*) establishment on summer soil moisture within and above its current elevation range. – *Oecologia* 171: 271–282.
- Paine, R. T. et al. 1998. Compound perturbations yield ecological surprises. – *Ecosystems* 1: 535–545.
- Parks, S. A. et al. 2012. Spatial bottom-up controls on fire likelihood vary across western North America. – *Ecosphere* 3: 1–20.
- Parnell, A. 2018. Bchron: radiocarbon dating, age-depth modelling, relative sea level rate estimation and non-parametric phase modelling. – R package ver. 4.2.7, <<https://CRAN.R-project.org/package=Bchron>>.
- Petrie, M. D. et al. 2016. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. – *For. Ecol. Manage.* 361: 328–338.
- Reimer, P. J. et al. 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. – *Radiocarbon* 55: 1869–1887.
- Romme, W. H. et al. 2011. Twenty years after the 1988 Yellowstone fires: lessons about disturbance and ecosystems. – *Ecosystems* 14: 1196–1215.
- Rother, M. T. et al. 2015. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. – *Can. J. For. Res.* 45: 1607–1616.
- Savage, M. et al. 2013. Double whammy: high-severity fire and drought in ponderosa pine forests of the southwest. – *Can. J. For. Res.* 583: 570–583.
- Stephens, S. L. et al. 2013. Managing forests and fire in changing climates. – *Science* 342: 41–42.
- Stevens, L. R. and Dean, W. E. 2008. Geochemical evidence for hydroclimatic variability over the last 2460 years from Crevice lake in Yellowstone National Park, USA. – *Q. Int.* 188: 139–148.
- Stevens-Rumann, C. S. et al. 2018. Evidence for declining forest resilience to wildfire under climate change. – *Ecol. Lett.* 21: 243–252.
- Tepley, A. J. et al. 2017. Vulnerability to forest loss through altered postfire recovery dynamics in a warming climate in the Klamath Mountains. – *Global Change Biol.* 23: 4117–4132.
- Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. – *Ecology* 91: 2833–2849.
- Turner, M. G. et al. 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. – *Ecol. Monogr.* 67: 411–433.
- Turner, M. G. et al. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. – *Ecosystems* 1: 511–523.
- Turner, M. G. et al. 1999. Prefire heterogeneity, fire severity and plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. – *Int. J. Wildl. Fire* 9: 21–36.
- Turner, M. G. et al. 2003. Postfire aspen seedling recruitment across the Yellowstone (USA) landscape. – *Landscape Ecol.* 18: 127–140.
- Turner, M. G. et al. 2007. Cone production in young post-fire *Pinus contorta* stands in Greater Yellowstone (USA). – *For. Ecol. Manage.* 242: 119–206.
- Vose, J. M. et al. 2018. Forests. – In: Reidmiller, D. R. et al. (eds), *Impacts, risks and adaptation in the United States: fourth national climate assessment, volume II*. U.S. Global Change Research Program, doi:10.7930/NCA4.2018.CH6
- Wagner, F. H. 2006. Yellowstone's destabilized ecosystem: elk effects, science and policy conflict. – Oxford Univ. Press.
- Westerling, A. L. 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. – *Phil. Trans. R. Soc. B* 371: 20150178.
- Westerling, A. L. et al. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. – *Science* 313: 940–943.
- Westerling, A. L. et al. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. – *Proc. Natl Acad. Sci. USA* 108: 13165–13170.
- Whitlock, C. 1993. Postglacial vegetation and climate of Grand Teton and southern Yellowstone National Parks. – *Ecol. Monogr.* 63: 173–198.
- Whitlock, C. and Bartlein, P. J. 1993. Spatial variations of Holocene climatic change in the Yellowstone region. – *Q. Res.* 39: 231–238.
- Whitlock, C. and Larsen, C. 2001. Charcoal as a fire proxy. – In: Smol, J. P. et al. (eds), *Tracking environmental change using lake sediments. Volume 3: terrestrial, algal and siliceous indicators*. Springer, pp. 75–95.
- Whitlock, C. et al. 2008. A 2650-year-long record of environmental change from northern Yellowstone National Park based on a comparison of multiple proxy data. – *Q. Int.* 188: 126–138.
- Whitlock, C. et al. 2010. Paleoperspectives on fire ecology: revisiting the fire regime concept. – *Open Ecol. J.* 3: 6–23.
- Whitlock, C. et al. 2012. Holocene seasonal variability inferred from multiple proxy records from Crevice Lake, Yellowstone National Park, USA. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 331–332: 90–103.
- Whitlock, C. et al. 2015. Climate change: uncertainties, shifting baselines and fire management. – In: Dellasala, D. A. and Hanson, C. (eds), *The ecological importance of mixed-severity fires: nature's phoenix*. Elsevier, pp. 265–283.

- Whitlock, C. et al. 2018. Land-use history as a guide for forest conservation and management. – *Conserv. Biol.* 32: 84–97.
- Williams, C. K. et al. 2003. Population dynamics across geographical ranges: time-series analysis of three small game species. – *Ecology* 84: 2654–2667.
- Williams, J. W. and Jackson, S. T. 2007. Novel climates, no-analog communities and ecological surprises. – *Front. Ecol. Environ.* 5: 475–482.
- Wirth, C. et al. 2008. White spruce meets black spruce: dispersal, postfire establishment and growth in a warming climate. – *Ecol. Monogr.* 78: 489–505.

Supplementary material (available online as Appendix ecog-04445 at <www.ecography.org/appendix/ecog-04445>). Appendix 1–4.