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# Spatial and temporal variability in the effects of wildfire and drought on thermal habitat for a desert trout

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ABSTRACT

We studied how drought and an associated stressor, wildfire, influenced stream flow permanence and thermal regimes in a Great Basin stream network. We quantified these responses by collecting information with a spatially extensive network of data loggers. To understand the effects of wildfire specifically, we used data from 4 additional sites that were installed prior to a 2012 fire that burned nearly the entire watershed. Within the sampled network 73 reaches were classified as perennial, yet only 51 contained surface water during logger installation in 2014. Among the sites with pre-fire temperature data, we observed 2–4 °C increases in maximum daily stream temperature relative to an unburned control in the month following the fire; effects (elevated up to 6.6 °C) appeared to persist for at least one year. When observed August mean temperatures in 2015 (the peak of regionally severe drought) were compared to those predicted by a regional stream temperature model, we observed deviations of −2.1°-3.5°. The model under-predicted and over-predicted August mean by > 1 °C in 54% and 10% of sites, respectively, and deviance from predicted was negatively associated with elevation. Combined drought and post-fire conditions appeared to greatly restrict thermally-suitable habitat for Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*).



## 1. Introduction

The influences of climate on Earth are often portrayed as systematic trends through time (Loarie et al., 2009), but change itself is not stationary (Milly et al., 2008). For example, as climate changes, it is broadly anticipated that the probability of episodic disturbances will also change (Running, 2008). Ecologically, this means that species will have to contend with a host of acute and chronic exposures (Foden et al., 2013) to changing climates. Such uncertainties regarding climate itself provide many challenges for anticipating ecological responses to climate change (Wenger et al., 2013). Here we focus on two common episodic, climate-driven ecological disturbances: drought (Lake, 2011) and wildfire (Westerling, 2016). Both of these disturbances are driven by the intersection of precipitation deficits and warm temperatures, and are thus likely to manifest at the same time within a given area (Diffenbaugh et al., 2015; Ganguli and Ganguly, 2016).

In this study we consider the influences of drought and wildfire on stream temperatures. Stream temperature is well-known to be sensitive to both meteorological variability (i.e. drought-related; Caissie, 2006; Diabat et al., 2013; Luce et al., 2014) and wildfires (Hitt, 2003; Dunham et al., 2007; Mahlum et al., 2011). In the northern Great Basin desert, the onset of meteorological and hydrological drought (Wilhite and Glantz, 1985) has increasingly coincided with large wildfires (Denison et al., 2014; Westerling, 2016). Wildfires often burn riparian vegetation, leading to loss of shade and warming of stream temperatures (Dunham et al., 2007; Mahlum et al., 2011), which may further warm if streams experience reduced flows during drought. Because a host of factors can influence stream temperatures and sensitivity to drought and wildfire (e.g., riparian and topographic shading, surface-subsurface

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heat fluxes) specific responses can be variable and difficult to predict. We used a combination of opportunistically available records of stream temperature (from temperature data loggers in operation before and after a large wildfire), a regional model of stream temperatures from before a wildfire and drought (Isaak et al., 2016a), and a network of temperature loggers deployed after a fire and during the height of an ongoing drought (i.e., 2015; Fig. 1) to evaluate how both wildfire and drought influenced temperatures across a large, desert stream network.

Specifically, our objectives were to: 1) quantify the magnitude and duration of influences of wildfire on stream temperature at sites with pre- and post-wildfire temperature data, 2) evaluate spatial variation in responses of summer stream temperature throughout the entire stream network during the latter stages of the drought to a baseline of predictions from a stream temperature model assembled with data from 1993 to 2011 (Isaak et al., 2016a), and 3) assess the ecological consequences of conditions observed during the 2015 drought year for a sensitive species (Lahontan cutthroat trout, [*Oncorhynchus clarkii henshawi*]; Jones et al., 1998). Collectively, results of this work provide novel insights into how aquatic ecosystems respond to the combined influences of drought and wildfire, two interactive disturbances that are more likely to occur as climate change proceeds (Lake, 2011; Diffenbaugh et al., 2015; Westerling, 2016).

## 2. Methods

### *2.1. Study area*

Our study was focused in the Willow and Whitehorse creeks watershed (hereafter, Willow-Whitehorse watershed) of southeast Oregon (Fig. 2). The watershed is characteristic of Great Basin sagesteppe, consisting mostly of open rangelands with elevations of 1300–2250 m, including 200–400 m deep canyons draining northward into the endorheic Coyote Lake Basin (Grayson, 2011). The watershed contains 262 km of intermittent-classified stream channels in the National Hydrography Dataset Plus V2 (NHDPlus; USEPA, 2012), and an additional 143 km of NHDPlus-classified perennial stream channels (all mapped at 1:100,000 scale). Natural overstory vegetation across the watershed is typical of the

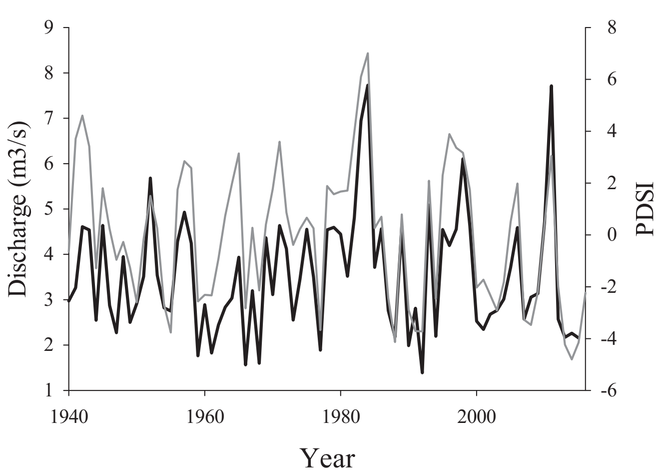


**Fig. 1.** Palmer Drought Severity Index (PDSI; gray) and annual discharge ($m^3/s$; black) for southeast Oregon, 1940–2016. Drought severity is from the Southeast Oregon climate division (3509) for this period of record, with monthly values aggregated to annual means to visualize general meteorological drought conditions in the region. Annual discharge is from the Donner und Blitzen River (10396000) in the Steens Mountain region, 70 km northwest of Willow-Whitehorse watershed.

region and composed of mostly sagebrush *Artemisia* spp. and pockets of quaking aspen *Populus tremuloides* in the higher elevations, bitterbrush *Purshia tridentata* and rabbitbrush (family: Asteraceae) flats at lower elevations, and willow *Salix* spp. dominated riparian zones (Grayson, 2011). Non-native cheatgrass *Bromus tectorum* has also invaded into much of the watershed, displacing native bunchgrasses (family: Poaceae) and has potentially altered its susceptibility to wildfire (Knapp, 1996). The watershed is also notable in that it supports one of the largest extant populations of Lahontan cutthroat trout *Oncorhynchus clarkii henshawi* (Jones et al., 1998; Warren et al., 2014), a federally listed threatened taxon (USFWS, 1995).

Our study system represents a progression of conditions associated with development of drought as a meteorological, hydrologic, and ecological phenomenon (Wilhite and Glantz, 1985). As with much of the western United States (Mote et al., 2016; Ganguli and Ganguly, 2016), the Willow-Whitehorse watershed experienced a period of severe meteorological drought that began in 2012 and peaked in 2015. The Palmer drought severity index (PDSI) suggested this was one of the most severe droughts on record in this watershed (Fig. 1). When combined with summer heat that is typical of the northern Great Basin (Hidy and Klieforth, 1990), these two factors led to manifestation of hydrologic drought, as evident from declining annual stream discharge recorded at a nearby gage in the Donner und Blitzen River, Oregon (Fig. 1). As drought conditions in the region intensified, major wildfires also occurred (Westerling, 2016). In the Willow-Whitehorse watershed, the Holloway Fire occurred August 5–17, 2012, and burned over 185,000 ha in northwest Nevada and southeast Oregon, including over 85% of our study area (Fig. 2). The fire resulted in significant loss of vegetation in both upland and riparian habitats (Fig. 3), and resulted in a mosaic of burn intensities across the Willow-Whitehorse watershed (P. Donnelly, University of Montana, unpublished data).

### *2.2. Field data collection*

We quantified spatial variation in stream temperatures by deploying a network of data logging sensors in the Willow-Whitehorse watershed September 24–27, 2014. We allocated 100 sampling points across stream reaches classified as perennial and intermittent by NHDPlus, and addressed specific research questions by ensuring that points represented several stratified landscape characteristics. We initially selected 7 locations within livestock exclosures to address management-related questions in the watershed. The remaining 93 sample locations were drawn from across the watershed using a generalized random tessellation stratified (GRTS) master sample created for the State of Oregon (Larsen et al., 2008). Use of the master sample was intended for distributing points across the stream network, rather than for generating unbiased estimates of conditions within the stream network based on known probabilities of inclusion for each point. Of the 100 sample points, 67 were selected from NHDPlus perennial streams and 33 in reaches classified as intermittent. We also selected these points such that 75 points were located inside and 25 outside of the perimeter of the Holloway Fire, and 50 inside and 50 outside of the Lahontan cutthroat trout distribution delineated during fisheries surveys conducted by Oregon Department of Fish and Wildlife (ODFW) between 2011 and 2013 (Jones et al., 1998; Kim Jones, ODFW, personal communication). This approach allowed us to attain a reasonable degree of spatial dispersion of points across the watershed, and to represent conditions believed to potentially influence hydrologic (stream flow permanence) or ecological (trout distribution) factors that could relate to stream temperature. In addition to these 100 points, 10 supplemental

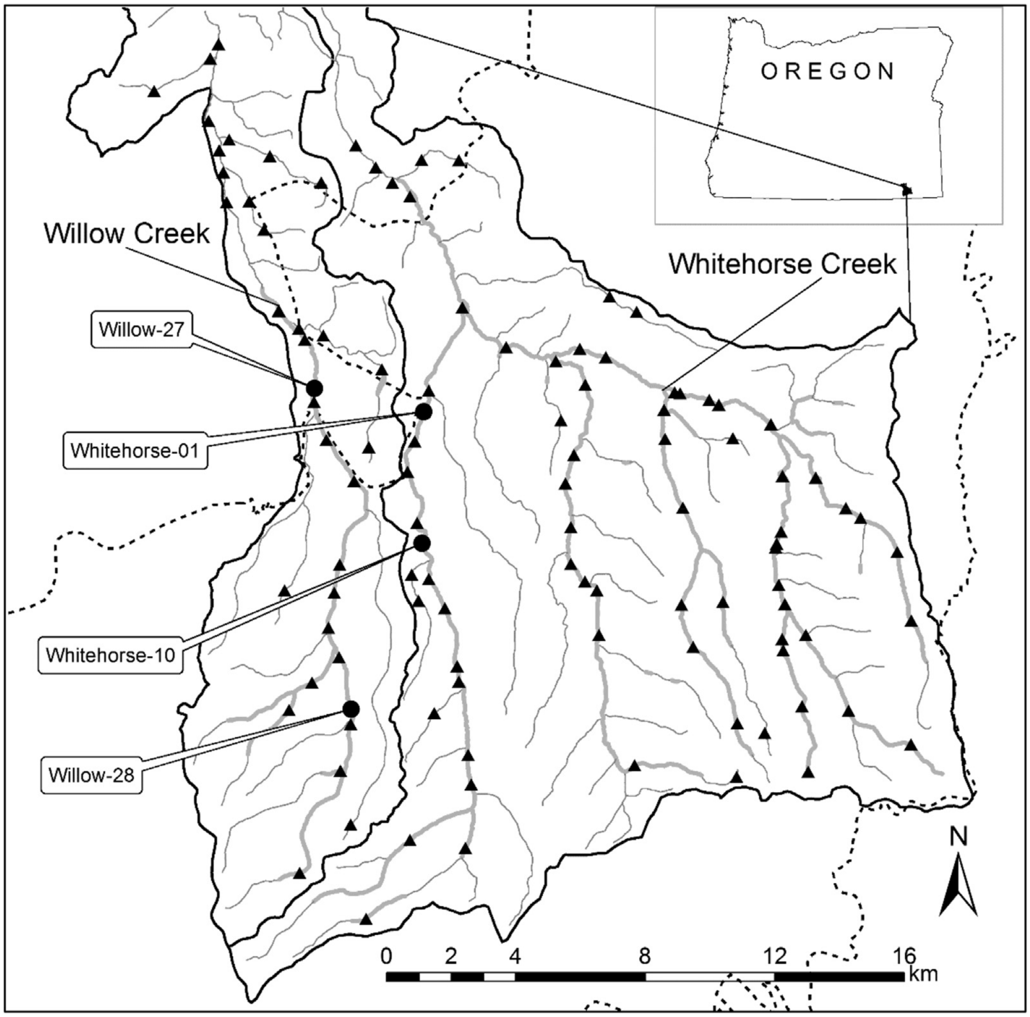


**Fig. 2.** Locations in the Willow-Whitehorse watershed of southeast Oregon where data loggers were deployed to evaluate stream temperature and flow permanence, 2014–15. The dotted line indicates the boundaries of the 2012 Holloway Fire. The 4 labeled sites (Whitehorse-10, Whitehorse-01, Willow-27, Willow-28) had complete temperature records from 2012 to 2015 and were used to evaluate the effects of the Holloway Fire on stream temperature.

points were established in the watershed in 2011 by ODFW for monitoring water temperature within the Lahontan cutthroat trout distribution. We had complete pre- (2011) and post- (2012–2015) fire temperature records from four of these sites, which allowed us to evaluate thermal responses to this fire in the Willow-Whitehorse watershed. The other sensors were either lost or had incomplete temperature records across this period.

At each of the 100 sample sites we installed a HOBO U-22 water temperature logger (Onset Computer Corporation, Bourne, MA) placed within a ventilated polyvinyl chloride (PVC) housing in the streambed (Dunham et al., 2005); the 10 additional points installed by ODFW had the same instruments. At all sampling points, we used global positioning system (GPS) receivers to navigate as close as possible to the pre-determined sampling locations. We placed temperature loggers in areas near the stream channel thalweg within 3–10 m upstream/downstream of the point to which we navigated to, and in locations we believed to be most likely to retain water and minimize probability of desiccation (Dunham et al., 2005), and that would maximize our ability to relocate them. Nearly all sites where we placed temperature loggers were completely dry or had continuous flow at the time of deployment (i.e. there were few sample points that were characterized by isolated pools). We used one of three methods to secure temperature loggers: 60 × 40 cm sand bags filled with cobble/gravel, metal stakes, or nylon zip ties to secure loggers to in-channel vegetation (Dunham et al., 2005). Of these, the majority (71) were secured using sand bags. For all temperature loggers, a measurement was recorded every hour throughout the course of the study.

We retrieved data temperature loggers over August 27–30, 2015. During the revisit, we again navigated to each of the sampling points and used site descriptions and field photographs to relocate the temperature loggers. For each temperature logger we used a HOBO Waterproof Shuttle (Onset Computer Corporation, Bourne, MA) to download data in the field. During both the initial and return visits to the study area, we noted whether stream channels at sampling locations contained surface water to compare NHDPlus classifications of perennial and intermittent streams against on-the-ground observations (e.g. Fritz et al., 2013).

### *2.3. Analysis of fire effects*

We developed a statistical model that described the relationship between observed stream temperature in streams in the Willow-Whitehorse watershed and those in an unburned control, the Little Blitzen River. In this approach, data from before the Holloway Fire were used to calibrate this predictive model. We then used this

**Fig. 3.** Photograph of the Little Whitehorse Creek watershed following the Holloway Fire (August 8–16, 2012). Both upland and riparian habitats were severely burned throughout the entire Willow-Whitehorse watershed. Photo credit: S. Hurn and P. Milburn, Oregon Department of Fish and Wildlife.

model to predict temperature at burned sites post-fire and evaluate the immediate- (1–7 days post-fire) and mid-term (1–3 years post-fire) effects (following Minshall et al., 1989) of fire on stream temperatures in the Willow-Whitehorse watershed. Because we lacked an unburned reference location for comparison within the Willow-Whitehorse watershed, we used stream temperature data from a time series collected by ODFW in the Little Blitzen River. This river is part of the Harney Lake basin, another endorheic system about 70 km northwest of our study sites in the Willow-Whitehorse watershed. The Little Blitzen River drains mountainous terrain that is similar in elevation and vegetation composition to the Willow-Whitehorse watershed. Temperature data from the Little Blitzen River were collected 2009–2015 with the same approach that we used in the Willow-Whitehorse watershed.

We visually evaluated the immediate effects of the Holloway Fire on thermal patterns by comparing plots of temperature at four burned sites in Willow and Whitehorse creeks to the unburned site in the Little Blitzen River. We quantitatively evaluated these patterns by examining the difference in paired daily maximum water temperature between the Little Blitzen and 2 sites each in Willow and Whitehorse creeks before and after the Holloway Fire (i.e., 1 June-30 September 2012). We relied on maximum temperatures as these have been found to be most responsive in past work on wildfire and stream temperature (Dunham et al., 2007).

For the mid-term fire effects, we used least squares regression with added autoregressive ('$p$') and moving average ('$q$') terms to evaluate stream temperature exceedances of observed stream temperature (Groom et al., 2011) from three sites in Willow and Whitehorse creeks (i.e. Whitehorse-01, Whitehorse-10, Willow-27; Fig. 2) against those predicted by the Little Blitzen River reference site. Because we lacked sufficient pre-fire data from an additional site (Willow-28) to acceptably calibrate the predictive model, we did not include this fourth site in this analysis. With this approach, we used stream temperature data collected in the Little Blitzen River prior to the fire to calibrate a model to predict daily maximum stream temperature in unique sites in Willow and Whitehorse creeks following the Holloway Fire, and noted if observed temperatures exceeded the upper 95% confidence intervals of those predicted. Warming and cooling patterns are highly correlated across multiple seasons, so we limited our analysis to the summer period of June 1- October 1. We used autoregressive and moving average terms to account for temporal and seasonal autocorrelation of temperature observations within the temperature time series, which were chosen by allowing $p$ and $q$ to separately vary from 0 to 4, while minimizing Akaike's Information Criterion (AIC) for the predictive models. We found that $(p, q) = (2, 1)$ was sufficient for both the daily mean and maximum temperature to model temporal autocorrelation in the data.

We evaluated model sufficiency by reviewing autocorrelation function plots, partial autocorrelation function plots, and residual plots to ensure independence and stationarity in model residuals. We also calculated 95% confidence intervals for the model by multiplying the overall model variance ($\sigma$) by three matrices: the design matrix of the regression model, the variance-covariance matrix, and the transpose of the design matrix. We inferred effects from the fire when observed mean temperatures exceeded the 95% prediction intervals following the fire. Models were completed using the *gls* function in the nlme package in program R (package nlme; Pinheiro and Bates, 2000), while predictions were generated using the *predict* function (R Core Team, 2015).

### 2.4. Analysis of the drought in 2015

To quantify drought-related temperature changes throughout the stream network in 2015, we compared observed mean August water temperatures throughout the Willow-Whitehorse watershed to those predicted by a regional statistical model (Isaak et al., 2016a). In this case we used mean rather than maximum temperatures, since the latter were not available from the regional statistical model. This spatial statistical model was fitted with thousands of empirical observations from throughout the northwest United States to predict mean August stream temperature as a function of air temperature, stream flow, elevation, latitude, reach slope, canopy cover, drainage area, precipitation, upstream lake cover and upstream glacier cover (Isaak et al., 2016a). The model assumed all covariates were constant through time except air temperature and stream flow (i.e., the model did not consider changes to canopy cover due to fires or other factors). For each sampling point that contained surface water at logger retrieval, we compared observed (2015) August mean water temperature to the grand mean of the model predictions based on data collected in 1993–2011 (sample locations found dry were removed from the analysis). This allowed us to examine how conditions from the drought compared to conditions expected from the 1993–2011 baseline, which spanned a mix of both relatively-wet and -dry years (Fig. 1).

We examined the Willow-Whitehorse watershed water temperature data in 2015 for observations that were outside of expected range of predicted August mean temperatures from the Isaak et al. (2016a) model. To do this we evaluated variability in predicted mean August stream temperatures for each of the 19 available years (1993–2011) for each of the 110 locations that corresponded to sites with temperatures recorded in 2015. For predicted temperatures, the maximum deviation in any year from the overall mean of predicted temperatures from 1993 to 2011 was 0.93 °C. Therefore, we conservatively considered any observed mean temperature from August 2015 that was within ±1 °C of the grand mean of the predicted estimates as within the expected range of variability represented by the model. Conversely, we considered observations that deviated >1 °C above or below predictions to be outside of the expected range of variability. We summarized these deviations by calculating the percent of individual observations that deviated by > ± 1 °C, as well as those that deviated by > ± 2 °C to consider thermal deviations that would have greater ecological significance. To evaluate overall patterns in temperature deviations for 2015, we plotted them as a function of elevation, a factor that is strongly associated with a host of characteristics influencing potential hydrologic processes (Isaak et al., 2016a) and fish distributions (Warren et al., 2014).

### 2.5. Ecological effects of the 2015 drought

To evaluate the potential ecological effects of the 2015 drought on Lahontan cutthroat trout in the Willow-Whitehorse watershed, we examined availability of suitable stream temperatures and flow permanence throughout the stream network. We considered the stream network at two extents: the potential distribution of Lahontan cutthroat trout based on elevation (Warren et al., 2014), and the subset of this network that is known to be occupied (accounting for upstream movement barriers, Jones et al., 1998). We classified suitability based on the number of sites that were found to be dry during sampling (during both deployment and retrieval) and calculated the percentage of sampled points with surface flow in the watershed that were thermally suitable. Thermal suitability was based on exceeding a maximum 7-day average daily maximum temperature threshold, where temperatures <20 °C (7-daily average daily maximum; 7-DADM) are considered less likely to cause sublethal stress to Lahontan cutthroat trout (Falke et al., 2016).

## 3. Results

The NHDPlus perennial classification was incorrect at >30% of sites visited in 2014 and 2015. In 2014, 51 of 73 perennial-classified sampling points (including both GRTS and re-located ODFW points) had surface water during initial visits, while 22 were completely dry; only 3 of the 33 intermittent-classified sample points contained surface water. Similarly, only 48 of the perennial-classified sites had surface water during 2015 fieldwork. With fieldwork in 2015, we successfully relocated temperature loggers at 106 of the remaining 108 sample points that covered the expanse of the study area (Fig. 2). Of the initial sites that were included, 2 of the 10 ODFW points were not located during fieldwork in 2014 and were presumed to have been lost. Our analysis for the immediate- and mid-term effects of the 2012 Holloway Fire include data from 4 sites that had continuous records from 2011 to 2015; other relocated loggers had records that either had gaps during this time period or were destroyed by the Holloway Fire.

### 3.1. Immediate- and mid-term fire effects

We observed immediate changes in both mean and maximum daily temperature in 2 sites in each of Willow and Whitehorse creeks following the Holloway Fire, but changes in the daily maxima were most pronounced (Fig. 4). At the onset of the fire (August 5 and 6), we observed a slight drop in mean and maximum daily temperature (1–3 °C) across 3 of the 4 sites in Willow and Whitehorse creeks. In the time period when the fire was actively burning these watersheds (i.e. August 8–10), mean and maximum daily water temperatures increased by ~2 °C and 4 °C, respectively, relative to the unburned control stream. These elevated temperatures appeared to persist for at least a month following the fire, but were variable through this time period.

Auto-regressive models from three sites that adequately calibrated to pre-fire data suggested that the mid-term effect of the fire in the Willow-Whitehorse watershed persisted in diminishing magnitude in the years following the fire, with the greatest exceedances occurring in 2013 and mostly isolated exceedances after 2014. At all sites, maximum stream temperature exceedances peaked in 2013 (Fig. 5), occurring in up to 80% of observed days (June-September) and averaging 3.3–6.6 °C above the predicted temperature (Table 1). We observed statistical exceedances from those predicted in 8.2–80.3% of days in 2013, 0–27.2% of days in 2014, and 0–29.2% of days in 2015 (Table 1). In all sites, the number of daily exceedances declined to <30% by 2014, and only Whitehorse-10 had exceedances in 2015. The persistence of fire effects was also heterogeneous across the three sites. Whitehorse-01 appeared to be the most sensitive post-fire, with >80% of observations in 2013 exceeding prediction intervals by a mean of 6.58 °C (SD: 2.08). Exceedances in Whitehorse-10 appeared to be of smaller magnitude (up to 5.88 °C, SD: 1.43), but exceedances occurred in almost 30% of observations in 2014 and 2015. In

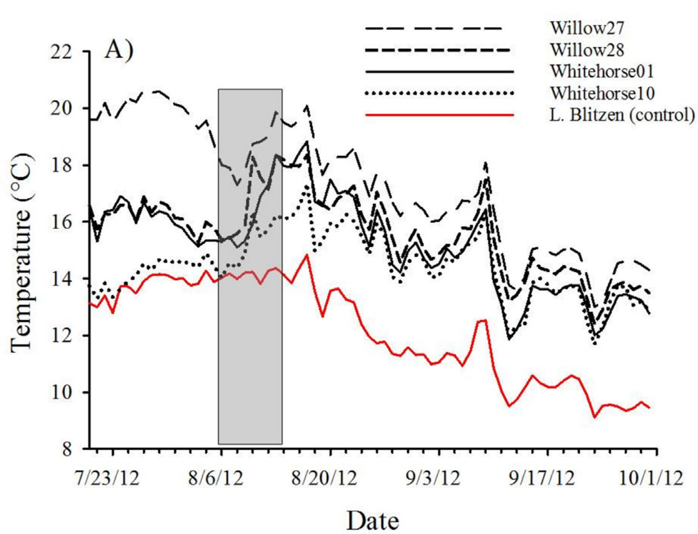


**Fig. 4.** Immediate effects of the Holloway Fire on stream temperature in the Willow-Whitehorse watershed, Oregon. Difference in mean (a) and maximum (b) temperatures between the Little Blitzen River and 4 locations in the Willow and Whitehorse watershed that burned in the large 2012 Holloway Fire (August 8–10, gray box). The Little Blitzen River was an unburned control site located about 70 km northwest of Willow and Whitehorse creeks on Steens Mountain. Note: the y-axis is different between panels.

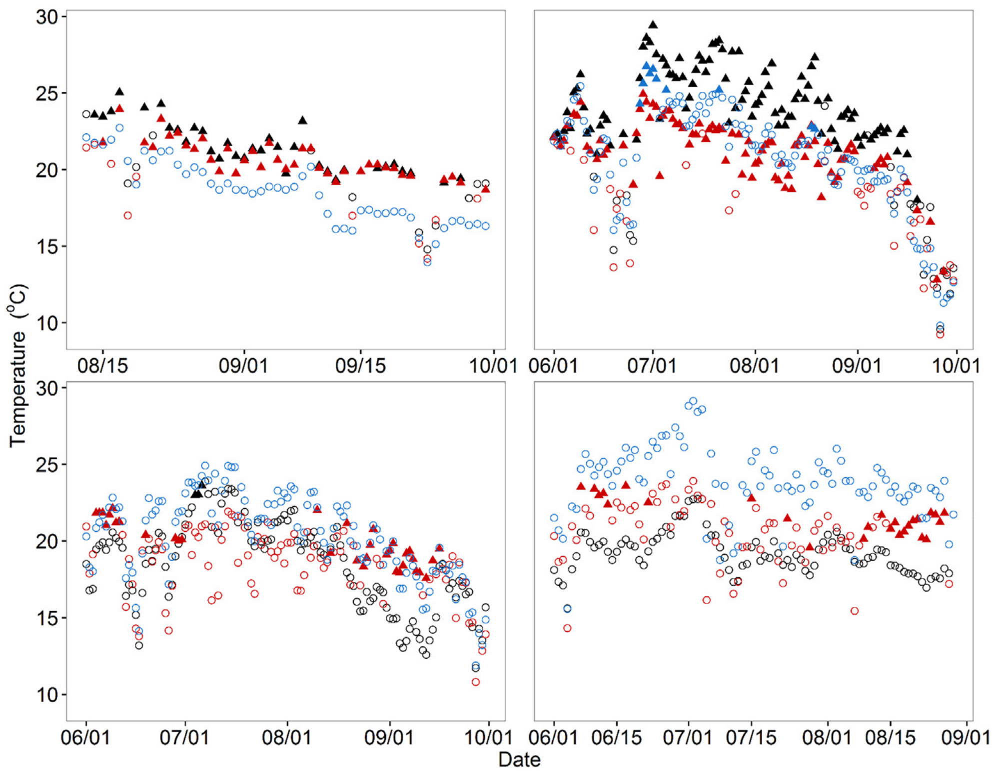


**Fig. 5.** Mid-term effects of the Holloway Fire on stream temperature in the Willow-Whitehorse watershed, Oregon. Predicted daily maximum stream temperature for June-September in three stream sites in the Willow-Whitehorse watershed, Oregon, for 2012 (upper left), 2013 (upper right), 2014 (lower left), and 2015 (lower right). Stream temperature was predicted with an auto regressive and moving averages approach using the Little Blitzen River, Oregon as an unburned reference site, and predicted for Whitehorse-01 (black), Willow-27 (blue), and Whitehorse-10 (red). For each site, hollow circles represent observations in which the daily maximum is within the expected range for these sites and exceedances are shown as solid triangles.

contrast, Willow-27 exceeded prediction intervals in only 8.2% of observations in 2013, and did not ever exceed the prediction interval after 2013.

### 3.2. Analysis of the drought in 2015

In general, the Isaak et al. (2016a) model (grand mean estimates) predicted lower stream temperatures than we observed in the Willow-Whitehorse watershed in 2015, but model performance was spatially heterogeneous across the watershed. The model predicted temperature in many reaches that were found dry during August 2015. Across all sites with surface water, predictions were within ±1 °C of the observed August mean temperature in 17 of the 48 sites included (35%). Deviations between observed and predicted values ranged from −2.1 °C to 3.5 °C, with the model underpredicting August mean temperature by > 1 °C and >2 °C at 27 (56%) and 21 (44%) of 48 sites, respectively. The model overpredicted stream temperature by > 1 °C and >2 °C in 4 (8%) and 2 (4%) sites, respectively (Fig. 6). Prediction deviance was negatively related to elevation ($r = -0.57$; Fig. 7) but the correlation between prediction deviation and drainage area was much weaker ($r = 0.39$).

### 3.3. Ecological effects of the 2015 drought

The combination of drought and post-fire conditions in the

**Table 1**
Summary of maximum daily stream temperature (°C) exceedances following a large wildfire in Willow and Whitehorse creeks, Oregon, 2012–2015. Exceedances are individual daily maximum temperature observations between June and September that were outside of prediction intervals from auto-regressive models that used pre-fire calibration data from the unburned Little Blitzen River, Oregon to predict stream temperature in Willow and Whitehorse creeks. The mean, 95% confidence interval (CI), and standard deviation is calculated from the difference between observed exceedances and the maximum temperature predicted by the auto-regressive models.

| Site | Year | Observations | Exceedances | % | Mean (°C) | 95% CI | SD |
|---|---|---|---|---|---|---|---|
| Whitehorse-01 | 2012 | 49 | 37 | 75.5 | 4.06 | 3.11 | 0.535 |
| | 2013 | 122 | 98 | 80.3 | 6.58 | 3.13 | 2.082 |
| | 2014 | 122 | 3 | 2.5 | 3.32 | 3.04 | 0.148 |
| | 2015 | 89 | – | – | – | – | – |
| Whitehorse-10 | 2012 | 49 | 38 | 77.6 | 5.83 | 3.74 | 0.78 |
| | 2013 | 122 | 87 | 71.3 | 5.88 | 3.74 | 1.434 |
| | 2014 | 122 | 34 | 27.9 | 4.71 | 3.75 | 0.637 |
| | 2015 | 89 | 26 | 29.2 | 4.49 | 3.72 | 0.386 |
| Willow-27 | 2012 | 49 | – | – | – | – | – |
| | 2013 | 122 | 10 | 8.2 | 4.76 | 3.57 | 0.986 |
| | 2014 | 122 | – | – | – | – | – |
| | 2015 | 49 | – | – | – | – | – |

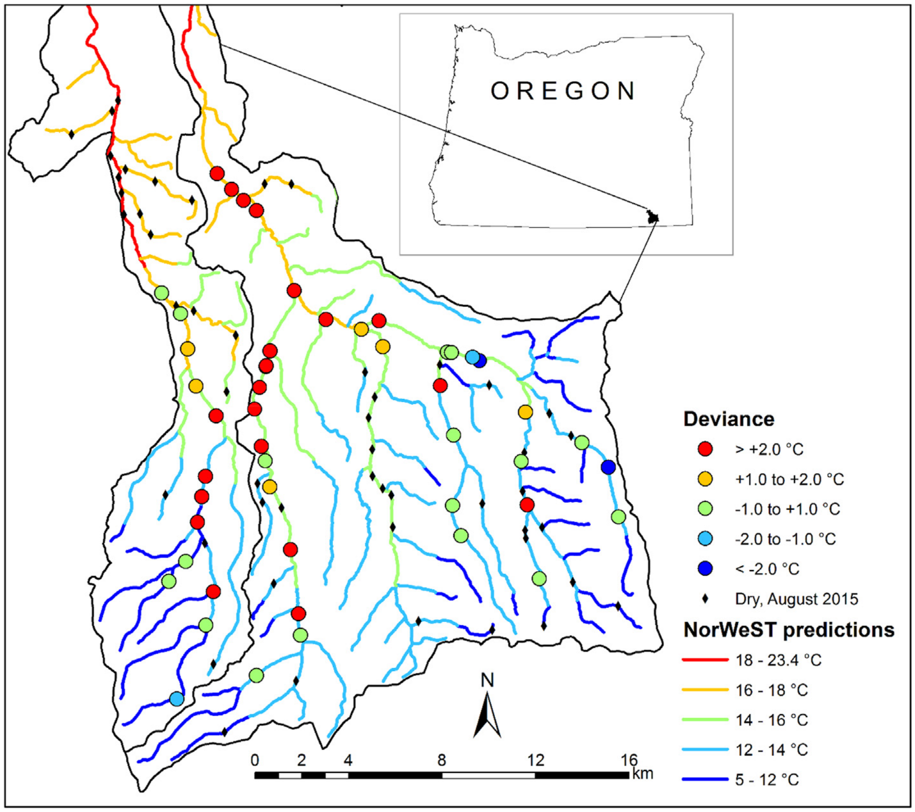


**Fig. 6.** Spatial distribution of deviations for observed August mean temperature from those predicted by a regional stream temperature model (Isaak et al., 2016a) in the Willow-Whitehorse watershed of southeast Oregon, 2015.

Willow-Whitehorse watershed appeared to restrict the amount of thermally-suitable habitat for Lahontan cutthroat trout across this network. Of the 102 sampling locations with data in 2015, 48 had surface water, 59 occurred within the known distribution of Lahontan cutthroat trout (Jones et al., 1998), and 91 occurred within the potential distribution (Warren et al., 2014). Of the sampling locations from the known distribution, 40 were found with surface water and only 9 did not exceed 20 °C 7-DADM; this represented 22.5% of sample locations with water and 15.2% of sample locations overall. Similarly, only 44 of the sampling locations in the potential distribution for Lahontan cutthroat trout contained water, and only 11 did not exceed 20 °C 7-DADM (25% of sampling locations with water and 10.7% of all points).

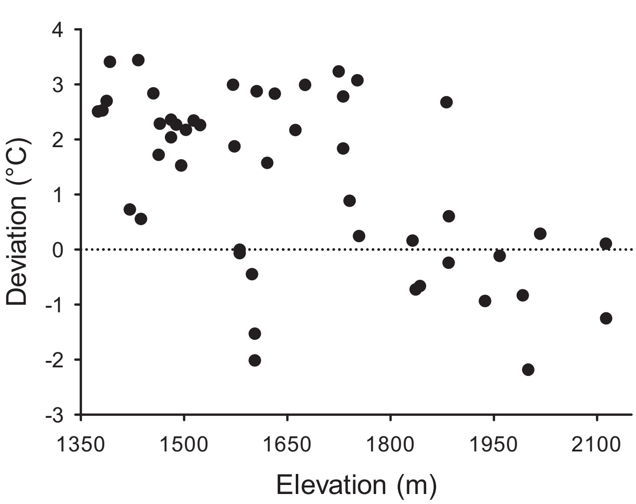


**Fig. 7.** Deviation between observed and predicted August mean stream temperature by site elevation in the Willow-Whitehorse watershed of southeast Oregon, 2015. Predicted temperatures were available from a stream temperature model for the western U.S.

## 4. Discussion

Results of this study provide unique insights into the progressive effects of drought on stream networks. Within the Willow-Whitehorse stream network, the effects of drought and wildfire were closely linked. The 2012 Holloway Fire coincided with a precipitous change in a major drought indicator, the Palmer Drought Severity Index (PDSI, Fig. 1), a relationship that is prevalent throughout the historical record in the region (Westerling, 2016). Stream temperatures warmed immediately in response to the Holloway Fire, but detectable changes were greatly diminished after two years. Continued persistence and intensification of drought conditions beyond this timespan appeared to sustain anomalously warm water temperatures within the stream network, and we observed potential ecological consequences for Lahontan cutthroat trout. Observed patterns of warming proved to be highly localized, however, indicating the role of local processes in hydrologic responses of stream networks to drought and other changes (Arismendi et al., 2012). Collectively, these findings provide one of the few detailed empirical examples of how entire stream networks may respond to the influences of climate (e.g. Isaak et al., 2010), and the only example we are aware of for the Great Basin, where many aquatic species may already be at the edges of their ecological limits (Warren et al., 2014).

The most obvious and immediate response to a regional trend of drier and warmer meteorological conditions in our study system was the occurrence of the 2012 Holloway Fire. We evaluated the immediate and mid-term effects (Minshall et al., 1989) of the fire on stream temperature, using opportunistic records of pre- and post-fire data within the Willow-Whitehorse stream network. Although our data were limited to just 4 locations, maximum water temperatures increased by up to 4 °C (to 20–24 °C) during and immediately following the Holloway Fire, and mean temperatures appeared to increase by 1–2 °C. We are not aware of comparable studies in the Great Basin, but the immediate effects of wildfires on stream temperatures in forested ecosystems in western North America have been reported to vary widely, ranging from ~4 °C (Rhoades et al., 2011) to nearly 8 °C increases (Hitt, 2003), as well as smaller increases of only about 1 °C (Beakes et al., 2014) or negligible effects (i.e. no change detected; Mahlum et al., 2011; Caldwell et al., 2013). In Mediterranean streams, precipitation following a fire regulates recovery of riparian vegetation and influences the recovery of stream thermal regions (Iraima et al., 2013). Results of analyses of mid-term responses of maximum daily stream temperatures to wildfire in the Willow-Whitehorse watershed indicated that statistically detectable temperature exceedances largely dissipated, or were undetectable (i.e., Willow-27), within two years, but that the magnitudes of exceedances were often quite large (>5 °C, Table 1). Given that we had only one year of calibration data for this analysis, as well as natural spatial variability in temperature among sites, our ability to detect more subtle changes may have been reduced. Furthermore, intensification of drought conditions across the region in 2015 may have obscured our ability to detect smaller absolute changes in temperature.

Analysis of observed stream temperatures across the Willow-Whitehorse watershed in 2015 suggested considerable spatial variability relative to historical baselines. In this case, our historical baseline consisted of modeled mean August stream temperatures using data from 1993 to 2011 (Isaak et al., 2016a, b), a period of record ending just prior to the 2012 Holloway Fire and the onset of meteorological drought in the region (Fig. 1). Observed deviations from this historical baseline in 2015 indicated warmer than expected temperatures at lower elevations, whereas a handful of higher elevation sites had temperatures that were cooler than expected. This could suggest either bias in the stream temperature model, spatial heterogeneity in thermal responses, or both. Evaluation of this model in additional (non-drought) years would be warranted to provide further information to assess bias within its predictions. Though we cannot speculate on the details of potential physical processes behind these patterns, an increasing body of work suggests that colder (and typically higher-elevation) streams are less sensitive to climate variability (Luce et al., 2014; Isaak et al., 2016b). More generally, the pervasive nature of local ($<10^3$ m grain) variability in responses of stream temperatures to climate (Arismendi et al., 2012; Mayer, 2012), as well as lack of stationarity in time (Arismendi et al., 2014) merit serious consideration in anticipating actual responses of streams to drought. Given these uncertainties and the fact that drought and associated disturbances such as wildfire can interact in complex ways to influence the heat budgets of stream ecosystems, it is impossible to simply attribute changes in stream temperature to any single factor (Caissie, 2006; Diabat et al., 2013).

Finally, it is worth noting that we observed a considerable number of dry sites within the stream network we studied (greater than 50% of those sampled). With such limited observations, we cannot draw strong conclusions about trends in streamflow permanence (e.g. Jaeger et al., 2014; Sando and Blasch, 2015), but prior empirical work in this region (Fritz et al., 2013) reported that current classifications of water availability often over-represent patterns of actual water availability across stream networks. From an ecological perspective, the implications of warming temperatures and declining water availability are clear for coldwater species such as Lahontan cutthroat trout. The Willow-Whitehorse watershed is one of the largest habitats occupied by this imperiled species (Jones et al., 1998; Warren et al., 2014), yet as we show here and elsewhere (Warren et al., 2014) it may be highly sensitive to climate-related influences.

Water availability is a concern for conservation assessments, not only for fish and other aquatic taxa in the Great Basin (e.g. Pilliod and Scherer, 2015), but for a host of terrestrial species of concern that are vulnerable to loss of stream and associated riparian and wetland habitats. These range from rare taxa such as greater sage grouse (*Centrocercus urophasianus*, Donnelly et al., 2016) to relatively common water-dependent game species such as mule deer (*Odocoileus hemionus*). Evidence from across the region points to the likelihood of drought increasing given that climates have warmed (Diffenbaugh et al., 2015), and other work suggests droughts of unprecedented duration (Ault et al., 2016) and spatial extent (Ganguli and Ganguly, 2016) could be more likely in the future. Such changes pose clear threats with potentially transformative implications for climate adaptation on both social and ecological fronts (Termeer et al., 2016). Although results from this study represent only a short-term view of these issues in a vast and remote region, they point to the value of understanding complex responses to drought that can be revealed through more intensive on-the-ground monitoring of streamflow permanence and temperatures.

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