

Impacts of beaver dams on riverscape burn severity during megafires in the Rocky Mountain region, western United States

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ABSTRACT

Megafires, defined as fires with burn areas greater than 100,000 acres (404.7 km²), result partly from increasingly short wet seasons coupled with consistently hotter, drier summers, and partly from past forest management decisions. Historically rare, megafires have become increasingly common in recent years. In this study, we examined the impact of megafires on riverscapes with beaver dams to explore the resilience of these habitats. We investigated whether beaver-modified riverscapes are more resistant to the impacts of megafires than geomorphically similar riverscapes lacking beaver dams. Our analysis utilized remotely sensed and field-collected data from three Rocky Mountain region megafires that burned in 2020. Our results showed that riparian areas with beaver dams (1537 beaver dams, which occurred in 658 out of

13,933 valley bottom segments evaluated) had significantly reduced burn severity compared to riverscapes without beaver dams or to areas outside the river corridor. Additionally, when riverscapes were classified according to their modeled beaver dam capacities (a metric closely linked to riparian habitat quality), areas with beaver dams had consistently lower burn intensities than those without beaver dams, even within the same theoretical dam capacity class. Our results indicate that riverscapes with a high degree of manipulation by beavers have significant resistance to burning during megafires. This resistance may also provide valuable secondary benefits in postfire ecosystem health, water quality, and biodiversity.

1. INTRODUCTION

1.1. Impacts of Megafires on People and Ecosystems

This study defines megafires as fires with burn areas greater than 100,000 acres (404.7 km²; Linley et al., 2022), consistent with the National Interagency Fire Center. These large and often highly destructive fires are partially the result of increasingly short wet seasons coupled with hotter, drier summers, year after year (Goss et al., 2020; Khorshidi et al., 2020; Swain, 2021; Syphard et al., 2007). Though megafires historically were rare, they have become increasingly common in recent years (Le Breton et al., 2022). These fires pose unique challenges: They have exceptionally fast rates of spread; they generate self-sustaining weather systems; and they can easily cause secondary ignitions in the surrounding landscape via ember spotting and lightning strikes from pyrocumulus clouds (Rodriguez et al., 2020; Stephens et al., 2014; Williams, 2013). These features culminate in an environment where the fire perimeter expands rapidly, posing significant risks to both humans and ecosystems (Williams, 2013).

Megafires are most common when two conditions are met: (1) There is severe fire weather (extreme heat, high winds, and convective instability; Prein et al., 2016), and (2) the landscape is predisposed toward intense and fast-spreading fires (Coen et al., 2018; Khorshidi et al., 2020; Stephens et al., 2014; Williams, 2013). Megafires have been linked to increasingly intense, long periods of severe fire weather fueled by climate change. At the same time, the role that forest management plays in making landscapes more or less susceptible to megafires remains understudied (Williams, 2013). Megafires are far less common than smaller wildfires, but they account for a disproportionately large amount of property damage, habitat destruction, fatalities, and fire-fighting costs (Jones et al., 2021; Williams, 2013). Land-management agencies have traditionally taken two approaches for addressing the rise of megafires: (1) aggressively increase the scale of fire-suppression efforts during the events, or (2) take preventative measures to reduce the likelihood that a megafire can form. Megafires often outpace containment efforts until large, naturally occurring fuel breaks or weather changes disrupt them. Scaling up the fire-fighting force alone has not been successful. The year 2020 was among the worst fire years on record

in terms of property damage and lives lost, and most of those losses occurred in megafires (Goss et al., 2020; Higuera and Abatzoglou, 2021; Swain, 2021). Therefore, shifting a portion of fire-management focus to making landscapes less favorable for megafires seems to be a prudent course of action.

Although it takes only one day of severe fire weather to start a megafire, it can generate its own hot, dry, windy weather system once initiated. Megafires, therefore, can create a positive feedback cycle of self-intensifying fire expansion, posing a major challenge for containment (Rodriguez et al., 2020). Wind spreads the fire at fast rates and enables long-distance fire spotting (ignition) from wind-driven embers. The air around megafires is dried to critically low humidities, which in turn rapidly desiccates any available fuel that is not actively being irrigated. Dry fuels and high wind allow the fire to rapidly expand (Coen et al., 2018; Khorshidi et al., 2020; Williams, 2013). As it does, the air gets drier, and the winds get stronger, further accelerating the spread of the fire and promoting a positive feedback loop. According to Williams (2013), landscapes are particularly prone to severe burning due to megafires under one or more of the following conditions (adapted from Williams, 2013):

- (1) Biomass and fuel accumulations dominate the landscapes;
- (2) rivers are disconnected from their floodplains;
- (3) woody debris and riparian vegetation are largely removed from floodplains;
- (4) wetlands are drained;
- (5) large, late successional stands are prioritized for recreation and aesthetics rather than fire prevention or resilience; and/or
- (6) vegetation mosaics are diminished, becoming more continuous high-hazard landscapes.

To help reduce the risk of excessive burning due to megafires, recommended practices for land-management agencies aim to achieve the opposites of these conditions. A landscape resistant to megafires would then have the following characteristics:

- (1) Fuel and biomass are regularly removed by natural processes (e.g., low-intensity managed or natural fires, herbivory, or mechanical methods such as thinning or back-burning/burnout to remove excess fuels in the face of wildfire);
- (2) rivers are well connected to their floodplains;
- (3) large wood is present across floodplain surfaces;

- (4) wetlands are reestablished;
- (5) strategic areas prioritize low-flammability new growth; and/or
- (6) vegetation mosaics are restored, and patch size of individual land-cover types is reduced.

Conditions to reduce risk of megafire can all be met through the reestablishment of healthy biologic and fluvial-geomorphic processes in watersheds. This suite of processes is broadly needed on watershed scales across North America to address the last two centuries of human impacts (Wohl et al., 2021). Nature-based, and specifically natural process-based, restorations of watersheds, including the activities of beavers, are cost-effective, scalable, low-tech, durable methods to return the natural function and resilience to rivers, streams, riparian areas, wetlands, and groundwater systems at the landscape scale (Jordan and Fairfax, 2022; Skidmore and Wheaton, 2022; Wheaton et al., 2019; Wohl et al., 2015).

1.2. Riverscapes as Climate-Resilient Natural Infrastructure

Large rivers already are utilized as fire breaks in small- to medium-sized fires. Fire-management plans take advantage of the fact that water does not burn. Riverscapes include far more than just the river channel itself. They include the floodplains, the wetlands, the wet meadows, the side channels, the subsurface hyporheic zone, and the shallow groundwater systems historically created and maintained by widespread native beaver activity across most river valley bottoms. In a functioning riverscape, these elements increase wetted area and fire resistance and refugia. Beavers, and their innate ecosystem engineering behaviors, are uniquely capable of restoring and rewetting riverscapes even under highly modified and simplified modern stream and river conditions. Key characteristics of functional riverscapes include the capacity for adjustment; structural forcing gained from wood jams, dams, and living vegetation; and flow-energy dissipation (Castro and Thorne, 2019; Wheaton et al., 2019). Together, these elements form a dynamic fluvial biogeomorphic system of positive feedback cycles that builds complex, wet, climate-resilient riverscapes (Wohl, 2021a; Wohl et al., 2021). In general, the structural forcing elements are biologically based (living vegetation and dead vegetation both typically increase as a result of beaver activity) and thus represent a continual input of energy (the biological processes) to the fluvial-geomorphic processes, thereby tying the transport-deposition state of a riverscape to the balance of its physical and biological processes (Johnson et al., 2019; Phillips, 2009, 2016). Thus, the climate resilience of wetted functional riverscapes is dependent on natural process complexity.

When degraded, riverscapes simplify to stable, dry, disconnected systems typically dominated by incised, high-energy single-threaded channels (Cluer and Thorne, 2014). The balance of the fundamental physical and ecological processes commonly shifts to a stable but functionally impaired state, where the lack of structural forcing leads to decreased lateral and vertical chan-

nel adjustment. Restoration of the function and form of degraded and simplified riverscapes has presented a distinct challenge to traditional form-based restoration approaches driven by engineering design (Wohl et al., 2015). Process-based restoration is a conceptual framework arguing for the management of processes, not form, when engaging in stream habitat restoration planning (Thompson and Stull, 2002; Beechie et al., 2010).

Low-tech process-based restoration (LT-PBR) is founded on a suite of well-established restoration principles within the process-based restoration paradigm (Wheaton et al., 2019). This approach emphasizes promoting natural processes in rivers with simple structural additions built from natural materials, rather than designing and building the riverscapes ourselves with extensive engineering or heavy machinery (Ciotti et al., 2021). Forming a partnership with beavers, and relying largely on them to do the physical work to restore riverscapes, is an established LT-PBR strategy that minimizes human time and effort and maximizes the reliance on natural ecohydrologic and biogeomorphic processes (Brazier et al., 2021; Dittbrenner et al., 2018; Jordan and Fairfax, 2022; Law et al., 2017; Macfarlane et al., 2015; Pollock et al., 2014, 2015; Scamardo and Wohl, 2019).

Numerous resources already exist to provide guidance on how, where, and at what cost restoration efforts can utilize LT-PBR strategies on a case-by-case basis (Dittbrenner et al., 2018; Macfarlane et al., 2015; Wheaton et al., 2019; Norman et al., 2022). While historically, LT-PBR has been used to improve fish habitat and water quality, the potential for its direct use as a fire-mitigation strategy is theoretically sound but lacking in application. Such restoration may support the desired landscape conditions that contribute to reduced megafire risk and increased fire refugia area by increasing channel and floodplain complexity and altering streamflow. They may additionally be enhanced by combining these LT-PBR strategies with current typical fire risk-reduction activities, such as fuel thinning, burnouts, and grazing management coupled with fuel thinning for understory maintenance, as described in Table 1, to further reduce risk.

Changing or increasing the scope and scale of human-based fire management is a multidimensional process involving prioritization in policy, budgets, and personnel. By allowing beavers to engage in natural ecosystem engineering behaviors, the scope and scale of restoration and the resulting climate resilience can increase with less human intervention (Law et al., 2017).

1.3. Does Beaver Ecosystem Engineering Accelerate and Expand Riverscape Restoration and Resilience?

Beavers, a keystone species, engineer their environment through the construction of leaky dams, coppicing or pruning trees and shrubs, and digging travel canals (Brazier et al., 2021; Larsen et al., 2021; Naiman et al., 1988; Pollock et al., 1995). Although beavers do this work to ensure a safe, stable habitat for themselves, these activities have significant impacts on the geomorphology and ecohydrology of riverscapes. Dams slow water down, create ponds, and induce more regular overbank flooding, and they

TABLE 1. COMPARISON OF STRATEGIES FOR INCREASING LANDSCAPE RESILIENCE TO FIRE THROUGH CURRENT TYPICAL FIRE MANAGEMENT, LOW-TECH PROCESS-BASED RESTORATION (LT-PBR), AND A COMBINATION OF PRACTICES

Desired landscape conditions	Current typical fire management techniques	LT-PBR of riverscapes	Current typical fire management techniques coupled with LT-PBR
Fuels and excess biomass are regularly removed from landscape. Debris is added to aquatic portions of watersheds.	Mechanical fuel thinning, prescribed burning for removing fuels, N/A for debris added to aquatic portions of watersheds.	Periodic flooding near in-stream structures mobilizes downed fuels and debris. Woody debris is added to river channels and floodplains to initiate natural, self-sustaining processes.	Mechanically thinned fuels are added to river channels as structures or building materials for beavers, forcing more complex pathways for conveyance of water and increasing inundated surface area while increasing the area from which the waterway can remove additional fuels and debris. Positive feedback cycle of riverscape restoration and fire resilience is established.
Wetlands are established. Low-flammability new growth is prioritized in strategic areas.	N/A for wetland establishment, prescribed or cultural burning for prioritizing new growth.	Beaver-based restoration creates and maintains wetlands throughout riverscapes. Can be accomplished with live beavers, beaver dam analogs, or a combination of the two. Beavers coppice or prune riparian trees regularly, which removes old growth vegetation, transports woody biomass into the rivers, and promotes the growth of younger, less flammable vegetation. Periodic flooding encourages new growth across the entire floodplain.	Riparian corridors rapidly regain the ability to withstand large-scale disturbances via LT-PBR. Prescribed burning can extend the buffer zone via strategic application near waterways and/or between patches of restored riverscape. Culminates in longer, wider, and more contiguous stretches of low-flammability, wet fuels.
Vegetation mosaics are established, increasing overall landscape disturbance resilience.	Prescribed or cultural burning with or without strategic reseeding.	Diverse habitats are naturally established and sustained within restored riverscapes.	Vegetation mosaics are broadly established and maintained both within riverscapes and surrounding landscapes.

contribute to groundwater recharge (Andersen and Shafroth, 2010; Feiner and Lowry, 2015; Lowry, 1993; Puttock et al., 2021; Westbrook et al., 2006). The canals help spread that water out throughout the floodplain, increasing the area influenced by beaver ecosystem engineering (Anderson et al., 2015; Hood and Larson, 2015; Bartelt, 2021). The combination of canal digging and dam building contributes to significantly more water storage both in the surface water system as well as subsurface in the nearby soils, even during dry periods. When beavers coppice trees and shrubs, they keep the ecosystem in a constant state of new growth and actively move large woody material from the broader adjacent landscape into the river and stream channels (Hyvönen and Nummi, 2008; Kirby et al., 2017; Rood and Mahoney, 1990). The presence of woody material in rivers—including beaver dams, lodges, and food caches—increases geomorphic and hydrologic complexity (Bashinskiy, 2020; Gurnell, 1998; MacCracken et al., 2005; Magilligan et al., 2008; Osei et al., 2015; Wohl, 2015; Wohl and Scott, 2016). This complexity accelerates process restoration and builds resilience to disturbances like flood, drought, and wildfire throughout a beaver's typical 1–2 km territory along a stream or river segment (Fairfax and Small, 2018; Fairfax and Whittle, 2020; Foster et al., 2020; Hillman, 1998; Hood and Bayley, 2008; Jordan and Fairfax, 2022; Puttock et al., 2021; Westbrook et al., 2006, 2020; Whipple, 2019).

Research shows the benefits and efficacy of beaver activity and beaver mimicry in the restoration of riverscapes. A factor that has not been explored is whether beaver-engineered climate resilience in riverscapes is maintained during the increasingly extreme wildfire behaviors that occur during megafires. Therefore, this study explored the extent to which beaver-modified areas are resistant to megafires. Additionally, we investigated whether this type of climate resilience is attributable to beaver activity or to a geomorphic setting that is itself conducive to beaver dam- and canal-building activity.

We hypothesized (H) that during megafires:

- (H1) riverscapes have lower burn severity than the rest of the landscape,
- (H2) beaver-dammed riverscapes have lower burn severity than riverscapes without beaver dams, and
- (H3) riverscapes with a higher capacity for beaver dams have lower burn severity than those with a lower capacity for beaver dams, driving increased climate resilience during extreme disturbance events.

2. STUDY AREA

This study included three megafires that occurred in 2020 in the Rocky Mountain region, western United States: Cameron

Peak (Colorado), East Troublesome (Colorado), and Mullen (Wyoming) (Fig. 1). Fire perimeters were downloaded as shapefiles from the National Interagency Fire Center (NIFC, 2022). Table 2 reports detailed information about each fire, including the area within the burn perimeter, the states and counties affected, the burn dates, the standardized precipitation evapotranspiration index (SPEI) drought conditions leading up to the fires (Vicente-Serrano et al., 2010), the 2019 National Land Cover Database dominant land-cover type (NLCD 2019 *in* Dewitz and USGS, 2021), and the number of satellite-visible beaver dams within each fire perimeter. Wildfires can be large in area but not necessarily destructive or damaging to ecosystems. In the American West, many landscapes are dependent on fire and should be burning regularly (Agee, 1998; Bowman et al., 2011; Dwire and Kauffman, 2003; Skinner and Chang, 1996; Syphard et al., 2007). These three fire locations exemplify fire-adapted, semi-arid, montane to alpine mixed conifer forest that historically experienced high-frequency, low-severity fire regimes but have been subject to systematic fire suppression and inadequate forest management for the last century. All three megafires included in this study exhibited extreme fire behavior outside of the natural fire regime. Each had varying amounts of satellite-visible beaver

activity within their perimeters. The Cameron Peak Fire had the least amount of beaver activity, and it tended to occur in isolated pockets along the river network. The East Troublesome Fire had more beaver activity, and it was more distributed throughout the river network. The Mullen Fire had the most beaver activity, and the majority of the river network was influenced by beaver ecosystem engineering.

3. METHODS

We applied three lines of evidence (described below) to test our three hypotheses on the wildfire resilience of riverscapes and beaver-modified riverscapes in the face of megafires in the Rocky Mountain region. First, we quantified burn severity using the remotely sensed differential normalized burn ratio (dNBR), and we qualitatively assessed burn severity with false-color imagery and field photographs. Next, we sampled data within and outside of the riverscapes. Finally, we further stratified the riverscape data by its extant beaver dam-building activity and theoretical beaver dam capacity provided by the Beaver Restoration Assessment Tool (BRAT; Macfarlane et al., 2015) model.

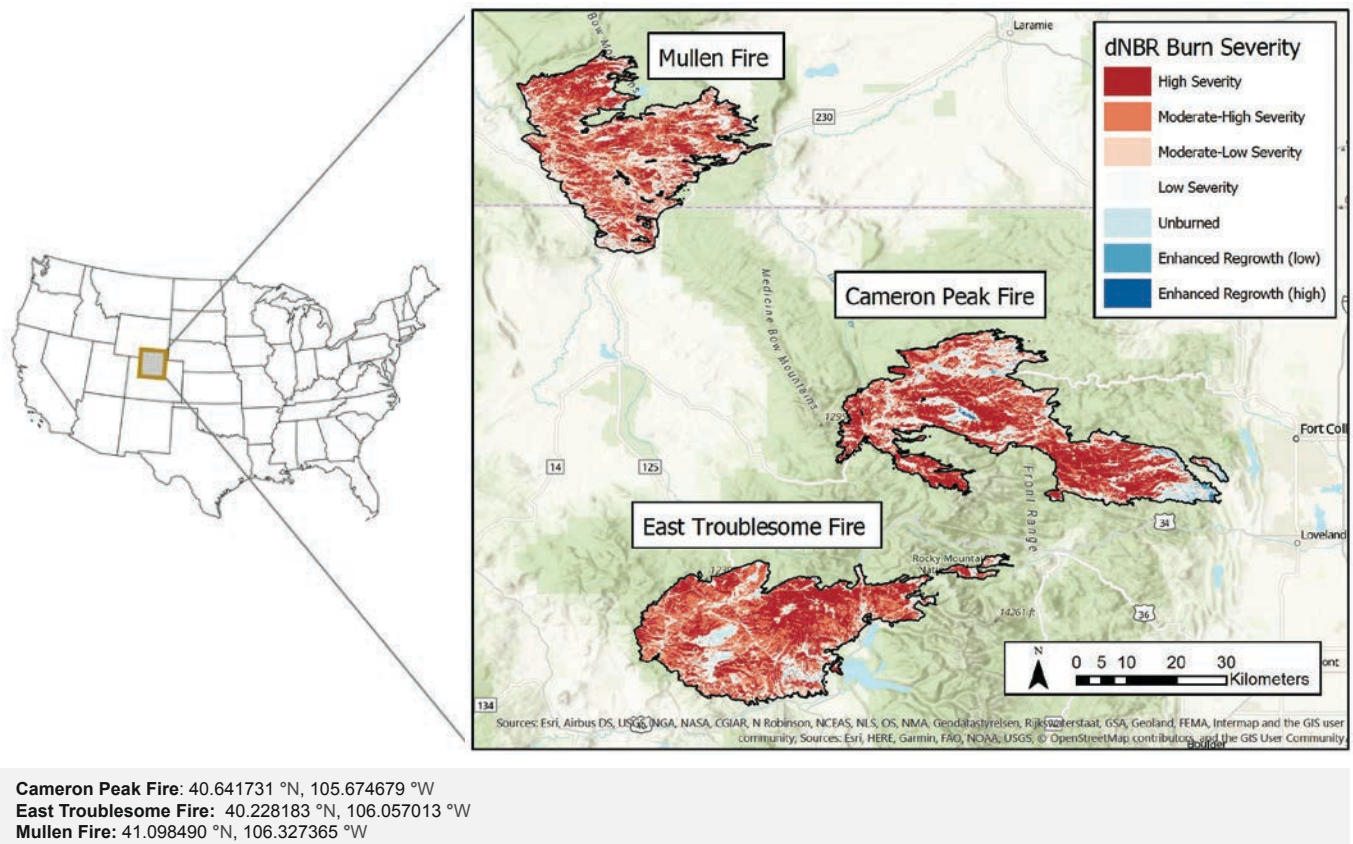


Figure 1. Study areas in Colorado and Wyoming. The three burn areas (Mullen, Cameron Peak, and East Troublesome Fires) are filled in according to their burn severity (dNBR—differential normalized burn ratio): red—high severity; white—low severity; blue—unburned.

TABLE 2. STUDY AREA INFORMATION BY WILDFIRE

Information	Cameron Peak Fire	East Troublesome Fire	Mullen Fire
State/counties affected	Colorado/Larimer	Colorado/Grand, Larimer	Colorado/Jackson, Wyoming/ Carbon, Laramie
Coordinates of fire center	40.641731°N, 105.674679°W	40.228183°N, 106.057013°W	41.098490°N, 106.327365°W
Area within burn perimeter (acres)	208,913	193,812	176,878
Active burn dates	13 August 2020– 2 December 2020	14 October 2020– 30 November 2020	17 September 2020– 4 January 2021
Satellite-visible beaver dams (no.)	99	512	926
Date(s) of imagery used to map beaver dams	August 2019	August 2019	September 2014 and June 2021
SPEI drought severity in month prior to fire	South Platte Hydrologic Region: –1.80, severe drought	Colorado Headwaters Hydrologic Region: –0.95, mild drought	North Platte Hydrologic Region: –2.02, extreme drought
SPEI drought severity in hydrologic year 2019–2020	South Platte Hydrologic Region: –1.11, moderate drought	Colorado Headwaters Hydrologic Region: –1.69, severe drought	North Platte Hydrologic Region: –0.91, mild drought
Dominant 2019 NLCD land cover	Evergreen forest	Evergreen forest	Evergreen forest

Notes: SPEI—standardized precipitation evapotranspiration index; NLCD—National Land Cover Database (Dewitz and USGS, 2021).

3.1. Identification of Beaver Dams

We identified and quantified beaver dams to show actual presence and density of habitats created by beavers in the study areas. At least three individuals identified and traced beaver dams manually using publicly available high-resolution optical imagery accessed via Google Earth Pro (Google, 2022). This imagery is typically sourced either from Maxar Technologies or Airbus. The lead beaver dam mapper had manually cataloged thousands of beaver dams in aerial imagery and ground-truthed hundreds before this study. Secondary dam mappers each had formal training by the lead mapper to find and identify beaver dams, canals, and ponds, and they had manually cataloged hundreds of beaver dams in aerial imagery and ground-truthed dams before this study. When disagreement occurred on whether a feature was a beaver dam, the secondary mappers consulted the lead mapper toward consensus. Once all mappers agreed on identifications of beaver dams, the traces were exported as a multipart polyline shapefile for further landscape area classification and burn severity analysis in ESRI ArcGIS Pro (ESRI, 2022).

3.2. BRAT Classification of Current and Historic Riverscape Beaver Dam Capacity

The capacity of a riverscape to support beaver dam building (beaver dam capacity) is a quantification of the number of beaver dams that a given channel reach could support given its geomorphic, hydrologic, and ecological conditions. Riverscapes that cannot support any beaver dams tend to be waterways that are very steep, very narrow, or very degraded, or those that do not contain any wetland or riparian-adapted vegetation (e.g., willow,

cottonwood, herbaceous wetland plants). Riverscapes that can support many beaver dams tend to be well vegetated. They also typically have perennial water, lower gradients, and more connected floodplains. The characteristics of riverscapes with high beaver dam capacity overlap significantly with the characteristics of fire refugia. For this reason, we consider a riverscape's beaver dam capacity to be a proxy for its baseline fire refugia potential.

To quantify beaver dam capacity, we used the Beaver Restoration Assessment Tool (BRAT). This is the most widely tested and proven tool for estimating beaver dam capacity of riverscapes in the American West. BRAT is typically run using nationally available geospatial data: LANDFIRE vegetation rasters (current/existing vegetation and historic/biophysical settings, <https://landfire.gov/vegetation.php>), digital elevation models from the National Elevation Data set, and hydrology/hydrography from the National Hydrography Data set (USGS, 2019). These data sets are used to quantify vegetation suitability within riverscapes, channel gradient, and low- and high-flow hydrology as variables, which then are used to estimate the maximum number of beaver dams per kilometer a given reach could theoretically sustain. Modeled estimates of beaver dam capacity were calculated via a fuzzy inference system model along a spatially explicit network and reported on a continuous scale, as well as by category, which are described in Table 3.

3.3. Burn Severity Data

3.3.1. Normalized Burn Ratio and Differential Normalized Burn Ratio Burn Severity Analysis

Variations in normalized burn ratio (NBR) and dNBR were estimated using quantitative burn severity data from the Monitoring Trends in Burn Severity database (MTBS, <https://www.mtbs>

TABLE 3. BEAVER RESTORATION ASSESSMENT TOOL (BRAT) BEAVER DAM CAPACITY AND CATEGORICAL CLASSIFICATIONS

Beaver dam capacity (dams/km)	Capacity category
0	None
>0–1	Rare
>1–5	Occasional
>5–15	Frequent
>15–40	Pervasive

.gov/). This database contains analyses by the U.S. Geological Survey Center for Earth Resources Observation and Science (EROS) and the U.S. Department of Agriculture Forest Service Geospatial Technology and Applications Center (GTAC). The Bureau of Land Management Land and Resources Project Office, as part of the National Integrated Land System (NILS; Eidenshink et al., 2007), compiled the data. Landsat 8 satellite imagery (16 d return interval) was used to determine the NBR (Eq. 1) and dNBR (Eq. 2) at 30 m pixel resolution in all three of the fire perimeters (Finco et al., 2012; Miller and Thode, 2007; Roy et al., 2014):

$$NBR = (NIR - SWIR)/(NIR + SWIR), \tag{1}$$

$$dNBR = NBR_{\text{prefire}} - NBR_{\text{postfire}}. \tag{2}$$

The NBR takes advantage of the strong differences in the way in which healthy vegetation and burnt areas reflect near-infrared (NIR) and shortwave infrared light (SWIR) (Ji et al., 2011; Plenou and Koutsias, 2013). Healthy vegetation reflects NIR strongly, while burnt areas absorb NIR light. Conversely, healthy vegetation absorbs SWIR, while burnt areas reflect SWIR light. The NBR is a standard-form spectral index used to differentiate between these landscape conditions.

Cloud-free imagery is required in the NBR calculations to ensure high-quality data and full coverage. Image dates were chosen to ensure consistent day-of-year timing of imagery in the prefire and postfire data, as well as to keep the day-of-year timing of the prefire image as close as possible to the fire ignition date without including cloud cover, smoke interference, or other nonfire disturbance artifacts. In the Cameron Peak Fire, the prefire Landsat scene utilized was from 15 September 2018, and the postfire Landsat scene was from 7 September 2021. In the East Troublesome Fire, the prefire Landsat scene utilized was from 4 September 2020, and the postfire Landsat scene was from 7 September 2021. In the Mullen Fire, the prefire Landsat scene utilized was from 4 September 2020, and the postfire Landsat scene was from 29 August 2021. The prefire and postfire NBR values, once calculated, were then used to calculate the dNBR values.

Burn severity was classified according to the dNBR values obtained from the Landsat 8 satellite imagery (Table 4; Keeley, 2009). Fire refugia are often defined as areas where the landscape is unburned or areas that only experience low burn severity (Med-

dens et al., 2018; Morelli et al., 2016). Moderate burn severity is associated with variable effects on overstory vegetation and a significant amount of vegetation loss (30%–80% killed). Some soil burning may occur at this level of severity. High burn severity is associated with large-scale vegetation loss (>80% killed) and extensive soil burning.

In some burn classification schemes and maps, such as those produced by many Burned Area Emergency Response (BAER) teams, the threshold for “high severity” burning starts at 440, “moderate–high severity” is included under “high severity,” and “moderate–low severity” burn classification is referred to as “moderate severity.” Enhanced regrowth is often interpreted as evidence that an herbaceous ecosystem benefited from low-intensity burning and regrew robustly postfire. It can also be more generally interpreted as an area that simply had more and healthier vegetation postfire than it did prefire, and this may or may not be due to fire effects in the ecosystem. In this study, when data are reported as quantitative distributions, they adhere to the more fine-grained classifications from Table 4. When reported as categorical classification, we used a threshold of dNBR = 440 as the cutoff for high severity. Our approach did not distinguish between high and low enhanced regrowth.

Before analysis, we assessed spatial autocorrelation within the fire perimeters by estimating Moran’s *I* value in 3 km × 3 km reference frames, where each pixel is represented by a unique sample point (Moran, 1950). The spatial autocorrelation in burn severity was high at the scale of the data resolution (sill [upper asymptote in the semivariogram] occurred at ~30 m), so point samples used in later analyses were spaced at a minimum of three 30 m pixels apart to ensure independent data. Statistical comparisons in burn severity and estimation of confidence intervals were conducted between beaver-dammed areas and areas without beaver dams using both Welch’s two-sample *t*-test and analysis of variance (ANOVA) plus post-hoc Tukey tests (Girden, 1992; Ruxton and Beauchamp, 2008; Welch, 1947).

3.3.2. False-Color Mapping

We accessed false-color (infrared [IR], red, green) and false-color urban (SWIR1, SWIR2, red) imagery from Sentinel-2 (5 d return interval) and used it to qualitatively assess the dNBR burn severity data as the second line of evidence in this study (Drusch et al., 2012). Sentinel-2 has 10 m pixel resolution in the IR, red,

TABLE 4. BURN SEVERITY CLASSIFICATION BY DIFFERENTIAL NORMALIZED BURN RATIO (dNBR) RANGE

Burn severity classification	dNBR range (×10 ³)
Enhanced regrowth postfire (high)	–500 to –251
Enhanced regrowth postfire (low)	–250 to –101
Unburned	–100 to 99
Low severity	100 to 269
Moderate–low severity	270 to 439
Moderate–high severity	440 to 659
High severity	660 to 1300

and green bands and 20 m pixel resolution in SWIR1 and SWIR2. We inspected all patches of fire refugia identified via dNBR analyses in cloud-free, snow-free false-color and false-color urban imagery as close to the burn date as possible. All three fires were blanketed with snow toward the end of their burn windows, so, occasionally, the closest date of cloud-free, snow-free imagery was immediately after snowmelt in spring 2021. Because minimal vegetation regrowth is expected while the landscape is under snow, images acquired immediately after snowmelt had minimal new vegetation that would obscure the patterns of burning and refugia that occurred in fall 2020 when the fires were active.

The dNBR burn severity was relatively coarse (30 m resolution) compared to the Sentinel-2 false-color imagery (10 to 20 m resolution). Burn severity calculations could also be sensitive to the scene dates used and amount of time elapsed on either side of the burn window between the scene data and the period of active burning. The false-color imagery, on the other hand, was viewable in near real-time during and immediately after burning occurred and could provide more insight into burn patterns, particularly for determining whether areas classified as enhanced regrowth experienced beneficial low-severity burning during the fire (Addabbo et al., 2016; Roy et al., 2019). Visual inspection of the false-color imagery throughout the burn perimeters created a second line of evidence to ensure that the burn severity of data points was correctly estimated and interpreted.

3.3.3. High-Resolution Optical Satellite Imagery and Field Visits

Inspection of the visible optical satellite imagery or field studies in places where the Landsat data may underperform (e.g., narrow riparian areas in steep-walled canyons or anywhere where significant time elapsed between the end of the burn and the collection of satellite data) created a third line of evidence to ensure that data points were not misclassified as burned or as fire refugia. All three fires had some postfire, high-resolution optical imagery collected by Maxar Technologies and made publicly available via Google Earth Pro. Burned (black) and unburned areas (green) could be readily visually identified in this imagery, which we used as part of our third line of evidence. The coverage of this imagery within the fire perimeters was not complete due to both smoke/cloud cover and limited data availability. Where it was available, dNBR burn severity rasters were overlaid on the optical imagery, and then the alignment between dNBR burn severity and visually observed extent of burning was visually assessed; i.e., we visually determined whether the low-severity burned areas and unburned areas as determined by dNBR were located in the same location as places that contained green vegetation in the optical imagery. The dNBR burn severity was relatively coarse (30 m resolution) compared to the optical imagery (15 to 30 cm resolution), so using the optical imagery allowed a finer-grained examination of burning patterns. We made three on-ground visits to two beaver complexes within the Cameron Peak Fire perimeter in May 2021, September 2021, and May 2022 for on-site verification of burn severity. These locations were chosen

as case studies because we could observe the landscape's ecological condition and recovery postfire and for use as context when interpreting remotely sensed data collected multiple months or years after the burn period.

3.4. Sampling Scheme

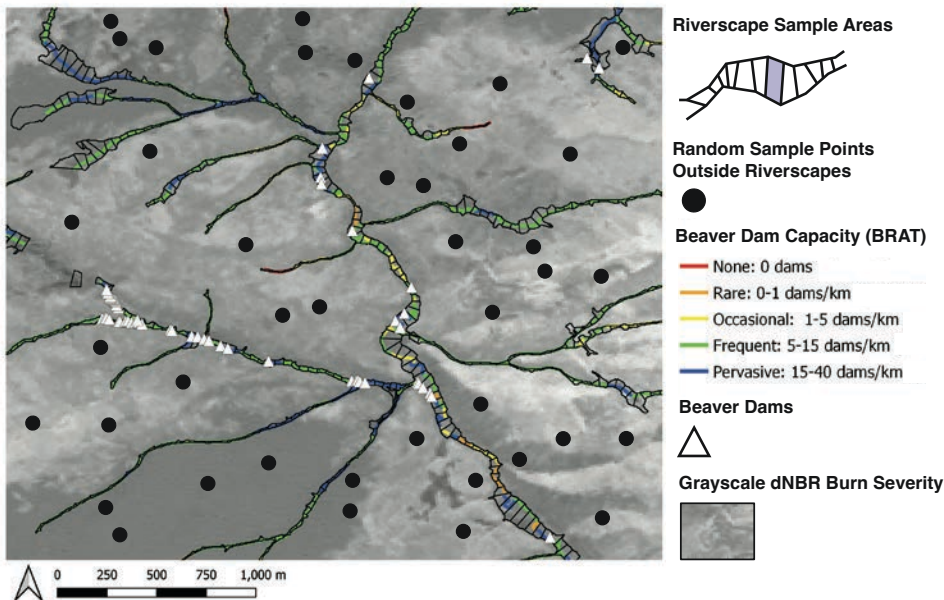
We considered dNBR values from three broad landscape types: sections of riverscapes without beaver dams ($n = 13,275$ sample areas); sections of riverscapes with beaver dams ($n = 658$ sample areas); and a random sample of points outside of the riverscapes spaced a minimum of 90 m (3 pixels) apart from each other ($n = 25,774$ pixels). To identify riverscapes, we extracted the valley bottom area, or potential channel migration zone between two confining valley walls, along the river networks using the Valley Bottom Extraction Tool (VBET; Gilbert et al., 2016). VBET uses topographic evidence to identify valley bottoms by transforming slope and height above drainage network values into likelihoods of being valley bottom using functions that vary based on stream size. VBET additionally breaks the delineated valley bottom into segments of a uniform length, creating discrete polygons that can be used as a sampling frame (i.e., portions of riverscape with dams and portions without). In this application, each riverscape sampling polygon consisted of 100 m of valley bottom length. Though all wildfires have some degree of spatial autocorrelation in the burn severity data, the effects of it are often weak compared to the fire effects driven by landscape treatments (Chou et al., 1993; van Mantgem and Schwilk, 2009), as represented by riverscape restoration via beaver ecosystem engineering in this study. By including all riverscape areas (i.e., all of the sampling polygons) in this analysis and taking the average value of pixels within each polygon, we further reduced the influence of small-scale spatial autocorrelation within the riverscapes in the dNBR data. Random point samples outside of the riverscapes were generated within the ESRI ArcGIS Pro software using the Create-Random-Points geoprocessing tool. The spacing of the random points was three times the threshold spatial autocorrelation distance determined with Moran's I to ensure that samples were independent of each other. Figure 2 illustrates the overall sampling strategy.

The current and historic BRAT beaver dam capacity data were recorded for each riverscape sample polygon. We extracted the individual pixel dNBR value at each random point outside of the riverscapes. We calculated the average dNBR of all pixels contained within each riverscape sample area. The presence or absence of beaver dams was recorded for each sample area using the Intersect tool, and the Distance-to-Nearest-Hub in QGIS determined the distance to the nearest beaver dam from the centroid of each sample area (QGIS.org, 2022).

3.5. Evaluation of Spatial Data Structure

To explore the relationship between reach- and riverscape-scale features and burn severity, we modeled dNBR as a function

dNBR Burn Severity Sampling Schematic



Lat/Lon: 40.263359 °N, 106.046930 °W

of reach-scale beaver dam presence, the predicted habitat suitability for beaver dam building, and the spatial occurrence of beaver dams across the burned watersheds. We parameterized the effects of riverscape covariates using generalized additive model (GAM) smoothers fit using the R package *mgcv* (Wood, 2018). We included interactions with the “by” function. We used smoothers and interactions to account for spatial patterns in riverscape covariates and for nonlinear relationships between reach and riverscape covariates. We fit simple GAMs to the data where dNBR was predicted by a spline smoother (s) on the interaction between the BRAT dam capacity and the distance to the nearest beaver dam using the restricted maximum likelihood method (Eq. 3):

$$\text{dNBR} \sim \text{BRAT category} + \text{s}(\text{distance to nearest dam, by} = \text{BRAT category}). \quad (3)$$

4. RESULTS

4.1. Differential Normalized Burn Ratio (dNBR) Burn Severity of Fires Overall and by Landscape Type

When evaluating the entire population of burn severity samples ($n = 39,707$), the bulk of the data ranged between low-severity and moderate–high-severity burns in each of the three study fires (Fig. 3).

This distribution of burn severity is commonly observed in megafires, though on its own, it does not give a clear picture of how the fire impacted the different parts of the landscape until

Figure 2. Example of the sampling strategy used for differential normalized burn ratio (dNBR) data collection. Valley bottom sample polygons are enclosed with thin black polygons, beaver dam capacity as modeled by Beaver Restoration Assessment Tool (BRAT) is color coded according to dam capacity category, and actual observed beaver dams are denoted with white triangles. Riverscape samples with and without beaver dams average all pixels within a given sample polygon. Random point samples were taken from outside of the riverscapes. Lat/Long: 40.263359°N, 106.046930°W.

stratified by landscape category: outside of riverscapes, riverscapes without beaver dams, and riverscapes with beaver dams (Fig. 4). The high-resolution imagery beaver dam mapping determined that the Cameron Peak Fire had 99 satellite-visible beaver dams, the East Troublesome Fire had 512 satellite-visible beaver dams, and the Mullen Fire had 926 satellite-visible beaver dams.

The population of burn severity samples outside of the river network and away from beaver-dammed areas ($n = 25,774$) had a roughly bimodal distribution. One peak was in the low-severity to unburned range, and a second peak was in the moderate–high-severity range (Fig. 4, top row). This shape of data distribution is reflective of the overall pattern of fire effects observed in the dNBR burn severity maps (Fig. 1). Many large patches of moderate- and high-severity burning intermingled with several small to mid-sized patches of low-intensity or unburned landscape, where often either alpine meadows with few trees were present or protected human infrastructure (roads, towns, housing developments, properties with cleared timber, etc.) was present.

In the population of burn severity samples that were in riverscapes without beaver dams ($n = 13,275$), the data from the Cameron Peak Fire had a roughly bimodal distribution. One peak was in the low-severity to unburned range, and a second peak appeared in the moderate–high-severity range (Fig. 4, middle row, left column). The data from the East Troublesome and Mullen Fires had a right-skewed distribution with a single peak in the low-severity to unburned range and then a thick tail extending out into the high-severity range (Fig. 4, middle row, middle and right columns).

When evaluating the population of burn severity samples within beaver-dammed areas ($n = 658$), the data from all three

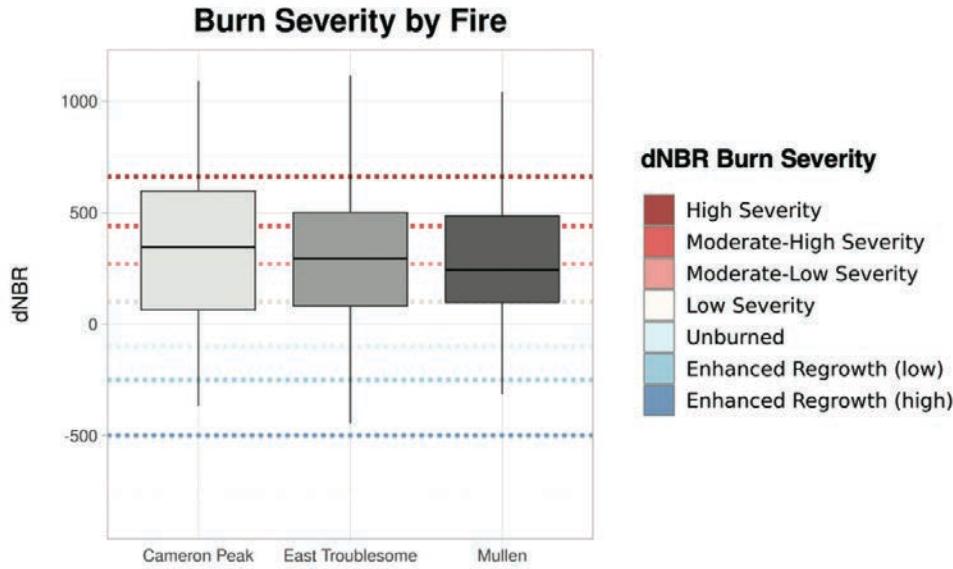


Figure 3. Distribution of sample differential normalized burn ratio (dNBR) burn severity by fire. Color-coded dashed lines are the lower thresholds of the burn severity classifications. Low-severity burning or less is considered fire refugia.

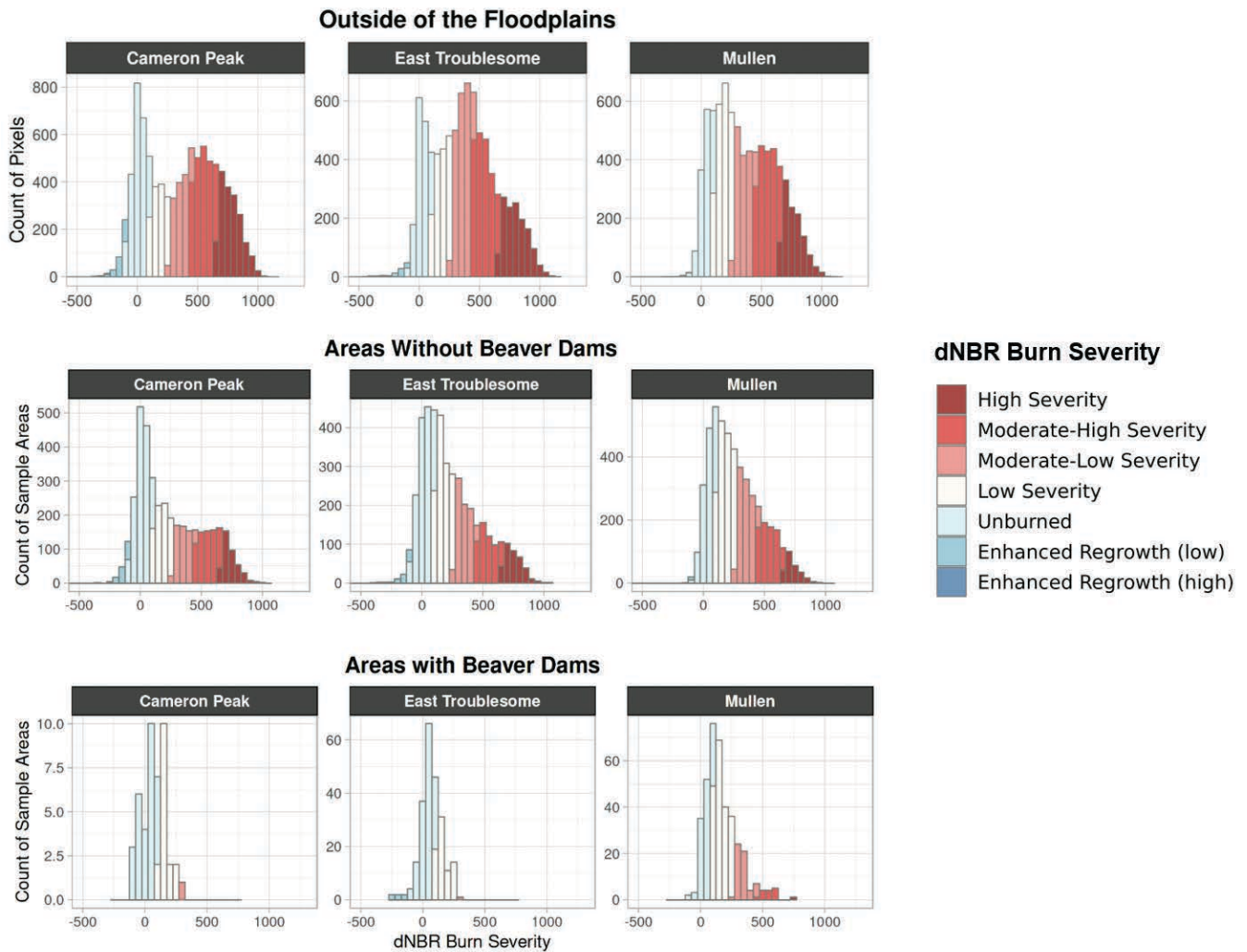


Figure 4. Distribution of sample differential normalized burn ratio (dNBR) burn severity by fire and landscape type.

TABLE 5. MEAN BURN SEVERITY BY FIRE AND LANDSCAPE TYPE

Landscape type	Cameron Peak Fire	East Troublesome Fire	Mullen Fire
Outside of the riverscapes	378 (M) <i>n</i> = 9332 pixels	369 (M) <i>n</i> = 8480 pixels	330 (M) <i>n</i> = 7961 pixels
Riverscapes without beaver dams	251 (L) <i>n</i> = 4002 sample areas	242 (L) <i>n</i> = 4303 sample areas	266 (L) <i>n</i> = 4970 sample areas
Riverscapes with beaver dams	72 (U) <i>n</i> = 45 sample areas	70 (U) <i>n</i> = 230 sample areas	167 (L) <i>n</i> = 383 sample areas

Notes: U—unburned; L—low severity; M—moderate severity; *n*—count of pixels or sample areas included.

fires had a roughly symmetric distribution around a sharp peak in the unburned range, with a slight right-skew and a short tail extending out into the moderate-severity range (Fig. 4, bottom row). These data distributions demonstrate that the majority of the landscape within the beaver-dammed areas was unburned or experienced low-severity burning, meeting the definition of fire refugia. The differences in burn severity data by landscape type (riverscapes with beaver dams, riverscapes without beavers, and outside of the riverscapes) were reflected in the mean burn severity values for each fire included in this study (Table 5).

The differences between the landscape types were statistically significant ($p < 0.05$) using both Welch's two-sample *t*-test and the ANOVA plus post-hoc Tukey tests (Girden, 1992; Ruxton and Beauchamp, 2008; Welch, 1947). Significant differences in burn severity were found within each fire and in all the fire data combined. The beaver dammed riverscapes experienced significantly less severe burning than the riverscapes without beavers and the areas outside of the riverscapes by a large margin (measured dNBR differences ranged from -99 to -306). The riverscapes without beavers experienced significantly less severe burning than the areas outside of the riverscapes by a smaller margin (measured dNBR differences ranged from -64 to -127).

4.2. Fire Refugia Area in Riverscapes

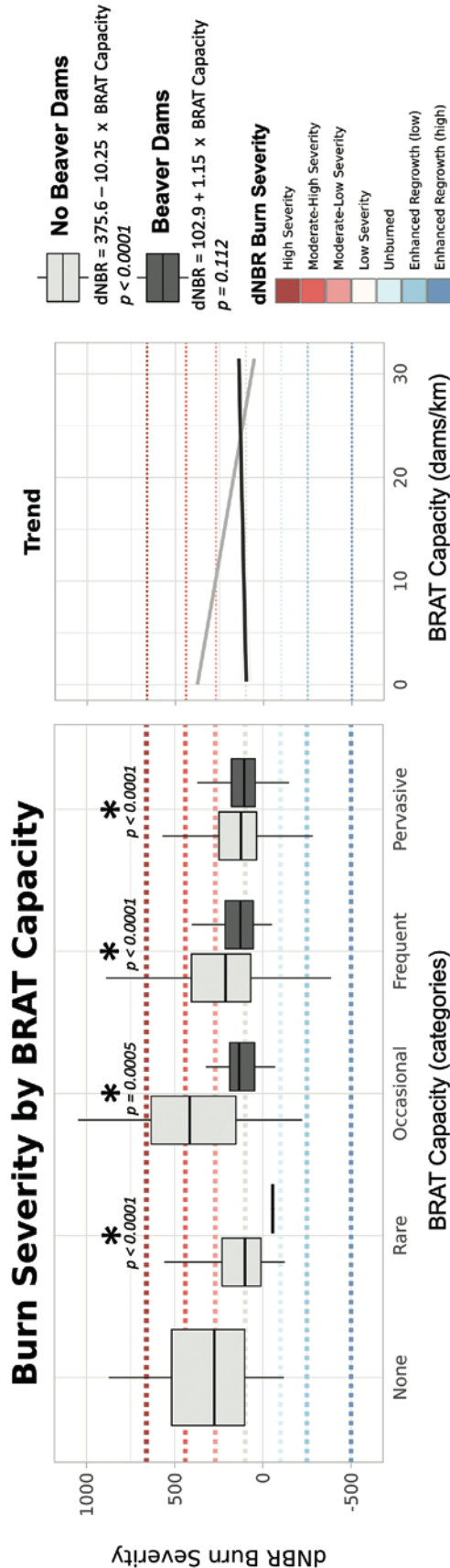
To further explore the potential ecological and human value of riverscapes as fire refugia, we calculated the total floodplain area that fell into each burn intensity classification in riverscapes with and without beaver dams (Table 6). Fire refugia were present in riverscapes with and without beavers. Beaver dams are relatively rare landscape features compared to riverscapes without beavers, so beaver-dammed riverscapes only constituted ~15% of total riverscape fire refugia by area. However, 89% of beaver-dammed riverscapes were classified as fire refugia compared to only 60% of riverscapes without beaver dams. The proportion of beaver-dammed riverscapes that were fire refugia was higher than the proportion of riverscapes without beaver that were fire refugia, so beaver-dammed riverscapes are more reliable fire refugia.

4.3. Beaver Dam Capacity as a Proxy for Riverscape Fire Refugia Potential

We compared burn severity across each BRAT beaver dam capacity category as well as within each category according to whether the sample area had beaver dams (Fig. 5).

TABLE 6. FLOODPLAIN AREA WITHIN EACH BURN CLASSIFICATION

Riverscapes with beaver dams		
Burn category	Area (km ²)	Portion of area (%)
Unburned or enhanced regrowth	6.58	46
Low intensity	4.65	43
Moderate intensity	1.3	9
High intensity	0.57	2
<i>Total</i>	<i>13.1</i>	<i>100.00</i>
Riverscapes without beaver dams		
Burn category	Area (km ²)	Portion of area (%)
Unburned or enhanced regrowth	37.18	32
Low intensity	28.38	27.5
Moderate intensity	16.71	17.5
High intensity	14.32	23
<i>Total</i>	<i>96.59</i>	<i>100.00</i>
Amount of fire refugia (burn severity of low, unburned, or enhanced regrowth)		
Riverscape type	Area (km ²)	Portion of area (%)
Riverscapes with beaver dams	11.23	89
Riverscapes without beaver dams	65.56	60



Beaver-modified riverscapes had significantly ($p < 0.001$) lower burn severities than riverscapes without beaver dams within each BRAT dam capacity category (Fig. 5). Table 7 reports average dNBR values, calculated differences in dNBR, and the 95% confidence interval for the estimated difference in means from the Welch’s t -tests. These results suggest that the presence of beaver dams lowers burn severity in all types of riverscapes, including those that already have many characteristics of good beaver habitat and fire refugia potential (e.g., perennial water, riparian vegetation, channel complexity). Simple linear models of burn severity as a function of BRAT capacity were created from the dammed and undammed riverscape data sets. The linear model fit to the undammed riverscape data set was statistically significant ($p < 0.0001$) with a negative slope (i.e., higher beaver dam capacity \rightarrow lower burn severity). The linear model fit to the beaver-dammed riverscape data set was not statistically significant ($p = 0.112$).

Within the beaver-modified riverscapes, no significant differences existed in dNBR between the riverscape beaver dam capacity categories when tested with ANOVA and post-hoc Tukey tests (pairwise p values in Table 8). The ANOVA test in beaver-dammed areas had an overall F value of 1.93 and p value of 0.123. Sample size in the “rare” category within beaver-dammed riverscapes was small ($n = 2$), so we report the differences here with the caveat that the statistical significance of those differences should be interpreted with caution. In the riverscapes without beaver dams, all BRAT dam capacity categories were significantly different from one another, except “rare \times pervasive,” which were not significantly different (pairwise p values in Table 8). The ANOVA test in areas without beavers had an overall F value of 540.2 and a p value < 0.0001 . The largest difference in burn severity between beaver-dammed riverscapes and riverscapes without beavers occurred in places that fell into the “occasional” dam capacity category.

4.4. Effects of Distance to Nearest Beaver Dam

The GAM-based evaluation of spatial structure in the burn severity data revealed moderate underlying spatial relationships between beaver dam (and beaver dam potential) and burn severity. The model (Eq. 3) explained 23.9% of the overall variance in

Figure 5. (Left) Distribution of sample differential normalized burn ratio (dNBR) burn severity by Beaver Restoration Assessment Tool (BRAT) capacity categories with and without beaver damming. All differences between beaver-dammed riverscapes and riverscapes without beaver dams marked with an asterisk were statistically significant ($p < 0.05$) using Welch’s two sample t -tests and analysis of variance (ANOVA) plus post-hoc Tukey tests. Test statistic information is labeled on the plot above. There were no beaver-dammed riverscapes in the “none” category. (Right) Trend in burn severity with increasing BRAT capacity with and without beaver dams. Both metrics are shown on a continuous scale with the equations and significance values labeled on the figure above.

TABLE 7. AVERAGE DIFFERENTIAL NORMALIZED BURN RATIO (dNBR) BY BEAVER RESTORATION ASSESSMENT TOOL (BRAT) CAPACITY

BRAT capacity category	Beaver dNBR	Beaver burn category	No-Beaver dNBR	No-Beaver burn category	Difference in dNBR (Beaver – No Beaver)	Welch <i>t</i> -test statistics
None	N/A <i>n</i> = 0	N/A	313 <i>n</i> = 437	Moderate	N/A	N/A
Rare	-56 <i>n</i> = 2	Unburned	155 <i>n</i> = 142	Low	-211	<i>t</i> = -11.266 <i>p</i> < 0.0001 CI: (-250, -170)
Occasional	131 <i>n</i> = 8	Low	398 <i>n</i> = 2844	Moderate	-267	<i>t</i> = -5.8 <i>p</i> = 0.0005 CI: (-374, -159)
Frequent	140 <i>n</i> = 137	Low	250 <i>n</i> = 6042	Low	-109	<i>t</i> = -10.2 <i>p</i> < 0.0001 CI: (-131, -88)
Pervasive	125 <i>n</i> = 523	Low	150 <i>n</i> = 3798	Low	-25	<i>t</i> = -4.1 <i>p</i> < 0.0001 CI: (-37, -13)

Notes: N/A—not applicable; CI—confidence interval; *n*—number of reaches.

dNBR values as a function of proximity to beaver dams, when allowing for separate interaction smooth by predicted beaver dam capacity. Visualization of the smooth functions by riverscape dam capacity (Fig. 6) detected a clear effect of proximity to beaver dams in the “rare,” “occasional,” and “frequent” dam capacity categories but not in the “none” or “pervasive” categories. The proximity effect began to plateau around 1000–1500 m from a beaver dam in the “rare” and “frequent” categories, and around 2000 m in the “occasional” category.

The best-fit model stabilized around a basis size (*k*) of 50 using thin-plate splines (Table 9). We tested basis sizes up to 100

but did not observe meaningful changes in test statistics with further increases in basis size beyond 50. This, in addition to the effective degrees of freedom for each smoothing term being significantly lower than the basis size, suggests that the basis size is appropriate for this data set (Pedersen et al., 2019).

4.5. Qualitative Burn Severity Observations

4.5.1. False-Color Mapping

No significant disagreements were detected between the fire refugia observed in false-color imagery (false-color and false-color urban; Fig. 7) and the measured dNBR burn severity that indicated fire refugia. The higher-resolution imagery from Sentinel-2

TABLE 8. PAIRWISE SIGNIFICANCE OF BURN SEVERITIES WITHIN RIVERSCAPE TYPE BY BEAVER RESTORATION ASSESSMENT TOOL (BRAT) CATEGORY

Beaver-dammed riverscapes	
Occasional × Rare	<i>p</i> = 0.2373261 (small sample size)
Frequent × Rare	<i>p</i> = 0.1282717 (small sample size)
Pervasive × Rare	<i>p</i> = 0.1778316 (small sample size)
Frequent × Occasional	<i>p</i> = 0.9974858
Pervasive × Occasional	<i>p</i> = 0.9991081
Pervasive × Frequent	<i>p</i> = 0.6068951
Riverscapes without beavers	
Rare × None	<i>p</i> < 0.0001
Occasional × None	<i>p</i> < 0.0001
Frequent × None	<i>p</i> < 0.0001
Pervasive × None	<i>p</i> < 0.0001
Occasional × Rare	<i>p</i> < 0.0001
Frequent × Rare	<i>p</i> < 0.0001
Pervasive × Rare	<i>p</i> = 0.9991153
Frequent × Occasional	<i>p</i> < 0.0001
Pervasive × Occasional	<i>p</i> < 0.0001
Pervasive × Frequent	<i>p</i> < 0.0001

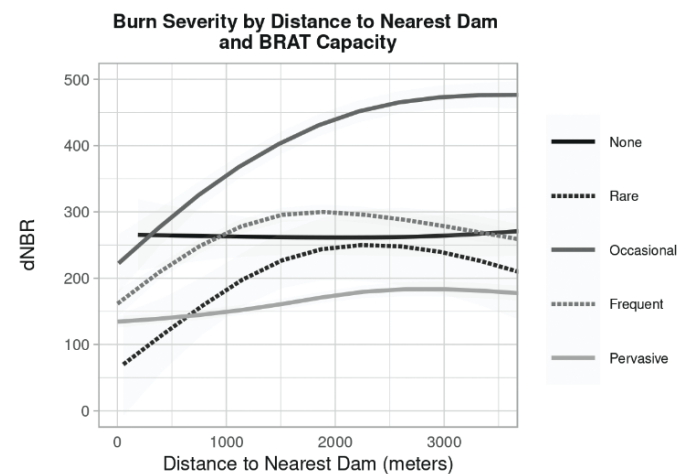


Figure 6. Generalized additive model (GAM) smoothing functions for differential normalized burn ratio (dNBR) as a function of distance to nearest beaver dam, separated by Beaver Restoration Assessment Tool (BRAT) riverscape dam capacity categories.

TABLE 9. GENERALIZED ADDITIVE MODEL (GAM) STATISTICS AS A FUNCTION OF DISTANCE TO NEAREST BEAVER DAM, SEPARATED BY BEAVER RESTORATION ASSESSMENT TOOL (BRAT) RIVERSCAPE DAM CAPACITY CATEGORIES

Smoothing function	Effective degrees of freedom	<i>P</i> value
Dam distance : BRAT-None	12.40	$p < 0.0001$
Dam distance : BRAT-Rare	5.41	$p = 0.00639$
Dam distance : BRAT-Occasional	31.27	$p < 0.0001$
Dam distance : BRAT-Frequent	31.25	$p < 0.0001$
Dam distance : BRAT-Pervasive	9.89	$p < 0.0001$

showed the gradient of transition from moderate- and high-severity burning outside of the river network to low-severity and unburned vegetation within the beaver complexes. The fires were not simply jumping over them due to their position in the valley bottom. Some imagery showed fire burning on all sides of the beaver complexes that was still unable to burn within them (Fig. 8).

4.5.2. Visual Inspection of Aerial Photographs and Field Visits

The fire refugia found in beaver complexes was clearly visible both in high-resolution satellite imagery (Fig. 9) and during field visits (Fig. 10). These visually identified fire refugia aligned with the dNBR identified fire refugia in all three fires. In the Mullen Fire, some very narrow ribbons of fire refugia in the riparian zone were visually identified as being unburned but appeared as low burn severity in the dNBR data. This result was likely due to the size of the dNBR pixels being on the same order

as the width of the riparian corridor, so the influence of pixels containing both riparian and hillslope landscape was disproportionately large. Based on this, the points within the beaver-dammed areas in the Mullen Fire may be biased toward higher dNBR values and burn severity classes. This bias happened with relative frequency in the Mullen Fire, but we did not observe it in the other fire areas. We were also able to observe the gradient of burn severity on-site that was noted in the false-color mapping observations (Fig. 9, bottom).

5. DISCUSSION

5.1. Beaver Complexes as Uniquely Fire-Resistant Landscape Features

The majority of riverscapes are fire refugia, but riverscapes without beaver dams are significantly less reliable fire refugia

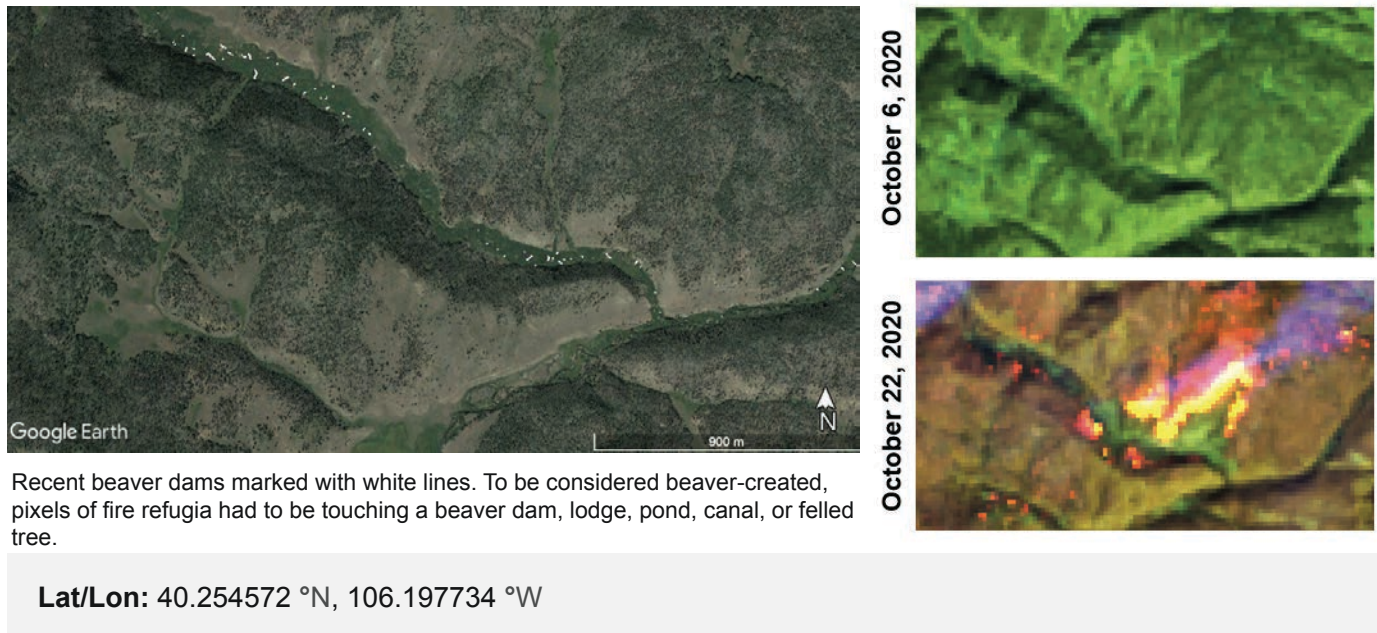
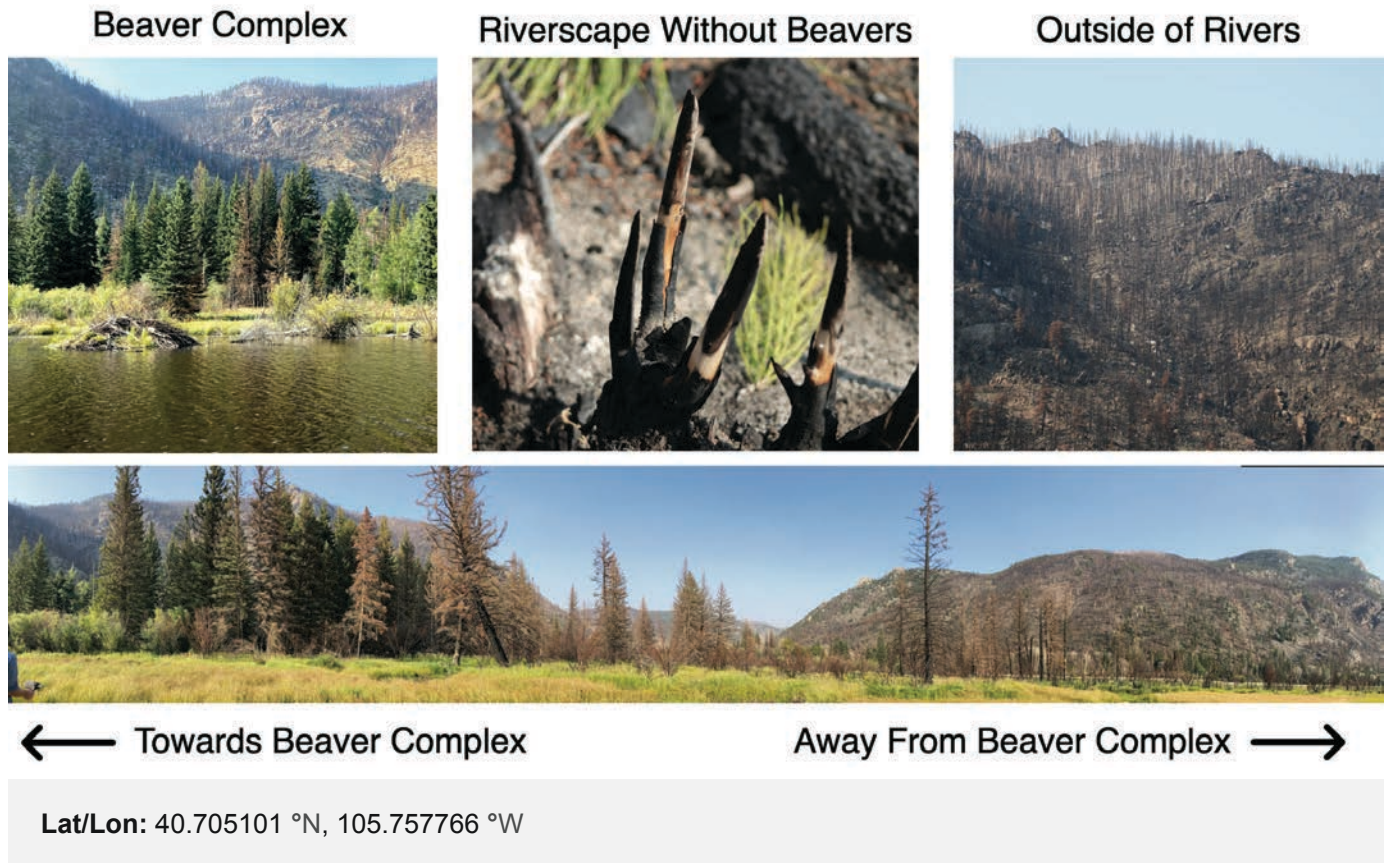


Figure 7. Example of qualitative assessment of burn severity within the fire perimeters using false-color mapping (green—unburnt vegetation, dark orange—burnt vegetation, bright orange and yellow—hot spots). Left: Satellite image of beaver complexes highlighted with semitransparent white polygons. Right top: Example of a false-color image immediately prior to the fire to assess prefire conditions. Right bottom: Example of a false-color image as close to the date of the fire as possible to assess postfire conditions.



Lat/Lon: 41.111878 °N, 106.379883 °W

Figure 8. Example of qualitative assessment of burn severity within the fire perimeters using true-color aerial and satellite imagery. Left: Landscape with beaver damming before the fire. Middle: Landscape with beaver damming after the fire where the beaver complexes are the only green left. Right: Differential normalized burn ratio (dNBR) burn severity raster overlain on top of the landscape showing the alignment between observed greenness and low burn severity around beaver dams (traced with black lines). 1000 ft = ~305 m.



Lat/Lon: 40.705101 °N, 105.757766 °W

Figure 9. Example of qualitative assessment of burn severity within the fire burn perimeters through field visits and on-site photography. Top left: Beaver complex after the fire with intact, mature vegetation. Top middle: Willow burnt to stumps after the fire in the river network outside of the beaver complex. Top right: Hillslopes surrounding the beaver complex with high-severity burning and total vegetation loss. Bottom: Panoramic photo of the landscape observing the gradient of burn severity changing with increased distance from the beaver complex.

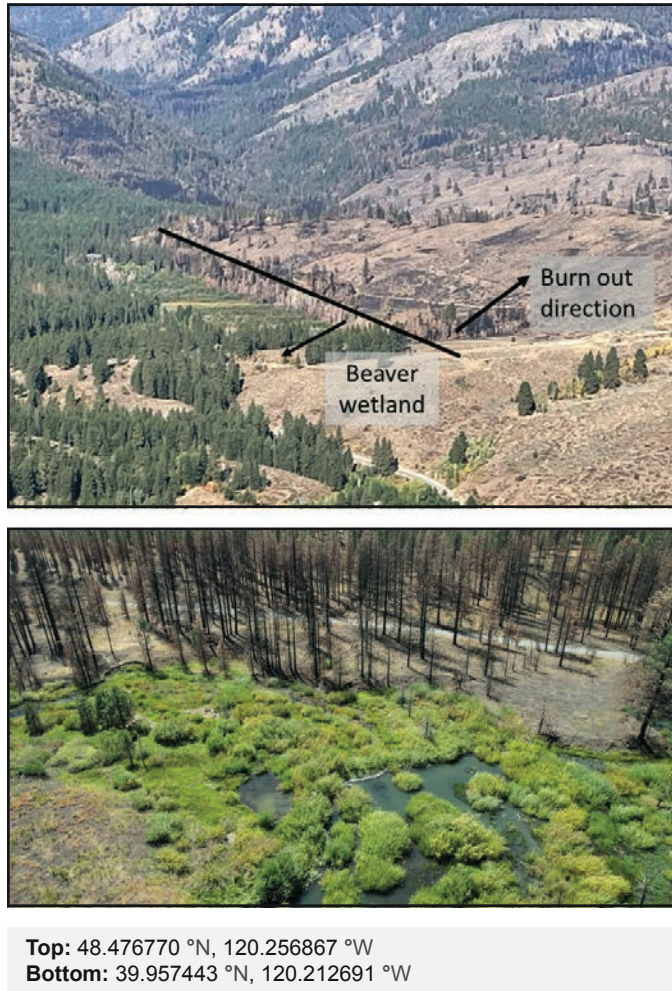


Figure 10. (Top) Example of a beaver complex assisting in our human wildfire management activities. The beaver complex provided a safe point from which to backburn to reduce fuel loads near Sun Mountain Lodge, Winthrop, Washington, 2021 (photo credit: Kamansky 2021). (Bottom) Example of a small patch of beaver-created fire refugia from the 2021 Beckworth Fire in California.

(60% refugia) than riverscapes with beaver dams (89% refugia). This finding supports H1, which hypothesized that riverscapes have lower burn severity than the rest of the landscape. Additionally, the beaver-modified riverscapes were significantly more resistant to burning during megafire than either the nondammed riverscapes or the nonriverine areas. This result supports H2, which hypothesized that beaver-dammed riverscapes have lower burn severity than riverscapes without beaver dams. This was true in all three fires individually and aggregated, as well as across all modeled beaver dam capacity categories. The relationships between burn severity and actual beaver damming, riverscape beaver dam capacity, and historic riverscape beaver dam capacity were nonlinear. A significant decreasing trend in burn severity was found in riverscapes without beaver dams as the dam capacity increased. However, there was consistently low burn severity

with no directional trend associated with dam capacity in riverscapes with beaver dams. This outcome only partially supports H3, which hypothesized that riverscapes with a higher capacity for beaver dams have lower burn severity than those with a lower capacity for beaver dams.

We had hypothesized in H3 that higher riverscape dam capacity would be associated with lower dNBR. In the case of the beaver-dammed riverscapes, all dam capacity categories had low dNBR, and no significant differences or trend existed between categories. In the case of riverscapes without beaver dams, a significant decreasing trend appeared (higher riverscape dam capacity = lower dNBR). It was not a uniform trend, however, as riverscapes with no dam capacity burned significantly less than riverscapes with a “rare” dam capacity, which may be related to the biophysical conditions in very narrow, steep, or sparsely vegetated catchments that are unsuitable for beaver occupancy and the relationship of those conditions to fire spread behaviors. The largest relative difference between the riverscapes with and without beaver dams occurred in the “occasional” dam capacity category (although sample size was low in that category at $n = 8$ sample areas) and decreased as dam capacity changed in either direction. This was the riverscape poorly represented in our data set, however, potentially influencing the magnitude of impact estimated and pointing to the need for additional attention in future work.

We determined that the distance to nearest beaver dam and current beaver dam capacity of a riverscape can explain 23.9% of the variance in burn severity data. Numerous different factors likely influence the remaining variability in burn severity in the Rocky Mountain region, including wind speed, wind direction, humidity, fuel age, fuel moisture, fuel volume, antecedent climate conditions, prior fuel treatments, and bark beetle tree kill. The consistency of resistance to fire observed in beaver-dammed areas and the magnitude of influence that beaver damming had on burn severity merit consideration in future fire management planning efforts in North America.

This study was not the first to demonstrate that beaver-dammed riverscapes are uniquely fire-resistant landscape features (Fairfax and Whittle, 2020; Foster et al., 2020; Markle et al., 2022; Weirich, 2020; Whipple, 2019; Wohl et al., 2022). It is the first to show, however, that the effect persists during the extreme wildfire behaviors common in megafires. The innate ecosystem engineering behaviors of beavers are complementary to fire risk-reduction strategies (Table 2). While this study focused on probing the upper limit of fire resistance that beaver complexes could maintain, many questions remain across the spectrum of wildfire burn severity, scale of impact, and influence of beaver-damming activity. For example, how and when can beaver-dammed riverscapes function as fire breaks? Anecdotal evidence from the 2021 Cedar Creek Fire in north-central Washington demonstrates a large beaver complex serving as a natural firebreak and a point for enacting strategic fire protection for human infrastructure. This beaver complex helped protect structures near Winthrop, Washington, by providing a safe point from which to backburn

to remove hazardous fuels from the oncoming wildfire path (Fig. 10, top). The ability for beaver wetlands to function as firebreaks has different potential applications in wildfire mitigation efforts than the more commonly discussed role they play in creating isolated fire-resistant patches (e.g., Fig. 10, bottom).

5.2. Potential Changes to Postfire Processes in Beaver-Supported Fire Refugia

Fire refugia are ecologically important postfire as well (Brazier et al., 2021; Meddens et al., 2018; Morelli et al., 2016). Mature vegetation can help reseed nearby burnt riparian areas more quickly postfire. It provides a distributed network of habitat patches for pollinators and seed dispersers throughout the burned areas (Andrus et al., 2021; Blomdahl et al., 2019; Downing et al., 2020; Landesmann and Morales, 2018). From a geomorphic standpoint, fire refugia patches are particularly well suited to slow incoming water and trap wildfire-mobilized sediment and nutrients, given how the redundant dam-vegetation structure of beaver-modified riverscapes reduces unit stream power by spreading the force of flow (Short et al., 2015). Expansion of beaver habitat across watersheds within their native range could prevent or reduce the severity of destructive, channel-incising debris-flow events that commonly occur after wildfires (Cluer and Thorne, 2014). For example, debris flows after wildfire can cause channel scouring and incision to bedrock (Cannon and DeGraff, 2009). These events straighten and deepen streams, removing in-channel and riparian vegetation and large wood by rapidly conveying it downstream. As a result, streams are further isolated from their floodplains, which damages the biological community within the channel. Numerous aquatic organisms cannot tolerate high suspended sediment loads and, in particular, struggle with ash that washes into the stream. Heavy loads of fine sediment in streams after wildfire can easily suffocate fish, macroinvertebrates, and amphibians by coating their respiratory organs (Bash et al., 2001; Gresswell, 1999; Rinne, 1996). The transport of high concentrations of limiting nutrients, like phosphate, with sediment after wildfire can also contribute to eutrophication in catchments downstream (Brass et al., 1996; Gresswell, 1999).

Wildfire in mixed conifer forests of western North America can stimulate regrowth of riparian deciduous shrubs that evolved with fire and regrow from their roots rapidly if not severely burned, as seen in the enhanced regrowth classification data (Schier et al., 1985; Shinneman et al., 2013; Stein et al., 1992). This rapid vegetation response can provide significant and critical food resources for beavers within a burned watershed, which may support their continued occupancy of a stream after fire or allow reestablishment where legacy human impacts such as livestock grazing had previously reduced or eliminated beaver food resources. For example, streams that have become severely incised following wildfire-induced debris-flow events but that have recovered fire-adapted riparian vegetation quickly have been targeted for beaver relocation and beaver-based restoration. These beaver translocation actions are meant to rapidly restore incision and reconnect

streams to their floodplains, and they have shown encouraging success (Dittbrenner et al., 2022). Success is reflected in recent research that shows significant changes in stream channel width/depth ratio and clear reductions in phosphate transport in streams where beavers have been able to establish following severe wildfire impacts, thus increasing refugia and resilience in preparation for the next wildfire (Whipple, 2019; Pollock et al., 2014).

5.3. Study Limitations

More research is necessary to compare how other types of restored riverscapes (e.g., stage 0 restoration, non-beaver LT-PBR, beaver mimicry via beaver dam analogs) respond to wildfire, and whether they create fire refugia at the same rates and as consistently as does beaver activity. Beavers are not ubiquitous, and not everywhere in the world has or had beavers controlling their waterways, and so other types of functioning, resilient riverscapes exist around the globe. Further investigation is warranted in expanding this style of analysis in future studies across fire-prone landscapes, especially in places where other types of river restoration activities affect portions of the river network within burn perimeters. Additionally, the three fires examined in this study were similar in fire and landscape characteristics, and, as such, expanded research on additional fires from a wider variety of physical and ecological settings that also include beaver damming within their perimeters would help to elucidate the sources of variability in burn severity as a function of riverscape and beaver activity state.

Given the widespread and profound influence beavers had historically in North America, it is possible that beaver presence is a requirement for full restoration in some watersheds. We know that many more beavers existed in North America historically than at present (100–400 million estimated before the industrialized fur trade and 10–40 million today; estimates from Naiman et al., 1988). Beavers were widely distributed on this continent, occupying the vast majority of watersheds from the east coast to the west coast, and from northern Mexico up into northern Canada and Alaska. The entire river network and flow of water across this continent was fundamentally different before beavers were systematically and intentionally removed from the landscape (Fouty, 2018; Wohl, 2011, 2021b). As such, it is reasonable to imagine that riverscapes without any influence of beaver activity were not as common of a phenomenon in the past (Wohl, 2021b). Thus, many historical riverscape fire refugia were likely in some way influenced by beavers.

To explore this assumption, more research is needed to model the historic population and distribution of beavers in the western United States, as well as the scale and duration of their impact on hydrologic and geomorphic riverine processes. In particular, a better understanding is necessary regarding how the activities and impacts of beavers varied over space and time when their populations and habitats were not as impacted by human activity as they are today. Beavers naturally cycle through locations as food resources wane or sediment accumulations turn

ponds into meadows, and local populations fluctuate with disease and predation cycles (Johnston, 2017; Gable et al., 2020). Evidence suggests that abandoned beaver dam complexes also play a significant role in riverscape processes (Ives, 1942; Polvi and Wohl, 2012; Ronnquist and Westbrook, 2021; Woo and Waddington, 1990). Abandoned complexes may continue to function as wildfire refugia, despite being unattended cyclically. Within the context of wildfire, current data are insufficient to characterize with certainty the durability of the biogeomorphic effects of beaver activity in fluvial systems during the periods when the beavers themselves are not physically present. This research, along with other recent work, does clearly demonstrate that beavers are a critical component of nature-based river restoration in North America and Eurasia, but many opportunities remain to deepen understanding of their role.

6. CONCLUSIONS

This study showed that beaver-modified riverscapes are resistant to megafire-scale disturbance. This resilience is directly attributable to beaver dam- and canal-building activity, although the geomorphic settings conducive to beaver activity also confer a degree of resilience. Therefore, even with the current degraded state of many river systems and the trajectory of increasing wildfire severity under a changing climate, beaver ecosystem engineering offers proven resilience to megafires and a reliable source of wildfire refugia for freshwater-dependent biological communities, including humans. Beaver ecosystem engineering is complementary to, not in opposition to, current fire-mitigation strategies. Beaver populations, and in turn beaver dam building, can be part of a comprehensive fire-mitigation strategy while offering additional benefits to biological communities, including humans, even when fire is not an active threat. Beaver conservation, beaver coexistence strategies, and beaver-based restoration should be strongly considered for inclusion when planning fire risk-mitigation strategies, and when developing or updating watershed and land management plans.

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REFERENCES CITED

- Addabbo, P., Focareta, M., Marcuccio, S., Votto, C., and Ullo, S.L., 2016, Contribution of Sentinel-2 data for applications in vegetation monitoring: *Acta Imeko*, v. 5, no. 2, 44, https://doi.org/10.21014/acta_imeko.v5i2.352.
- Agee, J.K., 1998, The landscape ecology of western forest fire regimes: *Northwest Science*, v. 72, p. 24.
- Andersen, D.C., and Shafroth, P.B., 2010, Beaver dams, hydrological thresholds, and controlled floods as a management tool in a desert riverine ecosystem, Bill Williams River, Arizona: *Ecology*, v. 3, no. 3, p. 325–338, <https://doi.org/10.1002/eco.113>.
- Anderson, N.L., Paszkowski, C.A., and Hood, G.A., 2015, Linking aquatic and terrestrial environments: Can beaver canals serve as movement corridors for pond-breeding amphibians?: *Animal Conservation*, v. 18, p. 287–294, <https://doi.org/10.1111/acv.12170>.
- Andrus, R.A., Martinez, A.J., Jones, G.M., and Meddens, A.J., 2021, Assessing the quality of fire refugia for wildlife habitat: *Forest Ecology and Management*, v. 482, <https://doi.org/10.1016/j.foreco.2020.118868>.
- Bartelt, K., 2021, Valley Bottom Inundation Patterns in Beaver-Modified Streams: A Potential Proxy for Hydrologic Inefficiency [M.S. thesis]: Logan, Utah, Utah State University, 78 p., <https://doi.org/10.26076/a66b-0708>.
- Bash, J., Berman, C.H., and Bolton, S., 2001, Effects of Turbidity and Suspended Solids on Salmonids: Final Research Report Research Project T1803, Task 42, prepared for Washington State Transportation Center, 92 p.
- Bashinskiy, I.V., 2020, Beavers in lakes: A review of their ecosystem impact: *Aquatic Ecology*, v. 54, no. 4, p. 1097–1120, <https://doi.org/10.1007/s10452-020-09796-4>.
- Beechie, T.J., Sear, D.A., Olden, J.D., Pess, G.R., Buffington, J.M., Moir, H., Roni, P., and Pollock, M.M., 2010, Process-based principles for restoring river ecosystems: *Bioscience*, v. 60, no. 3, p. 209–222, <https://doi.org/10.1525/bio.2010.60.3.7>.
- Blomdahl, E.M., Kolden, C.A., Meddens, A.J., and Lutz, J.A., 2019, The importance of small fire refugia in the central Sierra Nevada, California, USA: *Forest Ecology and Management*, v. 432, p. 1041–1052, <https://doi.org/10.1016/j.foreco.2018.10.038>.
- Bowman, D.M., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D'Antonio, C.M., DeFries, R., Johnston, F.H., Keeley, J.E., and Krawchuk, M.A., 2011, The human dimension of fire regimes on Earth: *Journal of Biogeography*, v. 38, no. 12, p. 2223–2236, <https://doi.org/10.1111/j.1365-2699.2011.02595.x>.
- Brass, J.A., Ambrosia, V.G., Riggan, P.J., and Sebesta, P.D., 1996, Consequences of fire on aquatic nitrate and phosphate dynamics in Yellowstone National Park, in Greenlee, J.M., ed., *Proceeding of the 2nd Biennial Conference on the Greater Yellowstone Ecosystem*, Sep. 19–21, 1993, Yellowstone National Park: Fairfield, Washington, International Association of Wildland Fire, p. 53–57.
- Brazier, R.E., Puttock, A., Graham, H.A., Auster, R.E., Davies, K.H., and Brown, C.M.L., 2021, Beaver: Nature's ecosystem engineers: *WIREs Water*, v. 8, no. 1, <https://doi.org/10.1002/wat2.1494>.
- Cannon, S.H., and DeGraff, J., 2009, The increasing wildfire and post-fire debris-flow threat in western USA, and implications for consequences of climate change, in Sassa, K., and Canuti, P., eds., *Landslides—Disaster Risk Reduction*: Berlin, Springer, p. 177–190, https://doi.org/10.1007/978-3-540-69970-5_9.
- Castro, J.M., and Thorne, C.R., 2019, The stream evolution triangle: Integrating geology, hydrology, and biology: *River Research and Applications*, v. 35, no. 4, p. 315–326, <https://doi.org/10.1002/rra.3421>.
- Chou, Y.H., Minnich, R.A., and Chase, R.A., 1993, Mapping probability of fire occurrence in San Jacinto Mountains, California, USA: *Environmental Management*, v. 17, no. 1, p. 129–140, <https://doi.org/10.1007/BF02393801>.
- Ciotti, D.C., McKee, J., Pope, K.L., Kondolf, G.M., and Pollock, M.M., 2021, Design criteria for process-based restoration of fluvial systems: *Bioscience*, v. 71, no. 8, p. 831–845, <https://doi.org/10.1093/biosci/biab065>.
- Cluer, B., and Thorne, C., 2014, A stream evolution model integrating habitat and ecosystem benefits: *River Research and Applications*, v. 30, no. 2, p. 135–154, <https://doi.org/10.1002/rra.2631>.
- Coen, J.L., Stavros, E.N., and Fites-Kaufman, J.A., 2018, Deconstructing the King megafire: *Ecological Applications*, v. 28, no. 6, p. 1565–1580, <https://doi.org/10.1002/eap.1752>.
- Dewitz, J., and U.S. Geological Survey, 2021, National Land Cover Database (NLCD) 2019 Products (ver. 2.0, June 2021): U.S. Geological Survey Data Release, <https://doi.org/10.5066/P9KZCM54>.
- Dittbrenner, B.J., Pollock, M.M., Schilling, J.W., Olden, J.D., Lawler, J.J., and Torgersen, C.E., 2018, Modeling intrinsic potential for beaver (*Castor canadensis*) habitat to inform restoration and climate change adaptation: *PLoS One*, v. 13, no. 2, <https://doi.org/10.1371/journal.pone.0192538>.
- Dittbrenner, B.J., Schilling, J.W., Torgersen, C.E., and Lawler, J.J., 2022, Relocated beaver can increase water storage and decrease stream temperature in headwater streams: *Ecosphere*, v. 13, no. 7, <https://doi.org/10.1002/ecs2.4168>.
- Downing, W.M., Krawchuk, M.A., Coop, J.D., Meigs, G.W., Haire, S.L., Walker, R.B., Whitman, E., Chong, G., Miller, C., and Tortorelli, C., 2020, How do plant communities differ between fire refugia and fire-generated early-seral vegetation?: *Journal of Vegetation Science*, v. 31, no. 1, p. 26–39, <https://doi.org/10.1111/jvs.12814>.

- Drusch, M., Del Bello, U., Carlier, S., Colin, O., Fernandez, V., Gascon, F., Hoersch, B., Isola, C., Laberinti, P., and Martimort, P., 2012, Sentinel-2: ESA's optical high-resolution mission for GMES operational services: Remote Sensing of Environment, v. 120, p. 25–36, <https://doi.org/10.1016/j.rse.2011.11.026>.
- Dwire, K.A., and Kauffman, J.B., 2003, Fire and riparian ecosystems in landscapes of the western USA: Forest Ecology and Management, v. 178, no. 1–2, p. 61–74, [https://doi.org/10.1016/S0378-1127\(03\)00053-7](https://doi.org/10.1016/S0378-1127(03)00053-7).
- Eidenshink, J., Schwind, B., Brewer, K., Zhu, Z.-L., Quayle, B., and Howard, S., 2007, A project for monitoring trends in burn severity: Fire Ecology, v. 3, no. 1, p. 3–21, <https://doi.org/10.4996/fireecology.0301003>.
- ESRI, 2022, ArcGIS Pro (Version 2.8): ESRI, Inc., <https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview> (accessed 30 October 2023).
- Fairfax, E., and Small, E.E., 2018, Using remote sensing to assess the impact of beaver damming on riparian evapotranspiration in an arid landscape: Ecohydrology, v. 11, no. 7, <https://doi.org/10.1002/eco.1993>.
- Fairfax, E., and Whittle, A., 2020, Smokey the Beaver: Beaver-dammed riparian corridors stay green during wildfire throughout the western United States: Ecological Applications, v. 30, no. 8, <https://doi.org/10.1002/eap.2225>.
- Feiner, K., and Lowry, C.S., 2015, Simulating the effects of a beaver dam on regional groundwater flow through a wetland: Journal of Hydrology—Regional Studies, v. 4, p. 675–685, <https://doi.org/10.1016/j.ejrh.2015.10.001>.
- Finco, M., Quayle, B., Zhang, Y., Lecker, J., Megown, K.A., and Brewer, C.K., 2012, Monitoring trends and burn severity (MTBS): Monitoring wildfire activity for the past quarter century using Landsat data, in Morin, R.S., and Liknes, G.C., compilers, Proceedings: Moving from Status to Trends: Forest Inventory and Analysis (FIA) Symposium 2012, 4–6 December 2012, Baltimore, MD: U.S. Department of Agriculture Forest Service, Northern Research Station General Technical Report NRS-P-105, p. 222–228 [CD-ROM], https://www.fs.usda.gov/nrs/pubs/gtr/gtr_nrs-p-105.pdf.
- Foster, C.N., Banks, S.C., Cary, G.J., Johnson, C.N., Lindenmayer, D.B., and Valentine, L.E., 2020, Animals as agents in fire regimes: Trends in Ecology & Evolution, v. 35, no. 4, p. 346–356, <https://doi.org/10.1016/j.tree.2020.01.002>.
- Fouty, S.C., 2018, Euro-American beaver trapping and its long-term impact on drainage network form and function, water abundance, delivery, and system stability, in Johnson, R., Carothers, S.W., Finch, D.M., Kingsley, K.J., and Stanley, J.T., technical eds., Riparian Research and Management: Past, Present, Future: Volume 1: U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station General Technical Report RMRS-GTR-377, p. 102–133, <https://doi.org/10.2737/RMRS-GTR-377>.
- Gable, T.D., Johnson-Bice, S.M., Homkes, A.T., Windels, S.K., and Bump, J.K., 2020, Outsized effect of predation: Wolves alter wetland creation and recolonization by killing ecosystem engineers: Science Advances, v. 6, no. 46, <https://doi.org/10.1126/sciadv.abc5439>.
- Gilbert, J.T., Macfarlane, W.W., and Wheaton, J.M., 2016, The Valley Bottom Extraction Tool (V-BET): A GIS tool for delineating valley bottoms across entire drainage networks: Computers & Geosciences, v. 97, p. 1–14, <https://doi.org/10.1016/j.cageo.2016.07.014>.
- Girden, E.R., 1992, ANOVA: Repeated Measures: Atlanta, Georgia, Sage Publications, Quantitative Applications in the Social Sciences 84, 88 p.
- Google, 2022, Google Earth Pro (Version 7.3): Google, <https://www.google.com/earth/versions/> (accessed October 2023).
- Goss, M., Swain, D.L., Abatzoglou, J.T., Sarhadi, A., Kolden, C.A., Williams, A.P., and Duffenbaugh, N.S., 2020, Climate change is increasing the likelihood of extreme autumn wildfire conditions across California: Environmental Research Letters, v. 15, no. 9, 094016, <https://doi.org/10.1088/1748-9326/ab83a7>.
- Gresswell, R.E., 1999, Fire and aquatic ecosystems in forested biomes of North America: Transactions of the American Fisheries Society, v. 128, no. 2, p. 193–221, [https://doi.org/10.1577/1548-8659\(1999\)128<0193:FAAEIF>2.0.CO;2](https://doi.org/10.1577/1548-8659(1999)128<0193:FAAEIF>2.0.CO;2).
- Gummell, A., 1998, The hydrogeomorphological effects of beaver dam-building activity: Progress in Physical Geography, v. 22, no. 2, p. 167–189, <https://doi.org/10.1177/030913339802200202>.
- Higuera, P.E., and Abatzoglou, J.T., 2021, Record-setting climate enabled the extraordinary 2020 fire season in the western United States: Global Change Biology, v. 27, no. 1, p. 1–2, <https://doi.org/10.1111/gcb.15388>.
- Hillman, G.R., 1998, Flood wave attenuation by a wetland following a beaver dam failure on a second order boreal stream: Wetlands, v. 18, no. 1, p. 21–34, <https://doi.org/10.1007/BF03161439>.
- Hood, G.A., and Bayley, S.E., 2008, Beaver (*Castor canadensis*) mitigate the effects of climate on the area of open water in boreal wetlands in western Canada: Biological Conservation, v. 141, no. 2, p. 556–567, <https://doi.org/10.1016/j.biocon.2007.12.003>.
- Hood, G.A., and Larson, D.G., 2015, Ecological engineering and aquatic connectivity: A new perspective from beaver-modified wetlands: Freshwater Biology, v. 60, no. 1, p. 198–208, <https://doi.org/10.1111/fwb.12487>.
- Hyvönen, T., and Nummi, P., 2008, Habitat dynamics of beaver *Castor canadensis* at two spatial scales: Wildlife Biology, v. 14, no. 3, p. 302–308, [https://doi.org/10.2981/0909-6396\(2008\)14\[302:HDOBCC\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2008)14[302:HDOBCC]2.0.CO;2).
- Ives, R.L., 1942, The beaver-meadow complex: Journal of Geomorphology, v. 5, no. 3, p. 191–203.
- Ji, L., Zhang, L., Wylie, B.K., and Rover, J., 2011, On the terminology of the spectral vegetation index (NIR – SWIR)/(NIR + SWIR): International Journal of Remote Sensing, v. 32, no. 21, p. 6901–6909, <https://doi.org/10.1080/01431161.2010.510811>.
- Johnson, M.F., Thorne, C.R., Castro, J.M., Kondolf, G.M., Mazzacano, C.S., Rood, S.B., and Westbrook, C., 2019, Biomic river restoration: A new focus for river management: River Research and Applications, v. 36, no. 1, p. 3–12, <https://doi.org/10.1002/rra.3529>.
- Johnston, C.A., 2017, Beavers: Boreal Ecosystem Engineers: Cham, Switzerland, Springer, 272 p., <https://doi.org/10.1007/978-3-319-61533-2>.
- Jones, G., Kramer, H., Berigan, W., Whitmore, S., Gutiérrez, R., and Peery, M., 2021, Megafire causes persistent loss of an old-forest species: Animal Conservation, v. 24, no. 6, p. 925–936, <https://doi.org/10.1111/acv.12697>.
- Jordan, C.E., and Fairfax, E., 2022, Beaver: The North American freshwater climate action plan: WIRES Water, v. 9 no. 4, <https://doi.org/10.1002/wat2.1592>.
- Keeley, J.E., 2009, Fire intensity, fire severity and burn severity: A brief review and suggested usage: International Journal of Wildland Fire, v. 18, no. 1, p. 116–126, <https://doi.org/10.1071/WF07049>.
- Khorshidi, M.S., Dennison, P.E., Nikoo, M.R., AghaKouchak, A., Luce, C.H., and Sadegh, M., 2020, Increasing concurrence of wildfire drivers tripled megafire critical danger days in Southern California between 1982 and 2018: Environmental Research Letters, v. 15, no. 10, 104002, <https://doi.org/10.1088/1748-9326/abae9e>.
- Kirby, K., Buckley, G., and Mills, J., 2017, Biodiversity implications of coppice decline, transformations to high forest and coppice restoration in British woodland: Folia Geobotanica, v. 52, no. 1, p. 5–13, <https://doi.org/10.1007/s12224-016-9252-1>.
- Landesmann, J.B., and Morales, J.M., 2018, The importance of fire refugia in the recolonization of a fire-sensitive conifer in northern Patagonia: Plant Ecology, v. 219, no. 4, p. 455–466, <https://doi.org/10.1007/s11258-018-0808-4>.
- Larsen, A., Larsen, J.R., and Lane, S.N., 2021, Dam builders and their works: Beaver influences on the structure and function of river corridor hydrology, geomorphology, biogeochemistry and ecosystems: Earth-Science Reviews, v. 218, <https://doi.org/10.1016/j.earscirev.2021.103623>.
- Law, A., Gaywood, M.J., Jones, K.C., Ramsay, P., and Willby, N.J., 2017, Using ecosystem engineers as tools in habitat restoration and rewilding: Beaver and wetlands: The Science of the Total Environment, v. 605–606, p. 1021–1030, <https://doi.org/10.1016/j.scitotenv.2017.06.173>.
- Le Breton, T.D., Lyons, M.B., Nolan, R.H., Penman, T., Williamson, G.J., and Ooi, M.K., 2022, Megafire-induced interval squeeze threatens vegetation at landscape scales: Frontiers in Ecology and the Environment, v. 20, p. 327–334, <https://doi.org/10.1002/fee.2482>.
- Linley, G.D., Jolly, C.J., Doherty, T.S., Geary, W.L., Armenteras, D., Belcher, C.M., Bliege Bird, R., Duane, A., Fletcher, M.S., Giorgis, M.A., Haslem, A., Jones, G.M., Kelly, L.T., Lee, C.K.F., Nolan, R.H., Parr, C.L., Pausas, J.G., Price, J.N., Regos, A., Ritchie, E.G., Ruffault, J., Williamson, G.J., Wu, Q., and Nimmo, D.G., 2022, What do you mean, ‘megafire’?: Global Ecology and Biogeography, v. 31, no. 10, p. 1906–1922, <https://doi.org/10.1111/geb.13499>.
- Lowry, M.M., 1993, Groundwater Elevations and Temperature Adjacent to a Beaver Pond in Central Oregon [M.S. thesis]: Corvallis, Oregon, Oregon State University Department of Forest Engineering, 134 p.
- MacCracken, J.G., Lebovitz, A.D., and Lewis, J.C., 2005, Selection of in-stream wood structures by beaver in the Bear River, southwest Washington: Northwestern Naturalist, v. 86, no. 2, p. 49–58, [https://doi.org/10.1898/1051-1733\(2005\)086\[0049:SOIWSB\]2.0.CO;2](https://doi.org/10.1898/1051-1733(2005)086[0049:SOIWSB]2.0.CO;2).
- Macfarlane, W.W., Wheaton, J.M., Bouwes, N., Jensen, M.L., Gilbert, J.T., Hough-Snee, N., and Shivik, J.A., 2015, Modeling the capacity of

- riverscapes to support beaver dams: *Geomorphology*, v. 277, p. 72–99, <https://doi.org/10.1016/j.geomorph.2015.11.019>.
- Magilligan, F.J., Nislow, K.H., Fisher, G.B., Wright, J., Mackey, G., and Laser, M., 2008, The geomorphic function and characteristics of large woody debris in low gradient rivers, coastal Maine, USA: *Geomorphology*, v. 97, no. 3–4, p. 467–482, <https://doi.org/10.1016/j.geomorph.2007.08.016>.
- Markle, C.E., Gage, H.J., Tekatch, A.M., Wilkinson, S.L., and Waddington, J.M., 2022, Wetland successional state affects fire severity in a boreal shield landscape: *Wetlands*, v. 42, no. 7, 87, <https://doi.org/10.1007/s13157-022-01606-x>.
- Meddens, A.J., Kolden, C.A., Lutz, J.A., Smith, A.M., Cansler, C.A., Abatzoglou, J.T., Meigs, G.W., Downing, W.M., and Krawchuk, M.A., 2018, Fire refugia: What are they, and why do they matter for global change?: *BioScience*, v. 68, no. 12, p. 944–954, <https://doi.org/10.1093/biosci/biy103>.
- Miller, J.D., and Thode, A.E., 2007, Quantifying burn severity in a heterogeneous landscape with a relative version of the delta normalized burn ratio (dNBR): *Remote Sensing of Environment*, v. 109, no. 1, p. 66–80, <https://doi.org/10.1016/j.rse.2006.12.006>.
- Moran, P.A.P., 1950, Notes on continuous stochastic phenomena: *Biometrika*, v. 37, p. 17–23, <https://doi.org/10.1093/biomet/37.1-2.17>.
- Morelli, T.L., Daly, C., Dobrowski, S.Z., Dulen, D.M., Ebersole, J.L., Jackson, S.T., Lundquist, J.D., Millar, C.I., Maher, S.P., Monahan, W.B., Nydick, K.R., Redmond, K.T., Sawyer, S.C., Stock, S., and Beissinger, S.R., 2016, Managing climate change refugia for climate adaptation: *PLoS One*, v. 11, no. 8, <https://doi.org/10.1371/journal.pone.0159909>.
- Naiman, R.J., Johnston, C.A., and Kelley, J.C., 1988, Alteration of North American streams by beaver: *BioScience*, v. 38, no. 11, p. 753–762, <https://doi.org/10.2307/1310784>.
- National Interagency Fire Center (NIFC), 2022, Wildland Fire Locations Full History: <https://data-nifc.opendata.arcgis.com/> (accessed 30 October 2023).
- Norman, L.M., Lal, R., Wohl, E., Fairfax, E., Gellis, A.C., and Pollock, M.M., 2022, Natural infrastructure in dryland streams (NIDS) can establish regenerative wetland sinks that reverse desertification and strengthen climate resilience: *The Science of the Total Environment*, v. 849, <https://doi.org/10.1016/j.scitotenv.2022.157738>.
- Osei, N.A., Gurnell, A.M., and Harvey, G.L., 2015, The role of large wood in retaining fine sediment, organic matter and plant propagules in a small, single-thread forest river: *Geomorphology*, v. 235, p. 77–87, <https://doi.org/10.1016/j.geomorph.2015.01.031>.
- Pedersen, E.J., Miller, D.L., Simpson, G.L., and Ross, N., 2019, Hierarchical generalized additive models in ecology: An introduction with mgcv: *PeerJ*, v. 7, <https://doi.org/10.7717/peerj.6876>.
- Phillips, J.D., 2009, Biological energy in landscape evolution: *American Journal of Science*, v. 309, no. 4, p. 271–289, <https://doi.org/10.2475/04.2009.01>.
- Phillips, J.D., 2016, Landforms as extended composite phenotypes: *Earth Surface Processes and Landforms*, v. 41, no. 1, p. 16–26, <https://doi.org/10.1002/esp.3764>.
- Pleniou, M., and Koutsias, N., 2013, Sensitivity of spectral reflectance values to different burn and vegetation ratios: A multi-scale approach applied in a fire affected area: *ISPRS Journal of Photogrammetry and Remote Sensing*, v. 79, p. 199–210, <https://doi.org/10.1016/j.isprsjprs.2013.02.016>.
- Pollock, M.M., Naiman, R.J., Erickson, H.E., Johnston, C.A., Pastor, J., and Pinay, G., 1995, Beaver as engineers—Influences on biotic and abiotic characteristics of drainage basins, in Jones, C.G., and Lawton, J.H., eds., *Linking Species & Ecosystems*: Boston, Springer, p. 117–126, https://doi.org/10.1007/978-1-4615-1773-3_12.
- Pollock, M.M., Beechie, T.J., Wheaton, J.M., Jordan, C.E., Bouwes, N., Weber, N., and Volk, C., 2014, Using beaver dams to restore incised stream ecosystems: *BioScience*, v. 64, no. 4, p. 279–290, <https://doi.org/10.1093/biosci/biu036>.
- Pollock, M.M., Castro, J., Jordan, C.E., Lewallen, G., and Woodruff, K., 2015, *The Beaver Restoration Guidebook: Working with Beaver to Restore Streams, Wetlands, and Floodplains*: Portland, Oregon, U.S. Fish and Wildlife Service, Version 1.02, 189 p., <https://www.fws.gov/media/beaver-restoration-guidebook>.
- Polvi, L.E., and Wohl, E., 2012, The beaver meadow complex revisited—The role of beavers in post-glacial floodplain development: *Earth Surface Processes and Landforms*, v. 37, no. 3, p. 332–346, <https://doi.org/10.1002/esp.2261>.
- Prein, A.F., Coen, J., and Jaye, A., 2022, The character and changing frequency of extreme California fire weather: *Journal of Geophysical Research: Atmospheres*, v. 127, e2021JD035350, <https://doi.org/10.1029/2021JD035350>.
- Puttock, A., Graham, H.A., Ashe, J., Luscombe, D.J., and Brazier, R.E., 2021, Beaver dams attenuate flow: A multi-site study: *Hydrological Processes*, v. 35, no. 2, <https://doi.org/10.1002/hyp.14017>.
- QGIS.org, 2022, QGIS Geographic Information System: QGIS Association, <http://www.qgis.org> (accessed 30 October 2023).
- Rinne, J.N., 1996, Management briefs: Short-term effects of wildfire on fishes and aquatic macroinvertebrates in the southwestern United States: *North American Journal of Fisheries Management*, v. 16, no. 3, p. 653–658, [https://doi.org/10.1577/1548-8675\(1996\)016<0653:MBSTEO>2.3.CO;2](https://doi.org/10.1577/1548-8675(1996)016<0653:MBSTEO>2.3.CO;2).
- Rodriguez, B., Lareau, N.P., Kingsmill, D.E., and Clements, C.B., 2020, Extreme pyroconvective updrafts during a megafire: *Geophysical Research Letters*, v. 47, no. 18, <https://doi.org/10.1029/2020GL089001>.
- Ronquist, A.L., and Westbrook, C.J., 2021, Beaver dams: How structure, flow state, and landscape setting regulate water storage and release: *The Science of the Total Environment*, v. 785, <https://doi.org/10.1016/j.scitotenv.2021.147333>.
- Rood, S.B., and Mahoney, J.M., 1990, Collapse of riparian poplar forests downstream from dams in western prairies: Probable causes and prospects for mitigation: *Environmental Management*, v. 14, no. 4, p. 451–464, <https://doi.org/10.1007/BF02394134>.
- Roy, D.P., Wulder, M.A., Loveland, T.R., Woodcock, C.E., Allen, R.G., Anderson, M.C., Helder, D., Irons, J.R., Johnson, D.M., Kennedy, R., Scambos, T.A., Schaaf, C.B., Schott, J.R., Sheng, Y., Vermote, E.F., Belward, A.S., Bindaschadler, R., Cohen, W.B., Gao, F., Hipple, J.D., Hostert, P., Huntington, J., Justice, C.O., Kilic, A., Kovalsky, V., Lee, Z.P., Lyburner, L., Masek, J.G., McCorkel, J., Shuai, Y., Trezza, R., Vogelmann, J., Wynne, R.H., and Zhu, Z., 2014, Landsat-8 and Sentinel-2: Science and product vision for terrestrial global change research: *Remote Sensing of Environment*, v. 145, p. 154–172, <https://doi.org/10.1016/j.rse.2014.02.001>.
- Roy, D.P., Huang, H., Boschetti, L., Giglio, L., Yan, L., Zhang, H.H., and Li, Z., 2019, Landsat-8 and Sentinel-2 burned area mapping—A combined sensor multi-temporal change detection approach: *Remote Sensing of Environment*, v. 231, <https://doi.org/10.1016/j.rse.2019.111254>.
- Ruxton, G.D., and Beauchamp, G., 2008, Time for some a priori thinking about post hoc testing: *Behavioral Ecology*, v. 19, no. 3, p. 690–693, <https://doi.org/10.1093/beheco/arn020>.
- Scamardo, J., and Wohl, E.E., 2019, Sediment storage and shallow groundwater response to beaver dam analogues in the Colorado Front Range, USA: *River Research and Applications*, v. 36, p. 398–409, <https://doi.org/10.1002/rra.3592>.
- Schier, G.A., Jones, J.R., and Winokur, R.P., 1985, Vegetative regeneration, in DeByle, N.V., and Winokur, R.P., eds., *Aspen: Ecology and Management in the Western United States*: U.S. Department of Agriculture Forest Service, Rocky Mountain Forest and Range Experiment Station General Technical Report RM-119, p. 29–33, <https://doi.org/10.2737/RM-GTR-119>.
- Shinneman, D.J., Baker, W.L., Rogers, P.C., and Kulakowski, D., 2013, Fire regimes of quaking aspen in the Mountain West: *Forest Ecology and Management*, v. 299, p. 22–34, <https://doi.org/10.1016/j.foreco.2012.11.032>.
- Short, L.E., Gabet, E.J., and Hoffman, D.F., 2015, The role of large woody debris in modulating the dispersal of a post-fire sediment pulse: *Geomorphology*, v. 246, p. 351–358, <https://doi.org/10.1016/j.geomorph.2015.06.031>.
- Skidmore, P., and Wheaton, J., 2022, Riverscapes as natural infrastructure: Meeting challenges of climate adaptation and ecosystem restoration: *Anthropocene*, v. 38, <https://doi.org/10.1016/j.ancene.2022.100334>.
- Skinner, C.N., and Chang, C., 1996, Fire regimes, past and present, in *Sierra Nevada Ecosystem Project: Final Report to Congress. Volume II. Assessments and Scientific Basis for Management Options*: Davis, California, Centers for Water and Wildland Resources, University of California, Wildland Resources Center Report 37, p. 1041–1069, https://pubs.usgs.gov/dds/dds-43/VOL_II/VII_C38.PDF.
- Stein, S.J., Price, P.W., Abrahamson, W.G., and Sacchi, C.F., 1992, The effect of fire on stimulating willow regrowth and subsequent attack by grasshoppers and elk: *Oikos*, v. 65, p. 190–196, <https://doi.org/10.2307/3545009>.
- Stephens, S.L., Burrows, N., Buyantuyev, A., Gray, R.W., Keane, R.E., Kubian, R., Liu, S., Seijo, F., Shu, L., Tolhurst, K.G., and van Wagtenonk, J.W., 2014, Temperate and boreal forest mega-fires: Characteristics and challenges: *Frontiers in Ecology and the Environment*, v. 12, no. 2, p. 115–122, <https://doi.org/10.1890/120332>.
- Swain, D.L., 2021, A shorter, sharper rainy season amplifies California wildfire risk: *Geophysical Research Letters*, v. 48, no. 5, <https://doi.org/10.1029/2021GL092843>.

- Syphard, A.D., Radeloff, V.C., Keeley, J.E., Hawbaker, T.J., Clayton, M.K., Stewart, S.I., and Hammer, R.B., 2007, Human influence on California fire regimes: Ecological Applications, v. 17, no. 5, p. 1388–1402, <https://doi.org/10.1890/06-1128.1>.
- Thompson, D.M., and Stull, G.N., 2002, The development and historic use of habitat structures in channel restoration in the United States: The grand experiment in fisheries management: Géographie Physique et Quaternaire, v. 56, no. 1, p. 45–60, <https://doi.org/10.7202/008604ar>.
- U.S. Geological Survey (USGS), 2019 National Hydrography Dataset, Version USGS National Hydrography Dataset Best Resolution (NHD): <https://www.usgs.gov/national-hydrography/access-national-hydrography-products> (accessed 30 October 2023).
- van Mantgem, P.J., and Schwilk, D.W., 2009, Negligible influence of spatial autocorrelation in the assessment of fire effects in a mixed conifer forest: Fire Ecology, v. 5, no. 2, p. 116–125, <https://doi.org/10.4996/fireecology.0502116>.
- Vicente-Serrano, S.M., Beguería, S., and López-Moreno, J.I., 2010, A multiscalar drought index sensitive to global warming: The standardized precipitation evapotranspiration index: Journal of Climate, v. 23, no. 7, p. 1696–1718, <https://doi.org/10.1175/2009JCLI2909.1>.
- Weirich, J., 2020, Beaver Moderated Fire Resistance in the North Cascades [M.S. thesis]: Cheney, Washington, Eastern Washington University, 56 p.
- Welch, B., 1947, The generalization of 'student's' problem when several different population variances are involved: Biometrika, v. 34, no. 1–2, p. 28–35, <https://doi.org/10.2307/2332510>.
- Westbrook, C.J., Cooper, D.J., and Baker, B.W., 2006, Beaver dams and over-bank floods influence groundwater–surface water interactions of a Rocky Mountain riparian area: Water Resources Research, v. 42, no. 6, W06404, <https://doi.org/10.1029/2005WR004560>.
- Westbrook, C.J., Ronnquist, A., and Bedard-Haughn, A., 2020, Hydrological functioning of a beaver dam sequence and regional dam persistence during an extreme rainstorm: Hydrological Processes, v. 34, no. 18, p. 3726–3737, <https://doi.org/10.1002/hyp.13828>.
- Wheaton, J., Bennett, S.N., Bouwes, N., Maestas, J.D., and Shahveridian, S.M., 2019, Low-Tech Process-Based Restoration of Riverscapes: Design Manual: Logan, Utah, Utah State University Restoration Consortium, 286 p.
- Whipple, A., 2019, Riparian Resilience in the Face of Interacting Disturbances: Understanding Complex Interactions between Wildfire, Erosion, and Beaver (*Castor canadensis*) in Grazed Dryland Riparian Systems of Low Order Streams in North Central Washington State, USA [M.S. thesis]: Cheney, Washington, Eastern Washington University, 114 p.
- Williams, J., 2013, Exploring the onset of high-impact mega-fires through a forest land management prism: Forest Ecology and Management, v. 294, p. 4–10, <https://doi.org/10.1016/j.foreco.2012.06.030>.
- Wohl, E., 2011, What should these rivers look like? Historical range of variability and human impacts in the Colorado Front Range, USA: Earth Surface Processes and Landforms, v. 36, no. 10, p. 1378–1390, <https://doi.org/10.1002/esp.2180>.
- Wohl, E., 2015, Of wood and rivers: Bridging the perception gap: WIREs Water, v. 2, no. 3, p. 167–176, <https://doi.org/10.1002/wat2.1076>.
- Wohl, E., 2021a, An integrative conceptualization of floodplain storage: Reviews of Geophysics, v. 59, no. 2, <https://doi.org/10.1029/2020RG000724>.
- Wohl, E., 2021b, Legacy effects of loss of beavers in the continental United States: Environmental Research Letters, v. 16, no. 2, p. 025010, <https://doi.org/10.1088/1748-9326/abd34e>.
- Wohl, E., and Scott, D.N., 2016, Wood and sediment storage and dynamics in river corridors: Earth Surface Processes and Landforms, v. 42, no. 1, p. 5–23, <https://doi.org/10.1002/esp.3909>.
- Wohl, E., Lane, S.N., and Wilcox, A.C., 2015, The science and practice of river restoration: Water Resources Research, v. 51, no. 8, p. 5974–5997, <https://doi.org/10.1002/2014WR016874>.
- Wohl, E., Castro, J., Cluer, B., Merritts, D., Powers, P., Staab, B., and Thorne, C., 2021, Rediscovering, reevaluating, and restoring lost river-wetland corridors: Frontiers in Earth Science, v. 9, <https://doi.org/10.3389/feart.2021.653623>.
- Wohl, E., Marshall, A.E., Scamardo, J., White, D., and Morrison, R.R., 2022, Biogeomorphic influences on river corridor resilience to wildfire disturbances in a mountain stream of the Southern Rockies, USA: The Science of the Total Environment, v. 820, <https://doi.org/10.1016/j.scitotenv.2022.153321>.
- Woo, M.-K., and Waddington, J.M., 1990, Effects of beaver dams on sub-arctic wetland hydrology: Arctic, v. 43, no. 3, p. 223–230, <https://doi.org/10.14430/arctic1615>.
- Wood, S.N., 2018, Mixed GAM Computation Vehicle with Automatic Smoothness Estimation: CRAN, <https://cran.uib.no/web/packages/mgcv/mgcv.pdf> (accessed 30 October 2023).

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