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Integrating habitat restoration and conservation planning for freshwater ecosystem resilience

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Integrating habitat restoration and conservation planning for freshwater ecosystem resilience

By

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Professor Albert Ruhí, Co-Chair
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Abstract

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Freshwater ecosystems support biodiversity, climate resilience, and ecosystem services around the globe, making them a conservation priority. To effectively conserve diverse freshwater ecosystems in an uncertain climate future, we must employ a portfolio of conservation strategies that tackle complementary aspects of freshwater restoration and conservation. This dissertation explores three conservation strategies - area-based conservation, local restoration, and wildlife reintroduction - as approaches to conserving freshwater ecosystems. Chapter one examines how state or national area-based conservation schemes must shift focus to specifically include freshwater ecosystems, providing climate, biodiversity, and societal benefits while also better protecting freshwater systems. Our recommendations for centering freshwater ecosystems are to 1) focus on watershed-scale conservation; and 2) consider five freshwater ecosystem priorities, including connectivity, watershed disturbance, flow alteration, water quality, and biodiversity. Chapter two zooms in to a local restoration project in the Klamath River watershed in northern California, where hydropower development and high river water temperatures threaten juvenile salmonids. We show that human-made off-channel floodplain ponds provide cooler and more stable thermal refuge habitat for salmonids, illustrating the value of small-scale restoration in systems that are highly impacted by human development. Chapter three takes a different perspective on habitat engineering by exploring how reintroducing a native wildlife species, the North American beaver (*Castor canadensis*), could have both biodiversity and climate resilience (water storage and fire risk) benefits at the landscape scale. Our results show that after centuries of overutilization, considerable capacity for beaver dams remains throughout the California Sierra Nevada region. We also show that beavers have the potential to store significant surface water and create fire resilient landscapes throughout the region, illustrating how restoring a keystone species can benefit both ecosystems and society. Overall, these chapters represent three valuable and intersecting approaches to conserving and restoring resilient and functional freshwater ecosystems.

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Introduction

The protection and restoration of freshwater ecosystems is increasingly recognized as a conservation priority. There is growing awareness that freshwater ecosystems are in peril, and that they can support a variety of biodiversity, climate, and ecosystem service goals around the globe. Rivers, lakes, and wetlands are unique ecosystems that harbor 10% of global biodiversity (Strayer and Dudgeon 2010), create movement corridors for aquatic and terrestrial species (Hilty and Merenlender 2004; Krosby et al. 2018), store carbon (Mitsch and Gosselink 2015; Nahlik and Fennessy 2016), and transport nutrients and sediments (Wohl et al. 2015). Freshwater ecosystems are also vital to humans, supporting agriculture, irrigation, drinking water infrastructure, recreation, transportation, fishing, and energy production, and have deep cultural and spiritual significance for many communities (Dudgeon et al. 2006). However, as an intersection between natural environments and human society, freshwater ecosystems are particularly vulnerable to human activity. Our dependence on ecosystem services from freshwater often disrupts the ecological processes that support us in the first place.

The diverse ways in which humans rely on freshwater ecosystems mean there is no simple solution to protecting them. Because of this, finding balance between humans and freshwater environments requires a portfolio of conservation and restoration approaches. The objective of this dissertation is to examine several strategies for conserving and restoring freshwater ecosystems, each of which tackles conservation from a slightly different perspective. These strategies explore freshwater ecosystems with different levels of impact and at different scales, but all focus on connections between water and people, and on how to balance human use with the maintenance of functional, resilient ecosystems.

Chapter one explores strategies to shift area-based conservation priorities to include river ecosystems. Area-based conservation is a framework that aims to set aside a certain amount of land and sea to achieve conservation goals, and our primary area-based conservation tool is to create protected areas like national parks or conservation easements (Dinerstein et al. 2019). However, many protected areas are not adequate for conserving river ecosystems (e.g. Abell et al. 2017; Dudgeon 2019). Protected areas developed for terrestrial systems often under-represent freshwater habitats or are ill-positioned in large river networks, leading to continued degradation of freshwater systems even inside protected areas (e.g. Leal et al. 2020). Studies demonstrate that area-based conservation initiatives that lack explicit freshwater priorities often deprioritize freshwater habitats, and therefore lead to the continued decline of freshwater species (Tickner et al. 2020).

In this chapter, we developed a framework for considering the unique needs of freshwater ecosystems in area-based conservation plans. We based our framework on two main concepts: watershed-scale conservation, or the idea that critical parts of the river network need to be protected for effective river conservation; and freshwater conservation priorities, including connectivity, watershed disturbance, flow alteration, water quality, and biodiversity, that should be considered when developing protected area plans.

The large-scale conservation of freshwater ecosystems emphasized in chapter one is not always feasible, especially in multi-use landscapes where human infrastructure is deeply ingrained. In these cases, small-scale local restoration efforts can effectively restore critical ecosystem structures or functions and support aquatic species. Often, small, localized restoration projects do not fully restore ecosystem processes that maintain habitats and species in the long term; but rather focus on re-creating essential habitat structures that can help species persist despite large-scale landscape alterations (Beechie et al. 2010).

Chapter two focuses on an ecosystem where large-scale process-based restoration and small-scale habitat restoration go hand in hand. In the mid Klamath River watershed in northern California, hydropower dams and poor water quality have devastated populations of native salmonids, and in particular, high summer water temperatures contribute to juvenile salmonid mortality. Four major hydropower dams were removed in the Klamath River in 2024, which will remedy some of the water quality issues that jeopardize salmonid populations (Klamath River Renewal Corporation 2020; Blumm and Illowsky 2022). However, dam removal was a multi-decade process, and in the meantime, salmonid populations needed access to higher quality habitat. To create cool water refuge habitat, the Karuk Fisheries Program constructed man-made off-channel floodplain ponds that are fed by groundwater and connected to Klamath River tributaries. We monitored water temperature in off-channel ponds, creeks, and the mainstem Klamath River and found that water temperature in the ponds is significantly cooler and more stable than in adjacent creeks and the river. This indicates that the ponds create an effective thermal refuge habitat for juvenile salmonids. This is an example of a small-scale, man-made restoration effort that successfully created refuge habitat for a threatened species, even as the Klamath River watershed was still heavily impacted by human use.

The potential benefits of local restoration initiatives are perhaps best exemplified by the wide-scale reintroduction of a native wildlife species. Chapter three explores the potential impacts of reintroducing the North American beaver (*Castor canadensis*) in the California Sierra Nevada region. Beavers are ecosystem engineers that build dams in stream channels, changing the movement of water and creating pond and wetland habitats that increase habitat diversity, store carbon and water, and create fire resilient landscapes (Brazier et al. 2021; Larsen et al. 2021). After being extirpated from the Sierra Nevada region during the fur trade in the early 1800s, beavers are now increasingly recognized for their potential water storage and fire resilience benefits in California, where water scarcity and wildfires threaten human communities and ecosystems (Fairfax and Whittle 2020).

To predict the potential landscape-scale benefits of beaver restoration, we examined the potential opportunities and benefits of restoring beaver dam-building activity in the context of global change in 31 watersheds in the Sierra Nevada region. We then estimated how much water those beaver dams could store and how much fire resilient landscape they could create. We identified five priority watersheds where potential dam capacity, water storage, and fire resilience overlapped considerably. These model outputs will allow land managers to prioritize not only where beavers are most likely to survive, but where they will specifically create water and fire benefits on the landscape.

Overall, this dissertation explores three different freshwater conservation strategies– area-based conservation, local restoration, and wildlife reintroduction– which represent three approaches for conserving and restoring freshwater ecosystems at different scales, in various conditions, and with unique priorities. The portfolio approach to ecosystem conservation and management is an important framework that accounts for both diversity and uncertainty by incorporating a suite of conservation strategies that target different populations, scales, and ecosystems (Schindler et al. 2015). This concept has been widely applied, from managing metapopulations of species (Anderson et al. 2015), to prioritizing conservation areas based on possible future climate scenarios (Aplet and McKinley 2017), to considering tributaries as part of a habitat portfolio for mainstem fishes (Bouska et al. 2023). In this dissertation, a portfolio approach addresses conservation in diverse freshwater ecosystems with different needs and priorities. Complementary, intersecting, and overlapping approaches are necessary to effectively conserve freshwater ecosystems in California and around the globe.

Chapter 1
Centering 30 × 30 conservation initiatives on freshwater ecosystems

This chapter has been previously published and is included here with permission from co-authors.

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Abstract
Regional, national, and international 30 × 30 conservation initiatives would be strengthened by including a specific focus on freshwater ecosystem conservation that supplements terrestrial conservation strategies. Globally, freshwater habitats support essential biodiversity and ecosystem services, yet are being lost at disproportionately high rates relative to terrestrial systems. Making freshwater ecosystems an explicit focus of 30 × 30 initiatives would assist in curtailing these losses while advancing 30 × 30's mission to address climate change, economic sustainability, food security, and equitable outdoor access across a variety of landscapes. Here, we explain how fresh water can serve as a key piece of 30 × 30 conservation efforts. We emphasize that to address the challenges of traditional area-based conservation programs, 30 × 30 should (1) focus on watershed-scale conservation planning and (2) evaluate conserved areas based on five freshwater priorities: connectivity, watershed disturbance, flow alteration, water quality, and biodiversity. We use examples from the US state of California to illustrate how addressing freshwater systems can help guide 30 × 30 conservation.

In a nutshell
- "30 × 30" is a collection of global initiatives that share a common goal of conserving 30% of land and sea area by 2030
- Well-conserved freshwater ecosystems can support 30 × 30 targets such as water quality, economic security, biodiversity, climate resilience, and outdoor access
- The 30 × 30 initiatives also present a valuable opportunity to better conserve freshwater ecosystems like rivers, lakes, and wetlands, and in so doing advance broader landscape-scale conservation
- Planning conservation at the watershed scale and evaluating conserved areas for a set of freshwater priorities will help 30 × 30 efforts leverage freshwater ecosystems to gain conservation benefits

Introduction

The next decade will be critical for slowing biodiversity loss and addressing climate change. Current efforts to advance biodiversity conservation focus largely on area-based targets, which aim to set aside a specific proportion of land and sea to achieve conservation goals. Scientific evidence suggests that at least 30% of land and sea area must be conserved by 2030 to reverse substantial biodiversity loss and mitigate the effects of climate change (Dinerstein et al. 2019). This goal, often referred to simply as "30 × 30", has been adopted by more than 50 governments around the world (Campaign for Nature 2021), including the US federal government (US Executive Order No 14008 2021) and many US state governments (e.g. California [CA] Executive Order N-82- 20). The mobilization of governments worldwide around the 30 × 30 concept creates an unprecedented opportunity to advance global conservation. However, policy makers still must determine how good intentions for biodiversity conservation and climate mitigation and adaptation can be converted into actionable plans.

We argue that centering freshwater ecosystems in 30 × 30 initiatives offers a unique opportunity to advance 30 × 30 objectives and to overcome persistent freshwater conservation challenges. Major goals of many 30 × 30 initiatives include supporting ecosystem services, biodiversity, and carbon storage. The conservation of freshwater systems can help meet each of these goals. For example, freshwater systems offer critical ecosystem services that enable agriculture, transportation, recreation, economic productivity, and drinking water systems. In addition, freshwater species compose 10% of global biodiversity (Strayer and Dudgeon 2010), and rivers and riparian habitat provide movement corridors for aquatic and terrestrial species to traverse landscapes (Hilty and Merenlender 2004; Krosby et al. 2018). Moreover, although covering a mere 5–8% of Earth's terrestrial surface area, freshwater wetlands store 20–30% of the world's soil carbon (Mitsch and Gosselink 2015; Nahlik and Fennessy 2016). However, despite the benefits of healthy freshwater systems, these environments are also acutely in need of additional conservation investment. Globally, freshwater systems endure impacts from development, fragmentation, pollution, biodiversity loss, invasive species, and climate change (Dudgeon 2019). In many situations, area-based conservation is inadequate for conserving freshwater systems. Area-based conservation often focuses solely on terrestrial areas, and many protected areas underrepresent freshwater habitats and are ill-positioned to protect large, interconnected waterways (e.g. Abell et al. 2017; Dudgeon 2019). As an effort that focuses on creating, improving, and connecting conservation areas, the 30 × 30 initiative provides an opportunity to refocus and reposition global conservation efforts to benefit freshwater systems and the habitats they support.

Here, we explore why and how freshwater ecosystems can be a central focus of 30 × 30 initiatives. Using the California 30 × 30 initiative as an example to explore 30 × 30 policy development and implementation related to freshwater ecosystems, we discuss how 30 ×

30 objectives could benefit from focusing on freshwater systems and how 30 × 30 can address persistent challenges in freshwater conservation, as well as priority actions for including freshwater ecosystems in the 30 × 30 framework.

30 × 30 background

In the US, the 30 × 30 initiative will largely rely on area-based conservation, meaning the protection of 30% of land area and coastal zones (Rosa and Malcom 2021). Parts of the landscape that contribute to 30 × 30 will likely include traditional protected areas (such as national parks or national monuments), along with other types of areas where conservation practices will be adopted (such as agricultural and forested working lands) (Rosa and Malcom 2021). The combination of these approaches gives 30 × 30 flexibility to initiate and improve conservation efforts in a variety of landscapes and land-use types. But with this flexibility comes the challenge of deciding where conservation efforts should be prioritized.

Another challenge confronting 30 × 30 is specifying what will be considered "conserved". Conservation goals are likely to be broadly defined in 30 × 30 policy documents (e.g.CA Executive Order N-82- 20) (Panel 1). Although broad goals may exist, in many cases the specifics of how to evaluate, achieve, and monitor 30 × 30 conservation goals are unclear, and policy makers at state and national levels must establish criteria for gauging whether conservation in a particular area meets standards for inclusion in 30 × 30.

Many 30 × 30 programs will likely employ a portfolio of management measures to address the primary challenges of prioritizing and defining conservation in a variety of land and sea ecosystems. As the portfolio of 30 × 30 conservation solutions is developed, we propose that freshwater ecosystems be used as focal ecosystems around which area-based conservation planning is centered (Panel 1; Figure 1). Importantly, both freshwater and terrestrial conservation planning are critical to the success of 30 × 30, and centering freshwater ecosystems in 30 × 30 need not replace sound terrestrial conservation strategies. However, protecting terrestrial habitats and species does not guarantee that freshwater systems are also protected, necessitating special consideration for freshwater systems (e.g. Abell et al. 2017; Leal et al. 2020).

How 30 × 30 can address persistent freshwater conservation challenges

Effective conservation of freshwater ecosystems requires unique strategies. Rivers, lakes, and wetlands exist in networks that span across terrestrial landscapes, and it is commonly assumed that freshwater ecosystems are implicitly protected through terrestrial conservation efforts (Thieme et al. 2016; Abell et al. 2017). As a result, area-based conservation plans rarely target freshwater particularities and needs specifically, instead treating freshwater systems as a subset of the terrestrial landscape. This approach is ineffective for protecting freshwater ecosystems, which depend on conservation of both a river network and its surrounding terrestrial drainage area (Leal et al. 2020). Indeed, recent studies demonstrate that land-based conservation initiatives that lack explicit freshwater priorities often deprioritize and contribute to the decline of freshwater habitats and species (Tickner et al. 2020). However, conservation efforts that focus on a freshwater network and the surrounding watershed have been shown to confer conservation benefits to both freshwater and terrestrial environments (Abell et al. 2010; Leal et al. 2020).

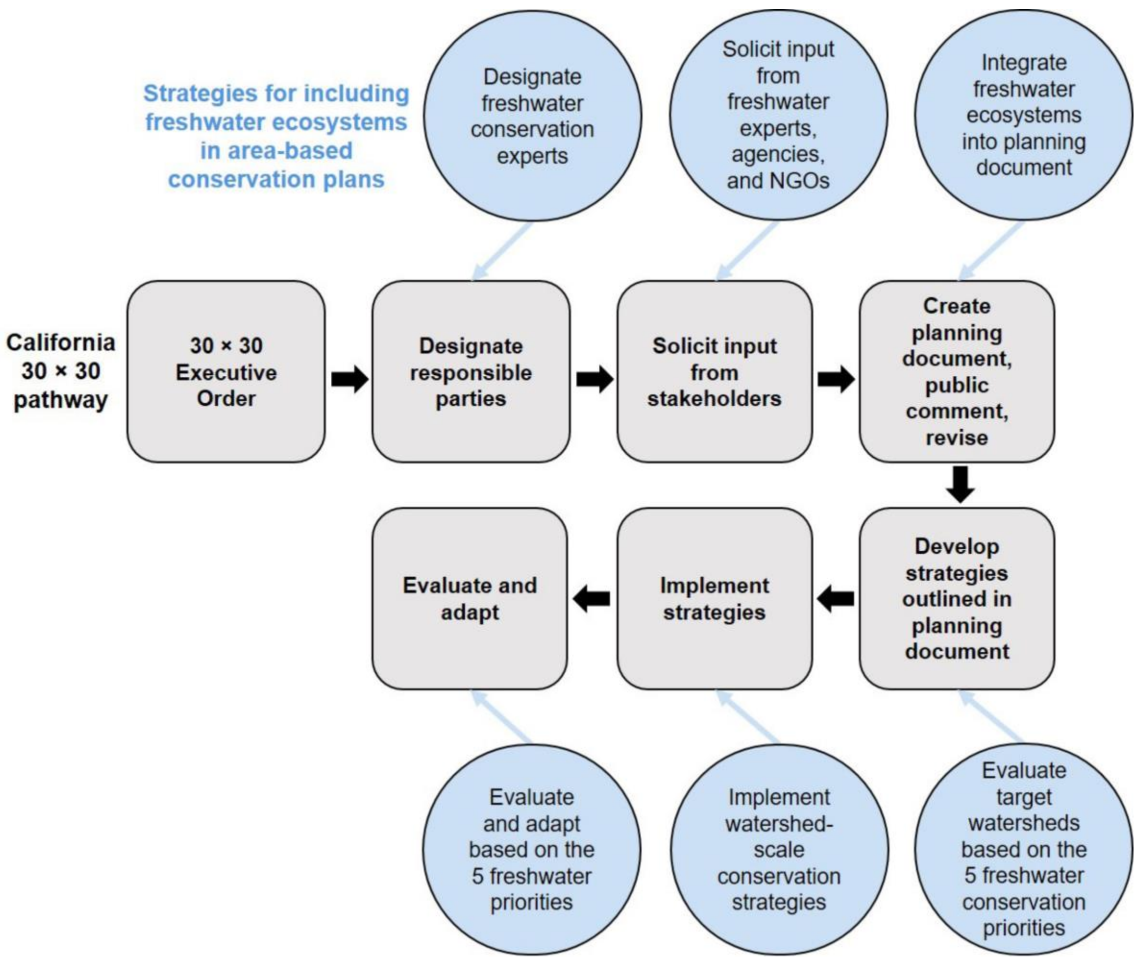

Figure 1. Stages of implementing a 30 × 30 conservation scheme using the California 30 × 30 initiative as an example (gray boxes). We emphasize ways to specifically include and address freshwater ecosystems in each step of the process (blue circles). The gray boxes and in particular the "Implement strategies" step of 30 × 30 involve a variety of conservation strategies that are described in greater detail in the California 30 × 30 Pathways document (www.californianature.ca.gov/pages/30x30).

To effectively include freshwater systems in area-based land conservation programs, 30 × 30 initiatives should proactively address several specific challenges that typically plague freshwater conservation efforts. First, a 30 × 30 initiative that effectively conserves freshwater systems must focus on conservation at the watershed scale. Disturbances that occur in one part of a watershed can easily result in downstream impacts throughout the full river network, and watershed-scale impacts such as habitat fragmentation, flow alteration, pollution, and landscape disturbances can affect entire river systems and the billions of people who rely on them. Land-based conservation programs often fail to address watershed-scale impacts because protected areas rarely include entire watersheds, and disturbances that happen outside a protected area can still affect waters within protected areas (Nel et al. 2009; Hermoso et al. 2015).

Second, effective 30 × 30 programs must include stipulations for specifically evaluating and protecting freshwater ecosystems within conserved lands. Even within protected areas, freshwater systems and waterways are not always well protected because human activities (such as building of dams, culverts, bridges, and roads) can directly alter stream networks and riverine processes (e.g. Thieme et al. 2020). Such alterations often negatively impact river ecosystems through habitat fragmentation, modified flow regimes, reduced riparian vegetation, increased sediment runoff, disrupted nutrient cycling, and transport of pollutants into waterways (Nel et al. 2009).
Third, 30 × 30 efforts must include both terrestrial and freshwater biodiversity targets. As noted above, land-based protected areas often do not explicitly target freshwater biodiversity, and freshwater and terrestrial biodiversity hotspots do not always overlap (Nel et al. 2009; Abell et al. 2017). For instance, in California, areas with the highest freshwater biodiversity generally occur outside of existing protected areas (Howard et al. 2018). To accommodate the frequent lack of overlap between freshwater and terrestrial biodiversity, 30 × 30 plans must explicitly consider biodiversity targets across multiple taxa and ecosystem types.

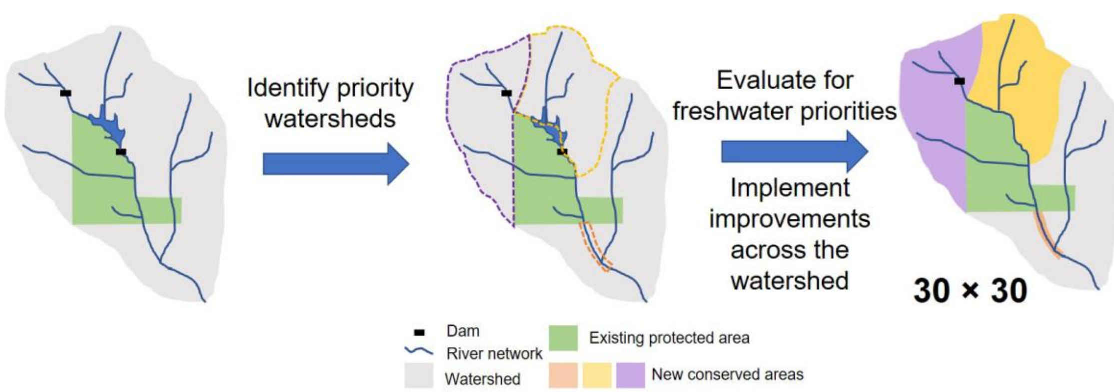

Figure 2. Two steps for incorporating fresh water into 30 × 30 conservation initiatives. First, area-based conservation planning should occur at the watershed scale. This includes identifying priority watersheds based on existing ecological integrity and/or restoration potential, and then implementing conservation strategies in those areas. Second, both newly conserved watersheds and existing protected areas should be evaluated for freshwater priorities (Table 1). This evaluation should be useful for identifying conservation improvements (such as dam removal, riparian corridor restoration, or other restoration activities) that should be implemented as part of inclusion in 30 × 30. These strategies will help guide 30 × 30 initiatives to focus on freshwater ecosystems.

Overall, 30 × 30 initiatives will not necessarily be effective for freshwater conservation simply because freshwater ecosystems happen to be included within conservation areas designed around and managed for terrestrial biodiversity. However, there are ways in which 30 × 30 can shift focus to center on freshwater ecosystems and address associated conservation challenges (Figure 1). In the next sections, we recommend ways to implement 30 × 30 that overcome traditional freshwater conservation challenges and meaningfully include the unique conservation needs of freshwater systems.

Incorporating freshwater conservation into 30 × 30

To incorporate freshwater conservation into 30 × 30 plans, we propose a two-step approach (Figure 2). First, we recommend that *areas for inclusion in 30 × 30 be identified and prioritized based on watershed boundaries*. Watershed-scale conservation protects stream networks as well as the surrounding terrestrial drainage area, and such areas can easily be mapped for inclusion at varying scales. Notably, a watershed-based

Figure 3. Freshwater ecosystem conservation under 30 × 30 should be based on five priorities, which should direct future conservation measures in both high-quality ecosystems and systems with high restoration potential. Priorities include connectivity, watershed disturbance, flow alteration, water quality, and biodiversity. For example, (a) Briones Dam reduces connectivity in Bear Creek, California (image credit: L Andrews); (b) wildfire in Hopland, California, creates widespread watershed disturbance (image credit: P Parker Shames); (c) poor water quality in Porter Creek, California, kills fish and reduces recreational opportunities (image credit: G Rossi); and (d) freshwater ecosystems support biodiversity in Klamath Lake, Oregon (image credit: J Shames).

conservation approach allows freshwater ecosystems to be protected in a manner consistent with a 30 × 30 area-based land conservation scheme.

Second, we suggest that *when targeting areas for conservation, practitioners should use five priorities to evaluate freshwater ecosystem status* (Table 1; Figure 3). We consider evaluating ecosystem status as a critical step in assessing both terrestrial and freshwater systems for inclusion in 30 × 30. The five priorities we outline below and in Table 1 will help practitioners assess whether current management strategies include, and are effective for protecting, freshwater systems and services (Table 1). If a particular area is included in 30 × 30 but does not reflect the five priorities for freshwater conservation, then 30 × 30 management plans should explicitly address how to improve freshwater conservation in that area.

Watershed-based conservation planning

Watersheds are natural area-based units around which 30 × 30 conservation planning can be structured (Figure 2). Watershed boundaries are naturally delineated areas that integrate across many ecological and social dimensions. Conservation at the watershed scale is critical because rivers occupy the lowest elevations on a landscape and are at the receiving end of both terrestrial and freshwater processes. Focusing on watersheds thereby broadens conservation initiatives to include both terrestrial environments as well as their downstream effects on freshwater systems. We strongly encourage 30 × 30 practitioners to use watersheds as convenient spatial units to structure conservation planning. Planning conservation efforts at a watershed scale can help identify how to connect existing protected areas, prioritize where to implement new conservation efforts, and involve stakeholders in the planning process (Howard et al. 2018; King et al. 2021).

Watersheds exist at many scales. Large watersheds can be broken down into smaller watersheds, which themselves can be further broken down into sub-watersheds. The scalable nature of watersheds is useful to 30 × 30 because it allows watershed-based conservation to occur at whatever scale is most relevant for a particular conservation effort. For example, 30 × 30 efforts in urban settings may include a small amount of land area, thereby focusing on small urban watersheds. On the other hand, 30 × 30 efforts involving conservation easements across large swaths of rural and agricultural land could focus on a larger watershed. In addition to protecting freshwater networks, protecting watersheds at different scales could be used to strategically support other conservation efforts. For instance, many terrestrial species use rivers and riparian areas as movement corridors (Hilty and Merenlender 2004), and conserving a small watershed could protect these corridors and enhance connectivity between existing habitat patches. Alternatively, focusing on a larger-scale watershed could help restore river network connectivity and enable long-distance migrations for freshwater species.

Table 1. Five freshwater conservation priorities and connections to the objectives of California 30 × 30

Priority	Definition	Importance	Issues	Connection to CA 30 × 30 objectives
Connectivity	Physical and biological connections between freshwater systems exist in four dimensions [1]. Freshwater connectivity occurs in longitudinal (e.g.along a river channel), lateral (e.g.between channel and floodplain), vertical (e.g.between groundwater and channels), and temporal (e.g.presence of water through time) dimensions.	The free movement of materials (e.g.nutrients, sediments, water) and organisms through a river network supports critical physical, chemical, and biological processes. Natural patterns of connectivity over space and time are critical to maintaining these processes and supporting freshwater species and habitats [2].	Dams and culverts that restrict movement of water, sediment, and organisms reduce longitudinal connectivity [2]. Wetland draining, floodplain development, and channel engineering reduce lateral connectivity [2]. Overdrawn aquifers reduce vertical connectivity [3]. Changes to a river channel, water abstractions, or changes in flow regime reduce temporal connectivity [4].	2,3,4
Watershed disturbance	Activities or processes within a drainage area that impact freshwater ecosystems throughout the watershed. Local disturbances include alterations to a riparian area or stream channel that impact part of a river [5].	River networks act as "endpoints" that integrate land and water processes throughout a watershed [6]. Protecting freshwater systems necessitates considering processes in the surrounding terrestrial environment.	Urban and agricultural development, mining, deforestation, and fire can alter flow, increase sediment and pollutant runoff, and impact groundwater. Loss of riparian vegetation can reduce shading and leaf litter, alter thermal and nutrient dynamics, and disrupt movement corridors [7].	1,2,3,4
Flow alteration	Changes in natural waterflow patterns, specifically changes in magnitude, frequency, duration, timing, and rate of change of streamflow [8].	River flow regimes are primary organizing forces in many freshwater systems. Flow regimes create physical habitat [9], govern life histories [10], and control invasive species [11].	Water diversions and dams that impede natural flow patterns alter the physical structure of rivers [9]. Changes to flow regimes disrupt biological patterns and life histories that are adapted to natural flow regimes [10].	2,3,4
Water quality	Quality as measured by physical (e.g.temperature, conductivity), chemical (e.g.pH, dissolved oxygen, nutrient concentration), and biological (e.g.bacteria, algae) factors [12].	Good water quality supports outdoor access and recreational activities; it is also a critical component of freshwater habitat and benefits native aquatic species [6].	Poor water quality can pose a risk for humans, degrade freshwater ecosystems, and endanger species that live in and depend on freshwater habitats [12].	1,2,5
Biodiversity	The number of species living in aquatic habitats, including algae, bacteria, fungi, plants, invertebrates, and vertebrates [6].	Freshwater systems contain 33% of vertebrate species and 10% of all species globally [13], and provide important habitat and movement corridors [14].	Freshwater habitats are vulnerable to invasive species, which can amplify the effects of disturbance, change native species behaviors, restructure food chains, and extirpate native species [12,15,16].	2,4

Notes: Numbers in the right-most column represent which of the five main objectives of the California 30 × 30 Executive Order (CA Executive Order N-82- 20) are met by each freshwater conservation priority. See Panel 1 for more details on California 30 × 30 objectives. [1] Ward (1989); [2] Ward and Stanford (1995); [3] Brunke and Gonser (1997); [4] Poff et al. (2007); [5] Abell et al. (2017); [6] Dudgeon et al. (2006); [7] Allan (2004); [8] Poff and Zimmerman (2010); [9] Wohl (2017); [10] Lytle and Poff (2004); [11] Kiernan et al. (2012); [12] Reid et al. (2019); [13] Strayer and Dudgeon (2010); [14] Hilty and Merenlender (2004); [15] Strayer (2010); [16] Gallardo et al. (2016).

To facilitate the use of watershed-scale conservation in 30 × 30, we recommend that conservation management practitioners at the local, regional, and national level identify priority watersheds. We view 30 × 30 as a mechanism to conserve high-value habitat and to support the restoration of degraded habitat. Therefore, the selection of priority watersheds should consider both existing ecological integrity (for example, pristine headwaters or areas within existing national parks) as well as restoration potential (for example, old hydropower dams that could be removed to restore connectivity). Apart from ecological integrity or restoration potential, watersheds might be prioritized because they contain diverse freshwater and terrestrial habitats or species, provide useful movement corridors for wide-ranging species, are of cultural importance, offer outdoor recreational opportunities, are vulnerable to climate change, and/or connect protected areas.

We envision that watersheds conserved under 30 × 30 could encompass a patchwork of conservation strategies that recognize local conditions, stakeholder values, and pre-existing conservation programs (e.g. Dudgeon et al. 2006). For example, parts of a conserved watershed might be included in a formal protected area, and other parts in working lands with conservation easements, tribally managed lands, urban areas with explicit freshwater and riparian management plans, or parts of a river that require dam removal or reoperation. In some areas, watersheds might already be well conserved, and these watersheds could also be incorporated into 30 × 30. A patchwork approach to watershed conservation will help negotiate trade-offs between protection and extractive uses of freshwater systems. Although freshwater conservation ultimately maintains the capacity of an ecosystem to provide services, trade-offs must be made between conservation and demands for water resources, and 30 × 30 must seek to balance resource extraction with the benefits of protecting ecosystems.

Freshwater priorities for evaluating existing and proposed protected areas

We recommend that practitioners use five freshwater priorities –connectivity, watershed disturbance, flow alteration, water quality, and biodiversity –to evaluate existing protected areas as well as areas that will be newly conserved under 30 × 30 (Table 1; Figure 3). These priorities should be evaluated in high-quality, intact ecosystems, as well as in systems with high restoration potential. Assessments of these freshwater priorities should occur alongside evaluations of conservation priorities for terrestrial and coastal ecosystems, and the combined results of these appraisals should guide 30 × 30 plans. In Table 1, we briefly define the five priorities, describe why each priority is important to freshwater conservation, discuss common conservation issues that fall under that priority, and connect each priority to specific goals from the California 30 × 30 initiative (Table 1). In addition, examples of how to measure and evaluate ecosystems for each priority are provided in Table S1.

Conclusion

The numerous 30 × 30 area-based efforts currently underway can achieve far-reaching results by leveraging and centering conservation actions on freshwater ecosystems. 30 × 30 is a broad set of initiatives that must take many conservation priorities into account, and freshwater ecosystems will certainly not be the only conservation focus of 30 × 30. However, we suggest that specific attention to freshwater ecosystems using a watershed-based approach will advance 30 × 30 goals and offer better protection of both terrestrial and freshwater systems (Figure 1). We present specific examples of the benefits of and opportunities for watershed-scale conservation using California as a case study (Panel 2), and we believe that comparable conservation programs that center on freshwater systems could reap similar benefits for the California 30 × 30 initiative. Conserved freshwater systems weave together multi-use landscapes, provide connectivity and habitat for aquatic and terrestrial species, integrate processes of upstream landscapes, and support a wide variety of ecosystem services including water quality, crop irrigation, biodiversity protection, climate resilience, and outdoor access. Therefore, the conservation of freshwater ecosystems should be an explicit focus of 30 × 30 initiatives.

Panel 1: Freshwater ecosystems advance 30 × 30 objectives: examples from California

The stated goals of the California 30 × 30 initiative demonstrate how explicitly centering freshwater ecosystems could support broad objectives of the 30 × 30 movement. The California 30 × 30 Executive Order was established in October 2020 (CA Executive Order N-82- 20) and includes five primary objectives to be accomplished through new conservation programs and acquisitions: (1) to safeguard California's economic sustainability and food security; (2) to protect and restore biodiversity; (3) to enable conservation on a broad range of landscapes; (4) to build climate resilience; and (5) to expand equitable outdoor access and recreation. Many types of environments, including terrestrial, coastal, marine, and freshwater systems, must be included to achieve these goals, but because freshwater systems are highly vulnerable, here we specifically focus on the benefits of fresh water.

Economic sustainability and food security: Much of California's three-trillion- dollar economy depends on access to water, and intact freshwater ecosystems maintain water quality (Hanak et al. 2012). Freshwater ecosystems can retain water during drought and minimize flood events (Lund et al. 2018). Freshwater fish support food security and culturally important foods. For example, declining populations of coho salmon (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) have resulted in negative socioeconomic, health, and cultural impacts for Indigenous peoples in northern California (e.g. Stercho 2006; Willette et al. 2016).

Biodiversity: Freshwater species diversity is a critical component of California's overall biodiversity, and freshwater systems are essential for meeting 30 × 30 biodiversity goals (Moyle 2002). Of California's 927 endemic freshwater species, 90% are vulnerable to extinction, and these species rely on habitat integrity such as flow regime and habitat complexity (Lytle and Poff 2004; Howard et al. 2015).

Broad range of landscapes: River systems tie landscapes together by flowing through multi-use lands (Abell et al. 2017; King et al. 2021). Watersheds define landscape boundaries in geologically and ecologically meaningful ways, and can be used to demonstrate how neighboring land users are linked by processes affecting water supply and quality (King et al. 2021).

Climate resilience: Inland freshwater wetlands store large amounts of carbon (Mitsch and Gosselink 2015; Nahlik and Fennessy 2016). Retaining soil moisture in waterways and groundwater systems can help buffer against catastrophic fire (Warter et al. 2021). Connected river networks provide large-scale movement corridors, which allow terrestrial and aquatic species to relocate as temperature regimes shift due to climate change (Krosby et al. 2018).

Outdoor access: Rivers support outdoor recreation activities like fishing, boating, wildlife viewing, and swimming. In urban areas, stream habitat enhancement can increase greenspace access for marginalized communities (Villamagna et al. 2014).

Panel 2. Opportunities for watershed-scale conservation: examples from California

Examples from California illustrate that multi-benefit freshwater conservation is achievable. For instance, the Yolo Bypass in northern California provides societal and ecological benefits on multiple scales. As an engineered floodplain in the Sacramento River watershed, the Bypass reduces flood risk and also creates agricultural land; serves as a wetland refuge for migrating waterfowl; provides habitat for native fish; and offers recreational opportunities for hunters, birders, and other community members. The Bypass is particularly valuable habitat for threatened splittail (*Pogonichthys macrolepidotus*) and Chinook salmon (*Oncorhynchus tshawytscha*), which often use associated flooded rice fields (Sommer et al. 2001). The Bypass exemplifies how large-scale watershed-based conservation strategies can help achieve 30 × 30 goals, as well as improve protections for freshwater habitats and species. Building and supporting programs that achieve multiple objectives could be a major strength of 30 × 30 initiatives around the world.

The Klamath River in northern California and southern Oregon provides an example of collaboration and conservation at a watershed scale that we envision could strengthen 30

× 30 initiatives. Dams along the Klamath River alter flow regimes, water temperatures, sediment movement, and salmonid disease prevalence, all of which have contributed to a 95% reduction in spring Chinook salmon populations from historical levels (Nehlsen et al. 1991). In response to declining river health, collaborative governance efforts that involve tribal, state, federal, and private interests have resulted in a plan to remove dams (Klamath River Renewal Corporation 2020). Removing four dams on the Klamath River will restore river connectivity and functional flow regimes, benefit salmonid populations, improve water quality, and address environmental justice issues. The dam removal process on the Klamath River highlights the importance of leadership and collaboration between tribes, local conservation groups, agencies, and state and national policy makers (e.g. Diver et al. 2022). Such collaboration could be an example for watershed-scale conservation as part of 30 × 30 initiatives.

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Supplementary Information

Table S1. Recommended freshwater conservation priorities and suggestions for how to measure each priority to evaluate areas for inclusion in 30 × 30

Priority	Examples of how to measure
Connectivity	• Presence and passability of longitudinal barriers (e.g. dams, culverts, and bridges) and lateral barriers (e.g. levees, artificial and buried channel structures) • Channel and floodplain morphology; degree of channel incision • Level of development within a floodplain that prevents river–floodplain connectivity • Frequency and magnitude of connection to groundwater sources • Aquifer levels • Fragmentation indices
Watershed disturbance	• Presence of specific watershed modifications (e.g. development, deforestation, mining, unnatural fire) • Changes in watershed land use or land cover • Changes in watershed Normalized Difference Vegetation Index • Loss of natural riparian vegetation • Amount of upstream protected watershed area
Flow alteration	• Presence of flow barriers (e.g. dams, culverts) • Impound runoff index • Change in unit hydrograph • Degree of annual flow regulation in impounded rivers • Inflation/deflation • Baseflow loss • Timing of flow regime components relative to species' life histories
Water quality	• Point-source pollution • Changes in dissolved oxygen • Presence and impacts of agricultural or urban runoff (e.g. high concentrations of nutrients, pesticides, or heavy metals) • Presence and impacts of livestock runoff (e.g. high nutrient concentrations) • Changes in sediment transport processes (e.g. increased turbidity or sediment load, sediment loss/winnowing) • Presence of harmful algal blooms • Changes in temperature dynamics
Biodiversity	• Native species richness • Native species status (e.g. unlisted, threatened, endangered) • Level of endemism • Invasive species presence • Benthic macroinvertebrate indices

Transition

State-wide, nation-wide, or global conservation of freshwater ecosystems as discussed in chapter one is not always achievable. In multi-use landscapes, where human infrastructure is essential and deeply ingrained, large-scale watershed conservation or restoration efforts may be impossible to implement. In lieu of comprehensive freshwater conservation, small-scale local restoration efforts can effectively restore critical elements of an ecosystem and support important aquatic species. In chapter two, I explore how a hyper-local restoration project successfully restored essential habitat structures that helped juvenile salmonid populations survive despite watershed-wide water quality issues. This chapter highlights how local restoration projects can not only help threatened species persist but can also complement large-scale conservation efforts like dam removal.

Chapter 2

Restored off-channel pond habitats create thermal regime diversity and refuges within a Mediterranean climate watershed

This chapter has been previously published and is included here with permission from co-authors.

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Abstract

Cool-water habitats provide increasingly vital refuges for cold-water fish living on the margins of their historical ranges; consequently, efforts to enhance or create cool-water habitat are becoming a major focus of river restoration practices. However, the effectiveness of restoration projects for providing thermal refuge and creating diverse temperature regimes at the watershed scale remains unclear. In the Klamath River in northern California, the Karuk Tribe Fisheries Program, the Mid-Klamath Watershed Council, and the U.S. Forest Service constructed a series of off-channel ponds that recreate floodplain habitat and support juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*O. mykiss*) along the Klamath River and its tributaries. We instrumented these ponds and applied multivariate autoregressive time series models of fine-scale temperature data from ponds, tributaries, and the mainstem Klamath River to assess how off-channel ponds contributed to thermal regime diversity and thermal refuge habitat in the Klamath riverscape. Our analysis demonstrated that ponds provide diverse thermal habitats that are significantly cooler than creek or mainstem river habitats, even during severe drought. Wavelet analysis of long-term (10 years) temperature data indicated that thermal buffering (i.e. dampening of diel variation) increased over time but was disrupted by drought conditions in 2021. Our analysis demonstrates that in certain situations, human-made off channel ponds can increase thermal diversity in modified riverscapes even during drought conditions, potentially benefiting floodplain-dependent cold-water species. Restoration actions that create and maintain thermal regime diversity and thermal refuges will become an essential tool to conserve biodiversity in climate-sensitive watersheds.

Key words

drought, habitat diversity, river restoration, salmonids, thermal refuge, thermal regimes, time series modeling

Implications for practice

- River floodplain restoration projects that create thermal refuge can help maintain suitably cool habitat in the face of climate extremes like drought and heat waves.
- Even during a severe drought, restored off-channel ponds in the Klamath River maintained diverse thermal regimes and created thermal refuge habitats that likely benefited cold-water fishes.
- Building off-channel ponds connected to river mainstems is a relatively quick way of creating thermal habitat diversity in a watershed.
- As climate change and drought increase the importance of thermal refuge habitats in riverscapes around the world, managing thermal regimes will be increasingly critical to the integrity of river ecosystems and to river restoration efforts.

Introduction

Restoring river habitat to support healthy fisheries, ecosystems, and human communities is a global conservation priority, especially as regional climates change (Palmer et al. 2008). River ecosystems are particularly sensitive to climate change, and studies have identified significant climate-related increases in water temperature and thermal heterogeneity across riverscapes (e.g. Isaak et al. 2012). Changing thermal regimes can have major impacts on aquatic species, which are highly sensitive to large changes in water temperature due to climate or other factors (e.g. Woodward et al. 2010; Sullivan et al. 2021). As irregular climate patterns such as extreme drought and variable temperatures become more common (Swain et al. 2018), understanding how watershed thermal regimes are poised to change is an increasingly important aspect of planning river conservation and restoration actions (Olden and Naiman 2010; Arismendi et al. 2013; Steel et al. 2017).

To address the thermal requirements of aquatic species in a changing climate, thermal refuges are an increasingly important riverscape feature. A freshwater thermal refuge is a spatiotemporally distinct habitat patch that organisms use to avoid stressful temperatures elsewhere in the river (Sullivan et al. 2021). In particular, cool-water refuges are critical for populations of aquatic species that exist in marginal habitats and frequently experience heat stress (Ebersole et al. 2020; Armstrong et al. 2021). Cool-water thermal refuges can form in many ways within a river system: tributary confluences (e.g. Brewitt et al. 2017), groundwater upwellings (e.g. Bilby 1984; Dugdale et al. 2015), deep pools (e.g. Tate et al. 2007), and off-channel floodplain areas (e.g. Dugdale et al. 2013) can all provide cooler habitats compared to the predominant temperature in the mainstem river (Sullivan et al. 2021). Cold-water fish such as salmonids especially benefit from cool-water refuges. Studies on both Pacific salmonids (*Oncorhynchus* spp.) and Atlantic salmon (*Salmo salar*) have shown that access to cool-water refuges allows salmonids to avoid stressful or lethal water temperatures during summer heat waves (Dugdale et al. 2015; Hess et al. 2016). Coho salmon and steelhead with access to coolwater refuges have been shown to forage more efficiently by reducing heat stress in cooler areas and foraging in warmer, more prey-dense parts of the watershed (Brewitt et al. 2017). In northern California, thermal refuges have been shown to reduce exposure of juvenile coho salmon to the myxozoan parasite, *Ceratonova shasta*, because cooler areas have fewer parasitic spores and alleviate disease effects (Chiaramonte et al. 2016). Cool-water refuges in the Klamath watershed have also been shown to reduce lamprey wounds on redband trout (Ortega et al. 2023). Understanding thermal refuge dynamics in rivers that support coldwater fish is critical for conserving, restoring, and managing these ecosystems.

A key challenge to managing thermal refuges is understanding the timing and spatial distribution of thermal regimes throughout a riverscape. Coldwater fishes, for example can thrive in riverscapes with diverse thermal regimes that create areas with warmer water and more food availability, and areas with cooler water and less food but that act as refuges from high temperatures, floods, droughts, disease, and invasive species (Brewitt et al. 2017; Ebersole et al. 2020). Historically, thermal refuge habitats in stream systems were created by complex floodplain features such as oxbow lakes, springs, seeps, and seasonal flooding (Sullivan et al. 2021). Thermal regimes in such floodplain habitats are often dictated by geomorphic and hydrologic context, and temperatures in floodplain waters can vary greatly depending on elevation, climate, groundwater influence, water level, and connectivity to other waterbodies (Arscott et al. 2001). In particular, connections between groundwater and floodplain habitats are complex, and variability in the temperature and flow of groundwater can create thermal mosaics across habitats (Arrigoni et al. 2008). Connections to groundwater can also influence the dissolved oxygen (DO) concentration in water: depending on the source, groundwater that creates cooler thermal habitats can have high or low DO concentrations, which influences the quality of floodplain habitat for fish (Larsen and Woelfle-Erskine 2018). In many cases, channelization, river regulation, riverbank development, agriculture, and water diversions have damaged river–floodplain connections, and these habitats are often no longer accessible to fish (Bond et al. 2019).

In certain contexts, restoration efforts that focus on reestablishing connections between rivers and floodplains and reactivating floodplains as thermal refuges can help restore thermal refuge options in degraded watersheds (Steel et al. 2017). This approach is exemplified in the Klamath River watershed in northern California. To create refuge habitat for juvenile coho (*Oncorhynchus kisutch*) and steelhead (*O. mykiss*), the Karuk Tribe Fisheries Program (KFP), in collaboration with the U.S. Forest Service and the Mid-Klamath Watershed Council (MKWC), collaborated to construct a series of human-made off-channel ponds throughout the mid-Klamath (Mid Klamath Watershed Council 2014; 2020; 2022; Wickman et al. 2020). These off-channel ponds connect to shallow groundwater within the floodplain (MKWC 2014, 2020, 2022; Wickman et al. 2020). Groundwater upwelling into the ponds is thought to sustain these ponds as cool-water refuges during hotter periods of the summer. These ponds are especially important cool-water habitat during extreme drought, when fish need refuge from high water temperatures caused by low flow and extreme air temperatures (Maher et al. 2019). Juvenile coho salmon in the Klamath River begin to seek cooler waters at around 19^{o}C, which occurs with increasing frequency in the Klamath River during summer, making the ponds a potentially critical refuge habitat (Sutton and Soto 2012; Asarian et al. 2020). Efforts to restore, create, or maintain cool-water refuge habitat are crucial restoration actions in systems like the Klamath River that support cold-water fishes. However, it is unclear whether localized restoration projects like off-channel ponds create a diverse selection of thermal refuges at a riverscape scale, particularly during stressful periods such as droughts. Additionally, few studies examine the long-term outcomes of thermal habitat restoration in a riverscape throughout recurring periods of drought. In this study, we analyze a decade of temperature data to explore thermal refuges and thermal regime diversity created by off-channel ponds in the mid-Klamath riverscape. We also measured DO in the off-channel ponds as a possible source of stress limiting refuge potential. We hypothesized that off-channel ponds would create cool thermal refuges because of groundwater connections, and that off-channel ponds would contribute to thermal regime diversity by adding unique regimes to the riverscape. Specifically, we predicted that: (1) off-channel ponds would have significantly different thermal regimes compared to creeks and the mainstem river; (2) off-channel ponds would provide cooler and more thermally stable habitats compared to creek and river habitats on daily and seasonal scales; and (3) thermal regime stability in ponds would increase over time. Testing these predictions may help reveal the potential and limitations of off-channel ponds for creating thermal refuges in degraded watersheds, especially under changing climate conditions.

Citation	Findings relevant to this study	Ponds/creeks included in this study
Witmore 2014)	• Evaluated movement patterns of juvenile coho in and out of ponds. • Juvenile coho growth and retention depends on pond-specific characteristics.	Alexander Pond
Krall 2016	• Assessed accessibility, habitat conditions, food availability, and salmon density in ponds. • Recorded high salmon occupancy in ponds in the summer. • Estimated salmon growth rates in ponds.	Alexander Pond, Stender Pond, Lower Seiad Pond, May Pond
Gorman 2016	• Used PIT tag data to track salmon rearing in off-channel ponds and non-natal tributaries.	May Pond, Seiad Creek, Horse Creek
Faukner et al. 2019	• Described numbers of juvenile coho PIT tagged in pond or creek locations in the mid-Klamath river watershed. • Fish tagged in off-channel ponds have low detection rates.	Horse Creek, Seiad Creek, Alexander Pond, Stender Pond, May Pond, Durazo Pond
Maher et al. 2019	• Evaluated temperature, DO, and fish presence in Fish Gulch pond and Horse Creek. • Recorded acceptable temperature and DO levels for juvenile coho and steelhead.	Fish Gulch Pond, Horse Creek
MKWC 2014	• Monitoring report detailing fish counts and temperature dynamics between 2010 and 2014.	Alexander Pond
Wickman et al. 2020	• Monitoring report detailing fish counts and temperature dynamics between 2014 and 2019.	Durazo Pond
MKWC 2022	• Monitoring report detailing fish counts and temperature dynamics between 2016 and 2022.	Goodman Pond
MKWC 2020	• Monitoring report detailing fish counts and temperature dynamics between 2014 and 2019.	May Pond

Table 1. Evidence of salmonid use in off-channel ponds. Upper Lawrence and Lower Lawrence Ponds are the only ponds not included here.

Methods

Study site

The Klamath River begins at Klamath Lake in southern Oregon and flows southwest through northern California to the Pacific Ocean. The watershed is heavily impacted by hydropower dams, agricultural water diversions, megafires, and poor water quality (including high water temperatures) that have devastated populations of native salmonids (Asarian et al. 2020; Sarna-Wojcicki et al. 2019). To create cool-water refuge habitat, the KFP, National Forest Service, and MKWC have constructed a variety of off-channel, groundwater-fed ponds that provide habitat for juvenile coho salmon and steelhead (see summary of previous research and findings on these systems in Table 1). Our study focused on nine human-made ponds constructed between 2010 and 2019 in the mid-Klamath watershed. The ponds are located on Horse Creek and Seiad Creek (Figure 1), which are both tributaries to the Klamath River. Goodman Pond is adjacent to Middle Creek, a tributary of Horse Creek. Ponds are human-made and are fed mainly by groundwater before flowing into the creek. Ponds range between 0.7 and 1.1 m average water depth during the summer but sustain higher water levels during the wet season (see Table 1).

As newly constructed habitats, these off-channel ponds were excavated with backhoes. They were sparsely vegetated at the start, and had large woody debris purposefully placed to enhance habitat heterogeneity. After construction, banks were stabilized with native

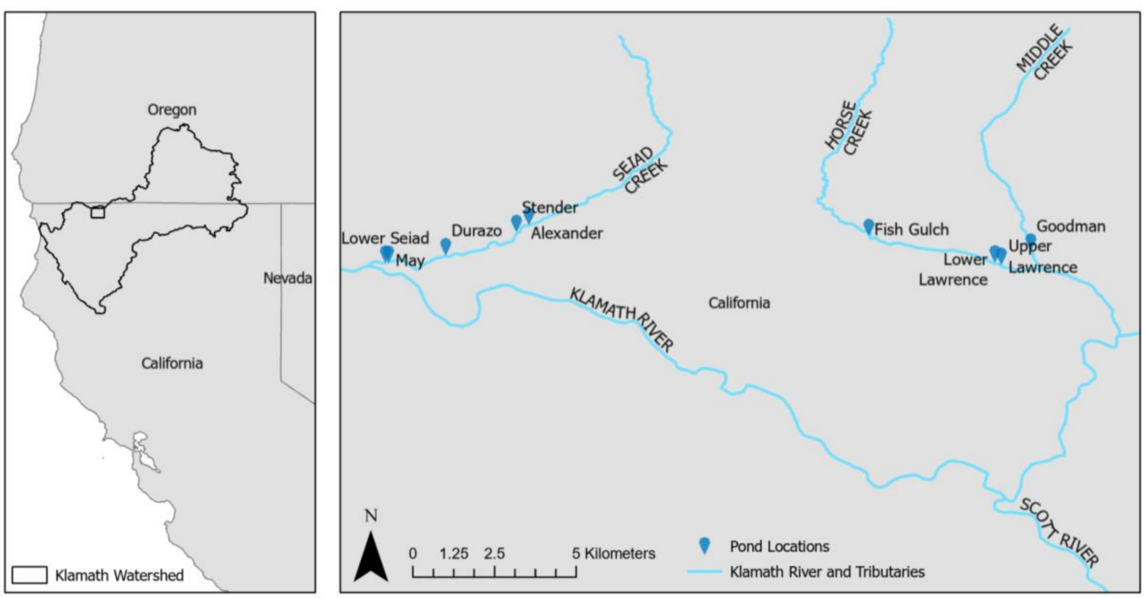

Figure 1: Seiad Creek and Horse Creek are neighboring watersheds feeding the Klamath River in northern California, United States. This study included five ponds on Seiad Creek (Alexander, Stender, Durazo, Lower Seiad, and May) and four ponds on Horse Creek (Fish Gulch, Goodman, Upper Lawrence, and Lower Lawrence). Goodman Pond is on Middle Creek, a tributary of Horse Creek.

grass seeding and weed-free straw, and additional native riparian plants were planted and tended at some ponds (MKWC 2014, 2020, 2022; Wickman et al. 2020). Aquatic vegetation was left to develop as time went on. As a result, ponds initially received full sun exposure, and the development and ongoing restoration plantings of riparian canopy cover and aquatic vegetation could influence thermal stability in these ponds over time.

Data collection

We examined water temperature and air temperature regimes in the Mid-Klamath riverscape using temperature sensors and data from long-term monitoring programs. These datasets included several habitat types: off-channel ponds, creeks, and the mainstem Klamath River. Importantly, much of our data collection took place during the severe drought of 2020–2021, the second driest year on record in California (California Department of Water Resources 2021).

In July 2020, we deployed 30 temperature sensors (HOBO MX2201, Onset Corporation, Bourne, Massachusetts, U.S.A.) programmed to measure temperature every 15 minutes in ponds and creeks. We placed one to four sensors in each pond to capture local-scale temperature variation. Sensors were installed at approximately one-third the water depth (at time of placement), except for two sensors in Goodman Pond, one in Upper Lawrence Pond, and one in Lower Lawrence Pond, where sensors were placed on the bottom of the pond. Sensors were placed near the outlet, around the sides, and as close to the center of the pond as possible. We chose these locations to capture within pond variation in thermal habitat, to maximize access and safety, and to facilitate future monitoring. We also placed one sensor in the creek upstream of the outlet of each pond. We placed sensors between 7 and 13 July, 2020 and read them out between 11 and 13 July, 2021. We removed incomplete sensor time series ($n = 6$ pond sensors and $n = 3$ creek sensors) resulting either from sensor malfunction or sensors that were no longer submerged because of drought-related decreases in water level. In ponds and creeks with multiple sensors, we averaged remaining sensor readings to obtain an average time series per site. In the five ponds with only one sensor, we used that sensor's time series. We averaged sensor readings per site because sensors in the same site captured very similar patterns (see Table S1; Figure S1). We calculated and modeled daily temperature means (instead of using sub-daily data) to avoid having to account for diel periodicity in the multivariate autoregressive model (MAR) models (Hampton et al. 2013; Holmes et al. 2023), which would have made these models unnecessarily complex.

Water levels in the pond fluctuated throughout the year, leading to different depths for the sensors throughout the study period, which could influence temperatures. We removed from analysis sensors that were completely out of the water (thus, recording air temperature rather than water temperature) because of depth fluctuations. To understand how well the remaining sensors represent thermal habitats in the ponds, we took post hoc temperature depth profiles in June 2023 at several locations in each pond (Figure S2). We found that the location and depth of our long-term temperature sensors placed in 2020 were generally representative of temperatures found in the 2023 depth profiles. To further quantify any error that was introduced by fluctuating water depths throughout the year,

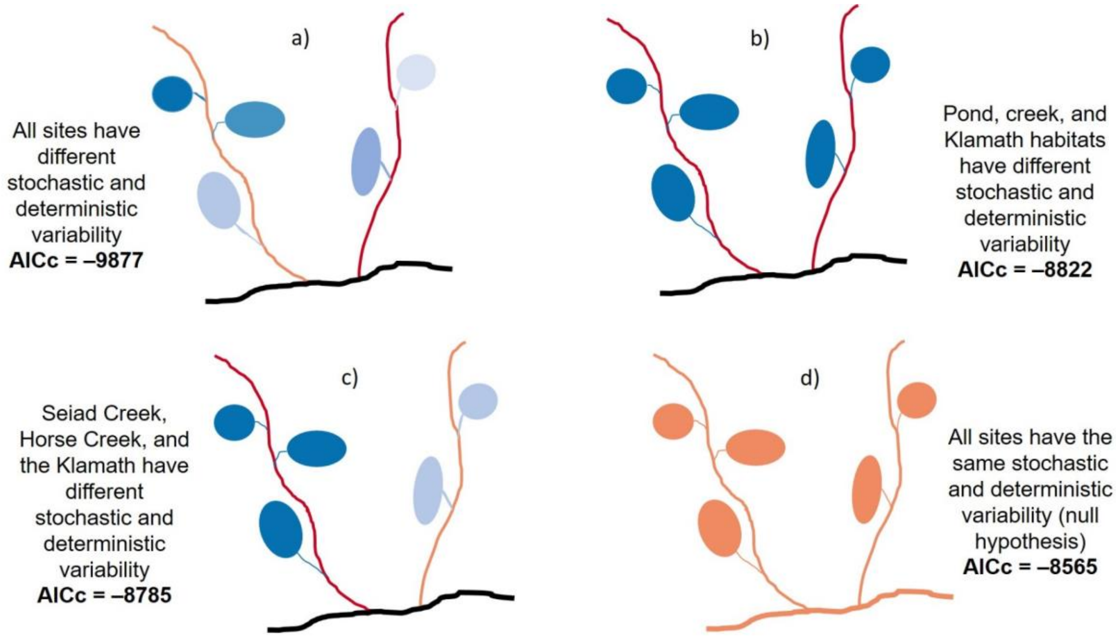

Figure 2: Four hypotheses representing different levels of thermal diversity in the riverscape. In the multivariate autoregressive (MAR) model, we allowed for different levels of complexity in stochastic variability (Q, variation due to random chance) and deterministic variability (C, variation due to changes in air temperature), ranging from a complex array of site-specific regimes (a) to a simple, watershed-wide thermal regime (d). Colors represent different configurations of deterministic and stochastic variability in ponds, creeks, and the mainstem river. We compared the four models using Akaike's Information Criterion corrected for small sample size (AICc), in which the best supported model has the lowest AICc score.

we compared sensors at different depths for sites with more than one sensor. We found that sensors at different depths captured very similar patterns (Table S1; Figure S1), suggesting that even if water depth fluctuated, sensor readings likely stayed relatively consistent.

Klamath River temperature data were collected by the Karuk Tribe and accessed with permission from the Karuk Tribe Water Quality Department (accessed 27 Sep 2022). We used data between May 2020 and February 2021. We used a combination of data readings from the Seiad Valley station as well as interpolated data using a linear regression from the Orleans station when Seiad Valley data was unavailable (5.5% of Seiad Valley data was interpolated). Additionally, we obtained air temperature time series from the National Oceanic and Atmospheric Administration's Climate Data Online database for Siskiyou County, California (NOAA 2020). We used the Slater Butte air sensor, located relatively close (13 km) to our study sites in Seiad Creek. Although these two sites differ in elevation (1423 vs. 430 m), we expected fluctuations in air temperature at these two locations to be correlated, and we note that our models quantify the effects of fluctuations around the mean rather than absolute values of air temperature (see next Section 2.3). Also, we measured DO in a single location in each pond over several days in July 2020 (Figure S3), and we took post hoc DO and temperature depth profiles in each pond in June 2023 (Figure S2). Finally, we analyzed historical temperature data from temperature sensors in Alexander and Stender Ponds, provided by MKWC. These are the two oldest ponds in the study and were constructed in 2010, and temperature data were collected hourly in these ponds from 2010 to 2021 via similar sensors to those we deployed (HOBO U22, Onset Corporation, Bourne, Massachusetts, U.S.A.). Each pond had a single HOBO U22 sensor that was placed in an accessible location near large woody debris on the side of the pond and suspended approximately one-third the depth of the pond.

Thermal diversity

To analyze variation in thermal regimes across the riverscape, we used MAR models. The MAR model is a time series model that takes advantage of temporal correlation in environmental variables to estimate the effects of a particular driver, while also accounting for stochastic process error (Ives et al. 2003; Ruhí et al. 2015). MAR models can also incorporate environmental covariate data, which allows us to quantify the effects of external drivers on the process of interest (in our case, variation in water temperature). A MAR model in the matrix form can be expressed as follows:

$$X_t = BX_{t-1} + Cc_{t-1} + w_t, \text{ where } w_t \sim MVN(0, Q) \quad (1)$$

where temperature at a given day (X_t) is a function of temperature the previous day (X_{t_1}) plus sensitivity to a covariate, here variation in air temperature (Cc_{t_1}); and process error (w_t). As a covariate (c_{t_1}), we used a time series of air temperature with a 1-day time lag, after examining support for other lags (results not shown); and the C matrix captured site-specific sensitivity to air temperature. In turn, process error (w_t) was drawn from a multivariate normal (MVN) distribution, with mean zero and covariance matrix Q. In our case, Q captured stochasticity in water temperature (i.e. temporal variation in water temperature that was unrelated to air temperature). B is an interaction matrix that can model the effect of each state on itself (diagonal parameters) and on each other (off-diagonal parameters). In our case, we set off-diagonal parameters to zero (as we did not expect sites to interact with each other) and estimated the diagonal parameters, often used to capture "density-dependence" in population processes, or pull-back to mean. When analyzing a thermal regime, these B parameters capture how fast temperature goes back to the mean after an anomalously high or low value (in our case, a warmer- or colder-than-average day).

To test our first prediction that off-channel ponds have significantly different thermal regimes compared to creeks and the mainstem, we developed four MAR model hypotheses that represent different levels of complexity in thermal regimes (as in Leathers et al. 2022). Each hypothesis was tested by manipulating the matrices of the MAR model, capturing stochastic or "unexplained" variation (Q matrix), and deterministic or covariate-explained variation (C matrix). This strategy allowed modeling mean daily temperatures among pond, creek, and river habitats in different ways (Figure 2).

The first hypothesis was that all sites had different levels of stochastic and deterministic variability (i.e. as many thermal regimes as sites). The second hypothesis was that each habitat type (pond, creek, and river) had some typical level of stochastic and

Hypothesis	Model Number	AICc
All states have different levels of stochastic (Q) and deterministic (C) variability	Model 1	-9877
Each habitat type (creeks, ponds, Klamath) have different levels of stochastic (Q) and deterministic (C) variability	Model 2	-8822
Each watershed (Horse Creek, Seiad Creek, and Mainstem Klamath) have different levels of stochastic (Q) and deterministic (C) variability	Model 3	-8785
All states have same levels of stochastic (Q) and deterministic (C) variability	Model 4	-8565

Table 2: MAR model hypotheses and AICc values. Model 1 was the best supported model with the lowest AICc score.

deterministic variability, but sites within the same habitat type did not differ from each other. The third hypothesis predicted that stochastic and deterministic variability depended on the watershed (Horse Creek vs. Seiad Creek vs. Klamath River), but not the specific site or habitat type. The fourth hypothesis predicted that all sites would have the same level of stochastic and deterministic variability (i.e. a single, watershed-level thermal regime). We used Akaike's information criterion corrected for small sample size (AICc) to compare support for the different hypotheses. All data and covariate data was z-scored, and model outputs were examined for normality and autocorrelation of residuals via the autocorrelation function. We used the MARSS package version 3.11.3 (Holmes et al. 2023) in R (R Development Core Team 2024).

Thermal buffering

To quantify thermal buffering of ponds (relative to creeks), we compared daily maximum temperatures (averaged across all sensors in a site, see Table S1; Figure S1) in each pond and creek during the three hottest months of 2020 (15 July–15 September), and then ran a one-way analysis of variance (ANOVA) of temperature as a function of site. We repeated the same process for the winter, focusing on daily minimum temperatures during the three coldest months (15 December, 2020–15 February, 2021). We assured that model residuals met assumptions of normality and homogeneity of variances.

We also assessed daily thermal buffering capacity of ponds and creeks by calculating the coefficient of variation (CV) for each day, using 15-minute temperature data. We then averaged daily CVs for each site over the yearlong study period. We used mean CV values to calculate the ratio of creek to pond CV for each pond/tributary pairing. If the creek:pond CV ratio was equal to or less than 1, that suggested no significant buffering took place. If the ratio was greater than 1, we considered the pond to "buffer" thermal fluctuations compared to the creek.

Thermal stabilization over time

We used wavelet analysis to examine thermal regimes in the frequency and time domains, and to determine whether some scales of variation strengthened over time. Wavelet analysis is useful because it localizes the contribution of each frequency to a given time series, and is not sensitive to the assumption of stationarity (Torrence and Compo 1998). Although the wavelet method does not require pre-specifying a frequency of interest, here we focused on temperature variation at diel (24 hours) and seasonal scales (12 months), and asked whether diel and seasonal variation changed over the years. We interpolated missing values in the historical temperature datasets for Alexander and Stender Ponds (3.3 and 3.9% of days, respectively) via an autoregressive integrated moving average model (ARIMA) and a Kalman filter. An ARIMA model is generally expressed as ARIMA(p, d, q), where p is the order of the autoregressive model, that is the dependence of the model on prior values; d is the order of non-seasonal differences, that is degree of differencing of raw observations; and q is the order of the moving average, that is the model's dependence on longer-term values and stochastic "shocks." After identifying the best-fit ARIMA model, we used the Kalman filter to interpolate missing data. We then ran wavelets on the complete time series, using the WaveletComp package in R (Roesch and Schmidbauer 2018). We used the Morlet wavelet function and compared observed power to a null background generated with red noise (i.e. temporally autocorrelated data).

Results

Off-channel ponds increase thermal diversity within the riverscape

Our analysis of riverscape temperatures showed that thermal regimes varied significantly between linked pond, creek, and river habitats (Figure 3A). The best supported MAR model (i.e. the model with the lowest AICc score, model 1) allowed all sites (each pond, creek, and river) to have different levels of stochastic (Q) and deterministic (C) variability (Table 2; Figure 2). As such, we can infer that each pond contributes a distinct thermal regime to the riverscape and increases thermal habitat options. Additionally, previous-day air temperature significantly influenced water temperature at all sites, as evidenced by the air temperature parameter not including zero at any sites. Notably, the creek habitats were more sensitive to air temperature (i.e. higher C parameter values) than pond or river habitats, as indicated by air temperature effects for creeks being higher and not overlapping with pond or with river habitats (Figure 3C).

Off-channel ponds provide diel and seasonal thermal buffering

Ponds buffered extreme hot and cold-water temperatures in winter and summer. Daily maximum temperatures for the three hottest months of the year were significantly cooler in most ponds compared to creeks on both Seiad Creek ($F_{[5,360]} = 125.70$, $p < 0.001$) and Horse Creek ($F_{[4,299]} = 300.90$, $p < 0.001$), except for Lower Seiad Pond, which was not significantly cooler than Seiad Creek in the summer ($p = 0.672$; Figure 4A & 4B). Daily minimum temperatures for the three coldest months were warmer in ponds compared to creeks on both Seiad Creek ($F_{[5,360]} = 168.80$, $p < 0.001$) and Horse Creek ($F_{[4,300]} = 170.00$, $p < 0.001$; Figure 4C & 4D), again with the exception of Lower Seiad Pond, which was not significantly warmer than Seiad Creek in the winter ($p = 0.999$).

Ponds also buffered daily water temperatures compared to creeks. The ratio of creek CV to pond CV was greater than one for all ponds, indicating that daily pond temperature varies less than creek temperature. However, we observed variation in the magnitude of buffering: the highest buffering was in May Pond (creek:pond CV = 5.3; Figure 3B) and Goodman Pond (creek:pond CV = 5.06), and other ponds exhibited less than half that value (Table S2).

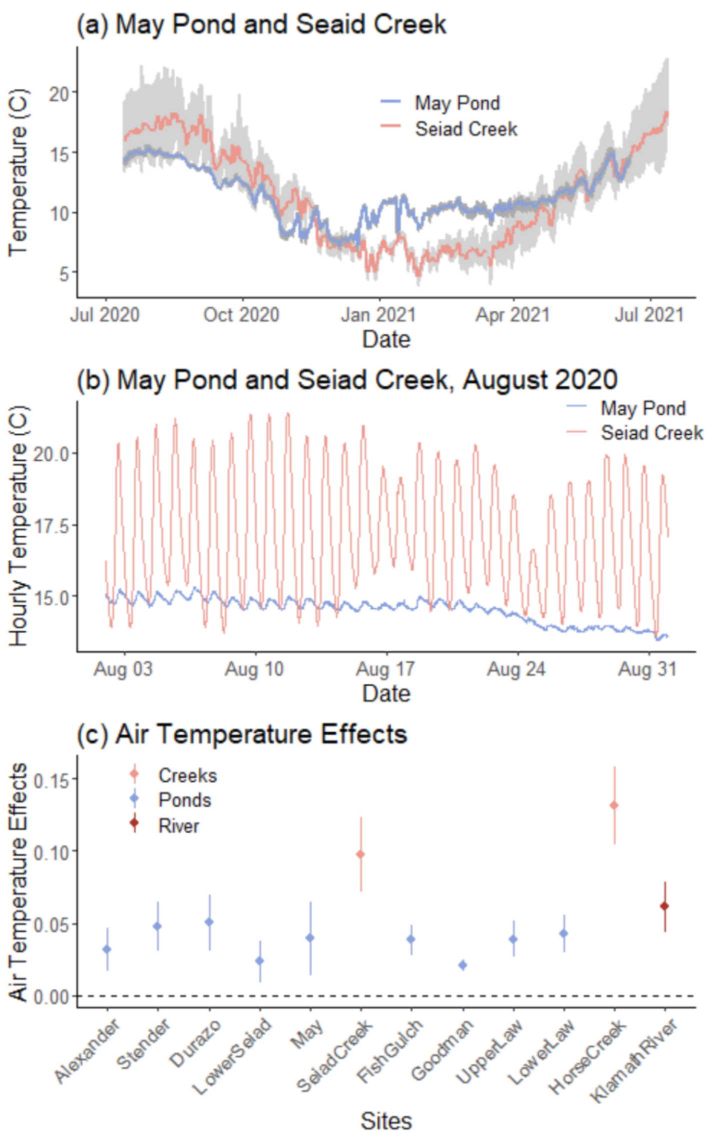

Figure 3: (a) Daily mean temperatures in May Pond (blue) and Seiad Creek (red) throughout the study period. Gray lines display 15-minute temperature readings. (b) Daily temperatures in May Pond (blue) and Seiad Creek (red) in August 2020. May Pond exhibits the strongest thermal buffering. (c) Air temperature (C) effects in the best supported multivariate auto-regressive model (MAR). Air temperature was a significant covariate for all ponds, and Horse Creek and Seiad Creek had particularly strong air temperature effects compared to ponds.

Off-channel ponds thermally stabilize over time

Wavelet analysis of the long-term series for Alexander and Stender Ponds (2010–2021) indicated fluctuations at the seasonal (1 year) scale and at the 24-hour scale (Figure 5). The annual signal remained important across the whole decade, indicating predictable, seasonal fluctuations in water temperature (i.e. winter vs. summer). However, the strength of the 24-hour signal declined over time (despite a small spike in 2021), suggesting that diel fluctuations in temperature (i.e. day vs. night) became less pronounced as pond succession advanced.

Discussion

Cool-water thermal refuges are increasingly critical habitat features for cold-water fishes in watersheds experiencing warming conditions (e.g. Steel et al. 2017). Restoration projects that create a diverse suite of cool-water thermal refuges, such as the off-channel ponds in this study, are examples of floodplain restoration practices that create large volumes of cooler water and restore thermal regimes; however, to what extent these habitats may be valuable under warmer, drier futures remains largely unknown. We found that (1) human-made, off-channel ponds had thermal regimes that were

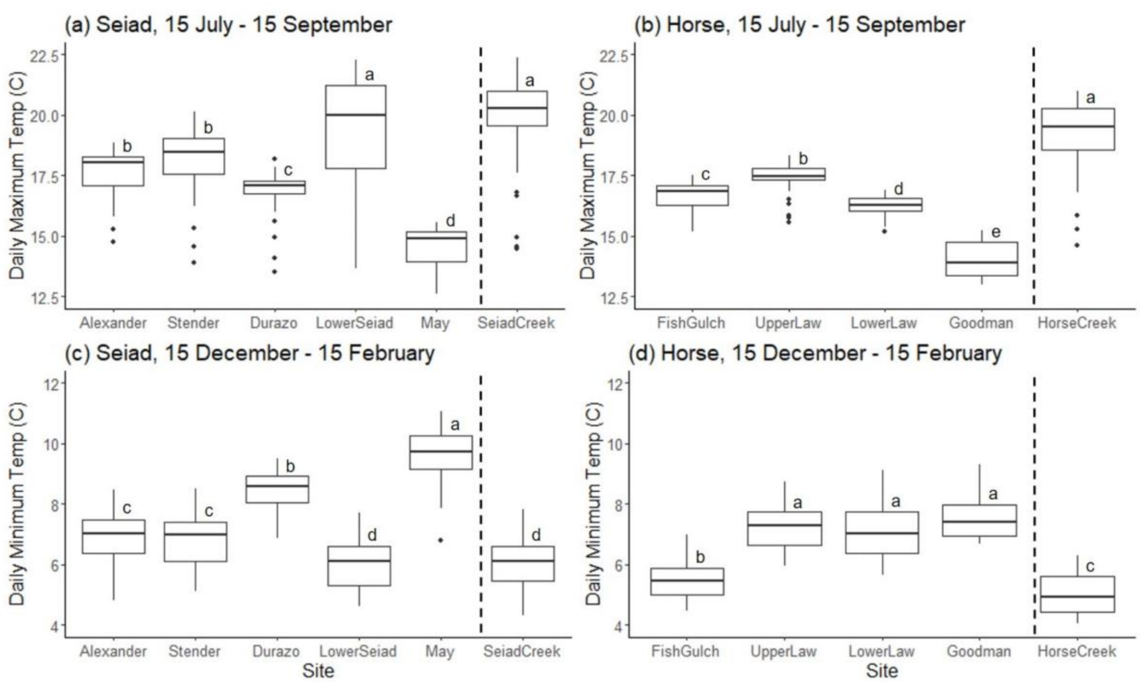

Figure 4: Boxplots showing daily maximum temperatures for the three hottest months in the study period (15 July - 15 September 2020) for (a) Seiad ponds and creek and (b) Horse ponds and creek. All ponds were significantly cooler than creeks except for Lower Seiad Pond. Figs. (c) and (d) show boxplots of the daily minimum temperature of the three coldest months in the study period (15 December - 15 February 2020-2021). Ponds were significantly warmer than creeks except for Lower Seiad Pond. Letters represent significant groupings from ANOVA analysis. The vertical dashed line in each graph is a visual aid to separate the pond and creek habitats (ponds are on the left of the line, and creeks are on the right).

significantly different than their adjacent creek and the mainstem Klamath River; (2) ponds provided cooler and more thermally stable habitats compared to creek and river habitats; and (3) thermal regime stability in ponds generally increased over time, with some exceptions in a severe drought year. Overall, our study shows that off channel ponds in the mid-Klamath watershed create thermal regime diversity and thermal refuges within the riverscape, adding to the growing evidence on the potential benefits of this restoration strategy. We contend that this approach may be particularly beneficial in Mediterranean-climate watersheds with seasonally and interannually variable hydroclimates, provided other critical conditions are met (e.g. access to the pond, sufficient DO). Understanding the spatial and temporal dimensions of restored cool-water thermal refuges is becoming critical, given the ongoing and projected warming trends (e.g. Albert et al. 2021).

Off-channel ponds increase thermal diversity within the riverscape

Based on the results of our MAR model, each of the nine offchannel ponds had a distinct thermal regime and contributed to overall thermal diversity. This finding supports our hypothesis that as large bodies of water with robust groundwater inputs (MKWC 2014, 2020, 2022; Wickman et al. 2020), off-channel ponds represent significantly different thermal habitats compared to creek or river sites. Diverse thermal regime options such as those created by these off-channel ponds are important features within a riverscape. Such habitat diversity allows mobile animals like fish to balance tradeoffs in food abundance and water temperature (e.g. Brewitt et al. 2017). In a system with stressful thermal conditions for salmonids, such as high summer temperatures in the mainstem Klamath River (Sutton and Soto 2012), the diverse thermal options provided by these ponds can be critical for salmonid survival. Other studies in the Klamath River identified tributary mouths as a source of cool thermal refuges for salmonids moving between the mainstem and tributaries (e.g. Sutton et al. 2007; Sutton and Soto 2012; Brewitt et al. 2017). In this ecosystem, juvenile salmonids in the mainstem Klamath River seek thermal refuge when temperatures reach around 19^{o}C (Sutton and Soto 2012). In the summer during our study, daily maximum water temperatures in Horse Creek averaged 19.14^{o}C and Seiad Creek were 19.9^{o}C, slightly exceeding the threshold for salmonids seeking refuge. Ponds, on the other hand, were several degrees cooler, averaging at daily maximums of between 16.1^{o}C in the Horse Creek watershed and 17.4^{o}C in the Seiad Creek watershed during the summer. Thus, our results suggest that off-channel ponds likely provide salmonids with a diversity of thermal habitats across the watershed—a facet of “biocomplexity” that may contribute to stabilizing population portfolios (Hilborn et al. 2003; Schindler et al. 2010). Thanks to the diversity of life-history, behavioral, and physiological traits in salmonid populations (e.g. Barrett and Armstrong 2022), floodplain ponds conferring thermal diversity likely help salmonid metapopulations cope with high summer temperatures.

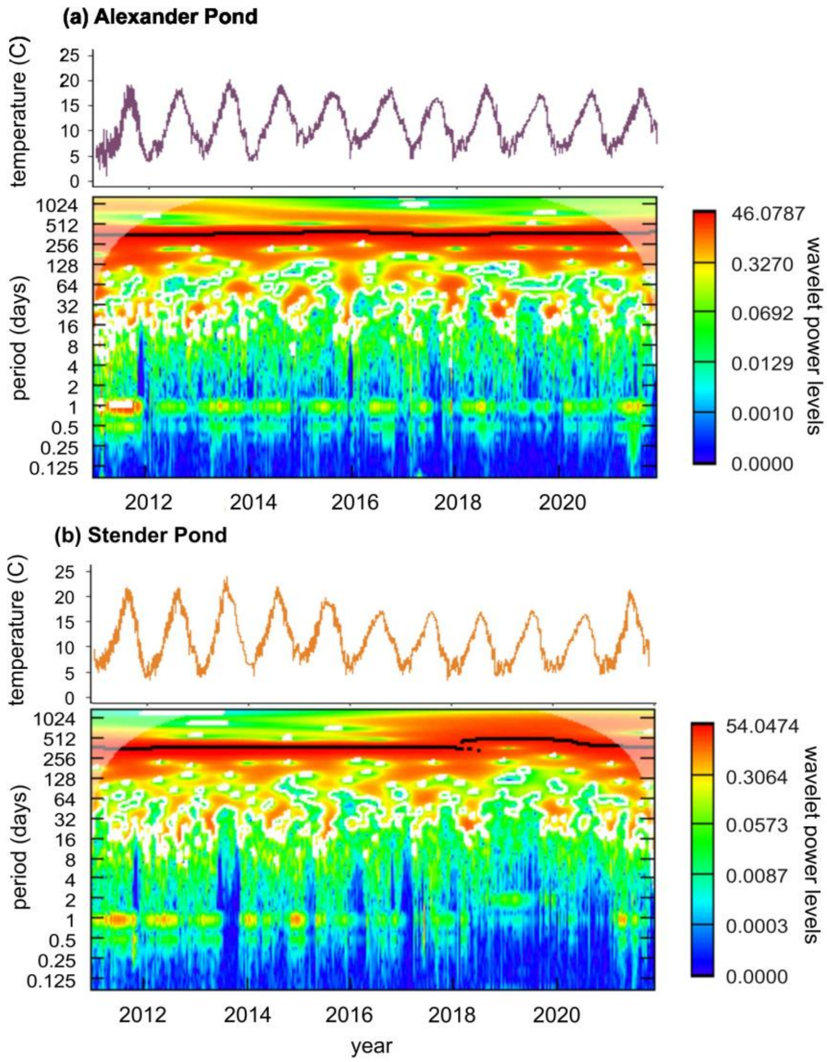

Figure 5: Hourly water temperatures from 2010 to 2020 and wavelet diagrams for Alexander (A) and Stender (B) Ponds. Wavelet diagrams identify the contribution of each frequency to the power, or strength, of a particular thermal regime. More powerful regimes with a stronger frequency are red, and less powerful regimes are blue. Statistically significant frequencies are outlined with a white line. Both ponds exhibit strong seasonal frequencies (period = 365 days) because of strong and regular temperature fluctuations in winter and summer. Both ponds also show strong frequencies at the daily scale (period = 1 day) because the cycle of day and night creates a strong and regular thermal fluctuation. In both ponds, the daily frequency becomes smaller and less red over time, indicating that daily temperature fluctuations decreased over the 11-year timespan. We predict this decrease in the power of daily regimes is due to the development of aquatic and riparian vegetation that provides shading.

Off-channel ponds provide diel and seasonal thermal buffering

In addition to increasing thermal diversity, off-channel ponds also buffered against changes in air temperature—a critical function in light of increasing frequency of heatwaves (Tassone et al. 2022). Our MAR analysis showed that off-channel ponds exhibited significant sensitivity to air temperature, but pond sensitivity was much lower than creek or mainstem river sensitivity. We suspect that ponds are less sensitive to changes in air temperature because they are deeper, have higher thermal mass and volume-to-surface ratios, and are more connected to groundwater compared to creeks (MKWC 2014, 2020, 2022; Wickman et al. 2020). Other studies measuring thermal sensitivity to air temperature in snowmelt-fed streams in California's Sierra Nevada (Leathers et al. 2022), or in high altitude streams in Alaska (Lisi et al. 2015), have generally reported higher thermal sensitivities than our study. Our measurements reflect an extreme drought period but still exhibited low thermal sensitivity compared to other published values. This highlights the strong buffering potential of ponds against hot periods, which may insure sensitive fish populations against transient heatwaves (Tassone et al. 2022) as well as long-term, directional warming (Arismendi et al. 2013). This is particularly important in the drought-stricken U.S. West: in the Klamath River, summer water temperatures have warmed over the last 20 years due to climate change, reduced snowpack, and decreased flows (Dettinger et al. 2015; Asarian et al. 2020).

We also found that the ponds created daily and seasonal thermal stability compared to adjacent creeks or the mainstem Klamath River. Daily maximum temperatures in the summer were up to 5^{o}C cooler in ponds compared to adjacent creeks, while daily minimum temperatures in the winter were up to 3^{o}C warmer in ponds compared to creeks. Overall, off-channel ponds buffer water temperatures throughout various seasons, meaning they likely stay closer to the physiological optima of cold-water fish in both summer and winter months. This buffering capacity also occurs within a day. Hourly temperature data showed that pond temperatures fluctuated far less than creek temperatures throughout day–night thermal cycles during summer months. Additionally, all ponds had thermal buffering capacity, as described by a ratio of creek to pond CVs as greater than one. Buffering capacity was highest in May Pond (5.3) and Goodman Pond (5.06), which are large, deep ponds with strong groundwater inputs.

Off-channel ponds thermally stabilize over time

The ponds received some assisted revegetation, and they were subsequently colonized by native and invasive vegetation that created canopy cover, habitat structure, and shading over time (T. Soto, Karuk Tribe Fisheries Program, personal observation July 2021). As canopy cover developed, we predicted that daily temperature fluctuations in the ponds would become more stable with increasing shade. As expected, wavelet analysis of Alexander and Stender Pond indicated that daily thermal stability increased over 10 years. However, the pattern of increasing daily thermal stability broke down in 2021, when daily temperatures fluctuated more widely than prior years in Alexander and especially Stender Pond. The years 2020–2021 were exceptionally dry and hot (California Department of Water Resources 2021), but the mechanism that caused pond thermal stability to break down during this drought is not clear, especially given that we did not observe similar patterns during the 2012–2016 drought (Lund et al. 2018). However, even though the daily thermal stability of Stender and Alexander Ponds declined in 2021 compared to prior years, the ponds retained buffering capacity compared to adjacent creeks and provided cooler, more stable thermal environments. This illustrates the importance of analyzing not only temperature averages and extremes, but also the scale and predictability with which regimes fluctuate (Arismendi et al. 2013). Extreme temperature variation at short timescales may be stressful to aquatic species (e.g. Nelson and Palmer 2007), and understanding this variation is important to classifying the impacts of climate events such as the 2021 drought.

Salmonid conservation

Sullivan et al. (2021) define a thermal refuge in the context of temperate river basins as "a cold-water patch used by poikilotherm (i.e. fishes) avoiding higher temperatures." We have not presented data on fish use of these ponds in this study; however, other studies have shown that juvenile salmonids used these ponds as refuge habitat throughout the year. Annual fish surveys by MKWC and the KFP indicated that these ponds are used by juvenile coho salmon and steelhead, although fish populations, community composition, and age structure in each pond vary by year throughout the watershed. Growth rates of juvenile salmonids rearing in the ponds depend on a variety of factors, including fish density (Witmore 2014; Krall 2016). Other studies of non-natal rearing in the Klamath watershed suggest that non-natal rearing, including in the ponds, can contribute to adult returns (Gorman 2016). Thus, the studied off-channel ponds likely provide important rearing habitats for juvenile salmonids in this watershed.

Critically, habitat intended as refuge can become an ecological trap (Schlaepfer et al. 2002) if a pond becomes isolated and fish are no longer able to leave when needed, e.g. to access better food sources, migrate to the ocean, or avoid predators. In several of these ponds, outflow channels connecting the pond to the creek can dry out by late summer, trapping salmonids in ponds and preventing other individuals from entering until winter rains rewet the outflow channel. In other cases, winter flows may create sediment plugs that cut off outflows. In this system, sediment plugs form most frequently in ponds with weak groundwater inputs and outflow channels connected at a 90^{o} angle to the creek, compared to oblique angled outlets (e.g. MKWC 2014). MKWC and the KFP have been experimenting with rock structures, beaver dam analogs, and post-assisted log structures that increase water level and connectivity of pond outlets. This work highlights an important point: restored floodplain habitats often require continued human intervention to maintain connectivity with the rest of the watershed, which is key to ensuring that these habitats operate as refuges rather than traps. The specific methods for maintaining lateral (river-to-floodplain) connectivity may vary across watersheds that differ in geomorphic and hydrologic background (e.g. Arrigoni et al. 2008). We do note that periodic connectivity is an inherent property of floodplains, and the risk– reward trade-off of using floodplain habitat has existed during the evolution of salmon using floodplains (e.g. Jeffres et al. 2020). Thus, occasional disconnect from the mainstem does not necessarily mean that these habitats are ecological traps. Further research on how intermittent access to pond habitats may affect salmonid behavior, foraging, and survival would help contextualize their role as thermal refuges (e.g. Krall 2016).

Another important consideration when restoring floodplain habitat for salmonids is DO availability. Inadequate levels of DO can impair activity, growth, and survival for juvenile salmonids (Carter 2005). In experimental settings at $15^{o}C$, juvenile coho salmon started to display oxygen growth dependence around DO concentrations of 4 mg/L and displayed zero growth below concentrations of 2.3 mg/L (Brett & Blackburn 1981). However, in northern California, juvenile coho salmon have been shown to survive in habitats with low DO concentrations by inhabiting microsites with higher DO (Woelfle-Erskine et al. 2017). In this study, we measured DO at a single location in each pond over several days in July 2020, and we took post hoc DO and temperature depth profiles in each pond in June 2023. In seven out of nine ponds, DO in at least the first 50 cm of the pond was above the 4 mg/L threshold. Additionally, in several ponds we recorded areas with DO supersaturation, likely due to photosynthesis from algae and macrophytes, indicating some pond microhabitats may provide relief from low-DO areas at least during the day (e.g. Woelfle-Erskine et al. 2017). However, Goodman and Lower Lawrence Ponds exhibited many DO measurements below 3 mg/L. Although fish have been recorded using Goodman Pond (e.g. MKWC 2022), this is cause for concern and DO in Goodman and Lower Lawrence ponds should be more thoroughly monitored.

Apart from floodplain restoration in general, our research calls attention to the importance of incorporating thermal regimes into restoration actions in dam-impacted rivers (Olden and Naiman 2010; Wohl et al. 2015; Palmer and Ruhi 2019). In the Klamath River, four dams in the upper part of the watershed are scheduled for removal in 2023 and 2024 (Klamath River Renewal Corporation 2020; Blumm and Illowsky 2022). The off-channel ponds in this study will be used for relocating fish from the mainstem prior to reservoir draw-down to protect them from fine sediment flushing during dam removal (Klamath River Renewal Corporation 2020; T. Soto, Karuk Tribe Fisheries Program, personal observation July 2021). Additionally, new off-channel ponds will be constructed in dam reservoir footprints post-dam removal. In addition to long-term restoration strategies such as dam removal, off channel ponds offer quick support to depressed coho populations, providing a relatively fast-acting restoration strategy that creates diverse thermal habitats for salmonids.

Our study has shown that in the mid-Klamath River watershed, human-made off-channel ponds are effective at creating diverse thermal refuge habitats that likely benefit cold-water fishes. These thermal refuges persist even during severe drought. However, beyond our study watershed, the geomorphic and hydrologic context of other riverscapes may lead to different results. Critically, the ponds described in this study have persistent sources of well-oxygenated groundwater that help create large volumes of cooler water, and these groundwater sources were investigated before pond excavation began (e.g. MKWC 2014). Ponds also require some level of continued human maintenance to ensure pond outflows stay connected to the rest of the river network (e.g. MKWC 2014). Use of these ponds as thermal refuge by salmonids and other cold-water species may be variable and influenced by other concurrent restoration efforts in the watershed. Thus, applying this restoration strategy to other river systems should be approached with appropriate consideration. Overall, as climate change and droughts increase the importance of access to thermal refuge habitats in riverscapes (e.g. Tassone et al. 2022), managing thermal regimes will be increasingly critical to the integrity of river ecosystems.

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Supplementary Information

Figure S1: Temperature time series from all sensors included in the study, grouped by site. In sites with more than one sensor, Pearson's correlation coefficient (r) and the p-value are shown for each time series pair.

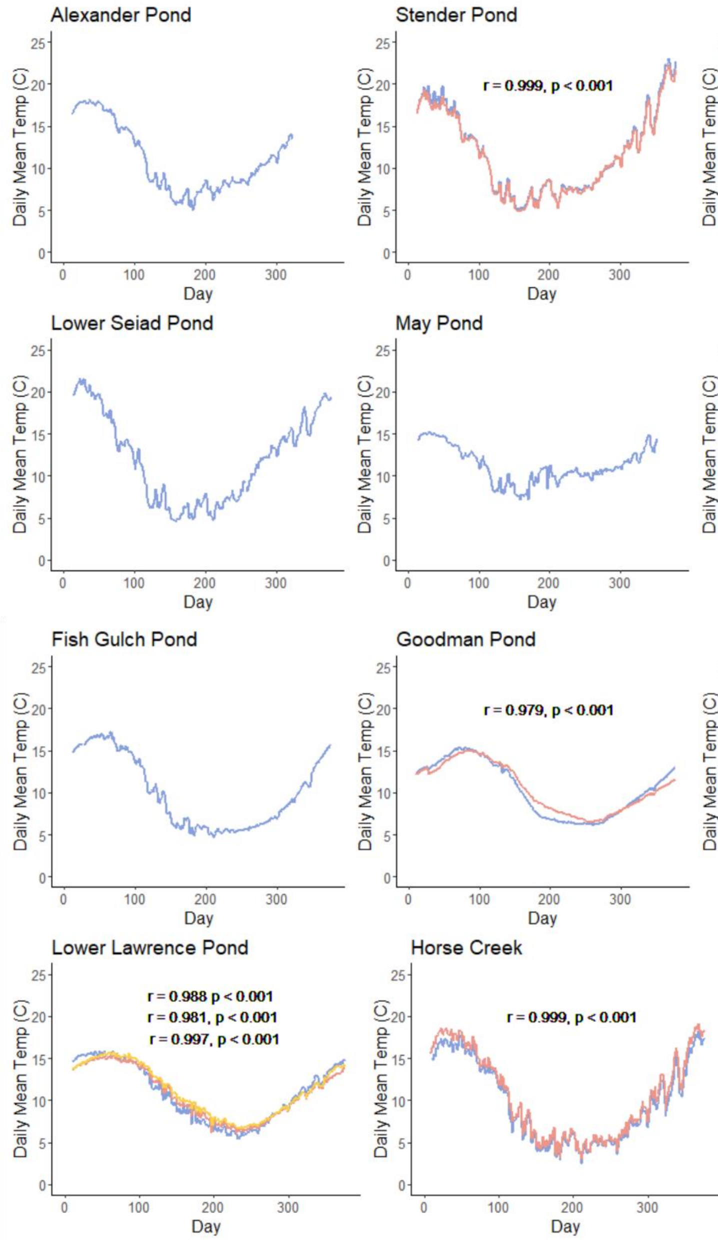
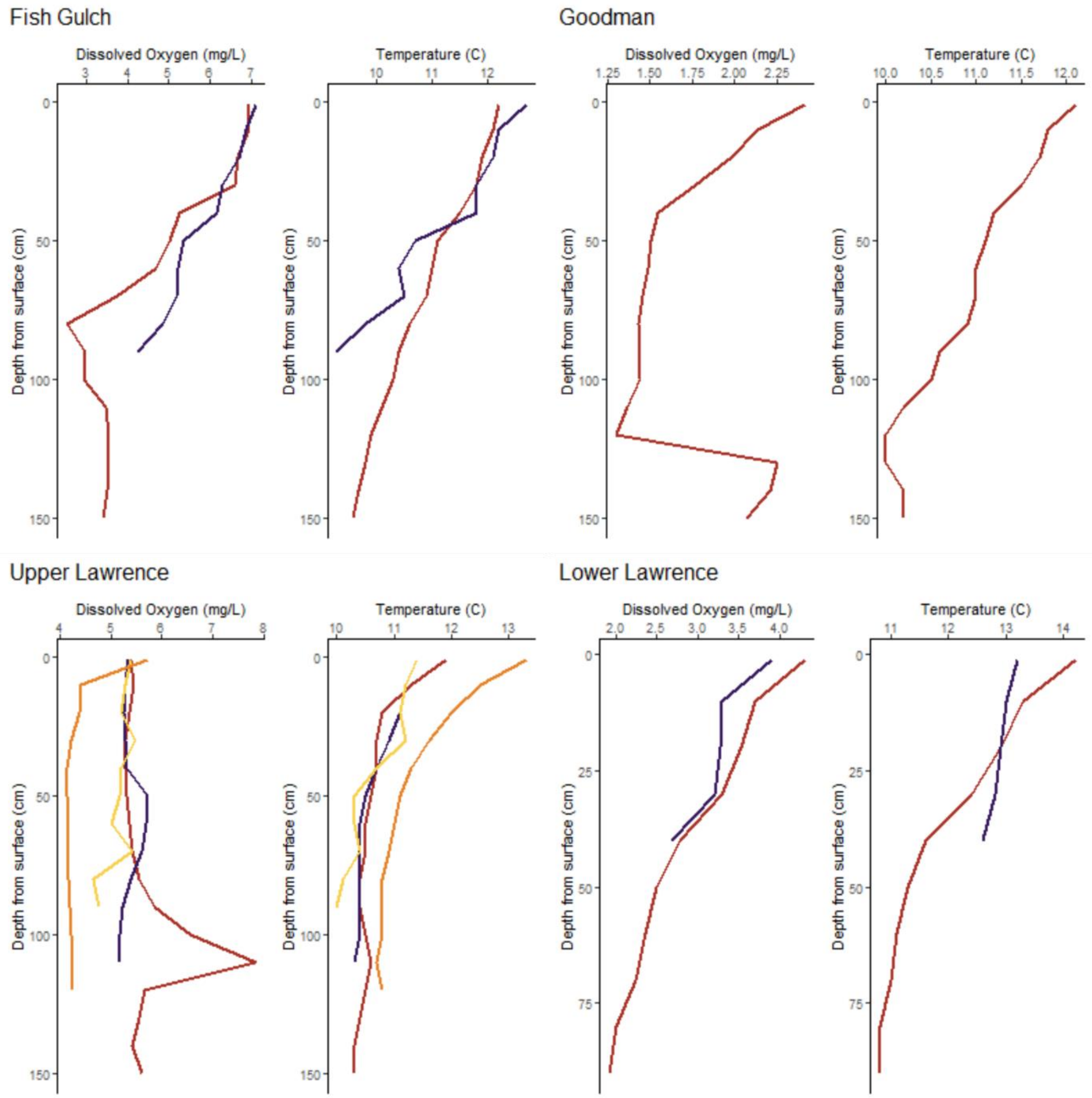


Figure S2: Depth profiles of dissolved oxygen and temperature taken in each pond in 2023 in the daytime during the DO maxima. Matching colors on dissolved oxygen and temperature plots for each pond represent profiles taken at the same time in the same location.



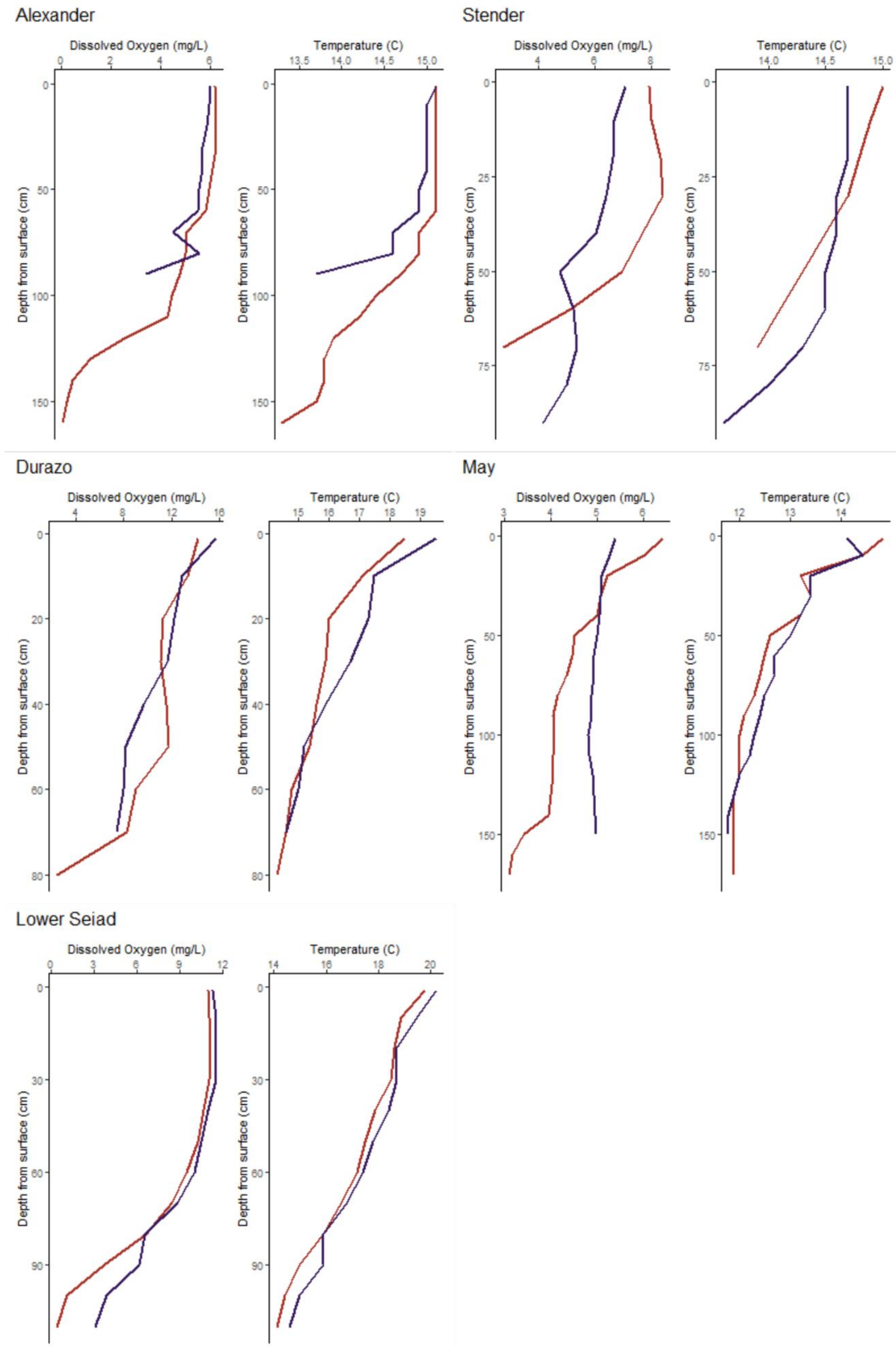

Alexander
Dissolved Oxygen (mg/L)
Temperature (C)
Depth from surface (cm)
Stender
Dissolved Oxygen (mg/L)
Temperature (C)
Depth from surface (cm)
Durazo
Dissolved Oxygen (mg/L)
Temperature (C)
Depth from surface (cm)
May
Dissolved Oxygen (mg/L)
Temperature (C)
Depth from surface (cm)
Lower Seiad
Dissolved Oxygen (mg/L)
Temperature (C)
Depth from surface (cm)

Figure S3: Dissolved oxygen data recorded in each pond in July 2020.

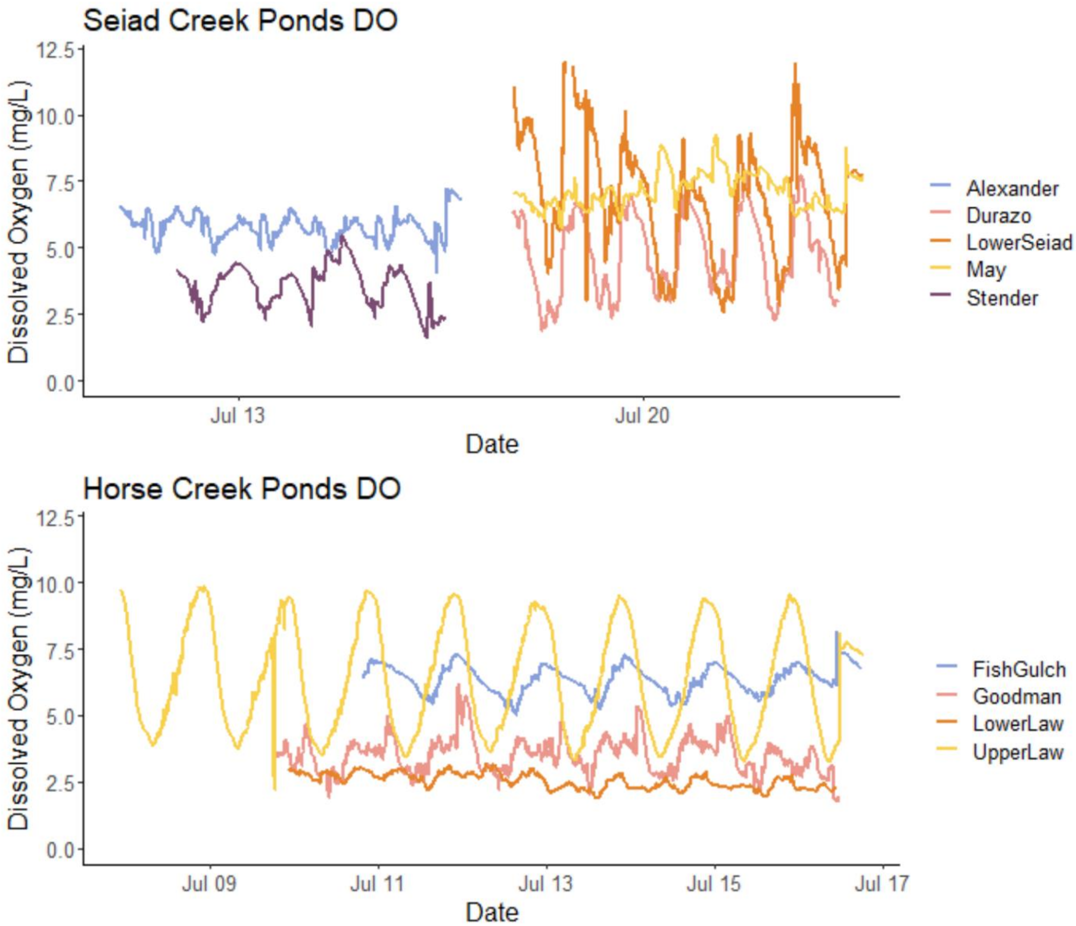


Table S1: For each site with more than one sensor, this table shows the mean difference and standard deviation of daily differences between each pair of time series.

Site	Mean Difference	Standard Deviation of Difference
Goodman Pond	0.134 ºC	0.708 ºC
Upper Lawrence Pond	0.812 ºC	0.655 ºC
Lower Lawrence Pond	0.655; -0.340; -0.346 ºC	0.647; 0.744; 0.212 ºC
Horse Creek	0.644 ºC	0.367 ºC
Stender Pond	0.255 ºC	0.286 ºC
Seiad Creek	0.105 ºC	0.259 ºC

Table S2: Coefficient of variation (CV) for each individual creek and pond. The last column is the ratio of creek to pond CV.

Watershed	Creek CV	Pond	Pond CV	CV Ratio
Seiad	9.68	Alexander	2.02	4.79
Seiad	9.68	Stender	3.08	3.14
Seiad	9.68	Durazo	2.02	4.80
Seiad	9.68	Lower Seiad	2.25	4.31
Seiad	9.68	May	1.83	5.30
Horse	9.94	Fish Gulch	2.21	4.49
Horse	9.94	Goodman	1.97	5.06
Horse	9.94	Upper Lawrence	5.09	1.95
Horse	9.94	Lower Lawrence	5.35	1.86

Transition

Man-made floodplain ponds, as explored in chapter 2, are an example of floodplain restoration at a local scale. Another approach to restoring river-floodplain connections at a regional scale is to reintroduce the North American beaver (*Castor canadensis*). Chapter three explores the potential local and regional impacts of reintroducing beavers in the California Sierra Nevada region. Beavers act as ecosystem engineers by building dams in stream channels, which creates wetland habitat, stores water, and creates fire resilient landscapes (Brazier et al. 2021; Larsen et al. 2021). In California, beavers are increasingly being recognized for their potential to help vulnerable landscapes, communities, and ecosystems be resilient to global change (Fairfax and Whittle 2020). This chapter uses modeling tools to describe the potential impact of widespread beaver reintroduction in California.

Chapter 3
Maximizing the potential benefits of beaver restoration for fire resilience and water storage

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Abstract

Restoring populations of native keystone wildlife species benefits biodiversity and can create landscape resilience to global change through the ecosystem-modifying actions of those species. The North American beaver (*Castor canadensis*) is an ecosystem engineer that creates both water storage and fire resilience on landscapes. Beaver populations in North America are significantly lower than they would have been historically, but over the last decade beavers have been increasingly recognized for their ecosystem service benefits, and beaver population expansion and reintroduction is becoming more prevalent. We modeled potential beaver dam-building capacity, water storage, and fire resilience in the Sierra Nevada region of California, a high-risk area for water and fire related climate catastrophes. We found that considerable beaver dam-building capacity exists in all watersheds in our study region, although only about 51% of dam capacity remains compared to historical levels. Beaver dams have the potential to store 0.12 km^3 of surface water and create 2,198 km^2 of fire resilience across this landscape. Areas where beavers have the greatest potential water and fire benefits frequently overlap with watersheds we identified as the highest risk in the region. We identified five priority watersheds that are both at high risk for drought and fire impacts and have high potential for ecosystem benefits from beaver restoration. These watersheds represent a starting place for localized beaver reintroduction work in California. The potential for the reintroduction of a native wildlife species to create landscape resilience to drought and fire is a valuable example of how biodiversity and nature-based solutions can be aligned.

Introduction

Sustaining biodiversity is an increasingly central priority for global conservation (Shin et al. 2022; Pettorelli et al. 2021; Veríssimo et al. 2014). In particular, there has been increasing conservation investment in restoring species that are strong interactors with their communities, like keystone species or ecosystem engineers, which can modify the physical environment for their own benefit (Power et al. 1996). Restoring populations of these species can support or be detrimental to other animal and plant communities, alter landscape structure, and create resilience to global change (Byers et al. 2006). Most of the time, restoration of keystone species is targeted in areas where they might persist, or where conflict with humans will be minimized. However, it is also useful to consider how restoring keystone wildlife species can directly address major challenges associated with global change, specifically drought and fire.

The North American beaver (*Castor canadensis*) is a highly adaptable ecosystem engineer that are the ideal test case for considering how wildlife restoration can create resilience to climate-related challenges. Beavers are widespread throughout North America (Brazier et al. 2021; Larsen et al. 2021), and they use riparian trees and shrubs to build dams in stream channels and change how water moves throughout a stream network (Naiman et al. 1988; Gurnell 1998). Beavers also dig channels that fan out into the surrounding floodplain area, which help them move around and contribute to water spreading throughout the surrounding area (Gurnell 1998; Fairfax and Whittle 2020). Dam-building and channel-digging activity by beavers is a defining process in aquatic and riparian ecosystems. Beaver ponds store carbon and sediment and alter nutrient cycling by storing carbon and sediment (Wohl 2021), help restore eroded and incised streams (Pollock et al. 2014), increase riparian vegetation wetness and landscape resilience to wildfires (Fairfax and Whittle 2020), and mitigate floods and droughts (Westbrook et al. 2020; Ronnquist and Westbrook 2021).

Critically, beaver dams slow the flow of water through the landscape (Brazier et al. 2021; Westbrook et al. 2006; Green and Westbrook 2009; Gurnell 1998), both by storing water and creating landscape “roughness”, which slows water as it moves around, through, over, or under beaver dams (Puttock et al. 2017; Green and Westbrook 2009; Jordan and Fairfax 2022; Gurnell 1998). Medium-sized beaver pond complexes have been shown to store up to 1000 m^3 of water (Puttock et al. 2017), which leaks out of the dam slowly over time, buffering streamflow even during dry seasons (Majerova et al. 2015; Puttock et al. 2017). In some cases, beavers have been shown to turn intermittent streams into perennial streams that are wet year-round, which can have some ecological impacts (e.g. for native desert fishes, Gibson and Olden 2014) but is considered beneficial in terms of reconnecting streams with groundwater sources and floodplain habitats (Pearce et al. 2021).

Beaver dams also create fire resilient landscapes. By building dams, digging channels, raising water tables, and reducing stream incision, beavers create zones of wet, well-connected floodplains (Weirich 2021; Jordan and Fairfax 2022; Whipple 2019). A study of wildfires in the western US found that stream segments with beaver activity maintained significantly higher vegetation greenness after fire than stream segments without beavers, indicating increased fire resilience associated with beaver ponds (Fairfax and Whittle 2020). Similarly, a study in the Rocky Mountain region found that beaver ponds in a stream system decreased burn severity in surrounding habitats during megafires (Fairfax et al. 2024). Even when beavers are not present, old beaver dams can help with fire recovery. Studies in the Rocky Mountains have found that after fires, abandoned beaver dams can trap sediment and promote overbank flow, which reduces bank erosion and facilitates post-fire floodplain vegetation regrowth (Wohl 2021). Based on these findings, beavers across the western US are increasingly recognized for their potential to create networks of fire-resistant ponds, potentially slowing the spread of fires and giving humans more time to mobilize firefighting resources (Fairfax and Whittle 2020; Jordan and Fairfax 2022).

Although beavers have landscape scale benefits and were historically widespread throughout North America, by 1900 populations had been severely depressed by the fur trade (Naiman et al. 1988). Over the last several decades, beaver populations have been recovering in much of North America, although in the United States beaver populations remain at about 10% of historical levels (CDFW 2023; Naiman et al. 1988). Similar to the rest of North America, beavers were once common in most of California, but populations have been slow to recover and are currently low throughout the state (CDFW 2023). As California becomes increasingly susceptible to drought (Berg and Hall 2017; Diffenbaugh et al. 2015; Liu et al. 2022) and wildfire (Brown et al. 2023), evidence of beavers' role in drought and fire mitigation has led to renewed investment in beaver restoration by the state of California (Castaneda 2023; CDFW 2023). As water storage and fire resilience solutions become increasingly critical across the state, and as beaver population restoration becomes more politically and socially realistic, it is important to understand the potential for restoring beaver dam-building activity, and how that dam-building activity could confer water storage and fire resilience benefits on a landscape scale.

The goal of this project is to examine the potential opportunities and benefits of restoring beaver dam-building activity to reduce damaging consequences of global change. We focused our study on the Sierra Nevada region of California, where water shortages and extreme wildfire events are critical issues and where beaver reintroductions are already occurring (Castaneda 2023). This will allow our results to inform future beaver restoration priorities. Our study covered a large, multi-watershed region and evaluated multiple beaver-related impacts, creating a unique perspective on the potential benefits of beaver restoration in this area. We quantified current beaver dam capacity in the Sierra Nevada and evaluated how dam-building capacity has changed compared to historical levels. We also measured the extent to which restoring dam-building activity could provide potential water storage and fire resilience benefits across the Sierra Nevada region, and evaluated how these potential benefits co-occur across the landscape.

We hypothesized that 1) current beaver dam capacity would be significantly lower than historical beaver dam capacity due to large-scale changes in land use over the last century, but that considerable dam building capacity would remain throughout the region. 2) We expected that some reaches with high beaver dam capacity would coincide with high fire risk stream corridors, creating the potential for enhanced fire resilience. 3) We also expected that some watersheds with high water scarcity would have the potential to benefit from beaver-related surface water storage. 4) Finally, we identified areas where restoring beaver populations could confer both water and fire resilience benefits, while also supporting the restoration of an important native mammal to California's ecosystems.

Methods

Study site

The Sierra Nevada mountain range spans much of eastern California and parts of Nevada (Figure 1). The Sierra Nevada Mountains have cool, wet winters and warm, dry summers, and almost all precipitation occurs between October and May (Melack and Stoddard 1991). In higher elevations, most precipitation falls as snow that starts melting in the spring. The western Sierra receives about ⅔ more rain than the eastern slopes. Vegetation is diverse and highly dependent on elevation, but generally consists of a combination of alpine meadow and pine forest at higher elevations, turning to deciduous oak forest in foothill regions, with riparian areas populated by willows and aspens (Landfire 2021).

Current beaver population size and distribution in the Sierra Nevada mountains are unknown. For most of the 20th century, beavers were considered non-native above 300m in the Sierra Nevada region (Lanman et al. 2013). However, Indigenous peoples in the Sierra Nevada region have long understood beavers to be a critical part of the local ecosystem (Keeble-Toll 2018; Sherriff 2021); and based on traditional ecological knowledge from Indigenous groups across California, as well as archeological evidence from ancient beaver dams, beavers are now recognized as a native species to the Sierra Nevada region (James and Lanman 2012). In 2023, the Mountain Maidu and Tule River Tribes spearheaded the first beaver reintroductions in the Sierra Nevada for over 75 years (Castaneda 2023). Other than this reintroduction, a few beaver colonies exist, notably in the Lake Tahoe region and the southern end of the range (Fairfax et al. 2023), but generally, beaver populations in the Sierra Nevada today are significantly smaller than those before European settlement (James and Lanman 2012).

For our study, we defined the Sierra Nevada region using regional classifications from Zimmerman et al. (2018). We focused on 31 USGS hydrologic units (HUC-8) watersheds overlapping with the Sierra Nevada region. Although parts of many of these watersheds extend outside our definition of the Sierra Nevada region, we included full HUC-8 catchments to understand how beaver dam capacity dynamics might vary throughout a watershed spanning different regions. We excluded watersheds that were outside the estimated historical range of beavers in California (e.g., watersheds in southern California such as the Antelope-Fremont Valleys watershed), even if those watersheds fall within the Sierra Nevada region (Lanman et al. 2013; Richmond et al. 2021).

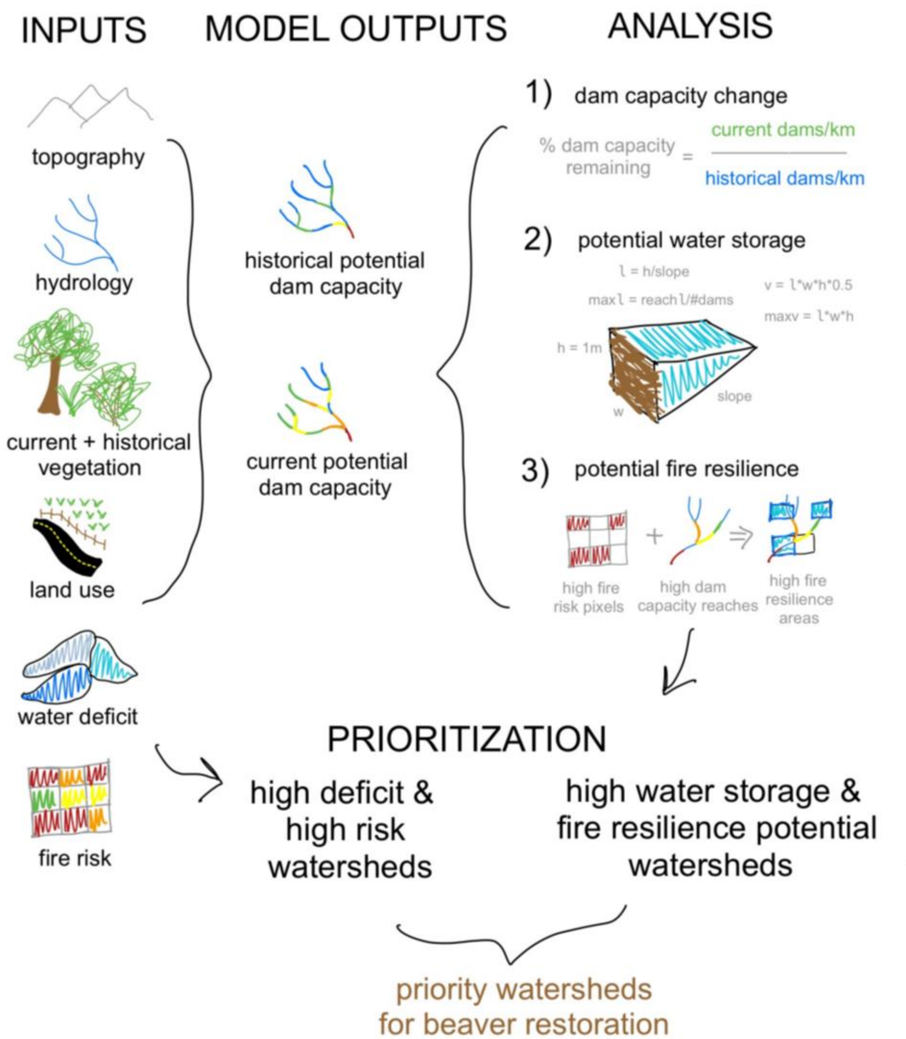

Figure 1: Schematic methods diagram of data inputs, model outputs, and analyses.

Modeling framework overview

This study relies on combining results from several models (Figure 1). We first modeled historical and current potential dam building capacity (see BRAT model below). We then used those model results to estimate current potential surface water storage. Then, we quantified potential fire resilience at the reach scale by identifying areas with both high fire risk and high potential dam capacity. We then identified "priority" watersheds, or watersheds with high water scarcity and high fire risk, where beaver-related water and fire benefits could have the most impacts. Finally, we overlaid potential water storage and fire resilience to identify areas where beaver restoration would create both benefits at the same time.

Beaver dam-building capacity

The Beaver Restoration Assessment Tool (BRAT) model was developed by Macfarlane et al. (2017) to estimate the maximum capacity of a stream network to support beaver dam-building activity. This model uses a fuzzy inference system to integrate topography, hydrology, vegetation, and land use spatial datasets to identify physical and ecological conditions that would allow beavers to successfully build and maintain dams (Figure 1). The beaver dam-building capacity output provides valuable information for understanding where and how to restore beaver populations. We obtained all data from publicly available national datasets and used pyBRAT 3.1 with modifications for use in ArcGIS Pro 3.1.

We used a ⅓ arcsecond (10m) digital elevation model (DEM) from The National Map (USGS 2024). We used the DEM to calculate the valley bottom footprint using the Valley Bottom Extraction Tool (VBET, Gilbert et al. 2016), which we hand-edited for accuracy, as well as stream channel slope and drainage area.

We mapped stream networks using the National Hydrography Dataset (NHD, (U.S. Geological Survey 2024a). We excluded streams marked as ephemeral or general in the dataset, since these streams do not have enough streamflow to support beaver dams (streamflow patterns in streams marked general are unclear, but often ephemeral). The resulting network included only perennial and intermittent streams and canals. We divided the stream network into 300m segments. We represented discharge using regional regression equations for a 2-year flood and baseflow. We used 2-year flood equations for hydrological regions that encompassed each watershed (Gotvald et al. 2012). Baseflow equations were calculated based on watershed specific variables for each watershed (Riverscapes Consortium 2018). We calculated elevation, precipitation, and slope for each watershed from USGS StreamStats (U.S. Geological Survey 2019).

We used historical and existing vegetation rasters from the Landfire dataset (Landfire 2021). For existing vegetation, we used the Landfire Existing Vegetation Type layer from 2020, and for historical vegetation we used the Landfire Biophysical Settings layer from 2016 (the most recent biophysical settings layer available). We edited the attribute table of each raster to include a vegetation suitability index for beaver dam building (Macfarlane et al. 2017). We coded each vegetation type 0-4, with 0 being no suitability and 4 being the best suitability. For example, vegetation like aspens and willows are highly suitable habitats for beavers and were coded as 4, while exposed rock, glacier, or cropland where beavers could not persist were coded as 0. The BRAT model bases historical beaver dam capacity estimates on a pre-European settlement vegetation layer. The model does not alter hydrology or topography to make historical estimates, meaning that all modeled dam capacity changes between historical and current levels are the result of vegetation change.

To represent land use, we edited the attribute table of the existing vegetation raster to include a land use code, following Macfarlane et al. (2017). The land use code ranges from 0-1 and represents very low to very high human land use. For example, the very low human land use category includes natural settings with limited land use, and the very high land use category includes urban areas. We also included road and railroad layers from the US Census Bureau Tiger dataset (United States Census Bureau 2023). We created a canal layer by selecting streams coded as canals in the NHD. We applied a land ownership layer from the Bureau of Land Management Surface Management Agency dataset (2024). We used a protected area layer and a conservation easement layer from the protected area database of the US (U.S. Geological Survey 2024b).

Estimating potential surface water storage in beaver ponds

Using dam-building capacity outputs from the BRAT model, we estimated surface water stored above each beaver dam. Following a method developed by Scamardo et al. (2022), we approximated beaver ponds as right triangular prisms. We assumed that beaver dams were 1m tall, which is a generally accepted average height for beaver dams, although actual dam heights vary (Hafen et al. 2020). We assumed that pond width was equal to channel width (i.e. no flooding outside the stream channel) for simplicity, and estimated channel width based on national hydraulic geometry relationships (Wilkerson et al. 2014). We calculated pond length as a function of slope and dam height, and we set a maximum pond length for reaches with multiple beaver ponds by dividing the length of the reach by the number of dams in that reach. If calculated pond length exceeded the maximum pond length for that reach, we used maximum length in calculations. We calculated approximate dam volume by taking the volume of a triangular prism (1):

$$\text{dam volume} = \text{dam height} \times \text{channel width} \times \text{dam length} \times 0.5 \quad (1)$$

We then calculated water deficit for each watershed using the Normalized Deficit Cumulated (NDC; Devineni et al. 2015). The NDC is the maximum cumulative deficit between average water demand and renewable water supply, divided by rainfall volume, for each county. NDC only includes internal sources of renewable water and excludes rivers and canals flowing through the county, therefore reflecting how much each county relies on non-renewable or external water sources. We calculated HUC-8 level NDC by taking the percentage of each county in each watershed and multiplying by the NDC of that county, treating NDC as cumulative over space (as in Ruhi, Messager, and Olden 2018; U.S. Geological Survey 2019).

Estimating potential fire resilience conferred by presence of beaver ponds

To quantify the spatial distribution of fire risk, we used a continuous raster of wildfire hazard potential (WHP) at a 270m resolution (U.S. Forest Service 2020). WHP values are based on the presence of fuels with the potential for extreme fire behaviors such as torching and crowning and are generally used for targeting long-term vegetation management. Although in this study we refer to WHP as "fire risk" for clarity, WHP values do not take into account weather forecasts or vegetation moisture conditions, and therefore do not measure fire risk for any specific day or season (U.S. Forest Service 2020). The WHP values ranged from 0 to 40000, and we classified pixels as "high risk" if WHP > 2000, which represented the top quartile of WHP values in this region. Like the BRAT model, the WHP values were calculated based on the 2020 Landfire vegetation dataset (Landfire 2021; U.S. Forest Service 2020).

To quantify the potential fire resilience conferred by beaver dams, we focused on areas with both high WHP and high dam capacity. We identified high-risk-high-capacity areas by overlapping raster cells with WHP > 2000 and stream segments with dams/km > 5. We quantified the percent of each watershed with high fire risk by dividing high risk area by total watershed area. We quantified the percent of high-risk-high-capacity area in each watershed by dividing total high-risk-high-capacity area by high-risk area along streams (we restricted this calculation to streams since potential beaver activity is also restricted to streams). We expect that our estimates of high-risk-high-capacity areas are an extremely conservative estimate of the fire resilience benefits conferred by beavers. Studies on megafires in the Rocky Mountains have shown that any number of beavers present on a landscape confers fire resilience, regardless of the BRAT-modeled dam capacity of the stream, indicating that our threshold of dams/km > 5 is conservative (Fairfax et al. 2024).

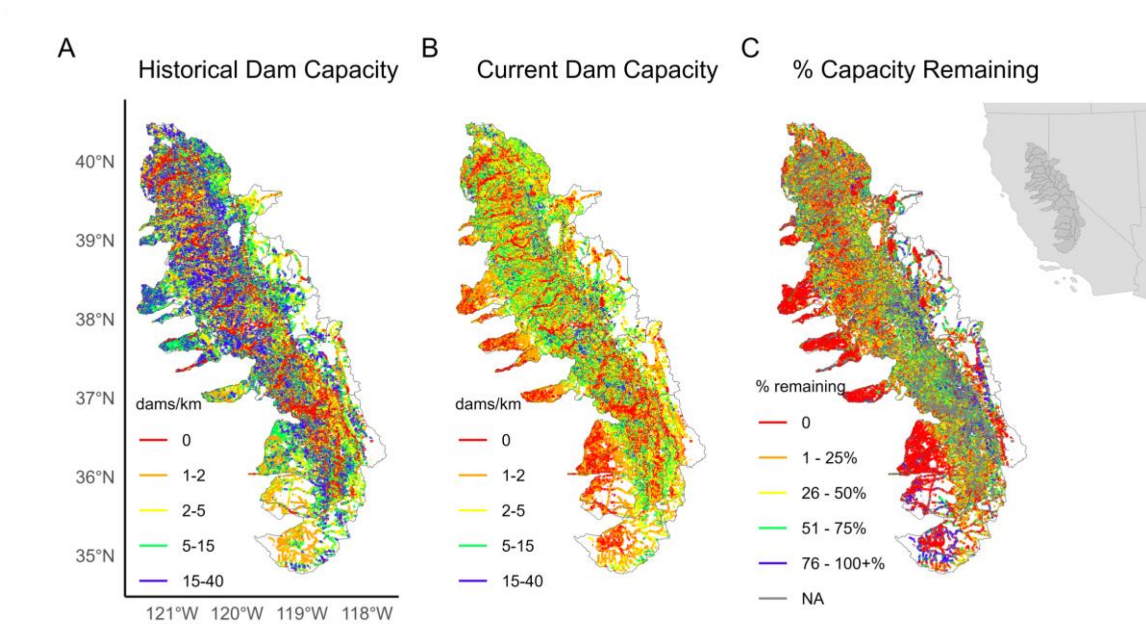

Figure 2: Change in beaver dam building capacity throughout the Sierra Nevada region (see inset) over time. a) Historical dam building capacity (dams/km) in the Sierra Nevada region, based on historical vegetation data. b) Current dam building capacity (dams/km) in the Sierra Nevada region. c) Change in dam capacity between historical and current times. Dam capacity in the region has declined about 60% compared to pre-European settlement, but significant dam capacity remains in every watershed in the region.

Watershed prioritization

Finally, to identify watersheds with high potential for beaver-related benefits, we summarized historical dam capacity, current dam capacity, percent historical capacity remaining, water deficit, fire risk, potential water storage, and potential fire resilience area for each of the 31 watersheds in our study region (Figure 4, Table S1). We identified high-risk priority watersheds by identifying watersheds with a water deficit (NDC > 1); and watersheds with more than 20% of land area at high fire risk (WHP > 2000). We also overlaid fire risk with potential water storage to identify watersheds where beaver restoration has the potential to support fire resilience, water storage, or both. For this overlay we used only fire resilience pixels that overlapped stream segments included in our study. We categorized potential water storage and potential fire resilience equally

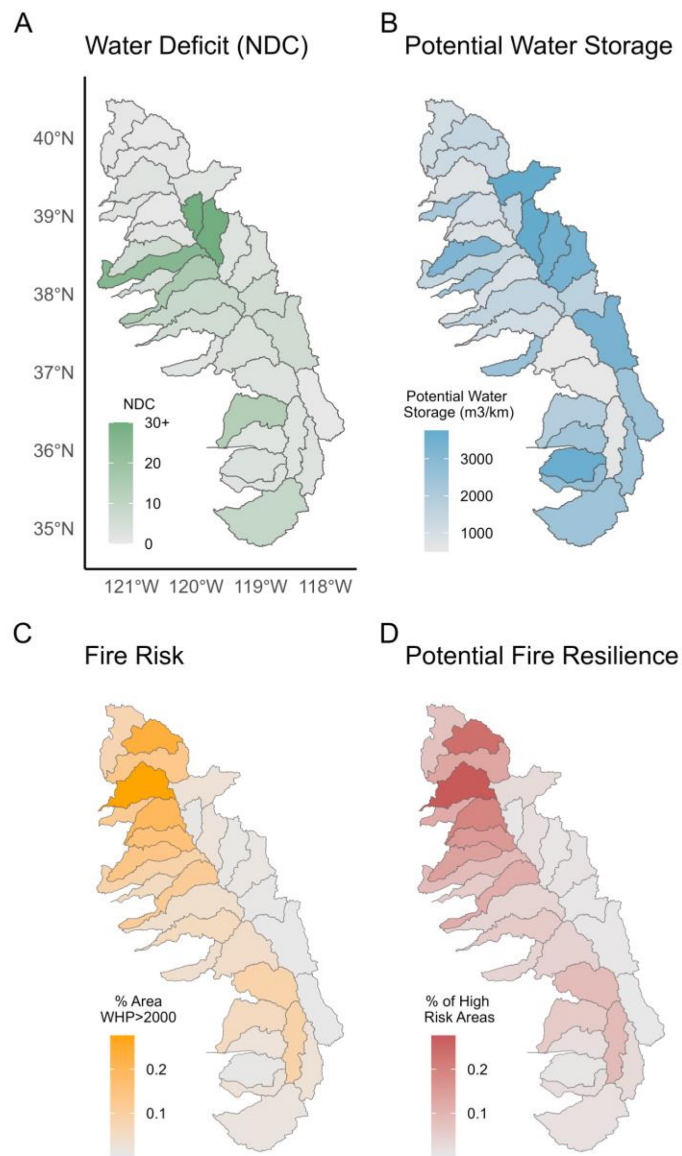

Figure 3: a) Watershed-scale water deficit (NDC); b) potential water storage as calculated by m^3 per stream kilometer for each watershed; c) fire risk, as calculated by percent area of watershed with a WHP > 2000; d) potential fire resilience, as calculated by percent area with high-risk-high-capacity overlap, restricted to stream corridors.

based on statistical quartiles. We identified watersheds with high percentages of overlapping co-benefits that were also high-risk watersheds. We also quantified the amounts of potential beaver dams, water storage, and fire resilience on private lands versus public lands (Table S3). All analyses were performed in R (R Development Core Team 2024).

Results

Change in dam capacity from historical levels

Our calculation of current and historical dam building capacity for 159,000km of stream in the Sierra Nevada region determined that historically, the region could have supported 897,000dams (Figure 2a), and it currently can support 51% of the historic estimate, or 440,000 dams (Figure 2b). Every watershed has seen declines in dam capacity compared to pre-European settlement (Figure 2c; Table S1), but considerable dam capacity remains across the region.

The differences in BRAT model estimates of dam capacity between historical and current time periods was based on changes in vegetation type between the time periods. Major vegetation shifts have occurred in this region since historical times, leading to a decline in beaver-favorable vegetation in most watersheds (Figure S1). Most of this vegetation shift is represented in changes from natural landscapes to agricultural or urban landscapes throughout the region (Landfire 2021).

Potential benefits of beaver dam restoration given current dam capacity

We found that in total, potential beaver dams in the study area could store up to 0.12 km^3 of water across the region as a whole (Figure 3b). For context, Lake Tahoe has a volume of approximately 157 km^3 of water (Coats et al. 2006). Potential water storage was not necessarily highest where potential dam capacity was highest. In this region, dam capacity tended to be highest in small headwater streams, but potential water storage was mostly concentrated in lower-elevation, wide, low-gradient streams with lower dam capacities. The geometry of these stream reaches creates more storage potential even with fewer beaver dams. Watersheds with the highest water deficits sometimes, but not always, overlapped with streams with highest water storage (Figure 3a).

We found that potential beaver dams conferred a total of 2,198 km^2 of fire resilience in areas with high fire risk (Figure 3d; an area slightly smaller than Yosemite National Park, Figure 3c).

Identifying priority watersheds for beaver restoration

We identified 10 watersheds at the highest risk of experiencing both water deficit and fire at the watershed scale (Figure 4a). Of those 10 watersheds, potential water storage from beaver dams ranged from 628 to 3760 m^3 (mean m^3/stream km per watershed, Figure 4b). Potential fire resilience gained by projected beaver restoration ranged from 2% to 28% of each watershed (% high-risk-high-capacity area/high risk area, Figure 4c).

A second approach to prioritize beaver restoration is to look at where water storage and fire resilience from beaver dams overlap. We overlaid potential water storage with potential fire resilience to identify stream segments with overlap (Figure 5a). Eight of the 31 study watersheds stood out in their potential for overlapping water storage and fire resilience benefits (Figure 5b). These eight watersheds had more than 8.7% (the third quartile) of stream area categorized as overlapping high potential for both water storage and fire resilience.

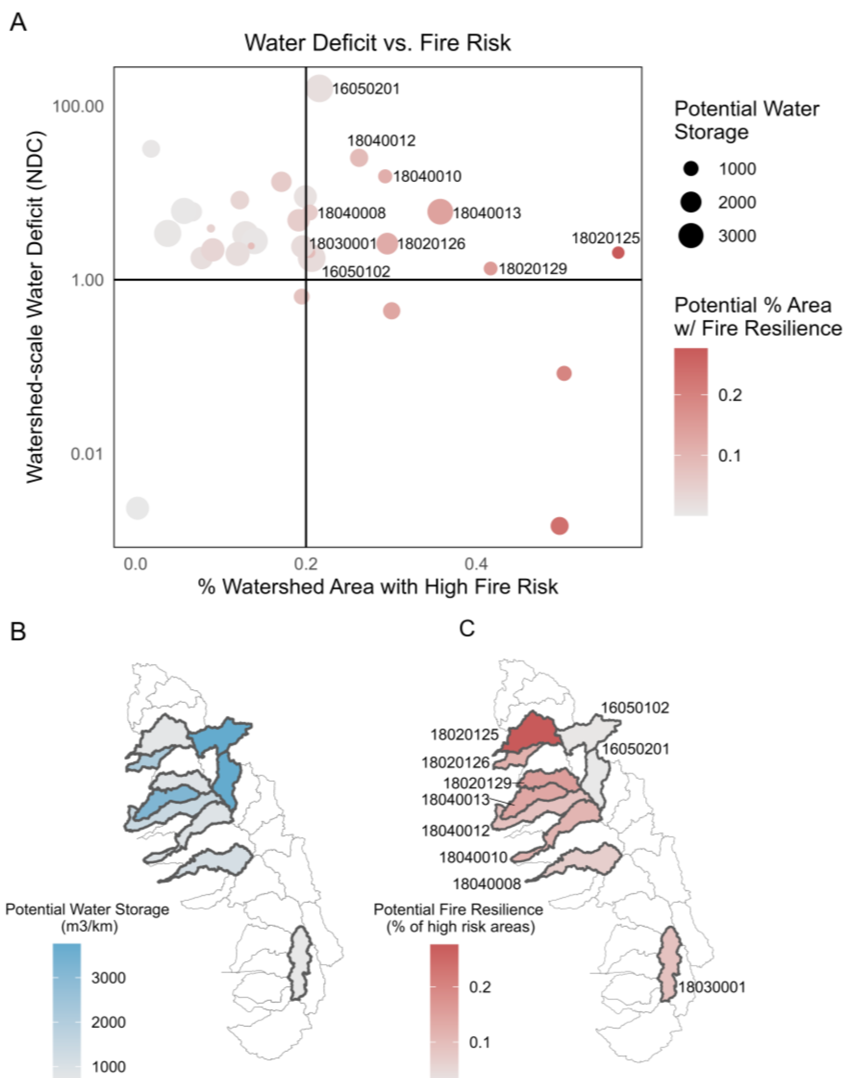

Figure 4: a) We identified priority watersheds by identifying watersheds with a water deficit (NDC > 1), and watersheds with more than 20% of area at high fire risk (WHP > 2000). We found 10 watersheds with both high NDC and high fire risk. These 10 priority watersheds had varying b) potential water storage and c) potential fire resilience.

Discussion

We found that current beaver dam building capacity in the Sierra Nevada region has declined nearly 50% compared to historical (i.e., pre-European) capacity, but the region retains considerable dam-building capacity across all 31 watersheds. Beaver restoration has the potential to increase water storage and fire resilience across the region, but the levels of water storage and fire resilience conferred by beaver dams varied by watershed. We identified the 10 most at-risk watersheds with the highest water deficit and fire risk and described the potential of beaver dams to store water and create fire resilience in those areas. We also identified eight watersheds with the most potential for overlapping water storage and fire resilience. Five of these high-potential watersheds were also identified as high-risk watersheds. Overall, restoring beaver populations and beaver dam-building capacity appears to be a promising component of water and fire resilience plans in the Sierra Nevada region.

Beaver dam capacity remains in all watersheds across the Sierra Nevada region

California's vegetation has undergone extreme change over the last three centuries, largely due to agricultural development (Shelton 1987). Conversion from natural landscapes to agricultural landscapes has significantly decreased vegetation suitability for beavers. The BRAT model scores all agricultural land use and agricultural vegetation types (such as orchards, crops, vineyards) as "0" or unsuitable for beavers, partially because some of these landscapes cannot sustain beaver populations and partially because beaver presence on highly agricultural landscapes can cause conflict (Macfarlane et al. 2017). Many of the watersheds in this study on the western side of the Sierra Nevada range extend into California's Central Valley, which is a highly agricultural area, and conversion of vegetation in this and other parts of the study region has led to a decline in vegetation suitability for beavers and a decline in potential beaver dam capacity throughout the region.

Despite extensive land-use change, considerable beaver dam building capacity remains in every watershed. Beavers are highly resilient and adaptable, and many areas retain the potential to sustain more than five beaver dams per stream kilometer, which would have considerable impacts on the ecosystem (Dittbrenner et al. 2022; Puttock et al. 2017). In this study region, areas with highest dam capacity tend to be concentrated in headwater streams, which are at higher elevations and tend to be in protected areas such as National Parks or National Forests. On the other hand, larger rivers that are too wide and swift or slope-limited stream corridors that are too steep for beavers to maintain dams have zero dam capacity (Macfarlane et al. 2017). The Central Valley region also has many areas

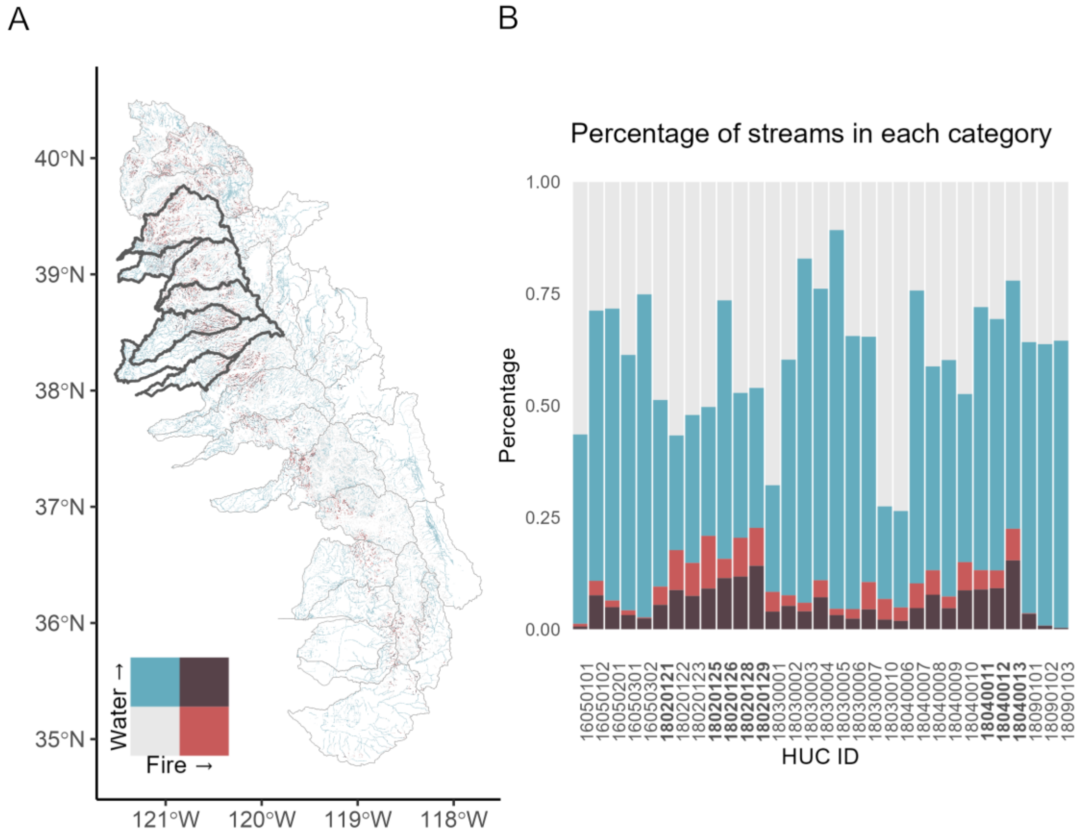

Figure 5: a) Map of the region showing areas that prioritize potential water storage, potential fire resilience, or both. We have categorized water storage and fire resilience equally based on statistical mean. b) We identified 8 watersheds where potential water storage and fire resilience was greater than 8.7% of stream area. These watersheds are highlighted on the map and in bold in the barplot.

with zero beaver dam capacity, mostly because of agricultural landscapes that would be unsuitable for beavers (Macfarlane et al. 2017).

We note that our analysis includes perennial and intermittent streams, with 47.5% of the streams included in our analysis identified as intermittent. We found that 23% of potential water storage and 53% of potential fire resilience are located on streams designated as intermittent in this region (Figure S2, Table S2). Studies have found that beavers can successfully build and maintain dams in intermittent streams, and often convert intermittent streams to perennial streams by raising water tables and creating flooded conditions (Gibson and Olden 2014). While often a positive outcome, this could be undesirable in some California streams, where intermittency is a natural occurrence that creates distinct community structures (Richmond et al. 2021; Fournier et al. 2023; Bogan et al. 2017; Bêche et al. 2006). Finally, it is important to note that the current dam capacity model results we present here represent a maximum beaver dam building capacity throughout this region and identifies places where beaver restoration is likely to be successful given landscape features and land use constraints. The next section of our study focuses on identifying where beaver restoration could maximize benefits for water storage and fire resilience on the landscape.

Potential water storage and fire resilience benefits from beavers

We identified 10 priority high-risk watersheds with both a water deficit and more than 20% of watershed area classified as high fire risk. Watersheds with a high water deficit generally have a high human development footprint, such as the Upper Carson (HUC 16050201), which includes Carson City, NV; and Lake Tahoe (HUC 16050101). These watersheds are cases where water demand is greater than renewable water supply. On the other hand, areas with high fire risk as defined in this study are associated with densities of natural fuels (e.g., forests, scrub or other vegetation), and do not take into account human development or structures at risk of fire damage (U.S. Forest Service 2020). Our analysis also identified areas where potential water storage and fire resilience benefits overlap, allowing us to maximize the broader ecosystem benefits of restoring beaver populations in this region. Five of the watersheds with the highest overlap of water-fire benefits were also priority high-risk watersheds, suggesting that restoring beaver populations in these watersheds could create considerable benefits in areas most at risk for the adverse effects of global change.

We note that areas with high potential water storage are not necessarily areas with the highest potential dam capacity. Often, potential water storage is highest in wider, less-steep stream channels in downstream parts of the watershed, which often have lower dam capacity but could store more water with fewer dams. In this study, we estimated that beaver ponds could store between 0 m^3 and 10,000 m^3 of surface water, with an average of 328 m^3 (SD: 1,047 m^3) These water storage estimates align with observations of water storage in beaver ponds around the world. Studies have estimated that beaver ponds store up to 11 km^3 of surface water in total globally, and large beaver dam complexes can store up to 10,000 m^3 of water at a given location (Karran et al. 2017; Dittbrenner et al. 2022). These literature values and the water storage estimates in our study only include surface water storage, but beaver complexes also increase groundwater storage. A study in Washington found that beaver complexes stored 2.4 times more groundwater than surface water (Dittbrenner et al. 2022), although the extent of groundwater response to beavers depends on valley width, channel confinement, and underlying soil types (Dittbrenner et al. 2022; Majerova et al. 2015; Westbrook et al. 2006; Hill and Duval 2009). Overall, our potential water storage estimates align with other observations of surface water storage in beaver ponds, but do not include potential groundwater storage, which represents even greater potential for storing water.

The connection between beaver dam-building activity and fire resilience is related to beavers flooding wetlands, raising water tables, and digging water-filled channels that fan into floodplain areas. Studies throughout the western US have found that streams with beaver activity maintain significantly higher vegetation greenness and decreased burn severity during fire events (Fairfax and Whittle 2020; Fairfax et al. 2024), and beavers are increasingly recognized for their potential to create fire resilient landscapes (Fairfax and Whittle 2020; Jordan and Fairfax 2022). While we restricted our fire resilience estimates to stream reaches with dam capacities of > 5 dams/km, studies of megafires in the Rocky Mountains have found that the presence of any number of beaver dams reduces burn severity, regardless of BRAT modeled dam capacity for that stream segment (Fairfax et al. 2024). Additionally, the areas we identified as high fire risk areas are not the only areas that are susceptible to wildfires. As such, beavers have the potential to create fire resilience anywhere on the landscape, and our estimates of where and how much beaver restoration could create fire resilience is extremely conservative.

Other considerations for prioritizing beaver reintroductions

Beavers have ecosystem impacts beyond their potential for water storage and fire resilience. In particular, beaver dam-building activity tends to benefit wetland taxa such as amphibians, waterbirds, and dragonflies, since they create slow-moving habitats, wet meadows, and improve stream-floodplain connection (e.g. Larsen et al. 2021). A variety of wetland species exist in California that could be specifically benefited by beaver dams. For example, the federally endangered Sierra Nevada Yellow-Legged Frog (*Rana sierrae*) has been observed in and around beaver ponds, which create slow-flowing lentic waters critical to this species (Brown et al. 2019; Yarnell et al. 2019; CDFW 2024). Similarly, beaver activity has the potential to benefit the federally threatened California Tiger Salamander (*Ambystoma californiense*). There is extremely limited work on the relationship between beaver activity and *A. californiense*, but studies on Barred Tiger Salamanders (*A. mavortium*) in the Rocky Mountain region found positive relationships between beaver ponds and tiger salamanders (Hossack et al. 2015; CDFW 2024). Overall, very little research exists about interactions between California endemic wetland species and beavers, and future studies are needed to examine how beaver restoration influences biodiversity of critical wetland species. Apart from wetland species, beavers create wet meadow ecosystems and influence food availability for herbivores such as deer, and may also interact with wolves, who predate both deer and beavers (Gable et al. 2020). Interactions between growing populations of wolves and beavers in California also merits further study.

The Sierra Nevada region included in this study represents a wide variety of land ownership and management types, including public and private lands. Specifically, in the five watersheds identified as high-risk/high potential, we found that the majority of land is owned by private entities, and the majority of potential beaver dams and water storage also occurs on private lands. However, potential fire resilience tends to be more prevalent on public lands. This indicates considerable potential for the state of California to spearhead beaver restoration on public lands, as well as the need to engage private landowners in beaver restoration. After beaver policy in California was updated in June 2023 to allow for beaver translocation within the state (CDFW 2023), the California

Department of Fish and Wildlife started accepting applications from land management entities and private landowners who wish to have beavers relocated to their property. In the future, incentives and cost sharing programs via Farm Bill conservation programs or California Wildlife Conservation Board resources could encourage additional beaver restoration activity on private lands and help mitigate any conflicts that might arise with increased beaver activity throughout the region.

Implications for prioritizing restoration of a keystone species

Prioritization, or identifying areas with the greatest need or greatest potential for restoration success, has guided ecosystem conservation and restoration for decades (Myers et al. 2000). Considering the outsized effects of keystone species is a crucial element of building restoration priorities. For example, the reintroduction and subsequent expansion of wolves into the greater Yellowstone ecosystem influenced migratory patterns of elk herds, their primary prey species (Middleton et al. 2013). Restoring salmonid populations to rivers in the Pacific Northwest can help restore nutrient exchange and food web connections between aquatic and riparian ecosystems (Moravek et al. 2021). Both of these examples also impact humans: Yellowstone wolves draw tourists but also create human-wildlife conflict by killing livestock and changing elk herd dynamics; and Pacific salmonids are a culturally important group of species that also support critical fisheries.

Beavers are no exception. Not only a keystone species but specifically an ecosystem engineer, beavers and their dam-building activity create critical ecosystem and biodiversity benefits as well as landscape-scale resilience to global change. This is an important example of how restoring an ecosystem engineer aligns biodiversity and climate resilience objectives at a landscape scale. Beaver reintroduction allows us to prioritize not only where beavers are most likely to survive, but where they will specifically create water and fire benefits and help us adapt to global change.

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Supplementary Information

Figure S1: Change in beaver vegetation suitability index between historical and current vegetation layers. Most dam capacity loss can be attributed to major shifts in vegetation type, especially in the Central Valley area where natural vegetation has largely been converted to agricultural landscapes. Beaver-favorable vegetation has changed over time. Blue represents an increase in beaver-favorable vegetation, and red indicates a decrease.

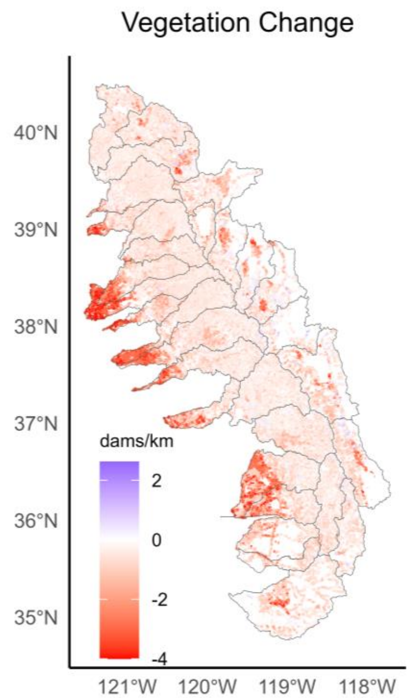

Figure S2: Potential beaver dam building capacity in intermittent streams. Intermittent streams make up 46.8% of all streams in this region. Intermittent streams store 23% of total potential water storage and create 52% of potential fire resilience area in this region, meaning that intermittent streams are disproportionately more important to fire resilience than perennial streams.

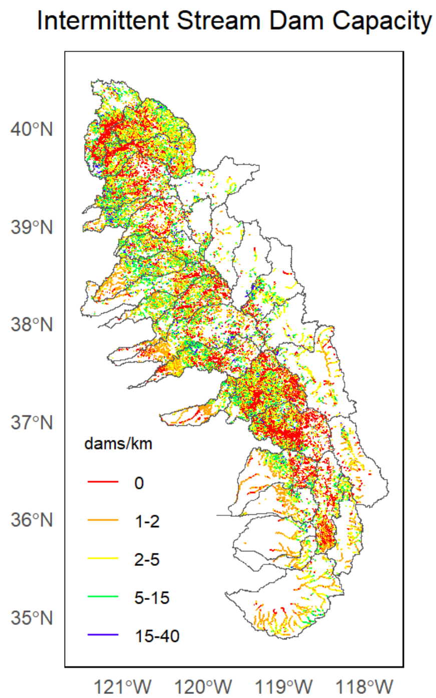

Table S1: Historical and current dam capacity (dams/km), percent dam capacity remaining (%), water deficit (NDC), fire risk (% of total area where WHP > 2000), and potential water storage (m^3/km) broken down by watersheds. Watersheds identified as high risk/high potential are highlighted in gray.

HUC ID	Watershed Name	Mean Historical Dam Capacity (dams/ km)	Mean Current Dam Capacity (dams/ km)	Mean % Dam Capacity Remaining	Water Deficit (NDC)	Fire Risk (% of total area where WHP> 2000)	Potential Water Storage (m^3/km)	Potential Fire Resilience (% of stream area with fire resilience)
16050101	Lake Tahoe	14.25	6.80	52.79	32.13	1.83	1398.38	0.50
16050102	Truckee	10.30	5.11	55.51	1.77	20.67	3760.23	2.52
16050201	Upper Carson	9.70	4.50	58.38	159.14	21.57	3755.90	2.09
16050301	East Walker	10.95	5.75	68.29	3.33	12.91	3393.05	1.11
16050302	West Walker	10.30	4.83	64.60	2.80	13.94	3461.71	0.65
18020121	North Fork Feather	10.48	5.00	52.50	0.64	19.50	1105.71	7.57
18020122	East Branch North Fork Feather	10.75	4.56	55.51	0.00	49.75	1432.34	23.61
18020123	Middle Fork Feather	9.80	4.41	60.16	0.44	30.05	1301.39	13.11
18020125	Upper Yuba	8.84	4.37	62.84	2.05	56.63	733.39	27.66
18020126	Upper Bear	13.09	5.21	51.80	2.60	29.54	2173.92	11.97
18020128	North Fork American	10.08	4.25	52.04	0.08	50.28	1013.67	19.56
18020129	South Fork American	12.60	5.50	50.78	1.35	41.66	854.36	15.49
18030001	Upper Kern	6.99	3.43	70.06	2.06	20.44	627.65	8.95
18030002	South Fork Kern	8.59	5.02	81.31	2.41	19.59	2389.69	2.61
18030003	Middle Kern	6.04	1.83	55.90	9.03	19.92	2429.41	1.48
18030004	Upper Poso	8.33	2.94	46.04	1.98	11.97	2721.92	2.29

18030005	Upper Deer-Upper White	5.95	1.77	44.29	3.41	3.77	3593.69	0.55
18030006	Upper Tule	9.49	2.49	30.52	1.78	7.77	2336.68	2.04
18030007	Upper Kaweah	9.33	2.82	37.33	13.40	17.11	1871.34	5.68
18030010	Upper King	6.40	4.09	80.44	2.45	13.57	491.87	8.67
18040006	Upper San Joaquin	7.30	4.74	81.00	3.89	8.84	506.75	4.39
18040007	Fresno River	9.06	3.11	38.99	2.21	9.06	2528.12	3.72
18040008	Upper Merced	11.54	5.37	54.74	5.94	20.44	1116.04	5.79
18040009	Upper Tuolumne	10.79	4.50	61.29	8.25	12.23	1526.60	3.80
18040010	Upper Stanislaus	10.72	3.89	44.24	15.49	29.29	888.22	11.41
18040011	Upper Calaveras California	15.68	4.46	33.45	4.83	19.13	2317.61	5.39
18040012	Upper Mokelumne	15.28	1.98	19.64	25.27	26.23	1459.40	8.91
18040013	Upper Cosumnes	13.69	4.30	38.45	6.07	35.75	3193.78	13.83
18090101	Mono Lake	10.86	6.85	104.51	6.06	6.66	1679.80	0.38
18090102	Crowley Lake	9.60	3.79	80.98	6.19	5.70	3300.41	0.24
18090103	Owens Lake	10.53	3.34	78.84	0.00	0.23	2466.65	0.07

Table S2: Current potential dam capacity broken down by percent of stream that is intermittent. The rest of the stream is perennial.

Dam Capacity	% intermittent (by length)
All streams	47.5%
0 dams/km	12.8%
1-2 dams/km	0.7%
2-5 dams/km	16.7%
5-15 dams/km	9.2%
15-40 dams/km	1.5%

Table S3: Private land and potential beaver dams, water storage, and fire resilience on private lands in each watershed. Watersheds identified as high risk/high potential are highlighted in gray.

HUC ID	Watershed Name	% Private Land	% Potential Dams on Private Land	% Potential Water Storage on Private Land	% Potential Fire Resilience on Private Land
16050101	Lake Tahoe	34.7	17.5	55.9	1.1
16050102	Truckee	14.1	30.7	19.4	9.2
16050201	Upper Carson	4.2	15.1	8.5	11.3
16050301	East Walker	6.7	21.8	8.4	7.2
16050302	West Walker	4.1	18.6	22.2	0.4
18020121	North Fork Feather	44.3	49.8	63.9	16.7
18020122	East Branch North Fork Feather	19.4	32.9	56.0	8.1
18020123	Middle Fork Feather	37.7	46.4	78.9	13.1
18020125	Upper Yuba	47.9	66.4	72.7	18.5
18020126	Upper Bear	89.1	91.5	92.7	44.6
18020128	North Fork American	34.5	45.9	40.3	17.2

18020129	South Fork American	49.1	57.3	61.3	34.7
18030001	Upper Kern	2.3	6.2	9.3	2.2
18030002	South Fork Kern	9.5	10.5	26.5	1.6
18030003	Middle Kern	80.7	82.3	97.2	14.1
18030004	Upper Poso	89.5	81.6	98.2	27.4
18030005	Upper Deer-Upper White	92.6	78.3	81.7	23.8
18030006	Upper Tule	71.6	63.8	93.2	10.2
18030007	Upper Kaweah	70.7	58.9	90.0	13.5
18030010	Upper King	5.8	10.1	12.6	4.8
18040006	Upper San Joaquin	13.7	13.0	22.0	18.4
18040007	Fresno River	92.2	72.7	95.0	34.4
18040008	Upper Merced	29.8	24.3	43.2	10.6
18040009	Upper Tuolumne	35.4	33.1	54.3	21.1
18040010	Upper Stanislaus	40.3	37.2	54.2	18.4
18040011	Upper Calaveras California	89.4	92.0	97.6	49.6
18040012	Upper Mokelumne	71.9	70.8	87.7	30.3
18040013	Upper Cosumnes	78.9	77.5	88.8	33.1
18090101	Mono Lake	4.0	19.3	42.4	15.8
18090102	Crowley Lake	3.2	10.3	12.3	3.0
18090103	Owens Lake	11.0	6.6	5.1	0.0

Conclusion

This dissertation explored three approaches to conserving and restoring freshwater ecosystems: area-based conservation, local restoration, and wildlife reintroduction. These three strategies have been applied at different scales, in watersheds facing different challenges, and in situations with different priorities, but all focus on balancing humans and ecosystems. Understanding the potential benefits and limitations of these conservation strategies will help policymakers, land managers, and wildlife agencies make informed decisions that lead to more resilient freshwater ecosystems.

In chapter one, I examined how area-based conservation plans can be shifted to specifically include freshwater ecosystems. Centering protected areas on river networks not only better protects rivers, but it also helps achieve the biodiversity, carbon storage, and environmental justice goals of many area-based conservation efforts. By focusing on watershed-scale conservation and considering freshwater connectivity, watershed disturbance, flow alteration, water quality, and biodiversity, protected areas can better conserve and benefit from freshwater ecosystems.

Chapter two explored local restoration efforts in the Klamath River watershed. Man-made off-channel floodplain ponds provided cool water thermal refuge habitat for juvenile coho and steelhead during the hottest summer months. Off-channel ponds also provided more stable thermal habitats, and thermal stability in these ponds increased over time. This small-scale restoration effort quickly and effectively recreated an essential structural element of the river ecosystem and provided valuable refuge habitat for a critical species.

In chapter three, I considered how reintroducing a native wildlife species, the North American beaver, has the potential to create landscape-scale resilience to global change. I modeled potential beaver dam building capacity in the Sierra Nevada region of California, and estimated how much water beaver dams could store and how much fire resilience they could create on the landscape. Considerable beaver dam building capacity exists in all watersheds in the study region, and there are several watersheds with high potential for both water and fire related beaver benefits. This study demonstrates how wildlife reintroduction can benefit stream ecosystems, biodiversity, and resilience to global change.

Area-based conservation, local restoration, and wildlife reintroduction are overlapping approaches to creating resilient freshwater ecosystems. However, no single strategy is applicable in all scenarios or able to solve all problems. The needs of freshwater ecosystems and the ways in which humans use them vary widely, and a diverse portfolio of conservation and restoration solutions are necessary to achieve ecosystem goals as we confront unpredictable and increasingly rapid global change (Schindler et al. 2015).

The portfolio theory was originally developed as an investment strategy that aims to reduce risk by diversifying assets (Schindler et al. 2015). In a similar way, diverse life histories, communities, habitats, and ecosystems have long been known to create biological stability (Schindler et al. 2015). For example, studies in Bristol Bay, Alaska show that diverse life histories of sockeye salmon led to overall stability in fishery yield, even as individual populations vary year to year (Schindler et al. 2010). Primary productivity in grassland communities with higher species diversity was shown to be more stable than lower diversity communities during drought (Tilman and Downing 1994; Doak et al. 1998). Habitat diversity can also create ecosystem stability: for example, adult chinook salmon in Oregon exploit cooler habitat patches in streams (Torgersen et al. 1999), and groundwater fed ponds in the Klamath River watershed provide cool water thermal refuges for juvenile salmonids (Chapter Two).

The concept of diversity promoting overall biological stability has also been applied to conservation planning. In an uncertain climate future, it is almost impossible to accurately predict threats to ecosystems (Eaton et al. 2019). To address this issue, a diversity of conservation strategies with different locations, scales, and critical ecosystem elements has been proposed as a risk reduction strategy to addressing uncertain future threats to functional ecosystems (e.g. Aplet and McKinley 2017; Mallory and Ando 2014). Similarly to this theory of conservation, the three freshwater conservation strategies presented in this dissertation deal with different scales, ecosystem elements, and conservation priorities that together create part of a complementary conservation portfolio. For example, chapter one tackles regional and national conservation planning, while chapter two examines hyper-local restoration efforts, and chapter three considers regional stream restoration through wildlife reintroduction. Each chapter also explores different ecosystem elements: chapter one addresses broad freshwater connectivity, chapter two focuses on habitat quality for a certain species, and chapter three investigates restoring a single species with broad ecosystem benefits. These strategies, along with many others, contribute to a diverse freshwater conservation portfolio that can hopefully weather widespread global change.

In the context of global conservation strategies, these three chapters are widely applicable outside that state of California. Chapter one, which explores how freshwater ecosystems can be effectively integrated into 30x30 conservation plans, can be applied to 30x30 initiatives at state, national, and international scales (e.g. Campaign for Nature 2021; US Executive Order No 14008 2021; California [CA] Executive Order N-82- 20). Chapter two, which explores how local restoration strategies can create valuable refuge habitat during longer-term efforts like large-scale dam removal, is pertinent as dam removal projects become more common across the Western US and in Europe (Habel et al. 2020; Jumani et al. 2023). Beaver restoration has gained attention in California and throughout the western United States as a valuable strategy for addressing drought and fire threat and for restoring freshwater ecosystem function and is also increasingly recognized in the United Kingdom as critical for restoring stream ecosystems and species (Fairfax and Whittle 2020; Stringer and Gaywood 2016).

Finally, developing and implementing a robust portfolio of conservation strategies requires input from people with diverse perspectives, priorities and backgrounds. The three approaches discussed here range from state- or nation-wide policy (Chapter One), to hyper-local restoration efforts that take place largely on private land (Chapter Two), to regional wildlife reintroduction that affects local landowners and communities as well as the larger landscape (Chapter Three). These far-ranging strategies were developed by people with many different perspectives and skill sets, all of which contribute to the overall freshwater conservation portfolio (e.g. Morrison and Steltzer 2021). Ultimately, balancing humans and freshwaters requires many perspectives, collaboration between many groups, and different, complementary strategies.

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