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To cite this article: Scott L Stephens *et al* 2021 *Environ. Res. Commun.* **3** 081004

Environmental Research Communications

OPEN ACCESS

RECEIVED
6 May 2021

REVISED
20 July 2021

ACCEPTED FOR PUBLICATION
26 July 2021

PUBLISHED
6 August 2021

LETTER

Fire, water, and biodiversity in the Sierra Nevada: a possible triple win

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Keywords: wildfire, resilience, mixed conifer, climate change, adaption, hydrology

Abstract

Reducing the risk of large, severe wildfires while also increasing the security of mountain water supplies and enhancing biodiversity are urgent priorities in western US forests. After a century of fire suppression, Yosemite and Sequoia-Kings Canyon National Parks located in California's Sierra Nevada initiated programs to manage wildfires and these areas present a rare opportunity to study the effects of restored fire regimes. Forest cover decreased during the managed wildfire period and meadow and shrubland cover increased, especially in Yosemite's Illilouette Creek basin that experienced a 20% reduction in forest area. These areas now support greater pyrodiversity and consequently greater landscape and species diversity. Soil moisture increased and drought-induced tree mortality decreased, especially in Illilouette where wildfires have been allowed to burn more freely resulting in a 30% increase in summer soil moisture. Modeling suggests that the ecohydrological co-benefits of restoring fire regimes are robust to the projected climatic warming. Support will be needed from the highest levels of government and the public to maintain existing programs and expand them to other forested areas.

Introduction

Fire has been an integral ecosystem process in western U.S. forests for millennia. Lightning was the primary ignition source, and later, American Indians added ignitions by burning for cultural purposes. The invasion of Euro-Americans in the mid-1800s disrupted natural fire occurrence by both reducing the influence of Indigenous burning practices and introducing widespread livestock grazing, which limited fuel continuity and fire spread (Taylor *et al* 2016, Pyne 2019). Active fire suppression, which began in the early 20th century, further disrupted natural fire occurrence and ultimately led to a widely adopted policy of full fire suppression across all U.S. federally managed lands (Stephens *et al* 2016). This suppression policy was highly effective at eliminating fire for decades but recent wildfire activity has increased and this has been accompanied with severe land management problems (Calkin *et al* 2015).

In 1962, the Secretary of the Interior asked a committee to investigate wildlife management problems in the U.S. national parks. This committee, named after its chair, Dr Starker Leopold, took the broader ecological view

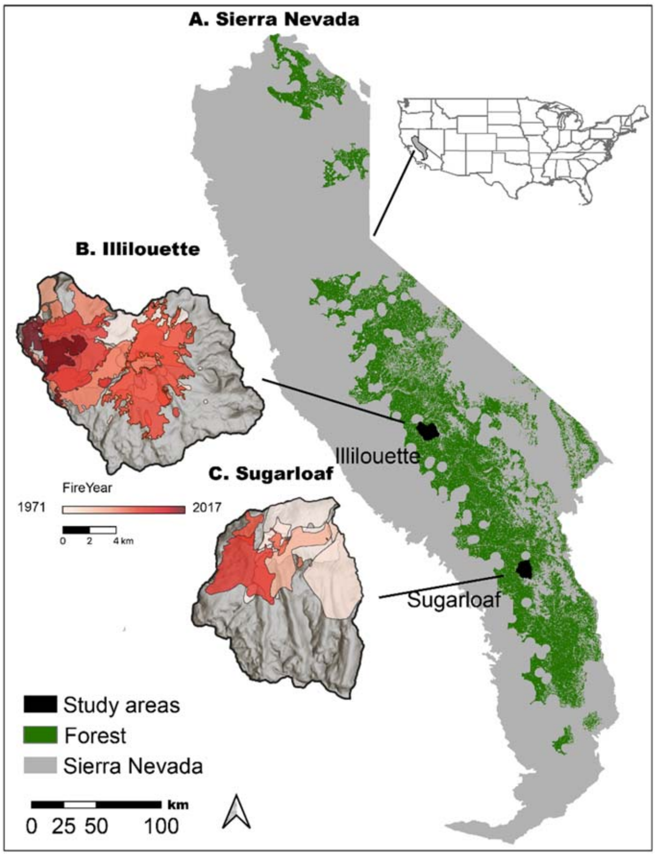

Figure 1. Sierra Nevada forests with managed wildfire potential, locations of study areas, and perimeters of wildfires that burned in Illilouette and Sugarloaf creek basins during the wildfire management program (~1972-present). Fire perimeters were obtained from a database generated by the state of California (FRAP 2020) and are shaded based on wildfire year (darker red = more recent). Forested areas with actual or potential managed wildfire use (green areas in A) are classified as those outside of the wildland urban intermix (WUI; Radeloff *et al* 2017) threat zone and where the contiguous land area is at least as large as our smaller study basin (Sugarloaf; ~13,000 ha). Forested areas are defined according to LANDFIRE biophysical settings data (Rollins 2009). WUI threat zone definition follows the strategic fire management zone alternative A of the Sierra National Forest land management plan (USDA 2019).

that parks should be managed as ecosystems (Leopold *et al* 1963). As a result, the U.S. National Park Service changed its policy in 1968 to recognize fire as an ecological process. Fires would be allowed to burn if they could be contained within fire management units and accomplished approved management objectives (figure 1).

Sequoia and Kings Canyon National Parks established a natural fire management zone in 1968 immediately after this policy change (Kilgore and Briggs 1972), and thus began the first tentative experiments with managing naturally ignited fires deep in park wilderness. This was followed in 1972 with a similar zone designation in Yosemite National Park (van Wagtendonk 1978). These three national parks have the longest periods of allowing lightning fires to burn in the USA. The objective of these programs was to restore the ecological role of fire under prescribed conditions (figure 2). Among land management agencies, these national parks have been world leaders in the increasingly difficult effort to allow lightning-ignited fires to burn. Concerns over smoke, at-risk species, the threat posed by fires to nonfederal lands, and the uncertainty of potential impacts should fires grow beyond expected boundaries have hindered full implementation of managed wildfire programs (Miller *et al* 2012). Even with these constraints, the parks and a few U.S. Forest Service wilderness areas remain committed to allowing wildland fires to play their ecological role. The U.S. Forest Service is currently moving ahead with plans to expand natural fire programs in California (Meyer 2015).

In this paper we summarize what has been learned from 50 years of managed fire programs in Sierra Nevada national parks. Very few areas with such a legacy of fire-use exist making these areas critical natural laboratories which have accordingly received increasing attention from scientists. As managers, policy makers, and the public work to create long-term solutions to conserve U.S. forests, these areas could prove invaluable in future program and policy design.

Figure 2. Repeat photographs taken from field plots in Illilouette Creek basin. The left two images (A), (B) were taken 1 and 9 years following low severity fire. The right two images (C), (D) were taken 1 and 9 years following moderate severity fire. Fire severity class for these plots was based on Landsat-derived Relative differenced Normalize Burn Ratio, using thresholds presented in Miller and Thode (2007). A small patch of fire-killed trees is also evident in Image D, just beyond the red oval, which contains numerous snags and saplings that regenerated following the 2001 Hoover Fire. Red ovals identify the same point in the photographs.

Fire severity and vegetation

Fire severity in the basins was assessed using the Relative differenced Normalized Difference Vegetation Index (RdNDVI) for fires prior to 1984 and Relative differenced Normalized Burn Ratio (RdNBR) for fires post 1984. RdNDVI and RdNBR were derived based on Parks *et al* (2018) Google Earth Engine algorithm. Both RdNDVI and RdNBR distributions for each fire was thresholded (Miller and Thode 2007), where values between 0 and 315 were classified as low severity, 316 and 640 as moderate severity, and values above 641 were classified as high severity. These thresholds were calibrated by Collins *et al* (2009), based on fires that occurred in Yosemite National Park. Despite 80–100 years of fire exclusion policies from ~1880 to 1970, the frequency of contemporary fire activity in both basins is similar to the pre fire exclusion period using dated fire scars (~1700–1880 C.E.; Collins and Stephens 2007). The long fire-free period (~1880–1970) coincided with substantial tree recruitment relative to the historical and contemporary natural fire periods (Collins and Stephens 2007) and allowed for considerable surface fuel accumulation (Parsons and Debenedetti 1979). Given these changes one might assume that fire severity, as measured using remotely sensed imagery (e.g., Miller and Thode 2007), would be elevated when fire was reintroduced. This was not the case in either basin. In Illilouette, the first widespread fire under the managed wildfire program, the 1974 Starr King Fire, burned nearly 1600 ha (van Wagtendonk 1978) and only 9% was at high severity (Collins *et al* 2009). Since then, only 14% of the total burned area in Illilouette was classified as high severity, and in Sugarloaf, high severity accounted for 16% of total burned area. For comparison, 27% of the area outside of the Illilouette and Sugarloaf basins in the Sierra Nevada burned at high severity from 1984 to 2018 (figure 3).

The return of fire to these basins has allowed investigation into the processes driving natural fire-vegetation dynamics. The fact that neither timber harvesting or road building occurred in either basin strengthens inferences from these investigations. Within individual fires, the dominant vegetation type (i.e., *Pinus*-dominated forest, *Abies*-dominated forest, montane chaparral) and weather were most strongly connected to fire severity (Collins *et al* 2007). At the landscape level, time-since-last-fire, previous fire severity (for reburns), and dominant vegetation type influenced fire severity (Collins and Stephens 2010, van Wagtendonk *et al* 2012).

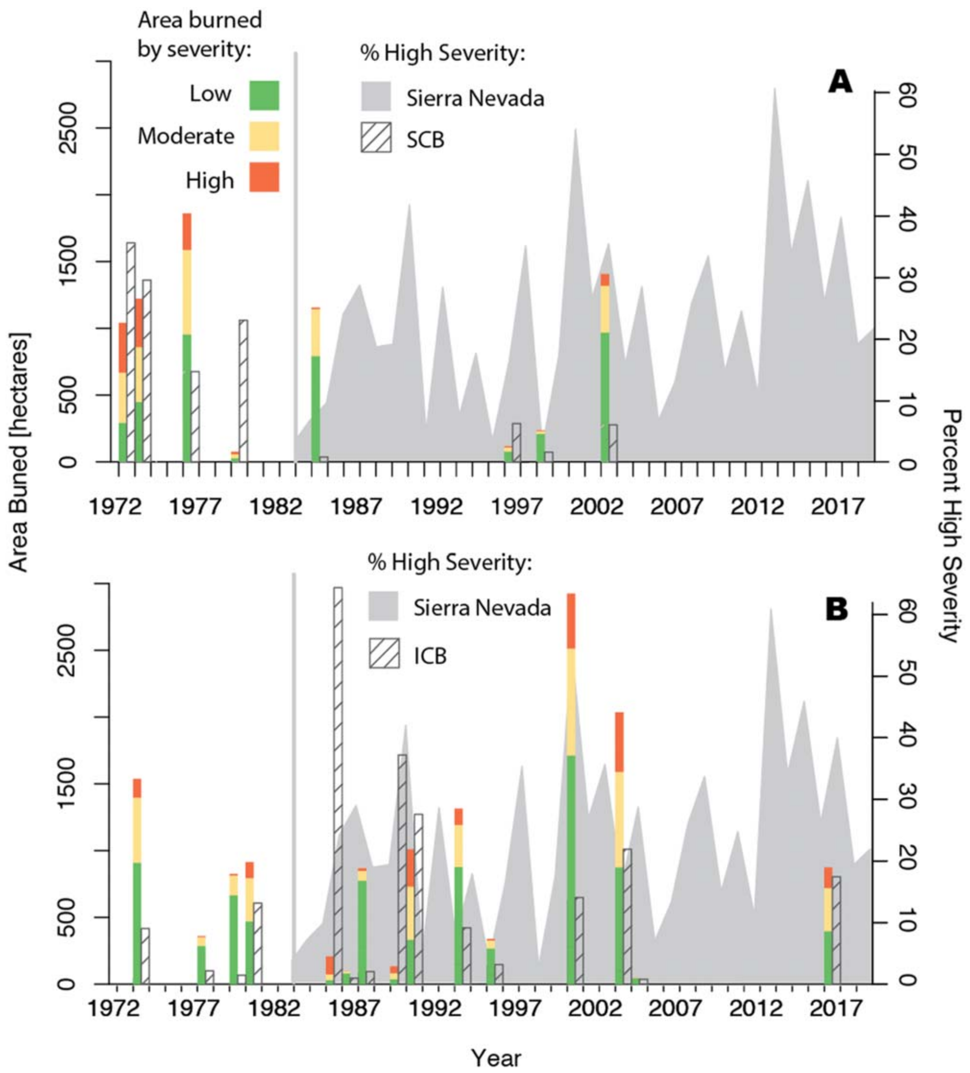

Figure 3. Proportion of fire area burned at low, moderate, and high severity as classified by LANDSAT-derived RdNDVI (prior to 1984) and RdNBR (post 1984) severity indices for fires burned in Sugarloaf Creek Basin-SCB (A) and Illilouette Creek Basin-ICB (B). Fire severity class thresholds were based on those in Collins *et al* (2009) and Miller and Thode (2007) for RdNDVI and RdNBR, respectively. Proportion of the yearly fire area burned at high severity is shown as vertical bars with diagonal line in both panels, which corresponds with the right vertical axis. For comparison, the proportion of yearly fire area burning at high severity in the entire Sierra Nevada bioregion (Rakhmatulina *et al* 2021a) is shown in light gray, also corresponding with the right vertical axis.

Time-since-last-fire also exerted a strong control on whether fires re-burned over previous fire areas (Collins *et al* 2009).

Assessments of landscape-scale vegetation change using aerial photography during the managed fire period revealed different outcomes for Illilouette (1970–2012; Boisramé *et al* 2017a) and Sugarloaf (1973–2014; Stevens *et al* 2020). In Illilouette, the proportion of the basin comprised of conifer forest decreased from 82% to 62%, being replaced by shrublands and meadows. In Sugarloaf, forest cover changed very little: from 83% to 82%. Accordingly, contemporary vegetation cover classes (forest, shrub, sparse and dense meadow) are more balanced, with greater landscape heterogeneity in Illilouette compared to Sugarloaf (Stevens *et al* 2020). Plot-level forest structure data collected in the early 1970s provided further evidence that forest stand structure in Sugarloaf did not change markedly as a result of the managed fire program (Stevens *et al* 2020). However, across both basins, conifer-dominated areas that burned in managed fires (including reburns) had highly variable structure and composition, ranging from open *Pinus jeffreyi* dominated forests, dominated by large trees (tree density: 104 ha^{-1}; basal area 19.5 m^2ha^{-1}) to dense, closed-canopy structures dominated by *Abies concolor and A. magnifica* (tree density: 446 ha^{-1}; basal area 53 m^2ha^{-1}) (Collins *et al* 2016). The two primary drivers of this variability were the local biophysical environment and recent fire severity. Despite this high variability, surface fuel loads and tree densities in both basins are markedly lower than in comparable portions of the Sierra Nevada where fire has been successfully excluded in the modern era (Collins *et al* 2016).

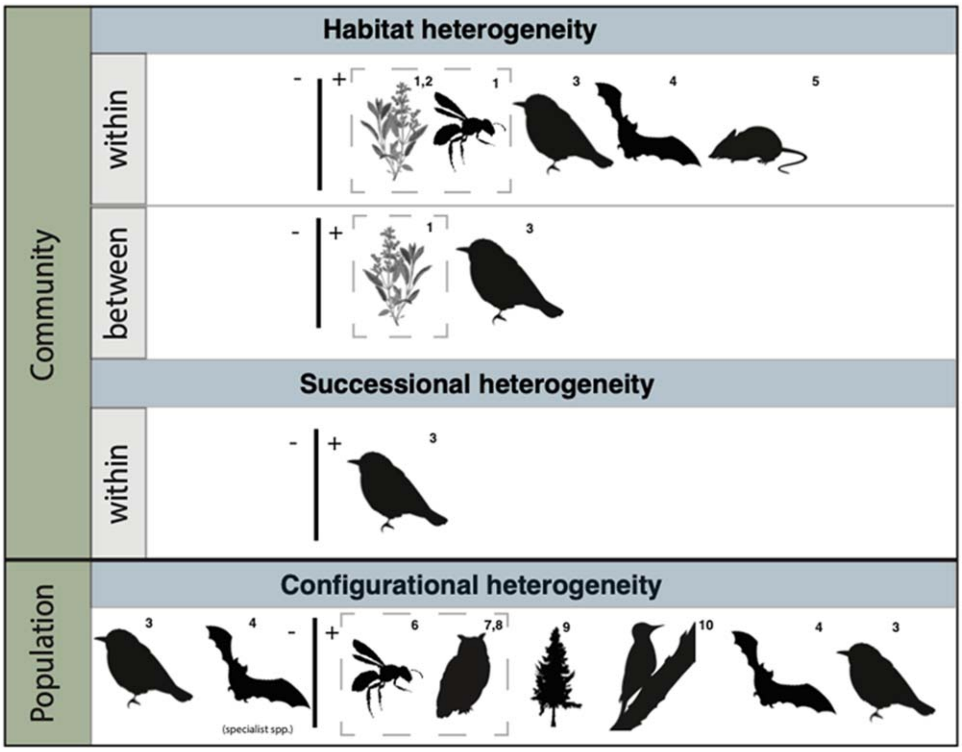

Figure 4. Studies finding evidence for (+) or against (−) the proposed mechanisms by which pyrodiversity begets biodiversity. Pyrodiversity may promote biodiversity by increasing variation in landscape composition (habitat and successional heterogeneity) and/or by increasing variation in the spatial arrangement of fire elements (configurational heterogeneity). The dashed grey boxes indicate studies were primarily conducted or at least partially in the Illilouette and Sugarloaf basins. Other studies examine the effect of mixed severity fires in the Sierra Nevada forests, the restoration of which is the intention of managed wildfire programs. 1 Flowering plants and bees- Ponisio *et al* 2016; 2 Understory plants - Wilkin *et al* 2021 (in press); 3 Birds - Tingley *et al* 2016; 4 Bats - Steel *et al* 2019; 5 Small mammals - Roberts *et al* 2015; 6 Bees- Ponisio 2020; 7,8 Birds (spotted owls) - Hobart *et al* 2021 and Kramer *et al* 2021; 9 Trees- Blomdahl *et al* 2019. 3,4 found evidence both for and against a specific mechanism depending on species.

The divergent effects of the managed fire program on vegetation in the two basins has several possible explanations. Illilouette has higher precipitation and vegetation productivity than Sugarloaf (Stevens *et al* 2020); therefore, it is possible that the increase in fuel during the fire exclusion period was greater in Illilouette, resulting in more frequent fires with larger high severity proportions that created larger patches of non-forest vegetation. Another possible reason for the difference is many fires have been suppressed in the last 15 years in Sugarloaf (Stevens *et al* 2020). The increase in vegetation heterogeneity in Illilouette is clearly related to the greater incidence of small high severity patches in this basin and the stability of fire severity classes over the decades (figure 3).

Biodiversity

Wilderness areas managed for wildfire in the Sierra Nevada support greater pyrodiversity (variability in fire severity, season, size, frequency) and consequently greater landscape heterogeneity (van Wagtendonk and Lutz 2007, Boisramé *et al* 2017a, Steel *et al* 2021) than comparable fire-suppressed areas. Ecological theory predicts that diversity, including pyrodiversity, begets biodiversity (Martin and Sapsis 1992). Multiple mechanisms by which pyrodiversity promotes biodiversity have been proposed at community and population scales (Kelly *et al* 2017, Jones and Tingley 2021, figure 4). Studies in Illilouette and Sugarloaf have shown that pyrodiversity created by managed wildfire is associated with higher biodiversity (bees and understory plants: Ponisio *et al* 2016, Ponisio 2020, Wilkin *et al* 2021 in press) and is compatible with at least some mature forest specialists (California spotted owl, *Strix occidentalis occidentalis*: Hobart *et al* 2021, Kramer *et al* 2021). Because few population- or community-level studies on the effect of fire management have been conducted primarily in Illilouette and Sugarloaf, we also considered studies conducted in similar Sierra Nevada landscapes. Corroborating Illilouette and Sugarloaf studies, pyrodiversity in other comparable regions is positively related to mammal, bird, bat, and tree biodiversity (Roberts *et al* 2015, Tingley *et al* 2016, Blomdahl *et al* 2019, Steel *et al* 2019) (figure 4). These lines of evidence suggest use of managed wildfire and restoration of pyrodiverse landscapes is broadly supportive of biodiversity in Sierra Nevada and similar ecosystems.

We also found support for a variety of mechanisms underlying the positive effect of pyrodiversity in and around the Illilouette and Sugarloaf basins. Within bird, bee, plant, and bat communities, habitat heterogeneity underlies enhanced biodiversity (figure 4). Specifically, pyrodiversity leads to local variation in fire history generating spatial niche diversity and allowing a greater number of species to coexist (Kelly *et al* 2017). Among communities, studies on flowering plants and birds found that the fire severity heterogeneity enhances beta-diversity (figure 4) because species are associated with different fire histories. These results highlight the potential for managed wildfire areas and their expansion to improve regional biodiversity, which is adversely affected by the homogenizing effects of both fire suppression and large high severity fires.

The successional heterogeneity mechanism has not been explicitly addressed for many taxa in the Sierra Nevada and is often conflated with habitat heterogeneity because different fire severities are often characterized as supporting species from different successional stages (e.g., higher severity fires support 'early successional' species) (Ponisio *et al* 2016). However, Tingley *et al* (2016) found that both habitat and successional heterogeneity enhanced bird coexistence in the Sierra Nevada. It is likely, therefore, that a combination of spatial and temporal heterogeneity of fire histories promotes biodiversity, as originally proposed by Martin and Sapsis (1992).

At the population scale, fire-generated heterogeneity promoted persistence in specific species of birds and bats that use areas with different fire histories for specific food resources/prey species, shelter, and/or avoid predation (Tingley *et al* 2016, Steel *et al* 2019, figure 4). For example, Black-backed woodpeckers (*Picoides arcticus*) benefited from configurational heterogeneity (number, size, and arrangement of habitat patches) along high severity patch edges perhaps reflecting the trade-offs of predation risk, nest site availability, and food resources within high severity patches (Stillman *et al* 2019, 2021). Similarly, fire refugia can support survival during and immediately following fire for California spotted owls (*Strix occidentalis occidentalis*) and some tree species (Blomdahl *et al* 2019, Hobart *et al* 2021, Kramer *et al* 2021). We would expect to find similar positive responses to configurational heterogeneity for other species that have resource/shelter needs associated with patches of different fire severities or unburned forest, but negative responses for some habitat specialists. In Illilouette, Ponisio (2020) found that the combination of local pyrodiversity enabled populations of species with the ability to switch floral interaction partners to persist through a severe drought. Fire-supported heterogeneity may therefore enhance community resistance to climate change in other species that, similar to bees, benefit from the different resources afforded by patches with disparate fire histories.

Together, the ample evidence across taxa (birds, mammals, insects and plants) and ecological scales (population, within and between communities) that pyrodiversity benefits biodiversity through a variety of mechanisms. This suggests that the expansion of the managed wildfire model to analogous areas in the Sierra Nevada mixed conifer forest would benefit biodiversity regionally and perhaps help ecological communities adapt to growing threats associated with global change.

Hydrology and climate change

The conversion of dense, fire-excluded forest to a mosaic of grasslands, wet meadows, shrublands, and forest stands of varying age and density changed the partitioning of the water balance in Illilouette (Boisramé, *et al* 2017b, figure 5). A statistical model trained on field moisture measurements suggested that the observed conversion of forest areas to meadows in the central area of the Illilouette basin between 1969 and 2012 led to increases in summer soil moisture by as much as 30 percentage points (Boisramé *et al* 2018). These estimates are supported by *in situ* soil moisture monitoring in Illilouette and Sugarloaf, which consistently shows soil water content under meadow and shrub canopies to be 10 to 30 percentage points greater than under neighboring forest canopies (Boisramé *et al* 2018, Stevens *et al* 2020).

Identifying the processes responsible for these relations between vegetation and water storage remains challenging. Simulation in Illilouette with ecohydrological models suggests that forest reduction was associated with reduced snowpack sublimation and summer transpiration so that 2012 vapor fluxes from the basin declined by approximately 40 mm year^{-1} relative to 1969, similar to the increase in streamflow (Boisramé *et al* 2019). Observations made with time-lapse cameras in Illilouette and Sugarloaf show that snowpack is thinnest and melts earliest beneath forest canopies compared to shrub and meadow areas (Boisramé *et al* 2019, Stevens *et al* 2020). Increased subsurface water storage and reduced transpiration demands probably contributed to very low tree mortality in Illilouette during the extreme drought years of 2014–2015 (Boisramé *et al* 2017b). Flow observations at the Happy Isles stream gauge on the Merced River and model predictions suggest that these water balance changes produced modest increases in annual streamflow, with approximately 50 mm year^{-1} additional flow from Illilouette after 40 years of managed wildfire (Boisramé *et al* 2019). Reassuringly, neither the modeling nor gauge observations show evidence of increased peak flows (floods), which are often identified as a potential hydrological risk of increasing fire frequency. In contrast to Illilouette, the less pronounced

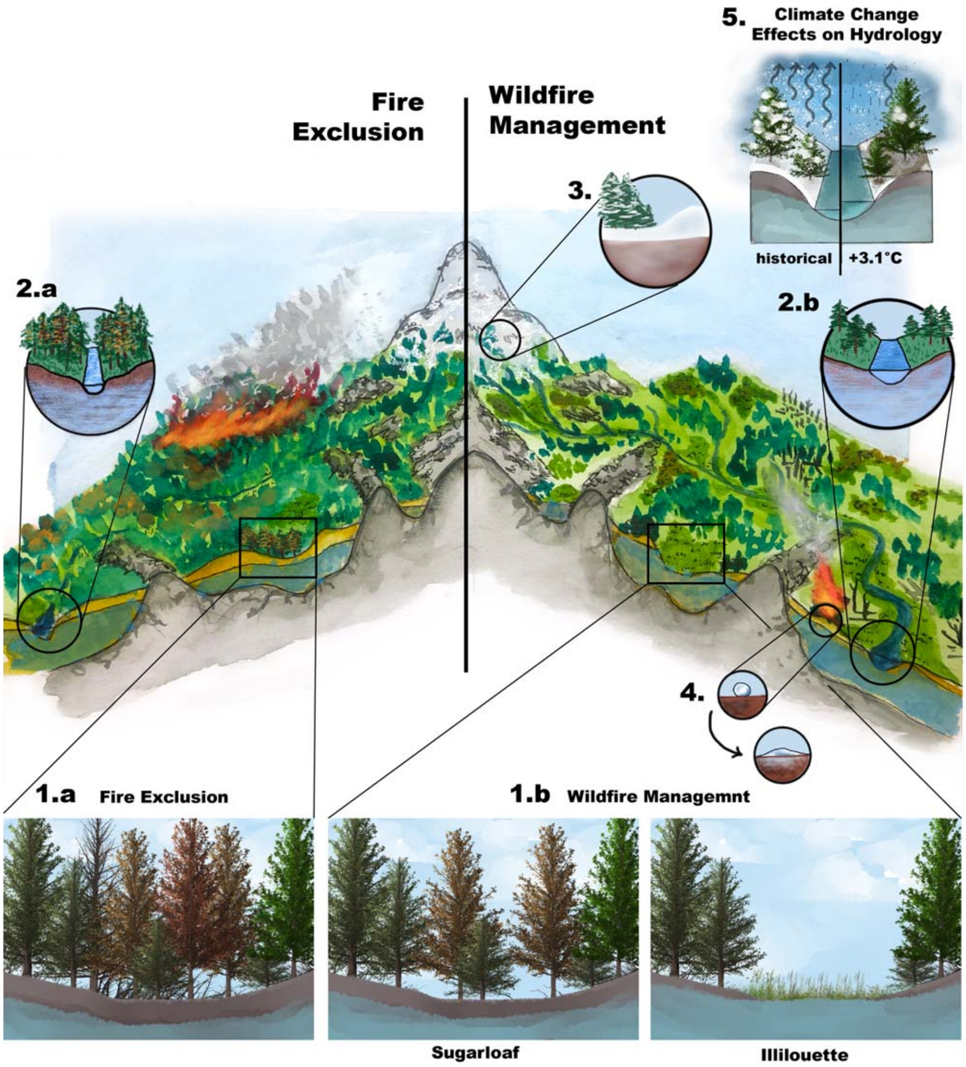

Figure 5. The left panel depicts a fire suppressed landscape, and the right panel shows a landscape experiencing frequent fires under a wildfire management strategy. The right panel is more representative of a landscape change that occurred in Illilouette basin, which experienced greater vegetation transitions from forest to shrublands and grasslands, resulting in an overall wetter landscape than Sugarloaf basin (1.b). As seen in Illilouette, wildfires increased basin streamflow (2), which is partially attributed to greater snow water equivalent in open areas compared to under canopies (3). No large-scale post-fire erosion is observed in Illilouette, likely due to frequent freeze-thaw cycles which reduce post-fire soil hydrophobicity (4). As climate is predicted to warm by 3.1 °C without significant change in precipitation totals, snowpack will be reduced, which is predicted to decrease basin evaporation through sublimation reduction, causing a marginal net increase in streamflow relative to historically observed conditions (5).

vegetation changes in Sugarloaf during the managed fire program do not appear to have resulted in noticeable hydrological changes (Stevens *et al* 2020).

Climatic warming is expected to impact the hydrology of the Sierra Nevada by increasing the fraction of precipitation falling as rain and moving peak streamflow earlier in the year (Rakhmatulina *et al* 2021a). Climate change is also likely to alter the characteristics of managed wildfires in Illilouette and Sugarloaf, although forecasting these changes is challenging (Gonzalez *et al* 2018). Observations over the past 50 years in Illilouette show no trends in fire severity or burned area in spite of climatic warming during that period (figure 3), presumably because both of these characteristics have been moderated by fuel consumption and associated disruptions in fuel continuity across the landscape (Collins *et al* 2009). Lightning ignitions, however, may become more frequent in Illilouette given warmer and drier weather. Increasing fire frequency from climate change accelerates the pace of hydrological changes without altering the long-term hydrological state (Rakhmatulina *et al* 2021a). These results suggest that the hydrological co-benefits of restoring fire regimes are robust to the projected climatic warming in the Sierra Nevada.

Considerable uncertainties remain, however, regarding the feedbacks between fire, vegetation, and the water cycle as climate changes. For instance, it is not clear how important the expansion of wet meadow areas might be in creating natural ‘fire breaks’ that constrain the extent of future fire. Even the modest increases in soil moisture that occurred in the basin to date could influence fires, with recent studies showing that fuel moisture can be significantly increased by wet soils, reducing ignition probabilities (Rakhmatulina *et al* 2021b). Similarly, several hydrological implications of the managed wildfire program, including the impacts on water quality, require more research. Examination of LIDAR imagery from before and after the 2017 Empire Fire in Illilouette, however, shows little evidence of large-scale erosion (Boisramé unpublished data 2020). The fact that freeze-thaw cycling in Sierra Nevada soils can rapidly erode post-fire hydrophobicity (Rakhmatulina and Thompson 2020) could contribute to rapid recovery of soil's ability to absorb and store water in these basins after fire.

Conclusion

Reducing the risk of large, severe wildfires while also increasing the security of mountain water supplies and enhancing biodiversity are urgent priorities. Here we found evidence for this synergism in Illilouette but not fully in Sugarloaf. While differences in the productivity of these forested areas could have contributed to this disparity, the shortage of managed wildfires in Sugarloaf is likely the biggest factor. The number of fires larger than 40 ha from 1973 to 2016 was much higher in Illilouette ($n = 21$) than Sugarloaf ($n = 10$). This disparity is particularly evident in recent decades, with Illilouette experiencing 12 fires larger than 40 ha since 1985 and Sugarloaf only experiencing 4 (Stevens *et al* 2020). The amount of recent fire activity in Sugarloaf may represent a deficit compared to the historical fire return interval (Collins and Stephens 2007). This recent fire deficit is illustrated by the fact that wildfires have burned only 1 ha in Sugarloaf between 2004 and 2017 with 59% of active ignitions suppressed, compared with 7,289 ha burned in Illilouette and only 23% of ignitions suppressed in the basin between 1969 and 2003 (Stevens *et al* 2020).

The challenges of maintaining a managed wildfire program are daunting, even in remote areas. Ignitions during droughts have been suppressed for fear of adverse fire effects or lack of public and political support in allowing fires to burn. Climate change is expected to create more alternating periods of drought and high precipitation (Abatzoglou and Williams 2016), which will probably be the environment that fire managers will have to adapt to. Political challenges were evident to Yosemite National Park managers when the 2017 Empire Fire was allowed to burn in Illilouette at the same time as the 2017 Wine Country fires were burning large areas of Napa, Sonoma, and Mendocino counties and destroying tens of thousands of structures. National park managers are to be commended for creating these managed wildfire programs and working to maintain them into the future.

Current revisions to the Land and Resource Management Plans for U.S. National Forests in the southern Sierra Nevada emphasize managed wildfire over 69% to 84% of National Forest land (Rakhmatulina *et al* 2021a). Areas that have similar characteristics to Illilouette and Sugarloaf in terms of forest type and remoteness are extensive in the Sierra Nevada (figure 1), demonstrating the potential to increase the area managed by wildfire. National Forest lands often have different land use histories than National Parks, including extensive historical logging which can change forest and fuel structures and create additional challenges to restoration by fire alone (Collins *et al* 2017, Jeronimo *et al* 2019), but the successes of the managed fire programs in the parks discussed here do provide a useful template for scaling up the landscape application of managed wildfire to other lands. If managers decide to implement managed fire programs they should be robust to climate change (fires continue to be self-limiting and fire severity classes remain stable) but may be more volatile as the time required to produce a fire mosaic is expected to be much shorter from the impacts of climate change (Rakhmatulina *et al* 2021a). Continued support at the highest levels of government, as well as from the public, would be needed to maintain existing managed wildfire programs and expand them to others forested areas. Were fire to be removed from managed fire areas, woody cover and water use would again increase, diminishing the positive impacts of these programs (continued fire use would produce relatively low levels of smoke for many months which could negatively impact some people). Perpetual support for these programs and for the scientific investigations that can interpret their effects is key if we want to avoid increasingly destructive high severity wildfires that damage ecosystems and human communities.

Acknowledgments

We thank all fire managers and line-officers who have created and supported the managed wildfire programs in Yosemite and Sequoia and Kings Canyon National Parks. Without their strong leadership this project would not have been possible. Previous funding from the US Joint Fire Sciences Program, UC ANR Competitive Grants Program, and the NSF Critical Zone Collaborate Network (award number 2011346) funded the research in this paper.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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