

## Widespread exposure to altered fire regimes under 2 °C warming is projected to transform conifer forests of the Western United States

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Changes in wildfire frequency and severity are altering conifer forests and pose threats to biodiversity and natural climate solutions. Where and when feedbacks between vegetation and fire could mediate forest transformation are unresolved. Here, for the western United States, we used climate analogs to measure exposure to fire-regime change; quantified the direction and spatial distribution of changes in burn severity; and intersected exposure with fire-resistance trait data. We measured exposure as multivariate dissimilarities between contemporary distributions of fire frequency, burn severity, and vegetation productivity and distributions supported by a 2 °C-warmer climate. We project exposure to fire-regime change across 65% of western US conifer forests and mean burn severity to ultimately decline across 63% because of feedbacks with forest productivity and fire frequency. We find that forests occupying disparate portions of climate space are vulnerable to projected fire-regime changes. Forests may adapt to future disturbance regimes, but trajectories remain uncertain.

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Altered fire regimes are now pervasive in western North America and elsewhere as a result of anthropogenic climate change<sup>1,2</sup>, timber harvest, livestock grazing, fire suppression, criminalization of Indigenous fire stewardship<sup>3,4</sup>, and changes in human ignitions<sup>5</sup>. Wildland fire is increasingly acting as a catalyst for abrupt change in ecosystem structure and composition in forests of the western U.S.<sup>6,7</sup>—ecological transformations—especially where fire frequency or intensity are misaligned with species traits or where moisture limitations constrain recovery of pre-fire species<sup>8</sup>. Well-documented feedbacks between vegetation and fire imply that ecological transformations can alter fire-regime characteristics and subsequent ecosystem responses<sup>9–11</sup>. However, these dynamics remain challenging to project, despite high consequences for ecological functions that maintain biodiversity and ecosystem services<sup>12</sup>, the efficacy of natural climate solutions<sup>13</sup>, and human well-being<sup>14</sup>.

Constraining the direction and strength of feedbacks between fire and vegetation is important not only for projecting future fire activity (including frequency and severity) but also because reduced burn severity (the magnitude of ecological change caused by fire, e.g., tree mortality<sup>15</sup>) could allow some forests to avoid fire-catalyzed transformations to non-forest and instead reorganize as alternative forest types<sup>6,16</sup>. Transformations from forest to non-forest are documented and expected to continue in western U.S. ecosystems on the climatic margins of forest cover<sup>8,17–21</sup>. However, where, when, and how feedbacks between fire and vegetation could create opportunities for forests to persist in an altered state remains unresolved. For example, an increase in the relative abundance of species with fire-resistance traits that enable individual trees to tolerate frequent low-severity fire<sup>22</sup> might confer ecosystem-scale adaptive capacity<sup>23</sup>. Because fire is a nearly ubiquitous process in conifer forests of the western U.S., projections of future fire activity, ecosystem responses, and associated risks to ecological and human communities are critical information for scientists and land managers<sup>24</sup>.

This study anticipates future ecosystem and disturbance dynamics in conifer forests of the western U.S. Rapid climate-driven changes are already altering the character and function of forests in the region and present novel management challenges<sup>25</sup>. Information about plausible ecological futures is vital to successful stewardship through the decades ahead<sup>26</sup>. Natural resource managers request finely resolved projections of the location and form of potential ecological transformations, which go beyond monitoring post-fire forest recovery<sup>27</sup>. Long-standing paradigms in ecological theory (focused on stability) and land management (focused on restoration) tend to view ecosystems relative to 19<sup>th</sup>- and 20<sup>th</sup>-century archetypes. As ecosystems continue to depart from historical conditions, such perspectives are failing to explain contemporary responses to disturbance or guide the management of rapidly changing systems<sup>28</sup>. Stewarding forests along socially desirable and equitable pathways requires understanding where locally novel ecosystems and fire regimes are likely to emerge in response to climate change—supporting frontline communities to make informed decisions about accepting, directing, or resisting change<sup>25,29</sup>.

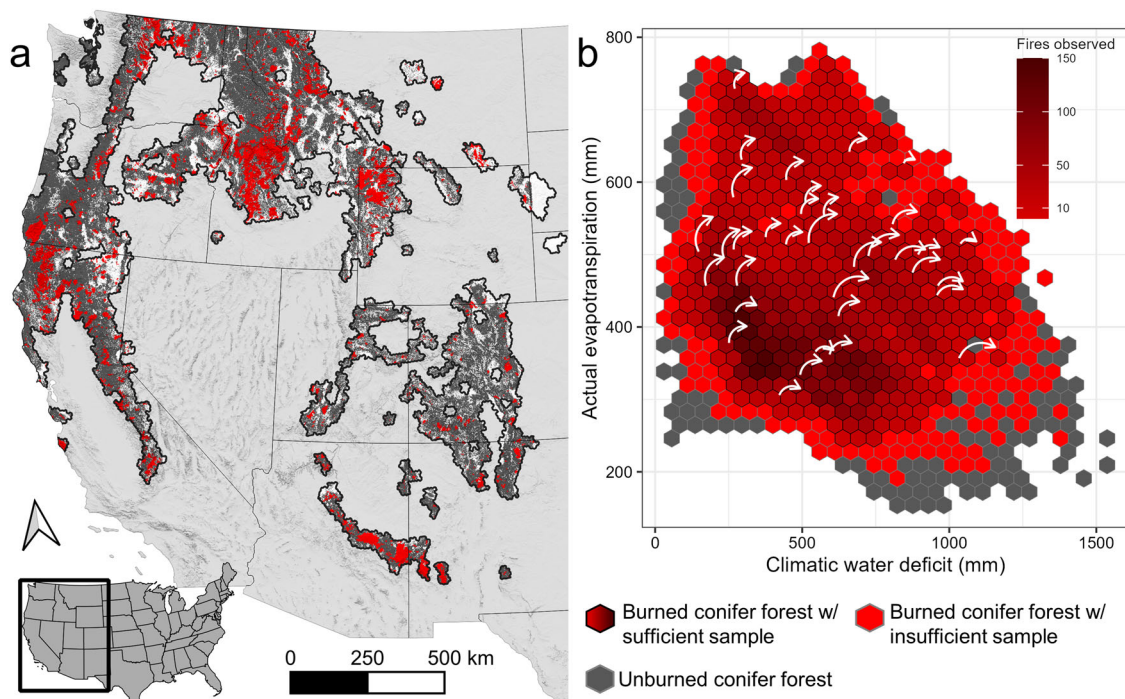
Expectations of future forest-fire activity are contingent upon whether and how vegetation dynamics are represented in predictive models. Correlative models use observed relationships between fire and climate metrics to predict changes in fire activity under projected climate scenarios. There is a clear consensus among these predictions of increasing annual area burned as fuel aridity increases<sup>30–33</sup>. While scalable and informative, correlative models assume stationarity in the relationship between fire and climate across time and space and do not account for dynamic feedbacks between fire and ecosystems<sup>34</sup>. And though fire activity and post-fire ecosystem responses are tightly coupled on real landscapes,

correlative frameworks generally consider them independently. Mechanistic models, by contrast, link together fundamental processes to simulate ecosystems dynamically from biophysical principles. Mechanistic approaches have not been used to project changes in burned area at the scale of the western U.S. because simulation models are challenging to run at sub-continental scales for computational and ecological reasons (but see ref. 35,36). However, these models effectively simulate time series or snapshots of plausible futures<sup>37,38</sup>, advance theory<sup>39</sup>, and perform experiments in silico that would otherwise be impossible<sup>40,41</sup>. Validation of future prediction is an inherent challenge in any framework. In practice, correlative and mechanistic models bookend approaches to a complex challenge and there are clear benefits to both paradigms.

Through advances across this modeling spectrum, some models represent interactions between vegetation and fire activity, but progress integrating fire occurrence, burn severity, and ecosystem responses is needed. Correlative models that incorporate vegetation suggest negative feedbacks could have a dampening effect on the rate and amount of increase in annual area burned in forests of the western U.S.<sup>42</sup>. Fine-scale correlative models show a reduced likelihood of fire within decades of an initial burn<sup>10</sup>, consistent with short-term successional dynamics assumed under, for example, state-and-transition modeling frameworks<sup>43</sup>. By simulating dynamics decades into the future, mechanistic models can reveal when persistent transformations emerge that reduce projected area burned<sup>44,45</sup> or alter the distribution of area burned among categories of fire-caused tree mortality<sup>37,40</sup>. Such modeling reinforces empirical evidence that vegetation feedbacks could manifest as ecologically important changes in burn severity even while the annual area burned remains higher than during the 20<sup>th</sup> century<sup>46</sup>. We posit that projecting future fire activity can be better achieved by modeling fire-regime attributes and vegetation together as a multivariate process<sup>47</sup>. Our approach treats vegetation, fire, and their feedbacks as emergent properties of a complex system, constrained at broad scales by climate but manifesting in non-deterministic ways in response to local variation in ecosystem characteristics<sup>48,49</sup>.

A diversity of conceptual frameworks and terminologies are invoked to understand and anticipate ecosystem vulnerability to climate-change impacts<sup>50,51</sup>. A commonality among frameworks is an understanding that vulnerability is not driven only by changes in climate but also by social-ecological elements of a system that modify impacts, confer resilience, or enable adaptation. We adopt a simplified framing of vulnerability that is specific to the ecosystem and disturbance-regime focus of our study. We define *exposure* to fire-regime change as significant multivariate dissimilarity between fire regimes supported by the contemporary and projected future climate, *adaptive capacity* as the ability of ecosystems to adjust to altered fire-regimes through changes in the relative abundance of species (here quantified using an atlas of tree community fire resistance) and *vulnerability* as the intersection of *exposure* and *adaptive capacity*. Our study is motivated by three objectives. 1) Quantify exposure of conifer forests to fire-regime change under a scenario projecting an increase of 2 °C in global mean surface temperature relative to the pre-industrial period (hereafter, “+2 °C”). 2) Explore the direction and spatial distribution of vegetation feedbacks reflected by changes in burn severity. And, 3) estimate the vulnerability of conifer forests to fire-catalyzed ecological transformation by intersecting exposure with information about tree species composition and fire-resistance traits.

We compared contemporary and projected future fire regimes across all forests of the western U.S. (Fig. 1) where conifers comprise > 50% of basal area<sup>22</sup>. We grouped remotely sensed observations of fire-regime attributes based on similarity in 30-year climatological means of climatic water deficit (CWD) and actual



**Fig. 1** Conifer forests of the western US in geographic and climate space. **a** Study area is outlined in black, which includes firesheds with > 45 ha of conifer forest. In both panels, conifer-forest area is shown in dark grey and portions that burned from 1984 to 2019 are colored red. **b** The climate space of conifer-dominated forests is divided into hexagons where red shading indicates the number of unique fire events observed within each; black outlines indicate hexagons that met criteria for statistical support (>10 unique fire events and > 1000 Landsat pixels). White arrows show, for a random sample of points, movement of points in climate space between the mean contemporary (1960–1990) and projected future (+2 C) climate.

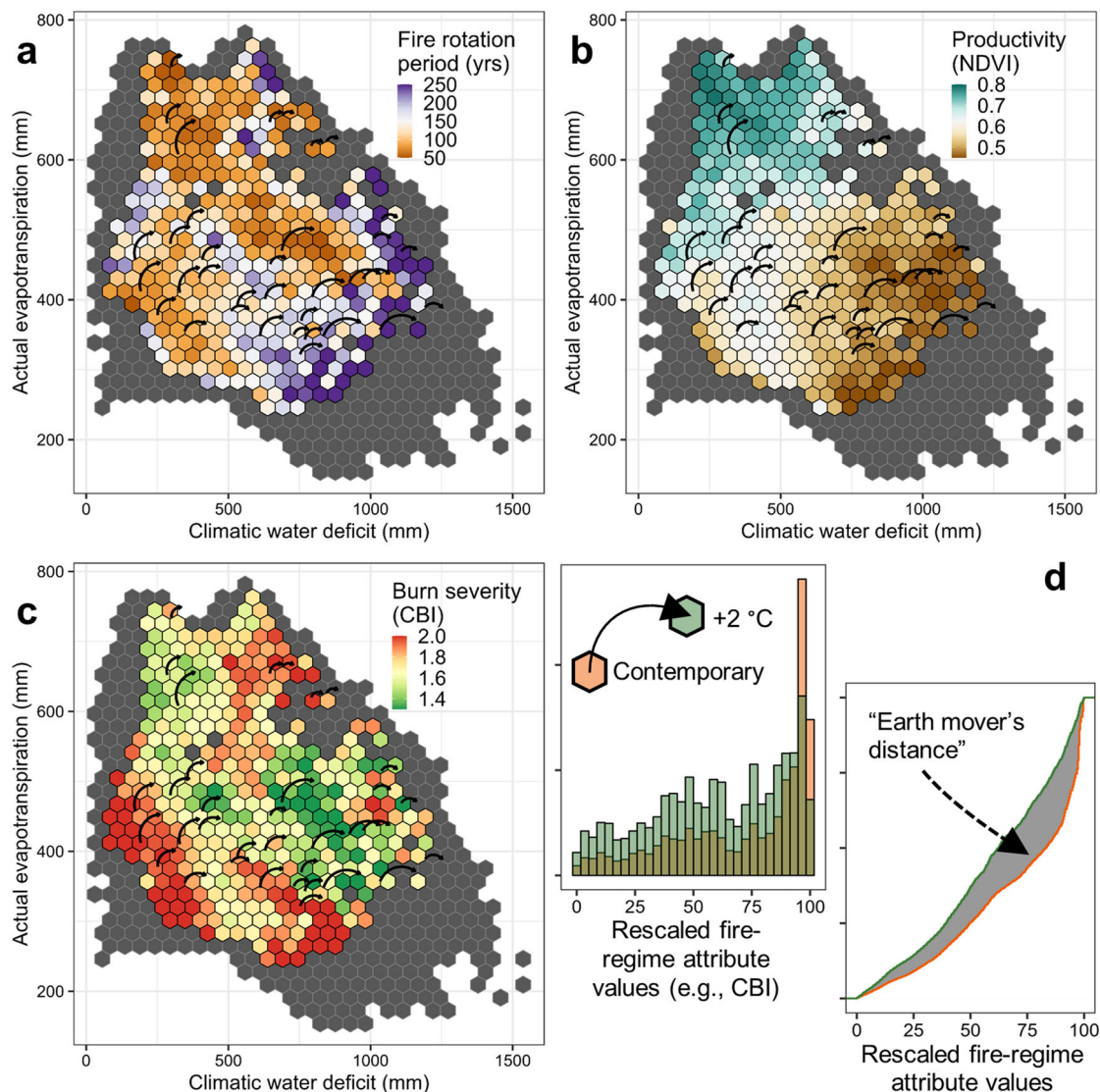
evapotranspiration (AET) and we projected movements in this space using climate analogs, which assume quasi-equilibrium between vegetation and climate over short time scales<sup>47</sup>. We defined exposure to fire-regime change as the multivariate dissimilarity between distributions of fire frequency, burn severity, and vegetation productivity supported by contemporary and projected future climates (Fig. 2). We quantified the direction and magnitude of changes in fire frequency, burn severity, and vegetation productivity individually to better understand the nature of exposure. Our approach does not permit extrapolation beyond the full range of empirical observations; thus, contemporary fire regimes define possible future fire regimes. The +2 °C scenario we used is agnostic of the timing of temperature increases, which vary among forcing pathways<sup>52</sup>; the +2 °C scenario incorporates but does not eliminate uncertainty among climate projections. We characterized one form of adaptive capacity—the potential for forests to adjust to increases in fire frequency through shifts in species composition—by intersecting our measure of exposure with an atlas of community-weighted, fire-resistance trait scores. These scores summarize the relative abundance of traits that allow individual trees to survive low-severity burning<sup>22</sup>. Finally, we linked our results with national Forest Inventory and Analysis (FIA) plot data to understand how vulnerability differs among forest types. To increase relevance to managers and frontline communities, we summarized our results within “firesheds,” a set of spatial containers delineated by U.S. federal fire managers as a basis for planning<sup>53</sup>.

## Results

A significant multivariate dissimilarity (a bootstrapped distribution of values did not overlap a null distribution, see Methods for detail) between the fire frequency, burn severity, and vegetation productivity supported by a location’s current and projected future climate—*exposure to fire-regime change*—was projected across 65% of western US conifer forests (Fig. 3). Median

dissimilarity was significant for >95% of conifer-dominated firesheds (776 of 819, SI 3). Projected changes in fire frequency, burn severity, and productivity were heterogeneous and did not correspond in predictable ways (Fig. 4). Reduced burn severity and productivity were dominant patterns. Firesheds and forest types vulnerable to ecological transformations exhibit a combination of high exposure and low adaptive capacity, which occurs across a broad climatic gradient (Figs. 5, 6).

**Exposure to fire-regime change.** The dissimilarity between contemporary and future fire regimes was significant for 52% of the 3999 pairwise comparisons we made, representing 65% of conifer forest area or approx. 495,000 km<sup>2</sup> (Fig. 3). Dissimilarity was not significant for 15% of conifer forest area, 4% had no measurable dissimilarity between contemporary and projected future fire regimes, and dissimilarity could not be calculated for 16% due to insufficient fire activity during the period of satellite records (Fig. 1b). The global median (IQR) dissimilarity between contemporary and projected future fire regimes was 7.6 (4.9–11.1), whereas median null dissimilarity was 2.2 (1.9–2.7). However, exposure varied substantially across geographic space, reflecting differences in the magnitude of projected changes in mean AET and CWD (Supplementary Fig. 1) and differences in observed fire activity during the contemporary period. For example, areas along steep climatic gradients and with large projected increases in AET, such as the crests of the Sierra Nevada and Cascade Range and the western slope of the northern Rocky Mountains, were projected to face high exposure (Fig. 3). Conversely, areas with low projected change in AET and CWD, such as coastal areas of California and Oregon, were projected to have low exposure. In these areas, small projected movements in climate space resulted in limited change between contemporary and future fire regimes (i.e., their climates may change but not enough to move between discretized climate bins). Arid regions



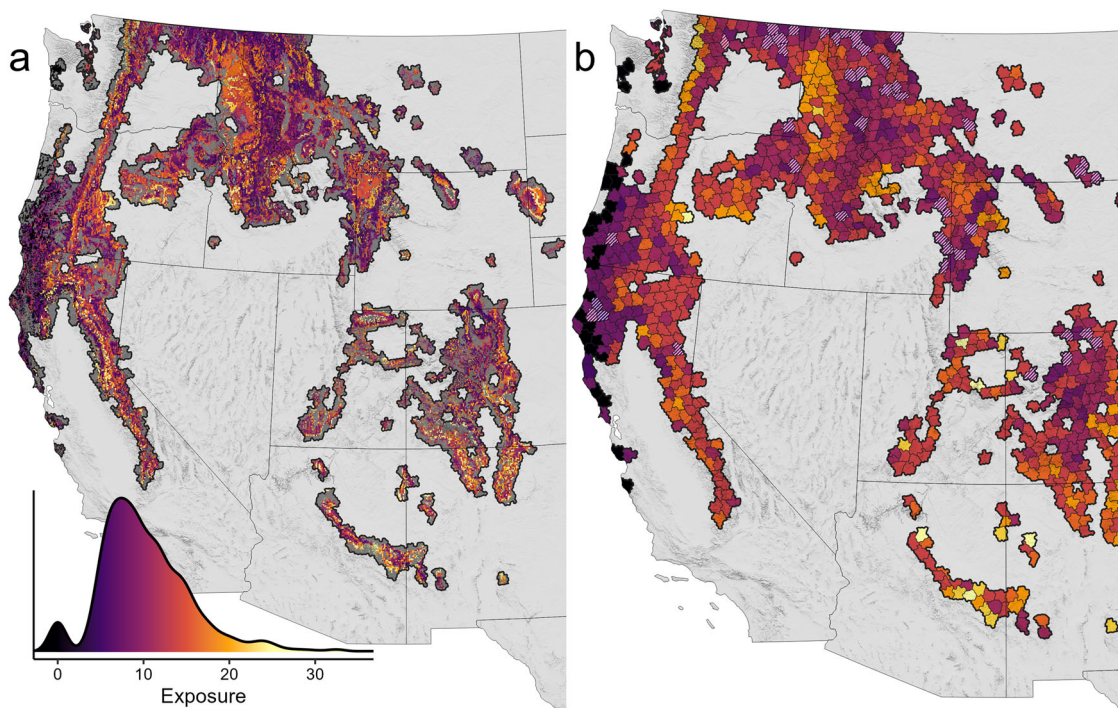
**Fig. 2 Fire-regime attributes in climate space.** The climate space of all conifer forest is shown in grey; burned conifer forest meeting statistical support criteria for this analysis are colored by the mean (a) fire rotation period (yrs), (b) vegetation productivity (NDVI), and (c) burn severity (CBI) values of all points within each hexagon. (d) Univariate histograms of burn severity data are shown for an example contemporary-future climate analog pairing. The area (grey) between empirical cumulative distribution functions (green and orange lines) is shown to visualize the earth mover's distance in one dimension. A multivariate earth mover's distance was calculated and is interpreted as exposure to fire-regime change.

tended to have higher exposure to fire-regime change than mesic regions, again reflecting projected amplification of aridity in these areas. The southern Rocky Mountains and the Southwest were hotspots for high exposure, driven by increasing CWD (Supplementary Fig. 1). Exposure to fire-regime change was low in areas with extensive and repeated fire activity during the contemporary period, for example, in southern Oregon and northern California (Supplementary Fig. 2). Even though contemporary fire activity in these areas may already exceed 20<sup>th</sup>-century observations, low exposure suggests that future climates and associated ecosystems are likely to support contemporary rates of burning in the future.

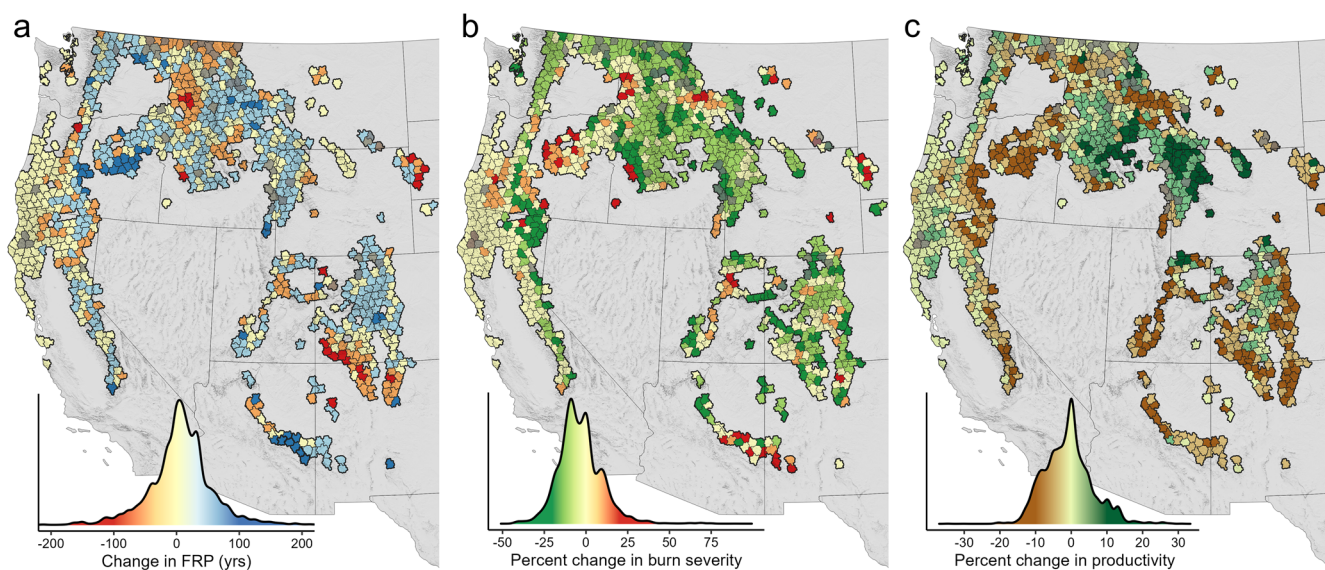
Changes in burn severity are inherently linked with changes in fire frequency and vegetation productivity, and changes in all dimensions were spatially heterogeneous (Fig. 4). The study-wide median (IQR) projected change in fire frequency (measured as FRP, yrs) was +8 yrs (16–33), but changes were highly variable across space (Fig. 4a). Contemporary fire frequencies are projected to be maintained in coastal Oregon and California. Fire frequency was projected to decline (FRP increases) in central

Idaho and Montana, central Colorado, and eastern Oregon and Washington, and Arizona. Conifer forests of northwest Montana, New Mexico, and southwest Colorado show notable projected increases in fire frequency (Fig. 4a). Future burn severity was projected to be lower than the contemporary period for 63% of conifer forests, higher for 32%, and no change was projected for 5% (Fig. 4b). The pattern of projected declines in burn severity was particularly consistent across the northern and central Rocky Mountains. We projected widespread declines in productivity of 0.1 NDVI units (~10%) or more (Fig. 4c), particularly in eastern Oregon, Utah, Colorado, New Mexico, and Arizona.

**Fire resistance among firesheds and forest types.** We identified vulnerable firesheds, those dominated by fire-sensitive species and with high projected exposure, by pairing exposure with fire-resistance trait scores (Fig. 5). Vulnerability to transformation is high in forest types where high exposure and low fire resistance intersect, for example, in pinyon-juniper, spruce-fir, and some



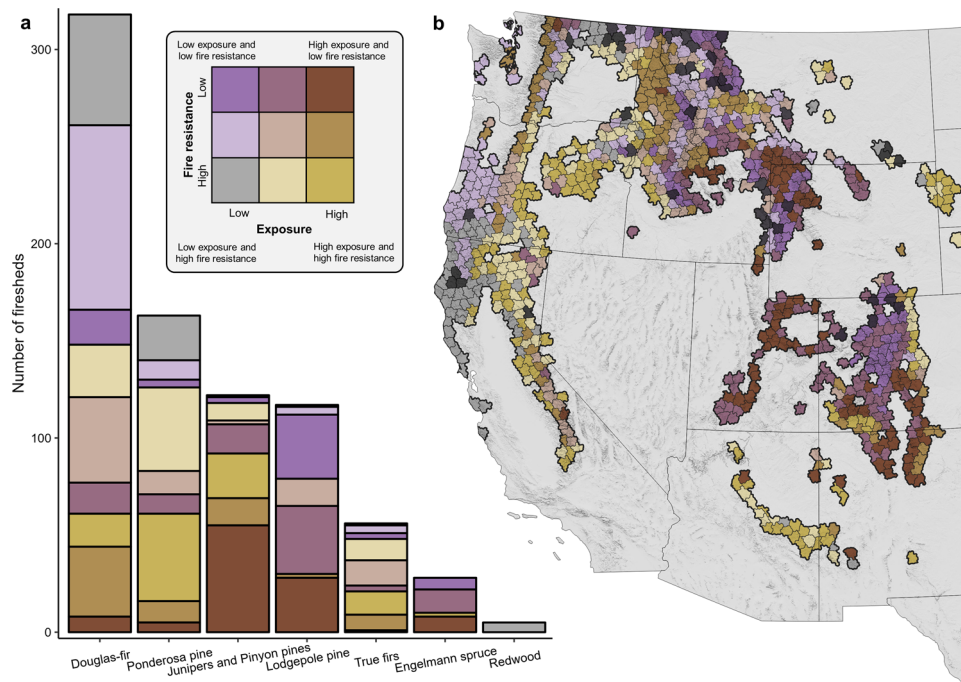
**Fig. 3 Projected exposure to fire-regime change.** Exposure is measured by the dissimilarity between the fire frequency, burn severity, and vegetation productivity supported by locations' contemporary and projected future climates, using the unitless earth mover's distance (Fig. 2d). Exposure at each sample cell (**a**) and the median exposure within firesheds (**b**). White hatching over firesheds indicates that median dissimilarity was not significant.



**Fig. 4 Projected changes in fire-regime attributes.** Firesheds are colored by the fireshed-level median change in fire-regime attributes between the future and contemporary period, for (**a**) fire rotation period (FRP), (**b**) percent change in burn severity, and (**c**) percent change in vegetation productivity. Grey shading over firesheds indicates that dissimilarity was not significant.

lodgepole pine and Douglas-fir forests (Fig. 5a). Median exposure values were significantly different from a null model for 95% of firesheds (Fig. 5b). High exposure was common for firesheds across Utah and the southern Rocky Mountains. Firesheds in coastal California and Oregon and central Washington exhibited a combination of low exposure and intermediate to high fire resistance. The northern Rocky Mountains spanned the range of both dimensions, with dry montane forests characterized by high exposure and high fire resistance, and subalpine forests characterized by low to intermediate exposure and low fire resistance (Fig. 5).

Forest types situated in arid landscapes—those dominated by junipers (*Juniperus* spp., incl. *Juniperus scopulorum*), piñon pines (*Pinus* spp., incl. *Pinus edulis*) or ponderosa pine (*Pinus ponderosa*)—were projected to face high exposure to fire-regime change but varied substantially in terms of fire resistance. Ponderosa pine forests have a moderate to very high proportion of fire-resistant traits, whereas juniper and piñon pine forests were among the least fire-resistant forests. Mesic forest types—those dominated by spruces (*Picea* spp.), firs (*Abies* spp.), and lodgepole pine (*Pinus contorta* var. *latifolia*)—tended to cluster



**Fig. 5 Conifer forest vulnerability to fire-driven transformation.** Axes representing exposure to fire-regime change and community-weighted fire-resistance are divided into classes defined by the 33<sup>rd</sup> and 66<sup>th</sup> percentiles. **(a)** A stacked bar plot indicates the number of firesheds (spatial containers for fire planning) in each class by dominant forest type. Forest types are named for dominant species but include multiple species. **(b)** Firesheds are mapped and colored by class. Only firesheds containing conifer forest are mapped. Black shading over firesheds indicates that mean dissimilarity was not significant.

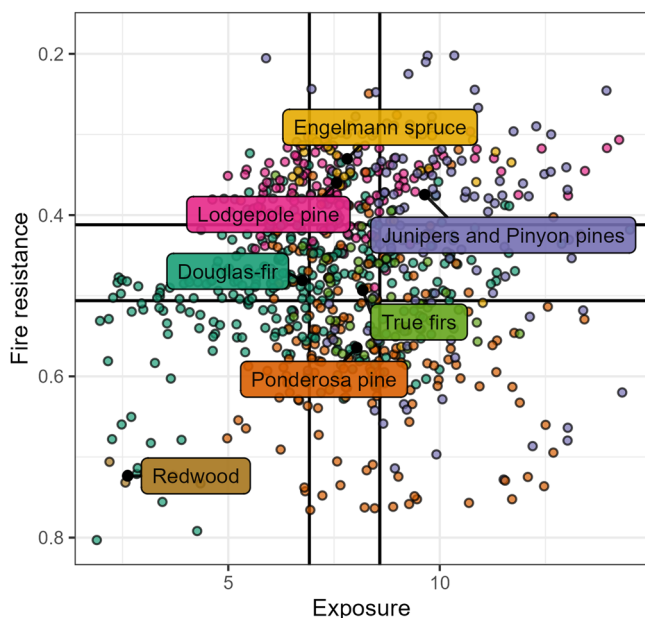
around intermediate exposure and low fire resistance scores (Fig. 6). In areas where these forests are exposed to large shifts in climate space, their vulnerability is high. Douglas-fir (*Pseudotsuga menziesii*) was the most common forest type across our study area (Fig. 6) and exhibited a wide range of exposure and fire-resistance scores (Fig. 6). Douglas-fir exposure spanned nearly the entire range of values. The Douglas-fir forest type includes two distinct varieties (coastal and interior; var. *menziesii* and var. *glauca*, respectively) and both co-occur with a wide range of species, creating communities that vary considerably in their proportion of fire-resistance traits. In general, however, the mean fire resistance of Douglas-fir-dominated firesheds reflected the species' individual score of 0.49.

## Discussion

A majority (65%, 495,000 km<sup>2</sup>) of western US conifer forest area is projected to face exposure to fire-regime change (significant multivariate dissimilarity between current and projected future fire regimes) under a +2 °C warming scenario. However, to anticipate whether exposure makes an ecosystem vulnerable to persistent transformation requires knowledge of its adaptive capacity<sup>23</sup>, in this case, through shifts in forest composition towards a higher relative abundance of species with fire-resistant traits. Our results suggest that shifts toward warmer and drier climates that alter vegetation productivity and fire frequency will drive associated shifts in species composition and burn severity, and in many places, impose ecological transformations. We follow a recent definition of ecological transformation, which generalizes concepts including transition, type conversion, abrupt change, collapse, and others, as “the dramatic and irreversible shift in multiple ecological characteristics of an ecosystem, the basis of which is a high degree of turnover in ecological communities.”<sup>7</sup> The paired metrics of exposure and fire resistance we present indicate where natural resource managers can expect high vulnerability to transformation.

Our projections are consistent with expectations that forests are likely to experience changes in fire frequency and severity during the 21<sup>st</sup> century<sup>2,13,54,55</sup>. Our results broaden the scope of landscape-scale studies documenting changes in composition in response to recent fire activity, including expansion of fire-resistant conifers in mixed-conifer forests with high trait diversity and contractions of serotinous and fire-sensitive obligate-seeding species<sup>56–62</sup>. An important way that our approach and findings differ from existing characterizations of forest and fire dynamics is that we describe fire regimes by recent remotely sensed observations, rather than archetypes, potential vegetation, or desired conditions. This means that exposure to fire-regime change can be low in ecosystems where substantial departures from 20<sup>th</sup>-century conditions have already been observed in the last several decades, for example, in northern California and southern Oregon<sup>63,64</sup>. We interpret low exposure in these settings as indicating that future climate and productivity will continue to support fire activity like the recent past (i.e., since 1984), which in many places already differs from historical references. This may be indirect evidence that some regions have transformed from conifer-dominated forests to, for example, fire-adapted mixed-hardwood forests that tolerate frequent, high-intensity fire activity<sup>65</sup>.

We projected both increases and decreases in fire frequency across our study region (Fig. 4a). This finding is consistent with the notion that relationships between aridity and fire frequency (or equivalently, area burned) are strongest at intermediate climatic water deficits<sup>34</sup> and weaken towards the margins of climate space occupied by forests (Fig. 2). Some studies project increases in area burned in climate-limited systems and decrease in fuel-limited systems<sup>11</sup>, whereas others project high area burned in the future in places that burned at high rates over the last several decades<sup>66</sup>. For example, area burned in the Greater Yellowstone Ecosystem has been projected to increase non-linearly through the 21st century<sup>67</sup>. However, vegetation dynamics are not characterized by these approaches, and thus, negative feedbacks to burn severity resulting



**Fig. 6 Vulnerability of forest types to transformation.** A random selection of firesheds is plotted in vulnerability space defined by exposure to fire-regime change and fire-resistant traits that confer adaptive capacity and colored by the dominant forest type. Forest types are named for dominant species but include multiple species. Labels point to black circles at the median values of each forest type. Black horizontal and vertical lines mark the 33rd and 66th percentiles in each dimension (as in Fig. 5). The scale of the x-axis was truncated to improve visualization.

from widespread increases in fire frequency are not explored. Our analysis in this region points toward a small decrease in fire frequency (Supplementary Fig. 3), increasing productivity (perhaps reflecting recovery from large 20th-century fires or relaxed climatic constraints on plant growth), and reduced burn severity (Fig. 3b), resulting in projections of moderate exposure (Fig. 3a).

Our analysis suggests negative feedbacks between fire and vegetation may emerge under 2 °C of warming, where burn severity in some ecosystems ultimately declines, perhaps independently of changes in area burned. These findings are in partial agreement with projections that show weak negative vegetation feedbacks to annual area burned after decades of increased burning<sup>42</sup>. While such studies emphasize that their models predict continued increases in area burned even when short-term (years-decades) fuel limitations from vegetation are represented, we note that models with fuel feedbacks predict as much as 30% less annual forest-area burned by 2050 compared to models without feedbacks. Our analysis suggests that models which do not include links among fire extent, burn severity, and productivity, nor regional variation in climate-fire relationships, could mischaracterize fire-regime changes and underestimate forests' resilience to altered fire regimes. Direct comparison of our findings with statistical and simulation models should be made cautiously. The impact of fire suppression and other management legacies cannot be removed from our model. However, we assume that management legacies are randomly distributed across climate space and that their potential impact on our findings is reduced by grouping observations that share climate but are not geographically contiguous. Our method does not explicitly account for ignitions, which are currently not a limitation on annual area burned in our study region but do affect the timing and location of fires<sup>5</sup>.

Our analysis underscores that exposure to climate change alone may not result in system transformation<sup>68</sup>. Theory and observation suggest that ecosystems possess the capacity to adapt to climate-

driven fire-regime change and persist as conifer-dominated forests through shifts in structure and composition when they remain within suitable climates<sup>6,69–71</sup>. Because ongoing climate change is largely forcing ecosystems in the western US toward more arid conditions that are more (often) suitable to burning, most projections indicate widespread increases in fire frequency<sup>31,42,72</sup>. Such a shift is also consistent with responses to a suppression-driven fire deficit in some western forests<sup>3,73</sup>. Our findings support these projections in many areas but also suggest that changes in fire frequency and burn severity may not unfold in predictable or consistent ways (Fig. 4). In this context, transformations that promote forest persistence are likely to favor increases in the relative abundance of species with fire-resistant traits that enable coexistence with frequent low-severity fires. For example, the proportion of highly fire-adapted western larch (*Larix occidentalis*) could expand in mixed-conifer forests of the northern Rocky Mountains that are today dominated by fire-sensitive spruce, fir, and pine species (Fig. 6), a process of ecosystem adaptation that would support resilience to a frequent mixed-severity fire regime<sup>61</sup>. This latent adaptive capacity is limited in contemporary tree communities with a small relative abundance of species with fire-resistant traits<sup>22,60</sup>. We view the capacity for species with fire-resistant traits to expand on the landscape as an essential characteristic of resilient, or perhaps more appropriately, adaptable, forests<sup>23,74</sup>. In places where traits align with projected future fire regimes, high exposure might be mitigated through landscape-scale ecosystem adaptation. Where the pool of available traits is insufficient or misaligned with future dynamics, high exposure could lead to abrupt ecological transformations<sup>6,70,71</sup>.

In addition to identifying ecosystems where changes in the relative abundance of species could enable forest persistence despite high exposure to fire-regime change, our findings also reveal forest types that are vulnerable to ecological transformation because of high exposure and low adaptive capacity. Forests with a small proportion of species with fire-resistant traits would undergo a high degree of turnover, either in the form of adaptation or transformation. Here, we find evidence of potential ecological transformations in forests at both the warm-dry and the cool-wet margins of climate space that supports forest, which differ in their suite of fire-related adaptations but are alike in exhibiting low individual fire resistance (Fig. 1b).

Fire-catalyzed contraction of forest has now been documented across the range of Douglas-fir and ponderosa pine, where increasingly arid environments constrain the window of opportunity for regeneration<sup>8,18,21,75</sup>. Our results are in partial agreement with this work; we project high exposure of these forests, but due to their high fire resistance, we suggest adaptation to increased fire frequency is possible when burn severity remains low enough to retain cone-bearing individuals<sup>16</sup>. Our findings indicate that warm-dry forests with low fire resistance, those dominated by pinyon pine and junipers, are highly vulnerable. Fire could catalyze or amplify ongoing range shifts in pinyon-juniper forests that today are driven primarily by drought<sup>76</sup>. In this case, ecological transformations might be aligned with management objectives, like reducing the encroachment of woody species into grasslands<sup>77,78</sup>.

At the other end of climate space, our analysis indicates that fire can also drive ecological transformations in areas that are, and will likely remain, climatically suitable for forests by undermining fire-adaptive traits like serotiny. Lodgepole and knobcone (*Pinus attenuata*) pines produce serotinous cones, in which seeds are bound by resin until heat releases them, enabling population-level persistence despite mortality of fire-sensitive individuals. However, mounting empirical and simulation modeling evidence<sup>37,61,62,79–82</sup> indicates that immaturity risk<sup>83</sup> can arise when fire return intervals are shorter than the time required for these species to mature and produce abundant serotinous cones and tall canopies that disperse seeds long distances<sup>59</sup>. Although

not present in our study area, immaturity risk has also been observed in boreal black spruce (*Picea mariana*) forests<sup>84–86</sup>. Fires can also create regeneration-limiting abiotic conditions because near-surface vapor pressure deficit increases after forest canopies are burned<sup>87,88</sup>. Topographic and postfire effects on microclimate are further amplified after unusually short fire-return intervals that eliminate residual structure<sup>89</sup>. These important effects of short fire-return intervals are not explicit in our approach; thus, their potential to drive transformation may be underestimated.

Our approach compares fire regimes supported by a single reference condition to those supported by a single future condition, identifying dynamics that are likely to unfold as the climate changes. This approach does not, however, reveal precisely when and how transient dynamics will emerge between time points<sup>71</sup>. Although ecological transformations in forests facing high exposure to fire-regime change might be mitigated by a high abundance of fire-resistant tree species, transitions from one forest type to another may not unfold in ways that are socially or ecologically desirable<sup>90,91</sup>. Importantly, our analysis may not accurately capture the consequences of events driven by extreme fire weather, which are likely to become more common in the future<sup>92</sup>. Abrupt shifts in fire regimes could trigger changes that occur too quickly for the adaptive capacity of forests to be realized, initiate prolonged periods of forest recovery that are not aligned with rates of adaptation in forest-obligate species, or are poorly matched with social expectations of forests.

Dispersal limitations and competition from alternative plant functional types could drive long transient dynamics<sup>93</sup> that prevent or delay ecosystem adaptation. Seed-source limitations arising from large or repeated high-severity disturbances<sup>94</sup> or abrupt increases in burn severity are a strong filter for postfire regeneration<sup>80,95</sup>. Long distances between seed sources and burned patches can delay forest regeneration even when abiotic conditions remain suitable<sup>57,61,62,81,82</sup>. In other cases, the velocity of climate change may exceed species' dispersal rates<sup>96</sup>, especially in the context of long-lived sessile organisms occupying complex terrain, i.e., forests in mountainous landscapes<sup>97</sup>. Fire-resistant species that are present on contemporary landscapes may not be able to expand as expected under increased fire frequency when they face strong competition from grasses or shrubs during the establishment phase<sup>98</sup>. Transformations to non-forest communities that are also highly flammable have proven to be resilient to repeated burning, further compromising the potential for fire-resistant conifers to expand under altered fire regimes when they do not regenerate while seeds are available, competition for light and moisture is low, and edaphic conditions are suitable<sup>64,99</sup>. While our study suggests a capacity in some conifer forest types to adapt to increasing exposure to fire regime changes, the road to adaptation that maintains such forests may be long and rocky, and these pathways are still unknown.

Frameworks for stewarding ecosystems through transformational change are developing rapidly, which is encouraging because our analysis suggests they are urgently needed<sup>100</sup>. Stewardship entails deliberately acknowledging possible, but uncertain, futures and taking action based on that knowledge<sup>26</sup>. This paradigm is fundamentally different from hands-off, reactive, and even “adaptive” management approaches where ecological dynamics unfold in the pseudo-absence of human intervention and undesirable consequences are (or are not) mitigated in response.

Calls for active management are not new in fire-prone forests and focus on restoring the application of fire where it is ecologically critical<sup>101,102</sup>. Our analysis suggests planned adaptation<sup>103</sup>—stewardship that facilitates changes in forest structure and composition to improve alignment with projected climates—is needed alongside

the expanded use of beneficial fire<sup>104</sup>, even in some forests where fire was historically infrequent. New and renewed thinking has recently been articulated under the “resist-accept-direct” (RAD) climate adaptation framework<sup>29</sup>. Applying this framework to our analysis can clarify management decisions in light of information about potential future conditions. Decisions to, for example, use mechanical fuel treatments to reduce future burn severity where fire resistance is high (*direct*), allow forests with high exposure and low fire resistance to transform (*accept*), or to promote forest persistence despite high exposure through intensive fire suppression or postfire reforestation (*resist*). Specific decisions should be made by local managers with place-based, experiential, and expert knowledge of their systems. By mapping fireshed-level exposure to fire-regime change and adaptive capacity, we offer a plausible vision of future fire regimes to managers and frontline communities. This knowledge helps inform critical stewardship decisions, which can nonetheless be especially fraught: whether and how to adapt ecosystems to likely future conditions or restore them to historical archetypes that may not be supported by future climates.

## Materials and Methods

**Research co-production process.** We conducted this analysis within a larger knowledge co-production process facilitated by the Northwest Climate Adaptation Science Center (<https://nwcasc.uw.edu/>). Knowledge co-production—collaboration among researchers and natural resource managers to make scientific outputs actionable—includes a spectrum of engagement<sup>105</sup>. We convened more than 100 natural resource managers and natural resource agency scientists to identify areas of consensus and gaps in knowledge around postfire ecological transformations in a changing climate. Here, we address specific research questions about the timing and location of fire-driven transformations, the properties of future fire regimes, and ecosystems' adaptive capacity, which participants identified during a two-day workshop in 2020<sup>27</sup>. We received feedback on our approach and initial findings at a subsequent workshop in 2022.

**Study area.** We conducted our analysis across all conifer-dominated forest area of the western U.S. that share climates with conifer forests that burned from 1984–2019, consistent with the availability of high-resolution fire data. We defined a maximum possible study area following Stevens et al. (2020), which includes areas where the combined basal area of any of the 27 conifers in their database comprise > 50% of the stand tree basal area and was > 5 m<sup>2</sup> ha<sup>-1</sup> (Fig. 1a). Ecosystems meeting these criteria represent a wide diversity of forests: they span low-elevation montane woodlands, subalpine mixed-conifer forests, and tree-line forests; are dominated by conifers but include broad-leaved species and shrubs; are situated within national forests, wilderness areas, national parks, wildland-urban-interface, and private timberlands; and are managed by tribal, state, federal, and private organizations. While shrublands, grasslands, and broadleaf-dominated forests cover large portions of the western U.S., conifer forests provide unique benefits to society, are almost universally fire-prone, and are especially vulnerable to fire-driven transformations in the decades ahead.

**Characterizing fire regimes.** The data sources used in our analysis differ in their native resolutions (with pixel dimensions ranging from 30 m to 4 km, as described below); we made inference on a grid with ~0.6 km<sup>2</sup> pixels. We summarized and visualized our findings within firesheds, spatial containers defined by similarity in estimated fire risk to infrastructure, containing > 45 ha of conifer forest (outlined in black in Fig. 1a). Our measure of exposure to fire-regime change is not equivalent to “fireshed exposure” presented alongside the fireshed dataset<sup>53</sup>, which focuses on near-term fire hazard to infrastructure.

We grouped locations into similar climates based on 30-year climatological means of climatic water deficit (CWD) and actual evapotranspiration (AET) from 1961 to 1990<sup>106</sup>. CWD and AET were calculated using a water balance model resolved at monthly timesteps and then summed annually<sup>106</sup>. We calculated climatological means across 30 years of annual data. We divided the climate space representing our study area, defined by AET and CWD, into a tessellation of hexagons (“climate bins”) and characterized fire regimes using observations from burned areas that fell in the same climate bin (Fig. 1b). Climate bins, and the fire regimes they define, are contiguous in climate space but not in geographic space. Climate data were extracted from the native ~4 km x 4 km grid at the centroid of burned 30 m x 30 m Landsat pixels. We excluded climate bins from our analysis that were represented by fewer than 1000 burned Landsat pixels and less than ten unique fire events (Fig. 1b). Testing confirmed that unequal statistical support among climate bins did not affect the results when these minimum support criteria are used. This procedure resulted in 659 unique climate bins and associated fire-



regime observations from the contemporary period, each representing a space of 53 mm CWD x 21 mm AET (Fig. 1b). The distribution of fire-regime attributes associated with a geographic location is defined by its position in climate space—its climate bin—and is populated by all observations of fire frequency, burn severity, and prefire vegetation productivity at locations in the same climate bin.

We quantified contemporary fire frequency by calculating a fire rotation period (FRP; years required to burn an area equal in size to the area of interest) as the proportion of forested area in each cell of a coarse grid (0.125° longitude x 0.125° latitude; 121–157 km<sup>2</sup>) that burned during the study period (1984–2019) divided by the number of years represented (Supplementary Fig. 3). Climate bins with a very small proportion of burned area (<0.036, equivalent to >1000 yr FRPs) were assigned a proportion randomly selected from a uniform distribution ranging from 0.036 to 0.720 (equivalent to 1000 and 500 yr FRPs, respectively), preserving the natural distribution of FRP values and allowing inference in areas where fire was rare during the satellite record. We estimated a field-based measure of burn severity, the composite burn index (CBI; bias corrected), within Monitoring Trends in Burn Severity (MTBS) fire perimeters using Google Earth Engine<sup>107</sup> with publicly available code<sup>108</sup>. Modeled CBI exhibits a stronger relationship to field measures of burn severity than unstandardized metrics (such as the delta normalized burn ratio, dNBR, and derivatives), reducing error and bias relative to other metrics<sup>109</sup>. Field-measured CBI is strongly related to several independent field measures of burn severity<sup>110</sup>. We filtered out locations where modeled CBI was <0.1, effectively excluding unburned pixels that can fall within MTBS fire perimeters. We quantified forest productivity using the Landsat-derived normalized difference vegetation index (NDVI) in the year prior to each fire from the same imagery used to model CBI; areas where prefire NDVI was <0.35 were excluded to remove low productivity sites that might be misclassified as forest<sup>108</sup>. To minimize computational burden, we conducted our analysis on a random sample of 5% of Landsat pixels that burned from 1984–2019 in flammable ecoregions of the western U.S. Observations from areas that burned more than once during this period were retained. Our final dataset included ~7.36 million observations from 4,016 different fire events. Analyses were conducted in R version 4.1.1<sup>111</sup> using the *tidyverse*<sup>112</sup>, *raster*<sup>113</sup>, *terra*<sup>114</sup>, *sf*<sup>115</sup>, and *hexbin*<sup>116</sup> packages.

**Quantifying exposure to fire-regime change.** We projected the future climate and associated fire regime of a focal location (i.e., a ~0.6 km<sup>2</sup> pixel) using climate analogs, a space-for-time substitution that uses observations from all present-day locations with a climate similar to a focal location's projected future climate. Related approaches are increasingly used to characterize climate-change impacts because they allow for inference into difficult-to-model responses, preserve latent information, and identify novel (i.e., “no-analog”) climates or conditions<sup>47,117–120</sup>. In our application, analogs were not limited by distance to the focal location and distributions of information from all analogs in the western US was considered. The projected future fire regime was characterized using observations of fire activity from all analogs that share the projected future climate of a focal location.

We used a future climate scenario representing 2 °C warming in global mean surface temperature relative to preindustrial conditions<sup>106</sup>, which applies pattern scaling factors to observed climate data during a reference period (here, 1986–2015) to project spatial and seasonal patterns of change in all modeled climate variables under a given increase in temperature above the reference period mean<sup>52</sup>. Scaling factors were based on a multi-model median from 23 CMIP5 global climate models, and thus incorporate uncertainties associated with concentration pathways, GCM structure, and the timing of temperature increases. We consider this to be roughly representative of a mid-21<sup>st</sup>-century scenario because modeled 2 °C exceedance years range from 2038–2071 under the SSP2-4.5 intermediate emissions mitigation scenario<sup>121,122</sup>, but this timing is dependent on the baseline period used to define warming, emissions policies, interannual climate variability, and unconstrained biophysical feedbacks in the climate system. This scenario is particularly useful in a forest stewardship context because it aligns with forest management planning horizons and is consistent with current federal emissions goals.

We measured the multidimensional dissimilarity between contemporary and future fire regimes using the earth mover's distance (EMD, also known as the Wasserstein metric), a distance measure that quantifies the amount of effort required to transform a reference distribution into a different distribution<sup>123</sup>. The EMD is a nonparametric dissimilarity index useful for comparing multivariate distributions that are not well described by parameters. We calculated the EMD between the future and contemporary distributions of FRP, CBI, and NDVI, all rescaled to a common domain of 00–100. In total, we made comparisons between 2583 unique combinations of contemporary and future fire regimes; 1377 climate-bin pairs lacked sufficient observations to make a comparison. Because calculating the multi-dimensional EMD is computationally expensive, we used an iterative sub-sampling approach (i.e., bootstrapping) where the EMD is calculated using 500 sample points drawn from each fire regime (climate bin), repeated 100 times, and the mean EMD is calculated. We performed EMD calculations using the *emd* package<sup>124</sup>. A high EMD reflects a large multivariate difference in fire frequency, burn severity, and vegetation productivity between contemporary and future fire regimes. Exposure values are

unitless and are only meaningful in a relative sense, as ranked against other exposure values; higher values suggest greater exposure to climate-enabled, fire-driven transformation than lower values. We calculated relative changes in specific attributes of fire regimes (FRP, CBI, NDVI) as the difference in the mean value between the future and contemporary period divided by the mean contemporary value. In the case of CBI and NDVI, we present the mean *percent* change, to account for potential differences in the meaning of these values among ecosystems and to improve interpretability. To map fire-regime statistics (exposure; change in mean FRP, CBI, and NDVI) across the study area, including conifer forests that did not burn during the study period, we identified the climate bin associated with each grid cell (its location in climate space) and applied the statistics for each climate bin to corresponding grid cells.

We compared the distributions of EMD values to a null distribution to assess whether projected changes in fire regimes differed from variability within current fire regimes (Supplementary Fig. 3). Using the bootstrapping approach described above, we recorded 100 EMD values for each pair of contemporary and projected future climate bins and calculated a 95% confidence interval of values. To build a null model, we followed the same procedure, but instead compared two distributions of samples randomly drawn from only the contemporary fire regime. We considered changes in fire regimes to be ‘significant’ when the 95% confidence intervals of the null (contemporary-contemporary) and alternative (contemporary-future) distribution of EMD values did not overlap (Supplementary Fig. 3). We calculated the median of the 5<sup>th</sup> and 95<sup>th</sup> percentiles of null and alternative comparisons of all pixels within each fireshed, assessed overlap in these statistics, and present this measure of significance at the fireshed level (Figs. 3b, 4, 5b).

**Fire resistance.** We provide ecological context to our measure of exposure to fire-regime change using an atlas of community-weighted conifer fire-resistance trait scores. This atlas represents the relative abundance of traits that enable conifer communities to burn yet resist mortality and survive fire<sup>22,125</sup>. This fire-resistance index integrates three traits relating to tree morphology and three relating to litter flammability and uses community-weighted averaging, based on relative abundance data from FIA plots, to estimate fire resistance scores across diverse tree communities. Fire-resistance trait scores reflect the capacity for conifer-dominated forests to support high-frequency, low-intensity fire and low burn severity<sup>126</sup>. Conifer forests—of any fire-resistance score—could also transition to broadleaf-dominated ecosystems that are resilient, via vegetative resprouting, to high fire frequency and high fire intensity<sup>64,127</sup>. Here, however, we only considered the adaptive capacity of conifer-dominated forests through changes in conifer composition; an expansion of fire-resistant species may allow forests to persist under increases in fire frequency and corresponding reductions in fire intensity. We did not consider shifts to broadleaf forests because the character and function of broadleaf ecosystems departs fundamentally from conifer forests and is beyond the scope of our datasets and analyses.

**Vulnerability among forest types.** To understand the biogeographic implications of our results, we explored variability in exposure and adaptive capacity among forest types. We used an index of imputed FIA plot identifiers at 30×30 m spatial resolution reflecting conditions ca. 2014<sup>128</sup> to summarize the dominant forest type within each fireshed. We calculated the proportion of total basal area in the fireshed in each FIA “tree species group code” and identified the group with the largest proportion<sup>129</sup>. These groups are named for the common name of the dominant species in the group, but may contain multiple species or variants (e.g., the “Douglas-fir” group contains all variants of *Pseudotsuga menziesii* and *Pseudotsuga macrocarpa*).

## Data availability

Data associated with this analysis are available here: <https://zenodo.org/record/8206101>.

## Code availability

Novel code used for this analysis is accessible in an external repository: [https://github.com/tylerhoecker/future\\_fire](https://github.com/tylerhoecker/future_fire).

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### Author contributions

Hoecker, Dobrowski, and Parks designed the study. Krosby provided funding and contributed to study ideation. Parks provided data. Hoecker conducted analyses and

produced figures. Hoecker wrote the manuscript with contributions from Dobrowski, Parks, and Krosby.

### Competing interests

The authors declare no competing interests.

### Additional information

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