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Mega-disturbances cause rapid decline of mature conifer forest habitat in California

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Open Research: Code (Steel et al. 2022a) is available in Zenodo at https://doi.org/10.5281/zenodo.7044555. Data (Steel et al. 2022b) are available in Dryad at https://doi.org/10.6078/D1W43V. Additional publicly available data sets utilized for this research are as follows: California fire perimeter geospatial data (FRAP 2022;

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/eap.2763

https://frap.fire.ca.gov/frap-projects/fire-perimeters/) and the California fire return interval departure dataset (Safford and Van de Water 2014; https://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=stelprdb5327836).

Abstract

Mature forests provide important wildlife habitat and support critical ecosystem functions globally. Within the dry conifer forests of the western United States, past management and fire exclusion have contributed to forest conditions susceptible to increasingly severe wildfire and drought. We evaluated declines in conifer forest cover in the southern Sierra Nevada of California during a decade of record disturbance by using spatially comprehensive forest structure estimates, wildfire perimeter data, and the eDaRT forest disturbance tracking algorithm. Primarily due to the combination of wildfires, drought, and drought-associated beetle epidemics, 30% of the region's conifer forest extent transitioned to non-forest vegetation during 2011-2020. Fifty percent of mature forest habitat and 85% of high density mature forests either transitioned to lower density forest or non-forest vegetation types. California spotted owl Protected Activity Centers (PAC) experienced greater canopy cover decline (49% of 2011 cover) than non-PAC areas (42% decline). Areas with high initial canopy cover and without tall trees were most vulnerable to canopy cover declines, likely explaining the disproportionate declines of mature forest habitat and within PACs. Drought and beetle attack caused greater cumulative declines than areas where drought and wildfire mortality overlapped, and both types of natural disturbance far outpaced declines attributable to mechanical activities. Drought mortality that disproportionately affects large conifers is particularly problematic to mature forest specialist species reliant on large trees. However, patches of degraded forests within wildfire perimeters were larger with greater core area than those outside burned areas, and remnant forest habitats were more fragmented within burned perimeters than those affected by drought and beetle mortality alone. The percent of mature forest that survived and potentially benefited from lower

severity wildfire increased over time as the total extent of mature forest declined. These areas provide some opportunity for improved resilience to future disturbances, but strategic management interventions are likely also necessary to mitigate worsening mega-disturbances. Remaining dry mature forest habitat in California may be susceptible to complete loss in the coming decades without a rapid transition from a conservation paradigm that attempts to maintain static conditions to one that manages for sustainable disturbance dynamics.

Keywords: Wildfire, drought, forest disturbance, spotted owl, fisher, habitat loss, climate change, forest conservation

Introduction

Mature forests characterized by large, old trees are essential ecosystems that support biodiversity conservation and ecological function globally (Lindenmayer and Laurance 2017). Additionally, these forests provide high levels of terrestrial carbon storage (Stephenson et al. 2014), which when managed in accordance with their natural disturbance regime can be strong carbon sinks (Liang et al. 2018). Mature forests in the western United States, particularly those composed of tall, old trees and complex understories, support numerous species of conservation concern including the spotted owl (*Strix occidentalis*) and fisher (*Pekania pennanti*) (Purcell et al. 2009, North et al. 2017). Conserving habitat for these species while also managing to reduce wildfire hazard has been a major objective of dry forest management for decades (Thompson et al. 2011, Stephens et al. 2019). Historically, mature forest patches characterized by large fire-resistant trees and varying densities made up a substantial component of the landscape vegetation mosaic

(Hessburg et al. 2015, Lydersen and Collins 2018) and were maintained by frequent, low to moderate severity fire ignited by lightning and Indigenous peoples (Anderson 2013, van Wagtendonk et al. 2018).

Through a combination of past logging and increasingly severe ecological disturbances, mature forests around the world are in decline (Lindenmayer et al. 2012). In the western United States, past timber harvesting that focused on large-tree removal is primarily responsible for the limited contemporary extent of mature forest habitat (Collins et al. 2017). Further, widespread fire suppression and exclusion of Indigenous burning during the 20th and 21st centuries has allowed small fire-sensitive trees and shrubs to replace the previously extracted large fire-resistant trees (Taylor 2004, Knapp et al. 2013, Bernal et al. 2022). These changes to forest structure and flammability plus a warming climate have led to increasingly severe disturbance cycles that may pose an existential threat to spatially-limited, remnant mature forests (Figure 1; Steel et al. 2015, Stephens et al. 2018). Patch size of forest loss due to severe wildfire is also increasing while unburned refugia within fire perimeters are becoming more fragmented and sustained in smaller patches (Steel et al. 2018), which can lead to slow or unsuccessful re-establishment of conifer species dependent on live seed trees (Welch et al. 2016). Forest densification can also lead to extensive tree mortality during drought due to a combination of elevated water stress and associated beetle attack (Fettig et al. 2019). This is particularly impactful for mature forests when beetle species preferentially select large host trees, such as sugar pine (*Pinus lambertiana*) and ponderosa pine (*P. ponderosa*) in the Sierra Nevada (Stephenson et al. 2019).

These recent and increasingly extensive losses of mature forests threaten the persistence of wildlife species that require a mosaic of seral stages, including stands of large trees and multi-layered canopies. Interiors of large high severity burn patches constitute poor habitat for mature forest specialists and support lower biodiversity for at least some taxa (Jones et al. 2020, Steel et al. 2022c). Even black-backed woodpeckers, long held up as an example of fire-dependent species in dry western forests (Hutto 2008, Odion and Hanson 2013), have recently been shown to be sensitive to fire patch size with large, homogenous high severity patches creating sink habitats for juveniles (Stillman et al. 2019, 2021). Further, the loss of fire refugia limits the capacity of many species to re-colonize the post-fire landscape (Cunningham et al. 2003, Vanbianchi et al. 2017, Thompson et al. 2021).

Several factors have led to documented or likely declines in populations of mature forest dependent species in the Western US, including the California spotted owl and the west coast population of fishers, with projected further loss of habitat posing a grave threat to these populations (Aubry et al. 2013, Gutiérrez et al. 2017, USFWS 2020). The southern Sierra Nevada in particular supports populations at-risk of climate-related shifts in drought and wildfire patterns, including the federally endangered Southern Sierra Nevada Distinct Population Segment of fishers. The region's complex topography and elevation range also provides potential climate refugia for these species, if such habitats avoid catastrophic disturbance. Policies adopted to protect remnant patches of mature forest habitat have been in place for several decades (Gutiérrez et al. 2017). Implementing such policies has led to land management designations such as spotted owl Protected Activity Centers in the Sierra Nevada National Forest Plans, and late successional reserves in the Northwest Forest Plan. Spotted owl Protected Activity Centers are a roughly 120-hectare land allocation designated wherever territorial owls are found in the Sierra Nevada portion of the California spotted owl range and delineated to include the best habitat (i.e., multi-story, large-tree, and dense canopy cover habitat). Late successional reserves are land allocations, representing 30% of the federal land within the range of northern spotted owls, designed to serve as habitat for late-successional and old-growth related species. While these policies have effectively ended the harvest of large, old trees on U.S. Forest Service lands, they also limit other management activities (e.g., thinning from below, prescribed fire) making restoration of these disturbance-adapted forests more difficult (Collins et al. 2010). Furthermore, these policies implicitly assume that "protected" habitat areas can be preserved, more or less in their current form, in perpetuity (USDA 2019). Recent disturbance trends in western forests create a test of this assumption and of the efficacy of a static approach to habitat conservation in disturbance-prone systems. Results from the Pacific Northwest suggest that in dynamic, disturbance-dependent forests, this assumption is not well supported (Davis et al. In Press). Under climate change, a static approach to mature forest conservation may be even less effective in drier and warmer regions such as the southern Sierra Nevada.

In this paper, we quantify change in the extent of mature conifer forests in the southern Sierra Nevada of California during 2011-2020, a decade and ecoregion characterized by compounding severe wildfires and drought follow prolonged fire exclusion. The primary objectives of this analysis are to: (1) quantify the decline of conifer forest cover and of mature forest habitat due to drought (and associated beetle attack) and wildfire between 2011 and 2020; (2) test the assumption that static areas of restricted management will conserve mature forest habitat over time by examining whether rates of decline differed within vs. outside of spotted owl protected areas; (3) compare the spatial pattern of drought/beetle-caused mortality with wildfire effects to better understand their differential impacts on mature forest habitat and the species that depend on it; and (4) assess whether and where forests have survived recent wildfires, potentially improving their resilience to future severe disturbance. Finally, considering the overall magnitude and extent of these disturbances, we discuss a potential shift in approach towards managing habitat for sensitive species, from one dominated by mega-disturbances toward a restoration of smaller, frequent disturbances necessary for the persistence of mature forests in fire- and drought-adapted ecosystems (Fig. 1).

Methods

Study Area

Our study area is defined by the southern Sierra Nevada ranging approximately from 35 to 39 degrees latitude and -121 to -117 degrees longitude (Figure 2). We focus on forests that were conifer-dominated as of 2011. Hardwood-dominated forests are also important habitat for mature forest specialists (North et al. 2000, Aubry et al. 2013, Green et al. 2019). However, we limit our analysis to conifer-dominated forests because the tree mortality data used (described below) has not yet been calibrated for non-conifer cover types. At lower elevations, conifer forests are dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), and incense cedar (*Calocedrus decurrens*), transitioning to a mixed conifer community at mid-elevations that also includes, sugar pine (*Pinus lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), giant sequoia (*Sequoiadendron giganteum*), and California black oak (*Quercus kelloggi*) (Mayer and Laudenslayer 1988, North et al. 2016). At higher elevations, Jeffrey pine (*Pinus jeffreyii*), red fir

(*A. magnifica*), lodgepole pine (*Pinus contorta* var. *murrayana*), and western white pine (*Pinus monticola*) become dominant (Mayer and Laudenslayer 1988, North et al. 2016). The southern Sierra Nevada has a Mediterranean-type climate where most precipitation occurs between November and May followed by an annual dry period broken up by sporadic summer thunderstorms (North et al. 2016).

Prior to Euro-American colonization, fire return intervals were short, especially in ponderosa pine and mixed conifer forests (Safford and Stevens 2017). Fire severity in these forests was predominantly low to moderate, resulting in the survival of most mature fire-resistant trees (Safford and Stevens 2017). Return intervals were longer and the share of high severity effects (i.e., >95% vegetation mortality; Miller et al. 2009) were somewhat higher in higher elevation red fir and subalpine forest (Meyer and North 2019). Due to 20th and 21st century fire suppression and exclusion, contemporary return intervals are much longer than their historical reference, although fire frequency and severity have both increased markedly in recent decades due to fuel accumulation, human ignitions, and climate change (Steel et al. 2015, Westerling 2016, Williams et al. In Revision). Severe drought was not uncommon in this region over the last two millennia (Swetnam 1993). However, the most recent drought (2012-2016) may have been the most severe event in the last 1200+ years (Robeson 2015).

Data and analysis

We used F^3 data of canopy cover and large tree height to map conifer forest and mature conifer forest cover as of 2011 (Huang et al. 2018). The F^3 product integrates Forest Inventory and

Analysis (FIA) field data with landscape and vegetation succession models to generate spatially-contiguous estimates of stand structure, which has been validated for Sierra Nevada forests (Huang et al. 2018). We defined conifer forests as areas with a minimum of 25% canopy cover dominated by conifer species. This threshold is consistent with the USDA's vegetation classification system where tree-dominated vegetation with a minimum height of 5m and 25-100% canopy closure is considered forest or woodland (Brewer et al. 2005). 10-25% tree canopy cover can be considered sparse woodland or savanna vegetation. We defined mature forests as a subset of conifer forests where the average height of the 40 largest diameter trees within the area equivalent to a FIA plot (0.4 ha) is at least 30 m. Cover of tall trees is particularly valuable for mature forest specialists such as the spotted owl (North et al. 2017). We further classified mature forests into sub-groups using the F^3 data and following the California Wildlife Habitat Relationships classification of moderate density (40-59% canopy cover) and high density ($\geq$ 60% canopy cover) forests, which support various life history requisites (foraging, nesting/denning) and demographic parameters (reproduction, survival) of mature forest wildlife (Table 1). For example, 56-61% cover may be optimal for fisher resting sites (Purcell et al. 2009) and California spotted owls tend to occupy nest sites with >70% canopy cover (Tempel et al. 2016). Forests characterized by tall trees, but less than 40% canopy cover may be considered low density mature forests. This forest type only covered 1076 ha in 2011, which constituted 1% of mature forest extent and 0.1 % of overall conifer forest extent. The savanna and low density mature forest sub-classes are not analyzed independently here as our focus is on species associated with higher canopy covers.

Estimates of live canopy cover decline (at 30 m resolution) were obtained from the Ecosystem Disturbance and Recovery Tracker (eDaRT) - an image analysis system that processes all usable historic Landsat imagery (normally at 8- or 16-day step). The eDaRT algorithm statistically models normal (e.g., phenology-driven) variability in multiple vegetation indices across the image time series, and tracks model residuals through time to detect disturbance events as anomalous changes in the residuals' trajectories, relative to the a recent baseline (Koltunov et al. 2015, 2020). For detected disturbances, the algorithm estimates the resulting loss of live tree canopy cover (as pixel area fraction) using the eDaRT Mortality Magnitude Index (MMI). In this paper, we used the MMI values integrated on an annual basis between 2011 and 2020 (detailed description in Appendix S1). Conifer forests and mature forests are considered to have transitioned to a different vegetation class if live canopy cover drops below their minimum canopy cover thresholds. Although increases in live canopy cover did occur in some instances over this time period, this new cover was predominated by seedling to sapling size trees following large tree mortality events (Young et al. 2020). Thus, only declines in canopy cover were considered here.

The current eDaRT version does not directly differentiate the cause of detected disturbances (e.g., fire vs. drought and beetle infestation), thus necessitating additional analyses to attribute detected disturbance to tree mortality. Specifically, we assumed eDaRT-detected reduction in canopy within wildfire perimeters of a given year to be attributable to a combination of wildfire and underlying drought conditions, and within management areas to be a combination of timber harvest or fuels reduction treatments and drought conditions. To delineate burned areas for each study year, we used California's interagency fire perimeter database (available at https://frap.fire.ca.gov/frap-projects/fire-perimeters/) (FRAP 2022). To delineate areas managed for timber harvest or fuels reduction treatments we used the Knight et al. (2022) dataset that combined spatially explicit activities data from the California Department of Forestry and Fire Protection (CalFire) and the US Forest Service (FACTS database); and cross-walked these activities by treatment type and intensity. Knight et al. (2022) also refined the spatial and temporal accuracy of the combined data using satellite imagery and the Continuous Change Detection and Classification algorithm. While these data include a wide range of activity types, we limited our assessment to activity types that can significantly reduce live canopy cover at the Landsat pixel scale (e.g., clear-cuts and thinning). This dataset does not include activities on National Parks land, where mechanical tree removal is minimal and at the time of writing does not include 2020 activities. Canopy declines in areas and years where no fire or management activity occurred are attributed to drought and associated beetle-kill only. This assumption likely resulted in a slight over-estimate of drought mortality in 2020 when management activity data were not available.

Spotted owl Protected Activity Center (PAC) polygons were obtained from a US Forest Service geospatial dataset and included a total of 651 PACs in our study area; 96% of which were established before 2011. A regular grid of non-PAC sample points was generated across our study area but limited to Forest Service lands and outside established PACs. Grid spacing (3.9 km) was set to allow an equal number of non-PAC points (651) within the 2011 extent of conifer forests. Sample points were buffered to create non-PAC areas equal to the mean size of study area PACS (128 ha). 2011 canopy cover, 2011 average large tree height, and relative decline in canopy cover between 2011 and 2020 were summarized for each PAC, all non-PAC Forest service lands, and for each non-PAC sample area. Relative canopy cover declines are calculated as the percentage of 2011 canopy cover that was lost between 2011 and 2020. Mean values within each PAC and non-PAC area were used for statistical comparison. To assess whether forest habitat within PACs were successfully preserved despite regional disturbances we modeled relative decline in cover as a function of sample class (PAC or non-PAC). Separately, we modeled relative decline in cover as a function of 2011 canopy cover and 2011 average large tree height. Structural and PAC class variables were not combined in the same model to avoid statistical confounding as PAC delineation is determined largely by forest structural characteristics (USDA 2004). We fit generalized linear models using a beta error structure with a logit-link because relative canopy cover decline is a proportion bounded between zero and one. Models were fit using the BRMs package in program R (Bürkner 2017, R Core Team 2021).

We compared landscape pattern within and outside of burned areas to contrast the effect of the combined impacts of wildfire and drought/beetles with areas only affected by drought and beetle attack. Patches of all forest and mature forest that transitioned to lower density classes between 2011 and 2020 were assessed for size and core area. Area ≥ 90 m (3 pixels) from non-transitioned edge is defined as core area, which approximates distance estimates of when conifer seed dispersal and habitat use of some forest-associated species become minimal (i.e., 100m; Jones et al. 2020, Kramer et al. 2021). Additionally, to assess the degree of fragmentation due to each combination of disturbances, we calculated the aggregation index of forest cover prior to the disturbances in question (2011) as well as within and outside of burned areas at the end of our study period in 2020. Assessments of landscape pattern were conducted for each forest class.

We focused this analysis on drought and wildfire pattern only because the extent of mechanical management activities during our study period were relatively minimal (see results).

To assess the degree to which forests survived a recent fire and potentially experienced partial restoration of the historic fire regime, we calculated years since last fire for all areas remaining as forest and mature forest each year. Forested pixels are considered to have experienced recent fire if years since last fire is equal to or less than twice the mean reference return interval for a given forest type (e.g., ≤ 2*11 years for dry mixed conifer) according to the California fire return interval departure dataset (Safford and Van de Water 2014). This measure has been used in previous work as an indication of uncharacteristically high fuel accumulation (North et al. 2012) and consequently greater vulnerability to severe fire (Steel et al. 2015). Spatial analyses were performed primarily using the *sf*, *terra*, and *landscape metrics* packages in the R statistical environment (Pebesma 2018, Hesselbarth et al. 2019, R Core Team 2021, Hijmans 2022).

Results

Conifer forest cover decline

As of 2011, there were a total of 1,407,597 hectares of conifer forest in our southern Sierra Nevada study region. 96,810 ha of these forests were classified as either moderate density (41,175 ha) or high density (55,634 ha) mature forest habitat (Table 2). Between 2011 and 2020, canopy cover across 30% of conifer forests declined below 25% constituting a change to either sparse woodland/savanna vegetation or in many cases a transition to non-tree-dominated vegetation (Figures 2 & 3). During this period, 50% of moderate or high density mature forest habitat saw canopy cover decline below 40% constituting a transition to lower density forest (22% of the original extent) or non-forest vegetation (28% of the original extent). Within the mature forest classification, higher density areas experienced more extensive declines, with 85% of this subclass falling below the 60% canopy cover definition of high density. The moderate density mature forests experienced little net change, with much of its declining area compensated by transitions from the high density mature forest group (Table 2; Figure 3).

Spotted owl Protected Activity Centers (PACs) saw rates of decline across conifer forest classes similar to the study area overall, with the exception of moderate density mature forests, which saw a net increase of 13% due to transitions from the high density class (Table 2). However, because of how they are delineated, PACs generally were biased towards containing denser forests than the study area as a whole resulting in differences in the average rates of canopy cover decline. In 2011, PACs were characterized by a mean canopy cover of 56%, mean large tree height of 24 m, and 20% of their conifer forest area was categorized as mature forest of moderate or high density. In contrast, all conifer forests in our study area in 2011 were characterized by a mean canopy cover of 36%, mean large tree height of 13 m, and 7% were categorized as mature forest of moderate or high density. By 2020, the mean absolute decline in canopy cover was greater inside PACs (26%) compared with all conifer forests in the study area (16%).

Statistical comparisons of PAC and non-PAC areas within Forest Service lands confirmed that the decline in relative canopy cover (percent of 2011 canopy cover) was greater in PACs and also showed clear effects of initial forest structure, with greater decline within areas characterized by higher 2011 canopy cover and less decline in areas characterized by greater 2011 large tree height (Figure 4). Models predict the average PAC lost 49% (95% prediction interval [PI] = 46, 51) of its 2011 canopy cover by 2020 while non-PAC areas lost 42% (PI = 40, 44; Figure 4a). Among both PAC and non-PAC areas, areas that had higher canopy cover in 2011 were more susceptible to percent canopy cover loss and vegetation class transition than areas with lower canopy cover (Figure 4b). For example, mean predicted declines at our density class thresholds of 25, 40 and 60% canopy cover were 31% (PI = 27, 34), 39% (PI = 37, 41), and 51% (PI = 49, 53) respectively (Figure 4b). The effect of large tree height on relative canopy cover decline was negative albeit with a smaller effect size, indicating the presence of large, tall trees had a moderating effect on disturbance. For example, a forest with a mean large tree height of 15 m was predicted to experience a 55% (PI = 49, 61) relative canopy cover decline, while a mean large tree height of 30 m was expected to result in a relative canopy cover decline of 52% (PI = 47, 57; Figure 4c) when controlling for 2011 canopy cover. Model uncertainty was low (95% credible intervals did not included zero) for all effect estimates (Appendix S1: Table S1).

Wildfire and drought patterns

Because drought conditions were ubiquitous during large parts of our study period, we compared three types of interacting forest disturbances: 1) drought and associated beetle infestation (jointly referred to as 'drought') in the absence of other disturbances, 2) the combination of wildfire plus drought, and 3) the combination of mechanical management activities (e.g., timber harvest and thinning) plus drought. A greater cumulative area of forests was converted to non-forest due to drought alone (213,000 ha; 51% of total area transitioned) than when wildfires were also a contributing factor (190,000 ha; 45%), or when mechanical activities were a contributing factor

(16,000 ha; 4%). The differential was even greater in the case of moderate and dense mature forests where transitions to non-forest or a lower density class was more attributable to drought alone (32,000 ha; 66%), than to the combination of wildfire and drought (15,000 ha; 31%) or mechanical activities and drought (2,000 ha; 4%).

For all forest classes, patch and core size of transitioned areas were greater within burned forest than those that were not burned during 2011-2020 (Figure 2; Table 3). Distributions of disturbed patch sizes were highly skewed with relatively few large patches accounting for a disproportionate amount of the area of transitioned forest. The largest transitioned forest patch (68,389 ha) and contiguous core area (25,186 ha) of transitioned forest were found within burned areas during this period. Likewise, the largest patch size (1119 ha) and contiguous core area (326 ha) of transitioned moderate and high density mature forest habitat occurred within fire perimeters (Table 3). These differences in spatial pattern of interacting drought and wildfire resulted in greater forest fragmentation than areas affected by drought alone as measured by the aggregation index. Low aggregation index values approaching 0 represent greater fragmentation and high values approaching 100 represent greater aggregation. For all forests the aggregation index declined from 93 in 2011 to 88 in unburned areas and to 75 in burned areas by 2020. Similarly, the aggregation index for mature forests declined from 85 in 2011 to 75 in unburned forests and 64 in burned forests (Table 4).

There was a clear temporal pattern of forest mortality attributable to drought and beetle infestation alone with a 2016 peak in forest cover decline corresponding to the last year of the 2012-2016 drought. Transitions due to the combination of wildfire and drought was less consistent and corresponded with individual large wildfire events (e.g., the 2013 Rim Fire and the 2020 Creek and Castle Fires). Transitions attributable to mechanical activities and drought were consistently limited between 2012 and 2019 (Figure 5a).

As of 2011 a large majority of the conifer forests and mature forests in the southern Sierra Nevada had not experienced a wildfire in at least twice their reference fire return interval. The absolute amount of forest that was within twice its reference return interval was largely stable across the study period, but the proportion of recently burned forest and recently burned mature forest increased due to an overall decline in forest cover (Figure 5b). Specifically, the percent of recently burned conifer forests increased from 25% in 2011 to 33% in 2020, while recently burned mature forests increased from 7% to 20% over the same period.

Discussion

Rapid decline of mature forest habitat

The 2010s was a decade characterized by severe and unprecedented ecological disturbance in California's conifer forests; one that portends a rapid reshaping of forested landscapes, the ecosystem services they provide, and their dependent wildlife communities. Here we documented a temporary or permanent conversion of 30% of the conifer forests and a transition of half of the moderate and high density mature forest habitat in the southern Sierra Nevada between 2011 and 2020 due to compounding megafires and a historic drought. Changes were particularly pronounced among dense mature forest habitat, which declined by 85% either by transitioning to lower density forest or through complete conversion to non-forest vegetation.

Spotted owl Protected Activity Centers (PACs), also saw dramatic declines with a loss of 49% of their 2011 canopy cover. Worsening wildfire and climate trends are expected to continue or accelerate in the coming decades (Abatzoglou et al. 2021), making continued decline of conifer forest extent likely and the complete loss of remaining moderate and high density mature forest habitats plausible (Westerling 2016, Stephens et al. 2016b).

Megafires create large high severity patches that can be inaccessible or inhospitable to mature forest specialists, and as a result they tend to support lower wildlife species diversity overall (Jones et al. 2020, Steel et al. 2022c). Further, large severe wildfires can increase fragmentation of limited mature forest habitat. Our results demonstrate that wildfire (in combination with drought) created distinctly larger contiguous patches of forest loss and increased forest fragmentation whereas tree mortality from drought and beetle-kill resulted in patchier, and more fine-scale spatial patterns with relatively moderate increases in habitat fragmentation. In the Sierra Nevada, suitable fisher habitat is distributed in a north/south pattern limited by elevational bounds and periodically disrupted by bottlenecks that occur near large river canyons (Thompson et al. 2021). These bottlenecks, which are typically associated with isolated stretches of linkage habitat, may be comprised of lower quality habitat but are crucial for maintaining overall population connectivity and gene flow (Tucker et al. 2014). Since 2013, habitat within key linkage areas has been lost to high severity fire at nearly twice the rate of habitat outside key linkage areas (USFWS 2020, Thompson et al. 2021), limiting population-scale connectivity and increasing the risk of genetic isolation (Tucker et al. 2014). The spotted owl is tolerant of or even selects for small high severity burned patches if mature stands survive in the nearby matrix, but they are intolerant of increasingly large high severity patches created by fires such as the 2013

Rim, 2020 Creek, and 2020 Castle fires in the southern Sierra Nevada (Jones et al. 2020, Kramer et al. 2021). A mosaic of burn severities consisting of predominantly low to moderate severity fire with small patches of high severity can create 'pyrodiverse' landscapes that contain early seral habitat including shrublands and recently killed 'snag forests' required by some species while also promoting persistence of key habitat structures for late seral dependent species (Jones et al. 2021b, Steel et al. 2021a). These disturbances also leave a network of residual habitat patches (i.e., fire refugia), which are critical to fisher re-colonization (Blomdahl 2018, Thompson et al. 2021). Without these refugia, the potential exists for a community shift to more generalist species (Green et al. 2022).

Low to moderate severity fire can create habitat for some wildlife species and increase forest resistance to future severe disturbance (Steel et al. 2021b), but drought mortality has the potential to add flammable fuels to the system and increase the likelihood of future forest loss due to wildfire (Stephens et al. 2018, 2022). The 2012-2016 drought and associated beetle epidemics resulted in the mortality of over 150 million trees in California's Sierra Nevada (USDA 2020), which was disproportionately concentrated among large conifers (e.g., among >38 cm diameter ponderosa pine; Fettig et al. 2019). Fishers rely on large trees for resting and denning habitat (Purcell et al. 2009, Green et al. 2019), and spotted owl population declines have been linked to losses of large, old trees used for nesting (Jones et al. 2018). Thus, the mechanism of canopy cover decline in mature forests is also important. For example, shifts from high density to moderate density mature forests may be restorative when wildfire is the causal agent because it consumes fuel and generally kills smaller trees, leaving larger trees intact and further insulated from subsequent disturbance. Fuels reduction treatments that target fine fuels can have a similarly restorative effect, especially when including the use of prescribed or cultural fire (North et al. 2021). Additional research is needed to better understand how mature forest specialist species respond to wildfire and wildfire surrogates that reduce canopy cover below known optimum, while maintaining important features such as large, tall conifers and restoring resilience to future disturbance (Jones et al. 2021a). However, when canopy cover declines are attributable to drought and beetle attack (Appendix S1: Figure S1), there is likely to be a corrosive effect on habitat quality because large trees are preferentially killed and dead fuel is added to the system, increasing vulnerability to subsequent wildfire effects.

Rapid loss in mature forest habitat in the southern Sierra Nevada and longer term trends in fire-related forest decline throughout California (Stevens et al. 2017, Steel et al. 2018) suggest that existing forest management paradigms may be inadequate for maintaining mature mixed-conifer forests under current and projected future disturbance dynamics (North et al. 2022). If these rates of decline continue, we are likely to see near total loss of southern Sierra Nevada mature conifer forests in the coming decades. This would be much more rapid than the time horizon of mature forest loss estimated by Stephens et al. (2016b) (by 2089, or ~75 years). However, Stephens et al. (2016b) did not consider drought-related mortality, and only analyzed fire activity up through 2014, which missed the record fire year of 2020 (Safford et al. 2022). It is worth noting that the extreme fire activity documented in California during 2020 was likely not a one-off anomaly; recent observations indicate similar, if not exacerbated fire activity in 2021 (Shive et al. 2021). The region has also reentered extreme drought (Williams et al. 2022) with implications for both drought and beetle mortality and severe wildfire. More optimistically, total loss of mature forests in this region could be delayed until mid-century if we enter a period of cooler, wetter years, if surviving mature forests within these fire footprints have gained resilience to future disturbances, or if recruitment of mature hardwood species compensate for losses of large conifers. Hardwood species may become a greater component of the Sierra Nevada landscape as conifers decline (Restaino et al. 2019, Steel et al. 2021b). Oaks, especially California black oaks, are relatively resilient to both wildfire and drought, and are utilized by species such as the spotted owl and fisher (North et al. 2000, Aubry et al. 2013, Green et al. 2019). However, loss of mature forest habitat, on any likely timeline, is unsustainable given that the recruitment of conifer or hardwood mature forests takes many decades to centuries. Stephens et al. (2016a) emphasize that policies prioritizing forest resilience over other resource concerns may be needed to meaningfully address the current backlog in forest management and shift course from forest decline to sustainable disturbance dynamics. Indeed, our analysis showed that areas of higher canopy cover are more at risk of loss, and that large areas of relatively homogenous moderate and higher density forests, like PACs, are at risk of larger declines if resilience needs are not addressed. Recognizing the dynamic nature of habitat in these forests, and prioritizing the restoration of these dynamics over the attempted strict preservation of existing habitat, may help minimize the impacts of these changes and maintain habitat functionality in the long term (Fabritius et al. 2017, Stoetzel et al. 2020, Gaines et al. 2022).

Management Implications: Toward more sustainable disturbance dynamics

Landscapes are naturally dynamic in space and time, but society's approach for conserving landscapes often views them as static entities (Stoetzel et al. 2020). Habitat conservation typically involves cordoning off lands for full or partial protection from human activities, while at the same time allowing for fire suppression activities to preserve current structure.

Conservation approaches that aim to keep ecosystems in stasis have been largely successful in conserving biodiversity and threatened species worldwide (Gray et al. 2016) by preventing threats to habitat such as infrastructure development and natural resource extraction (Barber et al. 2014). These approaches are heavily informed by conservation objectives in more naturally static ecosystems (e.g., Barber et al. 2014) as opposed to those adapted to frequent low intensity disturbance. Such “static” conservation approaches are heavily embedded in existing wildlife and ecosystem conservation policy (Leopold et al. 2018), as well as land management plans (e.g., USDA 2004) in North America. Yet recent disturbance patterns and their cumulative impacts have demonstrated that efforts to resist change are often falling short in dynamic ecosystems, such that achieving the specific conservation objectives and possibly the intent outlined in policy documents may no longer be feasible in disturbance prone areas (Davis et al. In Press). In fact, continued attempts to resist change may be counterproductive where a hands-off approach (but continued fire suppression) creates a higher likelihood of rapid, transformational, and undesirable changes in the form of large scale type conversion and habitat loss from disturbance (Rissman et al. 2018). In our study region spotted owl Protected Activity Centers are often managed using a static conservation approach but our analysis shows they have recently experienced more declines in canopy cover (49% relative to 2011) than outside of their borders (40%). This observation suggests that conservation of habitat for old-forest dependent species may require a more dynamic approach that increases resilience to disturbance while maintaining valuable habitat features such as large, tall trees.

As an alternative to the static approach to habitat conservation currently in practice, a landscape conservation paradigm that recognizes and incorporates ecological system dynamics (Hessburg et al. 2021, Gaines et al. 2022) may prove better suited for disturbance-prone forests. Collectively, we refer to this as the "managed dynamics" paradigm (Figures 1 & 6). While the overall goal of this alternative approach is similar to that of a more traditional static paradigm, i.e., to conserve a particular landscape feature (in this case, mature forests), the managed dynamics paradigm strives for something closer to a dynamic equilibrium (sensu Bonnicksen and Stone 1982) of habitat loss and recruitment. In Sierra Nevada dry forests that historically were highly dynamic, patches of mature forest were periodically lost or degraded but were balanced by continual successional changes supported by a frequent low severity disturbance regime (Miller and Safford 2017). Moving away from a "static" conservation paradigm in favor of a "dynamic" one does not prescribe eliminating protected areas or habitat preserves; nor would it involve removal of large trees, which our analysis shows supported forest resilience over the last decade. Rather it suggests greater active management is necessary (e.g., through fire use and ecologically based thinning; sensu North et al. 2021) with an eye for emulating fine scale heterogeneity and forest resilience likely supported by historic disturbance regimes (Jones et al. 2021a). Further, management tactics and tools may need to be similarly dynamic and allowed to shift when objectives are not being met, or when needs have changed (e.g., Spies et al. 2018, Wood et al. 2018).

Managing for sustainable dynamics also embraces the positive role of humans in actively managing ecosystems. For millennia, Indigenous peoples of western North America burned vast areas of land to increase access to natural resources (Anderson 2013, Hoffman et al. 2021). Indigenous burning as part of historic fire regimes also produced other ecosystem benefits such as increased forest resilience to subsequent disturbances (Eisenberg et al. 2019), enhanced biodiversity (Hoffman et al. 2021), and mutual protection for cultural and ecological resources (Slaton et al. 2019). A major part of implementing a managed dynamics paradigm in the Sierra Nevada includes increasing support for Indigenous fire use, as well as state and federally supported and ecologically-driven management. Specific management actions would likely include leveraging areas of low to moderate severity effects within unplanned wildfires as well as active fuels reductions across large landscapes with prescribed and managed fire in a "pyrosilviculture" framework (North et al. 2021). Such an approach would be expected to result in reduced forest conversion to non-forest, increased water supply, more stable carbon storage, reduced competitive stress, as well as both protection and promotion of growing conditions for large, old trees (Figure 6; Stephens et al. 2020, 2021, North et al. 2022).

A managed dynamics paradigm is not without its challenges. Implementing forest treatments and restorative actions is generally difficult due to insufficient funding and staffing, perceived and realized risks of employing prescribed, cultural, and managed wildfire, as well as other political and societal concerns (Schultz et al. 2019, North et al. 2021). Perhaps foremost among these obstacles where sensitive wildlife habitat is of concern is that a managed dynamics approach appears at odds with the precautionary principle, which has governed land management and wildlife conservation for decades (e.g., Kriebel et al. 2001). The precautionary principle “imposes a burden of proof on those who create potential risks, and it requires regulation of activities even if it cannot be shown that those activities are likely to produce significant harms” (Sunstein 2002). In the Sierra Nevada, the principle has led to resistance of managing disturbance dynamics because management activities such as fuels reduction and thinning have been perceived to pose a risk to spotted owls and fishers via habitat alteration (Tempel et al. 2015). Indeed, many past management practices have had negative impacts on old forest habitat features, including harvesting of the largest trees and removal of damaged trees that contain cavities or provide platforms for nesting and denning. Yet under current conditions characterized by rapid change, decision “paralysis” (Sunstein 2002) precipitated by the precautionary principle may lead to far greater harm to spotted owls and fishers via complete loss of mature forest habitat (Hessburg et al. 2021). For example, an estimated 10-14% of the global population of giant sequoia were lost in 2020 alone due to high severity wildfire within the southern Sierra Nevada with additional losses to giant sequoia groves incurred from two large wildfires in 2021 (Shive et al. 2021). Many of the affected giant sequoia groves had largely gone untreated (i.e., no large-scale fuels reduction activities have occurred) and there is concern that increased restrictions for the southern Sierra fisher population may add an additional barrier to restoration efforts. Yet avoidance of action is a management decision, and our analysis shows a hands-off approach is increasingly failing to preserve mature forests. Thus, we suggest that the managed dynamics paradigm is compatible with an interpretation of the precautionary principle that explicitly recognizes the risk of inaction. For example, as described in Wood et al. (2020), the precautionary principle could posit that management actions should be taken despite uncertainties if the cost of inaction is high.

Conclusion

Shifting disturbance patterns pose stark challenges to forest management and conservation. This has become particularly evident over the past decade in the southern Sierra Nevada of California, where compounding megafires and unprecedented drought have rapidly eroded already limited mature forest habitat. While this period of forest degradation appears exceptional at present, continued climate change and the lingering legacy of fire exclusion and suppression make continued mega-disturbances likely. Indeed, drought conditions returned to the region in 2019 and persist through the time of writing in 2022. To forestall continued loss and fragmentation of habitat critical to mature forest specialist species a shift from a static, preservationist paradigm of habitat conservation to one striving for sustainable disturbance dynamics is likely necessary in fire- and drought-prone forests. Encouragingly, some recent forest policy appears to be moving toward a recognition of the need for managing for desirable dynamics. For example, recent management strategies for both Sierra Nevada fishers and California spotted owls recognized the shortcomings of the static approach of identifying "protected" habitat areas with limited management allowed (USDA 2019). These new strategies call for a more dynamic approach to providing this habitat over time and space, while also incorporating the likelihood of disturbance. A broadscale shift in forest conservation paradigm faces challenges; but given the rapid rate of forest degradation and future outlook, an equally rapid adaptation of management approach is likely needed to maintain and restore mature forests in the coming decades.

Acknowledgements

We thank the USFS Region 5 remote sensing lab for providing the F^3 data used in this analysis, especially Laura Young-Hart and Leland Tarnay. Figure 6 was illustrated by the artist Allison Fitzmorris. Funding was provided by the California Department of Forestry and Fire Protection, grant #8GG21823.

Conflict of interest statement

The authors have no conflicts of interest.

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Table 1: Conifer forest classification definitions. Classifications are hierarchical with mature forests being a subset of conifer forest and mature forests further sub-divided into density classes.

Classification	**Canopy Cover Range**	**Large Tree Height Minimum**
Non-forest	0-25%	none
Sparse woodland/Savanna*	10-25%	5 m
Conifer Forest	25-100%	5 m
Mature Forest	40-100%	30 m
Low Density*	25-40%	30 m
Moderate Density	40-60%	30 m
High Density	60-100%	30 m

*The savanna and low density mature subclasses are not explicitly analyzed.

Table 2. Hectares (% of 2011 area) of conifer forests and forest class change between 2011 and 2020 for the full study area and spotted owl Protected Activity Centers (PACs). Conifer-dominated areas with >25% live canopy cover are considered forests. Within that class, mature forests are defined by a mean tall tree height of >30m. Further nested within the mature forest class are moderate density (40-60% canopy cover) and high density (>60% canopy cover) mature forests. Forests density classes either transitioned to non-forest (canopy cover dropped below 25%) or to a lower density class (e.g., a decline from 70 to 50% cover constitutes a transition from high density mature forest to the moderate density class).

Extent	Class	2011	2020	Transition to non-forest	Net change
	All Forests	1,407,597	988,601 (70%)	418,996 (30%)	-418,996 (-30%)
Study	Mature Forests[a]	96,810	48,385 (50%)	26,675 (28%)	-48,425 (-50%)
Area	Mod Density	41,175	39,957 (96%)	11,409 (28%)	-1,218 (-3%)
	High Density	55,634	8,427 (15%)	15,265 (27%)	-47,207 (-85%)
Protected	All Forests	76,819	49,936 (65%)	26,883 (35%)	-26,883 -(35%)
Activity	Mature Forests[a]	15,072	7,568 (50%)	4194 (28%)	-7,504 (-50%)
Centers	Mod Density	5,233	5,889 (113%)	1,690 (32%)	655 (13%)
(PACs)	High Density	9,838	1,679 (17%)	2,503 (25%)	-8,159 (-83%)

[a] Includes mature forests with >40% 2011 canopy cover (i.e., excludes low density mature forests).

Table 3. Summary statistics of disturbance patch size and core area size created by drought/beetles and wildfire between 2011 and 2020. Patches without core area are included in the patch size (area) metric but excluded from the core area (core) metric. N represents the number of patches in each group, and all other summary statistics are in hectares. In most cases disturbed patches are small (i.e., 50th quantile < 1 ha). Thus, we summarize the large end of data distributions (i.e., 95th quantile, and max) as these patches affect the greatest amount of area and are the most ecologically important.

Metric	Class	Disturbance	N	Mean	Q50	Q95	Max
area	Forest	Drought	233874	0.66	0.18	1.89	2246.04
area	Forest	Fire + Drought	36953	7.15	0.18	3.77	68372.36
area	High Density Mature	Drought	11467	2.25	0.27	5.84	1741.95
area	High Density Mature	Fire + Drought	5694	3.74	0.36	9.52	827.43
area	Mature Forest	Drought	20306	1.04	0.18	3.23	447.88
area	Mature Forest	Fire + Drought	9078	3.00	0.36	8.17	1115.57
area	Moderate Density Mature	Drought	14629	0.86	0.18	2.51	373.26
area	Moderate Density Mature	Fire + Drought	6939	1.54	0.27	4.49	970.91
core	Forest	Drought	1268	2.36	0.54	7.54	342.46

Metric	Class	Disturbance	N	Mean	Q50	Q95	Max
core	Forest	Fire + Drought	671	116.43	0.81	93.79	25179.57
core	High Density Mature	Drought	375	6.15	0.63	24.90	653.32
core	High Density Mature	Fire + Drought	322	10.15	1.39	41.56	295.41
core	Mature Forest	Drought	278	2.51	0.36	11.57	67.88
core	Mature Forest	Fire + Drought	400	8.41	0.99	32.24	326.03
core	Moderate Density Mature	Drought	124	2.68	0.45	10.98	58.63
core	Moderate Density Mature	Fire + Drought	156	5.40	0.72	19.64	292.45

Table 4. Aggregation index values prior to and following drought/beetles and wildfire in the southern Sierra Nevada during 2011-2020. Index values range from 0 to 100, where low values represent highly fragmented forest cover and high values represent highly aggregated forest cover.

Class	**Initial (2011)**	**Post-drought (2020)**	**Post-drought and wildfire (2020)**
All Forests	93	88	75
Mature Forests	85	75	64
Moderate Density Mature	77	63	52
High Density Mature	83	61	46

Figure 1: Conceptual figure showing trends in area of conifer forests and of mature forest habitat under regimes of (a) historical, (b) current, and (c) potential future dynamics (achieved via 'managed dynamics'). The late 2010s and early 2020s have been characterized by compounding mega-disturbances and extensive declines of mature forest habitat. Future managed dynamics include the restoration of small, frequent, low intensity disturbances that can help stabilize and perhaps reverse these recent trends. Vertical grey bars represent hypothetical disturbance events, with thicker bars indicating greater size/severity.

Figure 2. Map of forest and mature forest habitat transitions due to drought and wildfire mortality between 2011 and 2020. a) Areas of conifer forest persistence and transitions in the southern Sierra Nevada. b) An example of the spatial pattern of transition where drought and beetle infestation led to relatively small but widely dispersed patches of mortality. c) An example of where the combination of drought and wildfire led to larger and more aggregated patches of mortality (i.e., within the 2020 Castle fire). Forests and mature forest (moderate and high density) habitat are considered to have experienced transition if canopy cover declined below 25% and 40%, respectively. Areas initially considered mature were further limited to forests where the average height of the tallest trees exceeded 30 m. Black polygons show perimeters of medium to large (≥ 5,000 ha) wildfires during the study period and areas in the Sierra Nevada not dominated by conifer species are shown in grey.

Figure 3. Change in conifer forest habitat between 2011 and 2020 in the southern Sierra Nevada. Annual density distribution of canopy cover for a) all conifer forests (>25% canopy cover), and b) moderate and high density mature conifer forests (>40% canopy cover and >30 m mean height

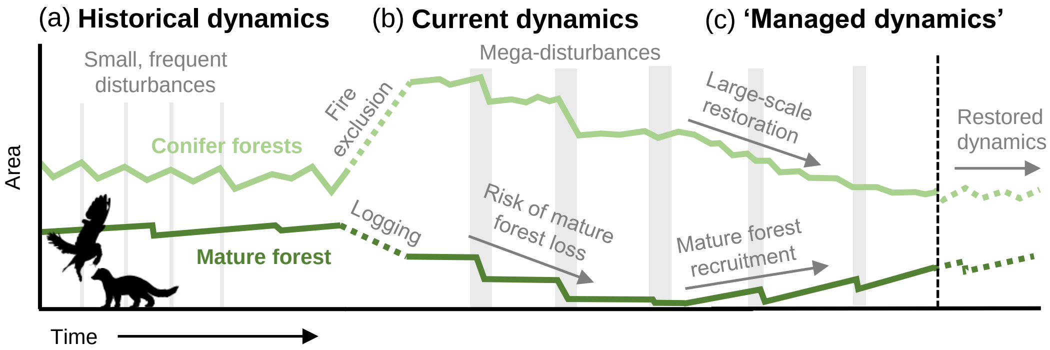
of tallest trees). Grey portions of density distributions illustrate area of transition since 2011 of each forest class. C) Change in area of all conifer forests and mature conifer forests relative to 2011. Mature forest sub-classes are shown as dashed lines in c) and illustrate the initial increase in moderate density mature forests (40-60% canopy cover) due to transitions from declining high density mature forests (>60% cover).

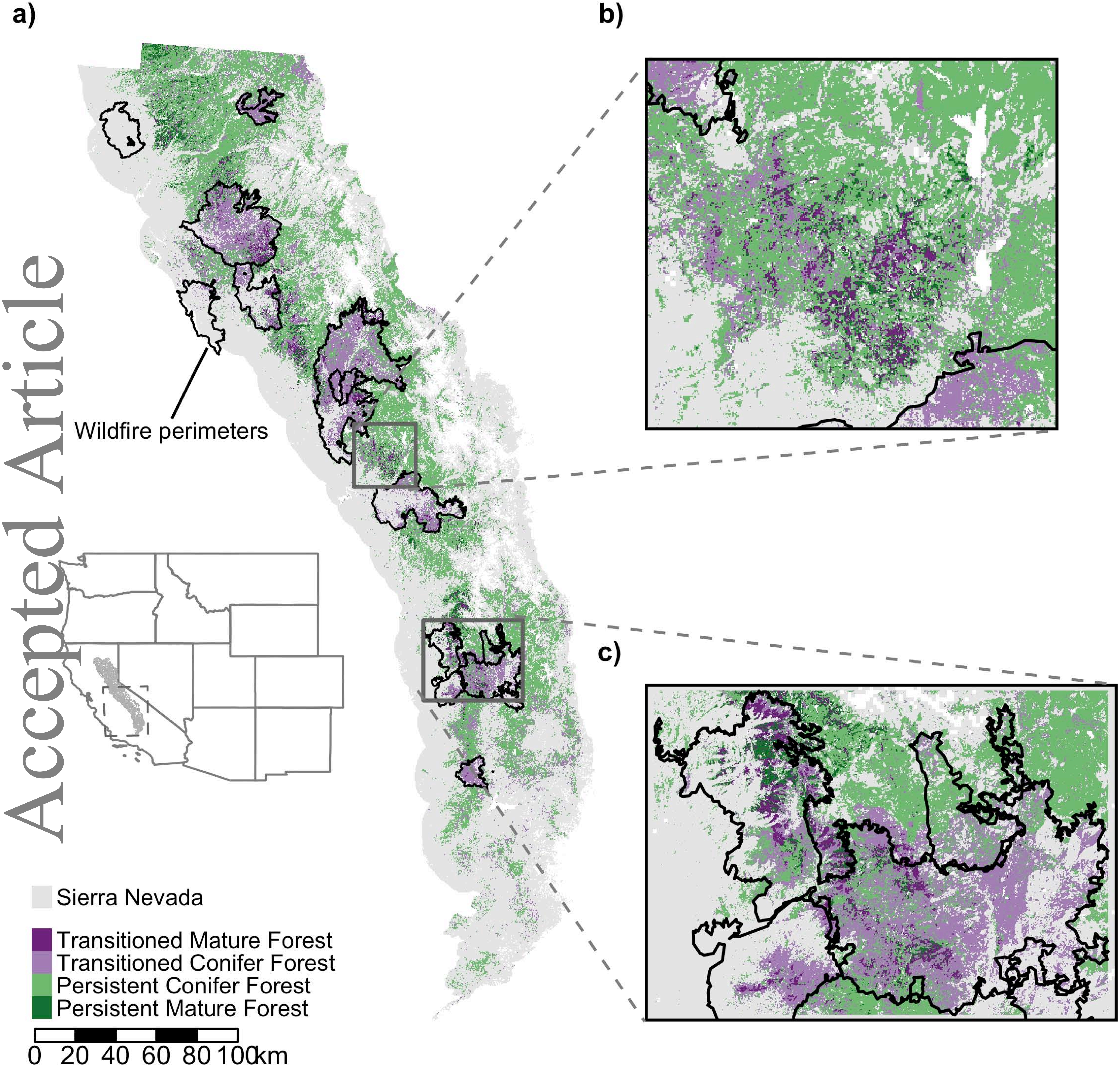
Figure 4. Expected relative canopy cover declines between 2011 and 2020 as predicted by a) spotted owl Protected Activity Center (PAC) class, b) 2011 canopy cover, and c) 2011 mean large tree height. Relative canopy cover declines are calculated as the percentage of 2011 canopy cover that was lost between 2011 and 2020. The effects of 2011 canopy cover and height are fit using data from both PAC and non-PAC sample areas. Tabulated model coefficients can be found in Appendix S1: Table S1.

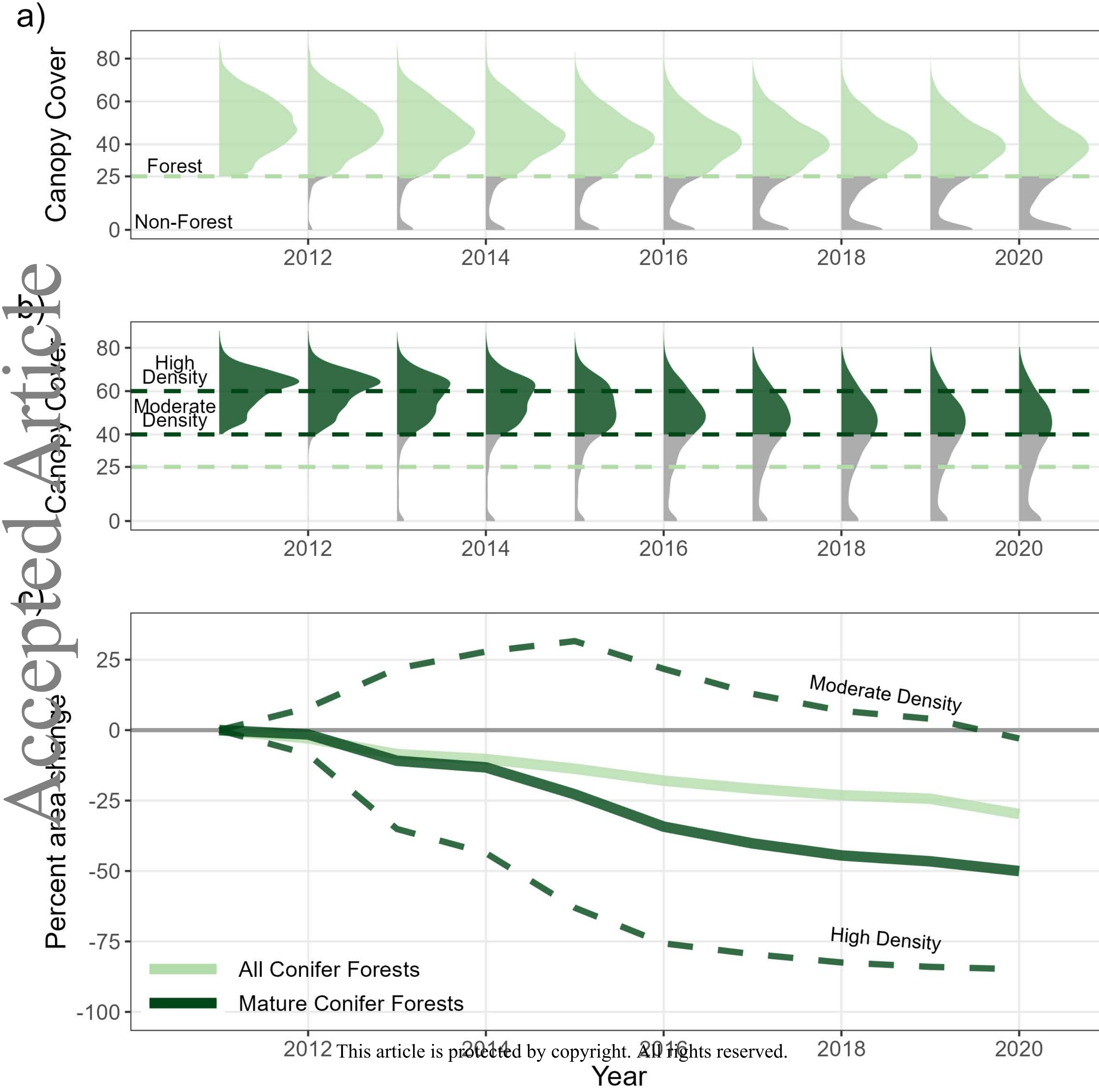
Figure 5. a) All forest and mature forest area transitioned annually due to drought, a combination of drought and wildfire, or a combination of drought and mechanical management activities (timber harvest or thinning) from 2011 to 2020. b) The total amount of area remaining as forest or mature forest as well as the amount of area that survived a recent burn (time since last fire was less than twice the historic fire return interval). Conifer forests are defined by a minimum of 25% canopy cover. Mature forests are defined as having a minimum of 30 m average height of the tallest trees as of 2011 and maintaining at least 40% canopy cover. The timing of three large fires and the final year of the 2012-2016 drought are noted with vertical dashed lines. No mechanical activity data was available during 2020 potentially inflating the

estimate of drought-only transitions for that year. Changes in mature forest density subclasses are shown in Appendix S1: Figure S1.

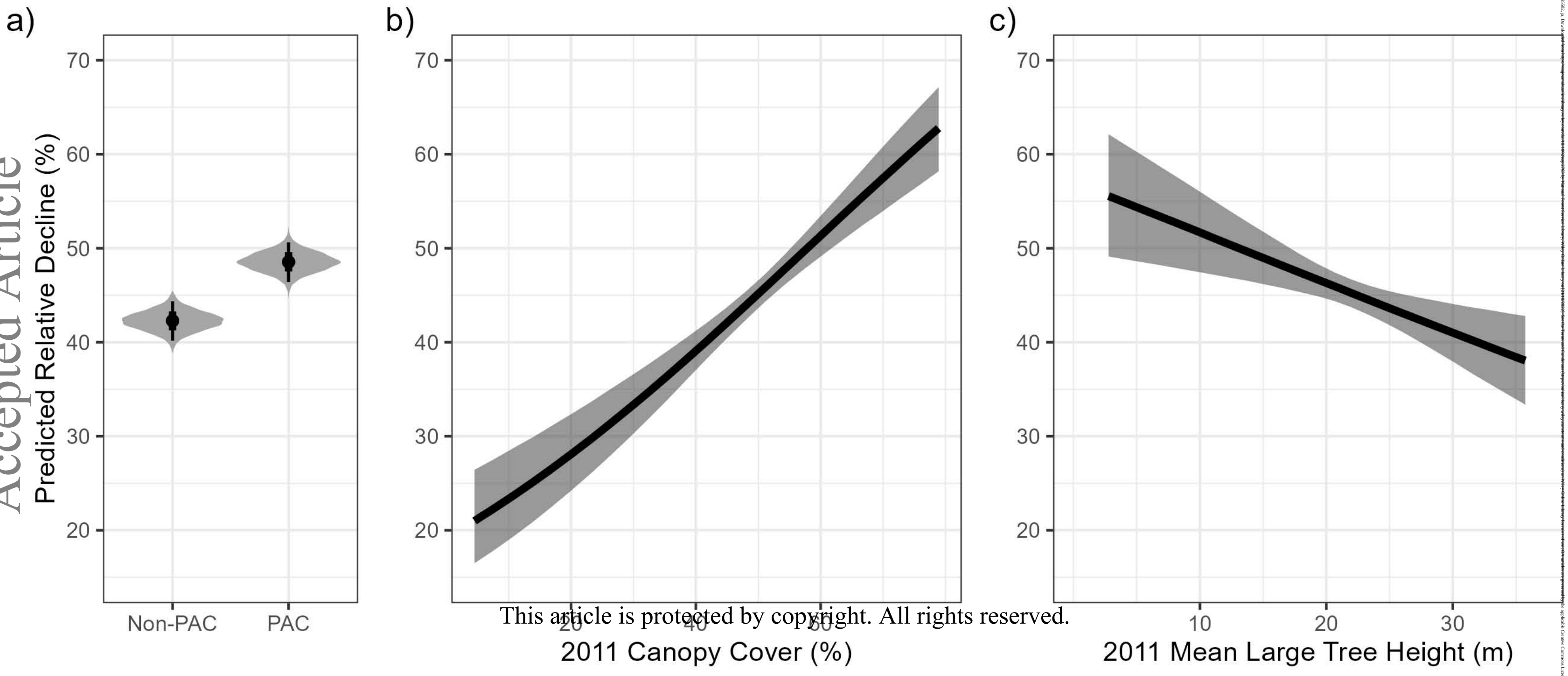
Figure 6: Illustration of two approaches to management in seasonally dry disturbance-prone California forests. Attempts to avoid and exclude all disturbance has led to mega-disturbances and transition from mature forests conditions (top scenario), while managing for sustainable disturbance dynamics can maintain forest resilience and wildlife habitat (bottom scenario).

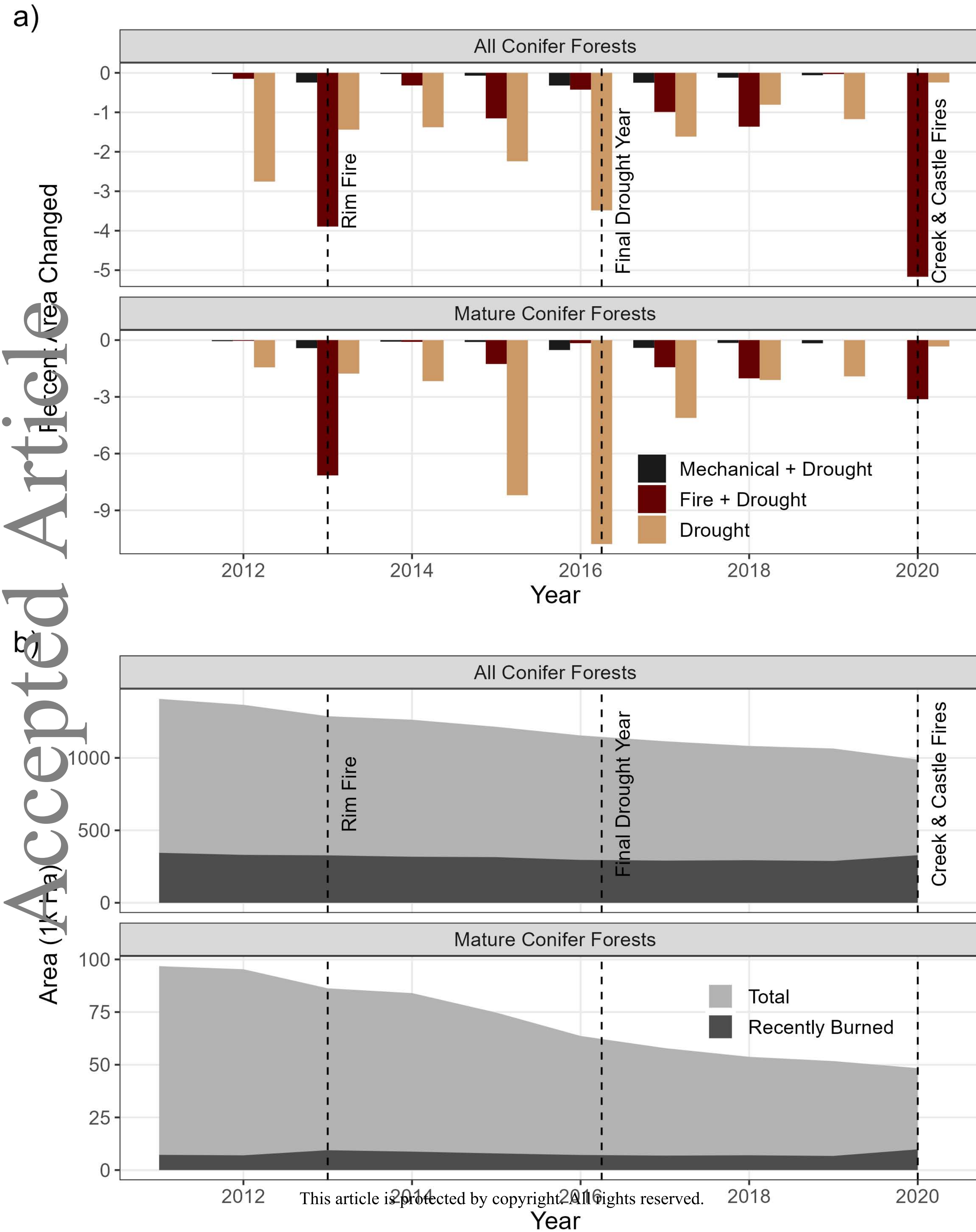

(a) Historical dynamics
(b) Current dynamics
(c) 'Managed dynamics'
Small, frequent disturbances
Mega-disturbances
Fire exclusion
Conifer forests
Large-scale restoration
Restored dynamics
Area
Logging
Risk of mature forest loss
Mature forest recruitment
Mature forest
Time

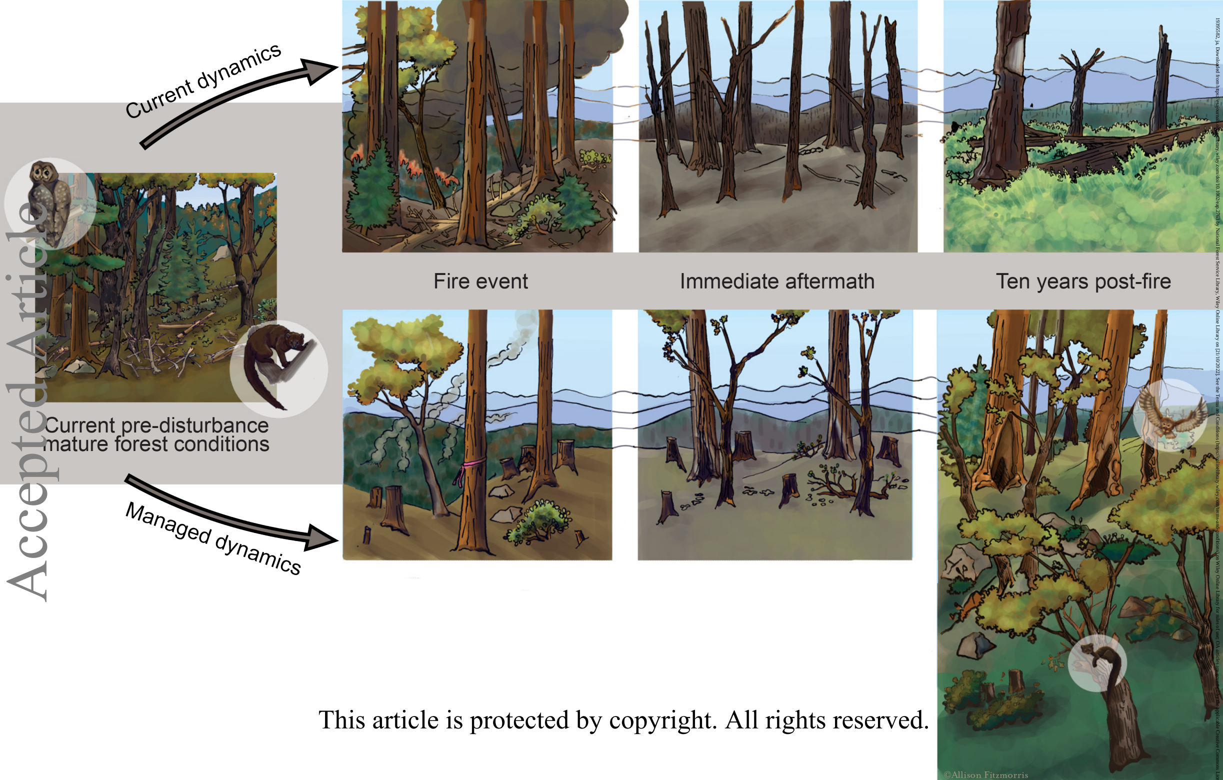

a)
b)
c)
Wildfire perimeters
Sierra Nevada
Transitioned Mature Forest
Transitioned Conifer Forest
Persistent Conifer Forest
Persistent Mature Forest
0 20 40 60 80 100 km



a)
Canopy Cover
80
60
40
25
0
Forest
Non-Forest
2012
2014
2016
2018
2020
Canopy Cover
80
60
40
25
0
High Density
Moderate Density
2012
2014
2016
2018
2020
Percent area change
25
0
-25
-50
-75
-100
Moderate Density
High Density
All Conifer Forests
Mature Conifer Forests
2012
2014
2016
2018
2020
Year


a)
b)
c)
Predicted Relative Decline (%)
70
60
50
40
30
20
Non-PAC
PAC
20
40
60
2011 Canopy Cover (%)
10
20
30
2011 Mean Large Tree Height (m)


a)
All Conifer Forests
Mature Conifer Forests
Percent Area Changed
0
-1
-2
-3
-4
-5
-3
-6
-9
Rim Fire
Final Drought Year
Creek & Castle Fires
Mechanical + Drought
Fire + Drought
Drought
2012
2014
2016
2018
2020
Year
b)
All Conifer Forests
Mature Conifer Forests
Area (1K Ha)
1000
500
0
100
75
50
25
0
Total
Recently Burned
Year


Current dynamics
Fire event
Immediate aftermath
Ten years post-fire
Current pre-disturbance mature forest conditions
Managed dynamics
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