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RECONCILING RESILIENCE ACROSS ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES

Research Article

Ecological resilience and vegetation transition in the face of two successive large wildfires

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Abstract

1. Wildfire can both promote and erode resilience to future disturbances in fire-adapted ecosystems. Through a combination of past fire exclusion and climate change, fire patterns and successional trajectories are shifting with potentially negative consequences for forest resilience. In particular, high-severity short-interval reburns can lead to permanent transitions from forested to persistent non-forested ecosystems.
2. To test conditions under which wildfires promote resilience or initiate vegetation transitions we leveraged high-resolution LiDAR data, field data and a natural experiment where two uncharacteristically severe wildfires burned the same area in California's Sierra Nevada mountains. Specifically, we evaluate what factors influence resistance to high-severity reburn and whether early forest recovery is evident following vegetation transition.
3. Our findings indicate that topography and vegetative structure influenced resistance to high-severity effects of a second wildfire and that environmental heterogeneity played an important role. Forests that survived the initial burn were most resistant to subsequent high-severity fire when they were characterized by relatively dense but heterogeneous upper strata and a sparse understorey, located in variable and mesic terrain and burned under milder fire weather conditions. Early seral vegetation was most likely to resist repeat high-severity fire and potentially continue post-fire forest recovery when it was located in variable and mesic terrain and was characterized by relatively sparse understorey vegetation and a heterogeneous subcanopy. Some early seral areas that reburned at lower severity showed signs of conifer forest recovery. Vegetation structure and composition of areas that repeatedly burned at high severity are consistent with a transition to persistent shrubland or hardwood forests.

4. *Synthesis*. Short-interval reburns close to historical fire intervals but of unusually high burn severity can create challenges for maintaining resilient forests, as sequential fires can expand upon and stabilize non-forest vegetation. However, forest communities that survive such disturbances appear partially restored with increased structural heterogeneity and greater resistance to future high-severity fire. If climate and fire regime trends continue, we are likely to see broadscale shifts towards vegetation types and species able to recover quickly from high-severity fire at the expense of forests and species resistant to frequent low-severity fire.

KEYWORDS

California, climate change, fire suppression, forests, LiDAR, resilience, resistance, wildfire

1 | INTRODUCTION

The countervailing ecological processes of disturbance and succession influence biome distributions globally and vegetation type composition regionally (Bond et al., 2005). This dynamic is especially important in frequent fire systems of the western United States including the seasonally dry forests of the Sierra Nevada in California. However, through a combination of land management policies and climate change, fire patterns and successional trajectories are shifting with potentially negative consequences for forest resilience (i.e. the ability to resist or recover from disturbance; Hodgson et al., 2015). In particular, there is concern that uncharacteristically severe wildfires combined with short-interval reburns will lead to permanent transitions from forested to non-forested ecosystems, with associated degradation of ecosystem function and services and declines of species associated with mature forest habitats (Coop et al., 2020; Coppoletta et al., 2016; Stephens et al., 2016). In this context, a greater understanding of the controls on vegetation-type transitions versus resistance to disturbance (Nagel et al., 2014) is needed as we continue to experience rapid global change and shifting fire regimes.

Ecosystem resilience is defined as the ability to respond to disturbance by reorganizing while maintaining basic structure and function (Table 1; Holling, 1973; Walker et al., 2004). The concept of resilience can be further decomposed into 'resistance' where a system maintains its previous state despite an exogenous disturbance, and 'recovery' where the system reverts to its prior state within a relatively short time (Figure 1; Hodgson et al., 2015). In fire-adapted conifer forests, low/moderate-severity fire (where <75% of the dominant vegetation is killed) can drive reorganization of vegetation structure and composition in a way that increases resistance to future disturbance (Collins et al., 2009; Jeronimo et al., 2019; Lydersen et al., 2017; Parks et al., 2014; Prichard & Kennedy, 2014; Stephens et al., 2008; Walker et al., 2018). Specifically, low/moderate-severity fire reduces cover of surface fuels (live and dead vegetation) and shifts community composition towards fire-resistant species with thicker bark and a tendency to self-prune low-lying foliage (Keeley et al., 2011). Conversely, plant communities can be maintained as shrubland by periodic high-severity fire (>75% mortality) when composed of species able to resprout after being top-killed or maintain a persistent seed bank (Coppoletta et al., 2016; Harvey et al., 2016; Lauvaux et al., 2016; Pausas et al., 2004).

TABLE 1 Usage of terms

Term	Usage
Resilience	The ability of a forest ecosystem to maintain basic structure and function by resisting or recovering from one or more wildfires
Resistance	A forest ecosystem maintains its original structure and function following wildfire
Recovery	A forest ecosystem changes state following wildfire but successfully returns to its previous state over time
Transition	A forest ecosystem changes state (e.g. to shrubland) due to wildfire. It can persistent in this state or recover back to forest over time
Early seral	Non-forested vegetation following high-severity fire, possibly including shrubland, herbaceous vegetation and/or regenerating trees. This vegetation type is produced by high-severity fire but may also occur in areas where productivity is too low to support forest growth
Persistence	Non-forest vegetation state remains over time due to recurring severe fire effects or a lack of forest recovery

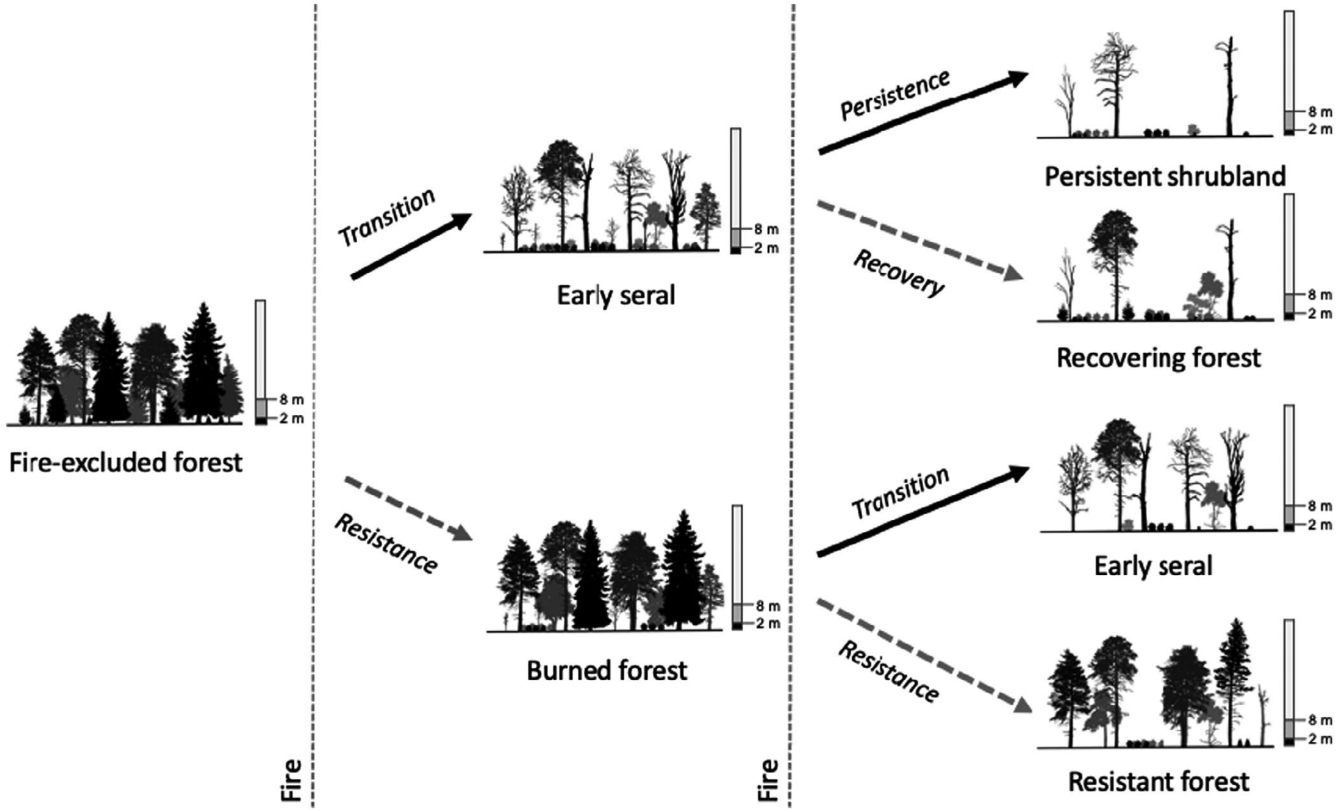

FIGURE 1 Theoretical trajectories of plant communities following repeated wildfire in the Sierra Nevada mountains of California. Forests are considered resilient if they resist state transition following multiple wildfires or are able to recover to a forested state over time following transition. One or more high-severity fires and a lack of forest recovery can lead to persistent shrubland communities. The height thresholds used to define canopy (>8 m), subcanopy (2–8 m) and understorey (1–2 m) strata for analysis are illustrated for reference

FIGURE 2 Representative images of vegetation types within the study area. (a) Persistent shrubland in areas dominated by forest prior to the initial fire, (b) vegetation in the early stages of forest recovery with a notable shift in composition from obligate seeder conifer to resprouting oak species, (c) forest conditions following two low/moderate-severity fires and (d) unburned, fire-excluded forest

The regional composition of vegetation communities and successional stages is a function of the baseline proportion of vegetation types, the rate at which forests transition to early seral vegetation through disturbance versus their ability resist such change and the rate at which forests recover through succession or remain as persistent shrubland (Miller & Safford, 2017). The rate of transition attributable to high-severity fire is in turn dependent on a number of factors including topography, fire weather and pre-fire vegetation structure. While topography is fixed, weather is highly dynamic at short (diurnal) and intermediate (annual) time-scales and sensitive to climate change at longer (multidecadal) time-scales (Abatzoglou et al., 2019; Collins, 2014). Plant cover and continuity of flammable vegetation at different heights are also important drivers of fire behaviour and effects, and are shaped by previous disturbances (Agee & Skinner, 2005). The spatial heterogeneity of vegetation and its resultant influence on fire behaviour and effects have thus far received less attention, but there is increasing evidence that Sierra Nevada forests were historically more heterogenous in structure (Fry et al., 2014; Hessburg et al., 2005; Larson & Churchill, 2012; Lydersen et al., 2013) and that such variation may promote resistance to high-severity fire and plant community transitions (Jeronimo et al., 2019; Kane et al., 2019; Koontz et al., 2020).

Changes to the disturbance regime threaten forest resilience and regional compositions of vegetation types (Coop et al., 2020; Johnstone et al., 2016; Reyer et al., 2015; Wu & Loucks, 1995). Mixed conifer forests in the Sierra Nevada were historically composed of a mix of forest and montane chaparral (Figure 2). Shrubs were common in the understorey of tree-dominated areas, especially where the tree canopy was relatively open allowing light to reach the forest floor (Knapp et al., 2013; Stephens et al., 2015), and often dominated in sites with limited soil moisture (Collins et al., 2015). Fire frequencies in the mixed conifer zone were short (10–20 years; Van de Water & Safford, 2011), and fire effects were mostly—but not uniformly—low/moderate-severity (92%–95% of area burned; Mallek et al., 2013). Under the historical fire regime, montane chaparral patches were often persistent and maintained by periodic fire, with longer but more variable fire return intervals than the surrounding forest (Lauvaux et al., 2016).

Fire exclusion and suppression over the past century have resulted in forests with uncharacteristically high canopy cover, increased dominance of fire-sensitive tree species and less understorey shrub cover (Safford & Stevens, 2017) as well as encroachment of forests into historically non-forested areas and a decline in landscape-level heterogeneity (Lauvaux et al., 2016). Where fires do escape suppression efforts, they increasingly burn at greater rates of high severity that transition forests to shrublands for the short to medium term (Steel et al., 2015). Such transitions can have negative consequence for ecosystems services such as carbon sequestration and storage (Gonzalez et al., 2015), as well as old forest-associated species such as the California Spotted Owl (Jones et al., 2020; Stephens et al., 2016). Furthermore, high-severity patches are becoming larger and more simple in shape, resulting in vast areas far from living tree seed sources (Steel et al., 2018; Stevens et al., 2017). For non-serotinous tree species unable to resprout following wildfire, long distances to seed source can lead to slow or failed forest recovery (Coop et al., 2020; Shive et al., 2018; Welch et al., 2016), which can be reinforced by subsequent high-severity fire that further threatens forest resilience. These trends are being exacerbated by longer fire seasons and more extreme fire weather associated with a warming climate (Abatzoglou & Williams, 2016; Pausas & Fernández-Muñoz, 2012; Westerling, 2016).

Due to fire suppression, areas of overlapping fire (i.e. reburns) are currently uncommon in the Sierra Nevada relative to historic norms and therefore understudied despite their ecological importance. Likewise, the limited availability of fine-grain data across large spatial extents pre- and post-disturbance has hindered investigation into the relationships between vegetation structure and rates of transition and resistance. The overlapping 2000 Storrie and 2012 Chips fires burned 12 years apart allowing for a natural experiment where two uncharacteristically severe wildfires burned at an interval typical of the historical fire regime in these forests. Additionally, availability of high-resolution LiDAR data collected between the two fires provides a valuable opportunity to test the conditions under which wildfires promote or degrade ecological resilience. To this end, we addressed the following questions: (a) How do fire severity rates differ between vegetation stages when wildfires burn through previously fire-excluded versus recently burned landscapes? (b) What are the drivers of resistance under repeated wildfire? (c) Are there signs of forest recovery following transition due to high-severity fire and a subsequent short-interval reburn?

2 | MATERIALS AND METHODS

2.1 | Study area

The study area is located on the Plumas and Lassen National Forests in the northern Sierra Nevada of California, United States. Due to the availability of repeat LiDAR data, our primary area of focus was on the large overlapping 2000 Storrie and 2012 Chips fires (Figure 3a). LiDAR data from an adjacent unburned site (1,774 ha) located approximately 10 km from the fire perimeters were used for reference. We also utilized field data from reburn areas of the Chips fire where either the Storrie or a smaller 2008 Rich fire constituted the initial fire. The Rich Fire was located 4.5 km east of the Storrie Fire and along the southern boundary of the Chips Fire. Topography is generally mountainous and steep, with elevations ranging from 673 to 2,144 m a.s.l. Climate in the region is characterized as Mediterranean, with most precipitation falling as rain or snow during the cold winter months, followed by hot and dry summers.

The Storrie Fire ignited in August of 2000 and burned 22,687 ha with a mixture of fire severity effects. In July 2008, the Rich Fire burned 2,473 ha. The Chips Fire ignited in July of 2012 and burned a total of 30,891 ha, including 45% (10,166 ha) of the Storrie Fire (Figure 2a) and 15% (379 ha) of the Rich Fire. Prior to the 2000 Storrie Fire, <0.1% of the area had experienced wildfire since at least 1950 (FRAP, 2020). Vegetation prior to the 2000 Storrie Fire was predominately lower montane mixed conifer forest, with approximately 95% of the stands classified as having moderate to dense overstorey canopy (CALVEG, 2004). Dominant species included ponderosa pine *Pinus ponderosa*, Jeffrey pine *P. jeffreyi*, sugar pine *P. lambertiana*, white fir *Abies concolor*, Douglas-fir *Pseudotsuga menziesii*,

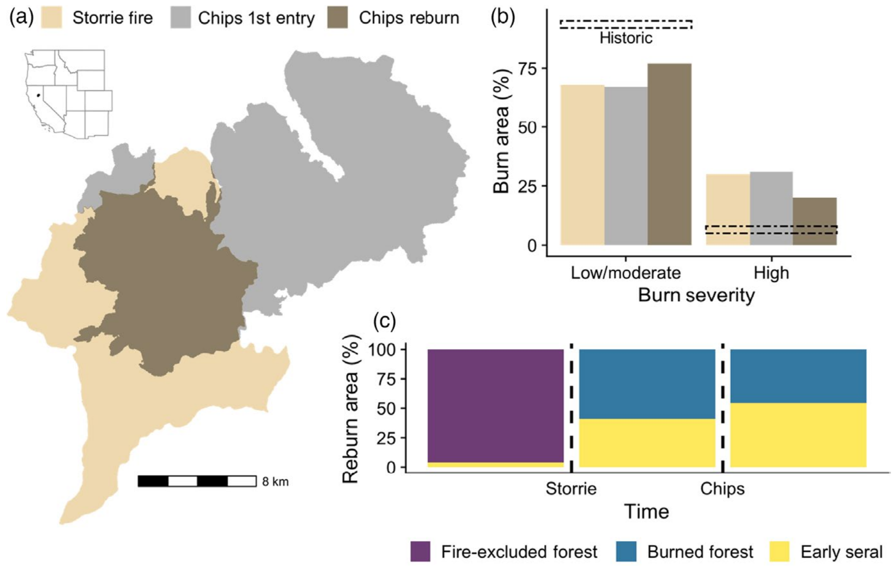

FIGURE 3 Primary study fires and vegetation history. (a) The 2000 Storrie and 2012 Chips Fires and the area of overlap (reburn). Inset map of the western United States shows the location of the study fires in northern California. (b) Burn severity percentage for the two wildfires. For the Chips Fire, percentages are calculated separately for first-entry (previously unburned) and reburned areas. Historic estimates of mean severity levels for Sierra Nevada dry and moist mixed conifer, and yellow pine forests (Mallek et al., 2013) are also noted. (c) Vegetation stage within the Storrie-Chips reburn area prior to, between and after the two wildfires

incense-cedar *Calocedrus decurrens* and California black oak *Quercus kellogii*. Stands of red fir *A. magnifica* occurred at higher elevations. Montane chaparral composed of *Ceanothus* and *Arctostaphylos* spp. was also present throughout, but dominated cover in lower elevation, drier and southeast-facing canyon slopes.

2.2 | Environmental data collection and processing

Vegetation community types were assessed across the study area prior to the Storrie Fire, between the Storrie and Chips fires, and following the Chips Fire using legacy versions of California's existing vegetation dataset (CALVEG, 2004). We categorize these data into two broad vegetation stages: (a) forest, which included conifer, hardwood and conifer–hardwood mixed vegetation and (b) early seral, which includes both shrub and herbaceous species. Due to some variation in imagery year within vegetation datasets (e.g. post-Chips vegetation was classified using 2014 and 2016 images), we limited our use of remotely classified vegetation data to identify broad vegetation stages, which are unlikely to change within the first decade after a fire.

We used fire severity estimates obtained from a US Forest Service maintained database (available at www.fs.usda.gov/detail/r5/landmanagement/gis). These data were derived from LANDSAT-TM satellite imagery and the Relative differenced Normalized Burn Ratio (RdNBR), and subsequently classified into levels of percent canopy cover mortality. This method of severity classification has been extensively calibrated and validated using field measurements (Miller et al., 2009; Miller & Quayle, 2015). Here, we use 75% canopy mortality as our cut-off between low/moderate- and high-severity. This threshold is often used to designate high-severity fire effects in conifer-dominated forests of California (Jones et al., 2020; Steel, Fogg, et al., 2021; Tingley et al., 2016; Welch et al., 2016), although other thresholds have also been used in the literature (e.g. Collins et al., 2017; Lydersen et al., 2016).

We used aerial light detection and ranging (LiDAR) data from two time periods. In July 2009, LiDAR data were collected over the entire Storrie Fire footprint by Watershed Sciences (now Quantum Spatial, Inc.) using a Leica ALS50 sensor mounted on a fixed wing aircraft. In September 2015, Quantum Spatial collected LiDAR over a wider area, including portions of the Storrie and Chips Fires as well as contiguous unburned forests. The 2015 LiDAR data were collected using a Leica ALS70 sensor mounted on a fixed wing aircraft. Data from each flight were delivered as discrete-return point clouds, with average first return density of 6.7 and 8 pulses m^{-2}, respectively. Preliminary analysis of undisturbed areas captured during the two LiDAR flights was similar indicating that measured differences within the 2012 Chips Fire footprint were due to fire activity rather than differences in return density.

LiDAR data were used to measure vegetation cover across three vertical strata at a 10 m resolution: 1–2 m above-ground height (understorey), 2–8 m (subcanopy) and 8–80 m (canopy). Cover was calculated using the LIDR package (version 2.1.3; Roussel et al., 2020), to implement a grid-based version of the methods described in Bouvier et al. (2015). Specifically, we used the equation:

$$C_i = \frac{N_{[z;z+dz]}}{N_{[0;z+dz]}},$$

where c_i is vegetation cover, z is the lower bound and dz is the depth of the focal stratum. $N_{[z;z+dz]}$ is the number of within stratum first returns, and $N_{[0;z+dz]}$ is the number of first returns from heights below $z + dz$ (i.e. those that reached the current stratum). A grid resolution of 10 m was the finest grain size that gave valid cover estimates for all strata (i.e. at least 1 first return below the lowest stratum per 10 m^2 pixel) over 99.99% of the study area. Horizontal heterogeneity in vegetation cover was assessed using the standard deviation of cover (log-scale) around each point and stratum using different radii (see below). Measurements of vegetation cover, and horizontal heterogeneity (structural complexity) at different heights adheres to Valbuena et al.'s (2020) framework for measuring ecosystem morphological traits, allowing comparisons among disparate data sources, ecosystems and sampling scales (Valbuena et al., 2020).

Elevation, topographic roughness and topographic wetness index (TWI) were calculated using a 10 m DEM obtained from Amazon Web Services public datasets using the ELAVATR package (version 0.2.0; Hollister & Shah, 2017). Roughness was calculated as the standard deviation of elevation within a focal area. TWI was calculated at 30 m resolution using the DYNATOPMODEL package (version 1.2.1; Metcalfe et al., 2018). The package authors caution that 30 m is the finest grain for which TWI is meaningful. Daily fire weather data (~4 km resolution) from the gridMET database (Abatzoglou, 2013) were combined with historical fire perimeter polygons from the GeoMAC database (National Interagency Fire Center, 2019) to describe the weather conditions (mean relative humidity and mean daily wind speed) under which each sample location re-burned in the Chips Fire. Gridded fire weather data were not available at a finer spatial resolution but were included in analysis because fire weather is an important driver of fire severity and fire-induced plant community transition.

To assess early forest recovery following high-severity fire, we utilized field data collected from permanent field plots established after the 2000 Storrie and 2008 Rich fires and resampled 5–6 years after the 2012 Chips Fire reburn. Field data were collected using the USDA Forest Service common stand exam protocol, which consists of two concentric circular plots originating from a single plot centre (USDA Forest Service, 2009). A larger plot is used to collect tree data, including species, status (live or dead), diameter at breast height (dbh) and height. A smaller nested circular plot is used to record the same measurements for smaller trees and saplings (>1.37 m tall). Total conifer and hardwood trees (including saplings, small and large sizes) per hectare were calculated for each plot and height strata (1–2, 2–8 and 8–80 m). As field data were compiled from multiple sampling efforts, there was some variation in methodology among plots, which is allowed under the common stand exam protocol. We conducted a comparison of data collection methods as part of a related study (Coppoletta et al., 2016) and found no significant differences in live tree density estimates among methodologies.

2.3 | Statistical analysis

Remotely sensed severity and vegetation data were summarized within fire perimeters to contrast first-entry wildfire and reburn severity as well as quantify fire-induced shifts in vegetation stage (Question 1). To assess drivers of resistance to high-severity fire (Question 2), we generated a 200 m point sampling grid across both the reburn and unburned reference areas. Analysing the complete census of data would have been infeasible when employing computationally intensive models (i.e. Gaussian process). Furthermore, given the fine-scale spatial autocorrelation inherent in fire effects, the additional spatially contiguous data were unlikely to improve model precision. Sampling and analysis were limited to areas that were lower montane conifer forests prior to the Storrie Fire, which had historical mean fire return intervals of <25 years (Moody et al., 2006; North et al., 2012; Van de Water & Safford, 2011). Lower montane conifer forests include the Calveg wildlife habitat relationship classification of Douglas-fir, Jeffrey pine, Sierran mixed conifer, white fir and mixed hardwood–conifer (CALVEG, 2004). Additionally, we used the Forest Service Activity Tracking System database to exclude areas that experienced management between the 2000 Storrie Fire and the relevant LiDAR sampling year (2009 or 2015). At each of these points, we sampled topographic variables, Chips Fire weather variables and vegetation structure prior to the second fire using the 2009 LiDAR data. To identify the scale at which variables of interest were most predictive of a point's severity (measured as the mean within a 25-m radius), we summarized environmental data at various scales using the following radii around each point: 25, 50, 75, 100, 125 and 150 m.

To assess the factors influencing resistance to high-severity fire, we built two classes of linear models for points characterized by Calveg (CALVEG, 2004) as (a) early seral vegetation (n = 836) and (b) forest (n = 1,197) after the initial fire. Specifically, points within herbaceous or shrubland vegetation types after the Storrie Fire but prior to the Chips Fire were included in the early seral models while those within lower montane conifer forest types were included in the forest models (middle panel of Figure 1). Forested points that burned at low/moderate-severity during the Chips Fire are considered to have resisted high-severity fire in the reburn (resistance pathway, Figure 1). For early seral vegetation, low/moderate-severity effects allow for potential continued forest recovery despite the reburn (recovery pathway, Figure 1), whereas repeated high-severity fire may lead to persistent shrubland vegetation (persistent pathway, Figure 1). For each class of model and scale, we fit the following model to assess the effects of vegetation structure, topography and fire weather on the likelihood of a point reburning at high severity:

$$\begin{aligned}
\text{high_severity}_i &\sim \text{Bern}(\phi_i) \\
\text{logit}(\phi_i) &= \alpha_0 + \beta_{\text{under}.mn} \times X_{1,i} + \beta_{\text{under}.sd} \times X_{2,i} \\
&\quad + \beta_{\text{sub}.mn} \times X_{3,i} + \beta_{\text{sub}.sd} \times X_{4,i} + \beta_{\text{canopy}.mn} \times X_{5,i} \\
&\quad + \beta_{\text{canopy}.sd} \times X_{6,i} + \beta_{\text{elev}} \times X_{7,i} + \beta_{\text{rough}} \times X_{8,i} \\
&\quad + \beta_{\text{TWI}} \times X_{9,i} + \beta_{\text{RH}} \times X_{10,i} + \beta_{\text{wind}} \times X_{11,i} + \text{GP}(x_i, y_i),
\end{aligned}$$

where high_severity_i is a binary response variable indicating whether point i burned at high-severity and α_0 represents the model intercept. Predictor variables describing vegetation structure included mean cover ($\beta_{\text{under}.mn}$) and heterogeneity ($\beta_{\text{under}.sd}$) of understorey, subcanopy ($\beta_{\text{sub}.mn}$ and $\beta_{\text{sub}.sd}$)

and canopy vegetation ($\beta_{canopy.mn}$ and $\beta_{canopy.sd}$). Variables describing topography include mean elevation (β_{elev}), topographic roughness (β_{rough}) and topographic wetness index (β_{TWI}). Fire weather variables included relative humidity (β_{RH}) and wind speed (β_{wind}). We applied a Bernoulli error structure with a logit link and a partial Gaussian process estimating the spatial covariance among points where x_i and y_i represent sample point coordinates (GP(x_i, y_i)). The partial Gaussian process term was included to describe any remaining spatial autocorrelation following our 200-m grid subsampling. Predictor variable summary statistics are tabulated in Table S1. For modelling, all continuous predictor variables were standardized with a mean of zero and standard deviation of one. Effects estimates are marginal and are conditional on the data and model structure.

We compared the predictive performance of models of different spatial scales using the leave-one-out information criteria (Vehtari et al., 2017). Models were fit using the BRMS and RSTAN packages (Bürkner, 2017; Stan Development Team, 2020) in the R statistical environment (R Core Team, 2020). The full model was fit using regularizing priors and was run with four chains, each for 2,000 samples with a warm-up of 1,000 samples and 4,000 total post-warm-up samples. Traceplots and R-hat values were assessed for proper mixing and model convergence.

We used both gridded 2015 LiDAR data collected in the Storrie-Chips reburn area as well as available field survey data within Storrie-Chips and Rich-Chips reburn areas to assess post-reburn indicators of forest recovery (Question 3). Specifically, if forest recovery occurred following an initial high-severity and subsequent low/moderate-severity reburn, we would expect to observe greater canopy and subcanopy cover as compared to areas that burned twice at high-severity. Where field data were available post-reburn, measures of conifer and hardwood trees per hectare were also used to directly quantify early forest recovery or lack thereof.

Using LiDAR data sampled from points composed of early seral vegetation after the Storrie Fire, we compared those that reburned at high-severity ($n = 179$) with potentially recovering points that burned at low/moderate-severity during the subsequent Chips Fire ($n = 137$). Contrasts were made using linear models where the response variable was the mean or standard deviation of vegetation cover for each stratum (1–2, 2–8 and 8–80 m) and Chips Fire severity was the sole categorical predictor. Generalized linear models with a zero-inflated Poisson error structure were used to assess field measures of forest recovery following an initial high-severity fire and a subsequent reburn. Data from 23 field plots were available in areas that initially burned at high-severity and reburned at low/moderate-severity, while 12 field plots were available where two high-severity events occurred. The model response variables were either conifer or hardwood trees per hectare with severity level (low/moderate or high) of the Chips Fire used as the sole fixed effect.

3 | RESULTS

3.1 | Fire severity and vegetation stages

Fire severity patterns and the resulting composition of vegetation stages differed depending on whether the burn represented a first-entry wildfire (i.e. where fire had previously been excluded for >50 years) or a 12-year interval reburn (Figure 3). Within the first-entry Storrie Fire, 31% burned at high-severity where greater than 75% of the pre-fire vegetation was removed. An equivalent percentage (31%) burned at high-severity during the 2012 Chips Fire in places where the Chips Fire represented a first-entry fire. Where the Chips and Storrie fires overlapped (i.e. the reburn area) the proportion of high-severity fire was lower (20%), but still greater than the historic average (Figure 3b). As a consequence of these two fires, the proportion of the landscape characterized as forest decreased, with the reburn area experiencing a shift from one dominated by unburned fire-excluded forest prior to both fires (96% of the subsequent reburn area) to only a slight forest majority (59%) after the first fire and a slight minority of forest following the second burn (45%; Figure 3c). Most of the early seral vegetation created by the initial Storrie Fire reburned at high-severity in the subsequent Chips Fire (67%) suggesting non-conifer forest vegetation will persist for at least the medium term. Conversely, the 33% of early seral vegetation that reburned at low/moderate-severity may allow for forest recovery through succession.

3.2 | Controls on resistance

Average vegetation cover and heterogeneity (standard deviation of cover) within 75 m of sample points showed clear differences in canopy (>8 m), subcanopy (2–8 m) and understorey (1–2 m) structure among vegetation groups. Canopy and subcanopy cover were greatest within fire-excluded forests as compared to both once-burned forest and early seral vegetation. Conversely, understorey cover in once-burned early seral vegetation was greater than both the burned and fire-excluded forest groups (Figure 4). Variation in canopy cover was greatest in the early seral group compared to both forest types, while variation in understorey cover was lowest in the early seral group.

To assess the factors that influence resistance to high-severity fire and consequently vegetation persistence or transitions, we fit early seral vegetation and once-burned forest models where predictor variables were summarized using different size circular radii. Leave-one-out information criterion model selection indicated predictors sampled within a 125-m radius of forest points and a 50-m radius of early seral points produced models with the greatest out of sample predictive performance. Models fit using a 75-m radius performed second best for both model types (Table S2). Due to the coarseness of fire weather data (~4 km grain), differences among models of different scales are predominantly attributable to vegetation structure and topography.

The final early seral model showed vegetation structure and topography, but not weather, influenced reburn severity. The likelihood of early seral vegetation reburning at high severity is estimated to decline with increasing subcanopy cover ($\beta_{sub.mn} = -1.07$; 90% credible interval [CI] = −1.45, −0.70), topographic roughness ($\beta_{rough} = -0.95$; CI = −1.20, −0.71), subcanopy heterogeneity

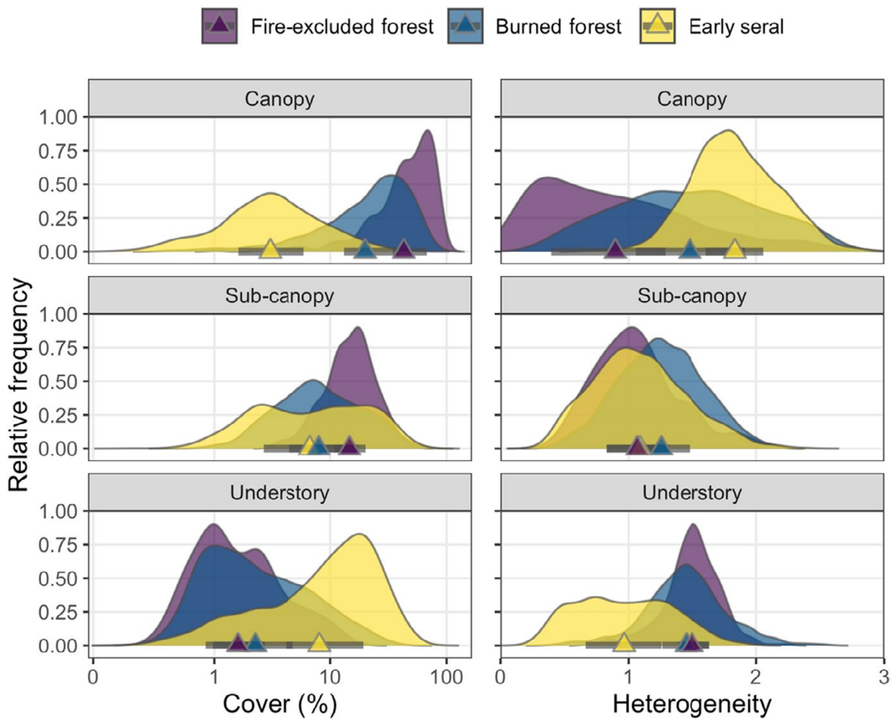

FIGURE 4 Sample distributions for once-burned early seral vegetation, once-burned forest and fire-excluded forest as measured within the canopy (>8 m), subcanopy (2–8 m) and understorey (1–2 m). Triangles and bars below distributions indicate mean and 50% interquantile ranges respectively. Heterogeneity is measured as the standard deviation of percent cover (log-scale). Structural variables were sampled from 10 m grids and summarized using a 75-m radius around sample points. The vertical axis indicates the frequency of samples relative to a panel's distribution maximum

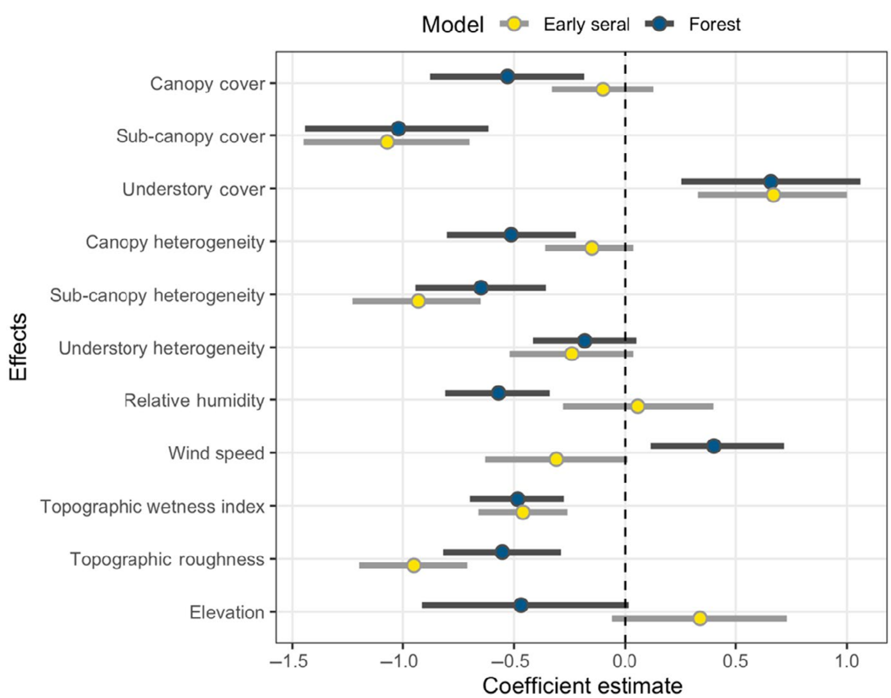

FIGURE 5 Coefficient estimates for once-burned early seral (yellow) and forest (blue) models. Values indicate standardized marginal effects on the probability of reburning at high-severity. Points and bars represent mean estimates and 90% credible intervals respectively. All estimates are tabulated in Table S3

($\beta_{\text{sub}.sd}$ = −0.93; CI = −1.23, −0.65) and topographic wetness index (β_{TWI} = −0.46; CI = −0.66, −0.26). Conversely, understorey cover was positively associated with high-severity reburns ($\beta_{\text{under}.mn}$ = 0.67; CI = 0.33, 1.00; Figures 5 and 6). Neither weather, elevation, understorey heterogeneity, canopy cover, nor canopy heterogeneity showed clear effects (Pr. < 95%; Figure 5). Taken together, these results indicate that once-burned early seral vegetation that was situated in variable and mesic terrain and characterized by relatively sparse understorey vegetation and heterogeneous subcanopy vegetation was most likely to avoid repeat high-severity fire and potentially continue recovery towards a forested state.

The final forest model showed vegetation structure, weather and topography all influenced the likelihood of burning at high-severity during the second burn. The likelihood of once-burned forests reburning at high-severity is estimated to decline with subcanopy cover ($\beta_{\text{sub}.mn}$ = −1.02; CI = −1.44, −0.62), subcanopy heterogeneity ($\beta_{\text{sub}.sd}$ = −0.65; CI = −0.94, −0.36), relative humidity (β_{RH} = −0.57; CI = −0.81, −0.34), topographic roughness (β_{rough} = −0.55;

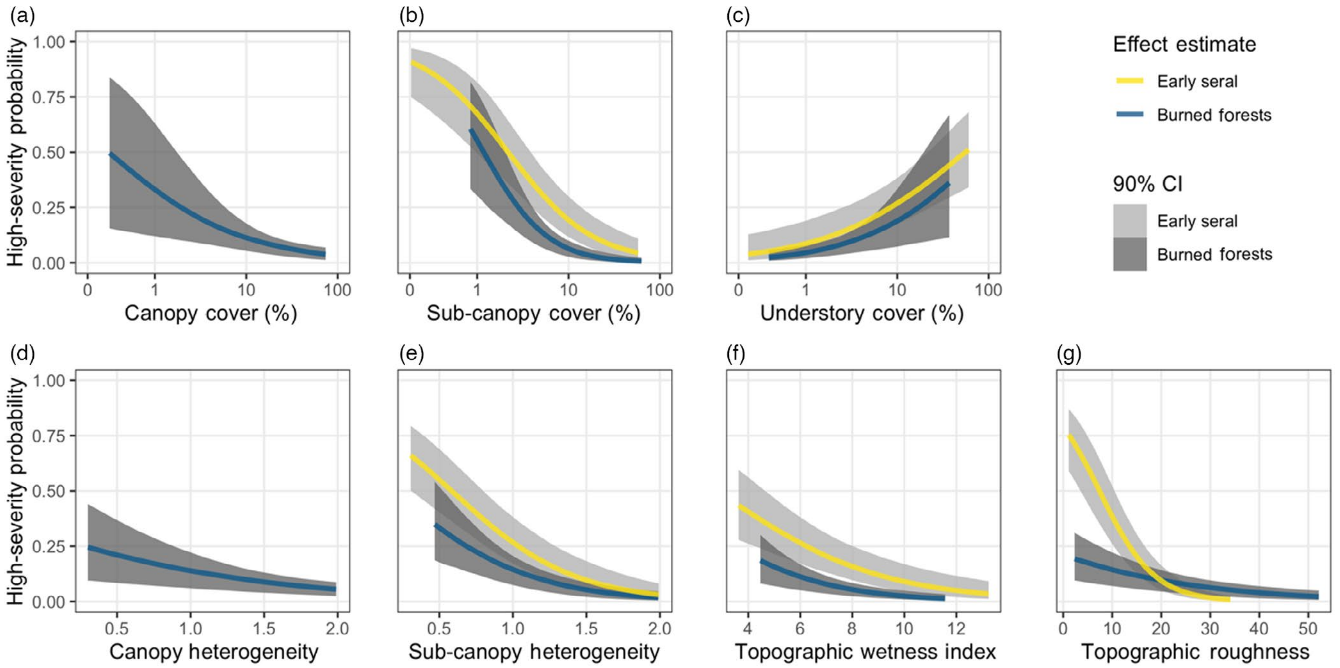

FIGURE 6 Marginal effects of vegetation structure and topography on the probability of reburning at high-severity for once-burned (12 years prior) early seral (yellow) and forest (blue) models. (a) Percent canopy cover (>8 m), (b) subcanopy cover (2–8 m), (c) understorey cover (1–2 m), (d) canopy heterogeneity (standard deviation of log-scale cover), (e) subcanopy heterogeneity, (f) topographic wetness index and (g) topographic roughness. Lines represent mean estimates and bands show 90% credible intervals. Only predictor variables with greater than a 95% probability of a positive or negative effect are shown

CI = −0.82, −0.23), canopy cover ($\beta_{can.mn}$ = −0.53; CI = −0.88, −0.19), canopy heterogeneity ($\beta_{can.sd}$ = −0.51; CI = −0.80, −0.22) and topographic wetness index (β_{TWI} = −0.48; CI = −0.70, −0.28). Conversely, understorey cover ($\beta_{under.mn}$ = 0.66; CI = 0.26, 1.06) and wind speed (β_{wind} = 0.40; CI = 0.12, 0.72) were positively associated with high-severity in the second burn (Figures 5 and 6). Neither understorey heterogeneity nor elevation showed clear effects (Pr. < 95%; Figure 5). Taken together, these results indicate once-burned forests characterized by relatively dense but heterogeneous upper strata and sparse understorey, located in variable and mesic terrain and burning under moderate fire weather conditions are most likely to resist high-severity fire.

3.3 | Potential forest recovery

The combined LiDAR and field data indicate low/moderate-severity reburns in early seral vegetation may support some forest recovery. Following the Chips Fire reburn, LiDAR sample points classified as potentially recovering forest (i.e. early seral vegetation that subsequently burned at low/moderate-severity) had higher (Pr. > 95%) mean cover and heterogeneity in both the canopy and subcanopy as compared to persistent shrubland (early seral points that experienced repeat high-severity fire). There was little discernable difference between the persistent shrubland and recovering groups in understorey cover and heterogeneity (Figure 7). Field surveys showed clear (Pr. > 95%) differences in tree density between plots that experienced repeated high-severity fire (persistent shrubland) and those that burned at high-severity followed by low/moderate-severity (recovering forest). Plots in persistent shrubland supported no conifer regeneration 5–6 years post-reburn. However, a robust hardwood tree response in the subcanopy was observed in 17% of these plots (Table 2). In contrast, plots that burned at high-severity in the initial fire but at low/moderate-severity in the reburn exhibited some conifer recovery (9% of plots) as well as hardwood tree regeneration (9% of plots; Table 2).

4 | DISCUSSION

The 2000 Storrie and 2012 Chips fires provided an opportune natural experiment of how multiple fires in long fire-excluded forests promote or erode ecosystem resilience. The initial fire greatly modified vegetation type and structure of forests with two distinct pathways: cover reduction coupled with increased heterogeneity in surviving forests, or stark vegetation transition from forest to early seral communities. Surprisingly, both post-fire conditions demonstrated some ability to resist high-severity effects when reburned after 12 years. This resistance was contingent on both biophysical and vegetation structural factors. At the landscape scale, these overlapping wildfires appear to have produced a mix of partially restored forest and early seral vegetation, with the latter divided between

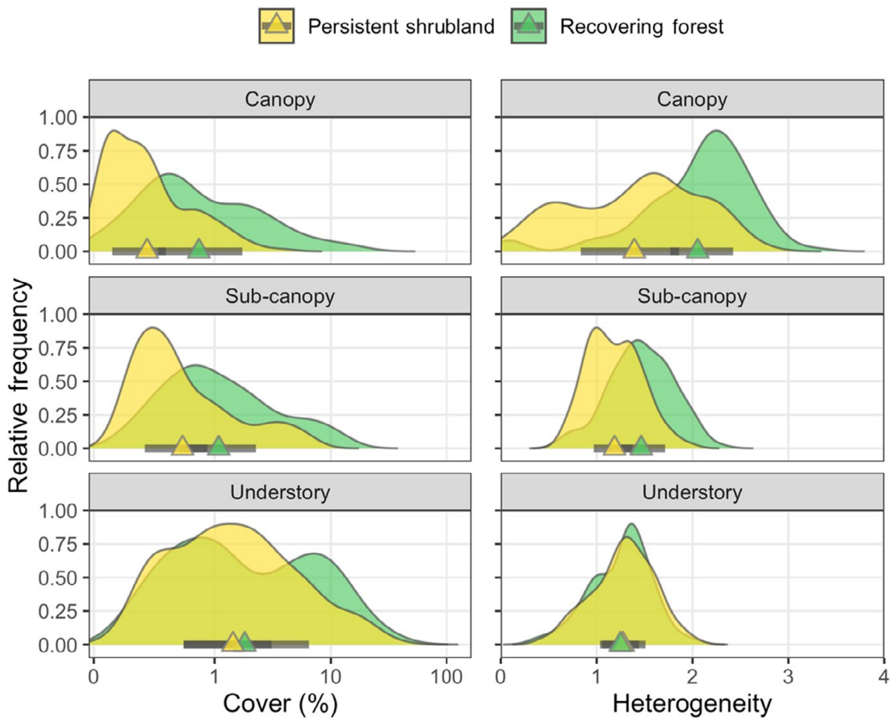

FIGURE 7 Sample distributions for twice-burned early seral vegetation as measured within the canopy (>8 m), subcanopy (2–8 m) and understorey (1–2 m). Vegetation groups are defined by their potential successional trajectory according to their reburn severity. Early seral vegetation that reburned at high-severity is labelled persistent shrubland, while areas that experienced low/moderate-severity reburn effects are labelled potentially recovering forest. Triangles and bars below distributions indicate mean and 50% interquantile ranges respectively. Heterogeneity is measured as the standard deviation of percent cover (log-scale). Structural variables were sampled from 10 m grids and summarized using a 75-m radius around sample points. The vertical axis indicates the frequency of samples relative to a panel's distribution maximum

TABLE 2 Mean (range) trees per hectare of field plots that initially burned at high-severity and reburned at either low/moderate- (H-LM) or high-severity (H-H)

	Conifers		Hardwoods	
Stratum	**H-H severity**	**H-LM severity**	**H-H severity**	**H-LM severity**
Canopy (>8 m)	0 (0, 0)	15 (0, 108)	0 (0, 0)	0 (0, 62)
Subcanopy (2–8 m)	0 (0, 0)	3 (0, 81)	382 (0, 2,327)	40 (0, 793)
Understorey (1–2 m)	0 (0, 0)	52 (0, 1,217)	0 (0, 0)	13 (0, 317)

areas potentially recovering towards a forested state and other areas likely to persist as montane chaparral.

As compared to long unburned forests, forests that experienced one low/moderate-severity burn had lower cover but higher spatial heterogeneity in the canopy and subcanopy. Because fire-suppressed forests are currently much denser and more homogenous than they were historically (Hessburg et al., 2005; Larson & Churchill, 2012; Lydersen et al., 2013), these shifts moved forest structure closer to historical reference conditions and a potentially more resilient structure (Kane et al., 2019). Species with fire-resistant traits (e.g. thick bark and high crown base; Stevens et al., 2020) are more likely to survive initial burns, dominate post-fire communities and further promote forest resilience (Larson et al., 2013).

4.1 | Resistance versus vegetation transition

Topography strongly influenced the ability of both once-burned early seral and forest vegetation to resist high-severity effects in the reburn, while fire weather was also highly influential for forest types (Figure 8). In areas where topography was homogenous and xeric, once-burned forests and early seral vegetation were less likely to resist subsequent high severity and consequently transition to, or persistence as, non-conifer forest vegetation. Once-burned forests that reburned when relative humidity was high and wind speeds were low were less likely to experience high-severity fire effects. Topographic roughness may moderate fire effects if rapid changes in terrain disrupt fire behaviour and break up patches of high-severity (Estes et al., 2017; Povak et al., 2018). Given that

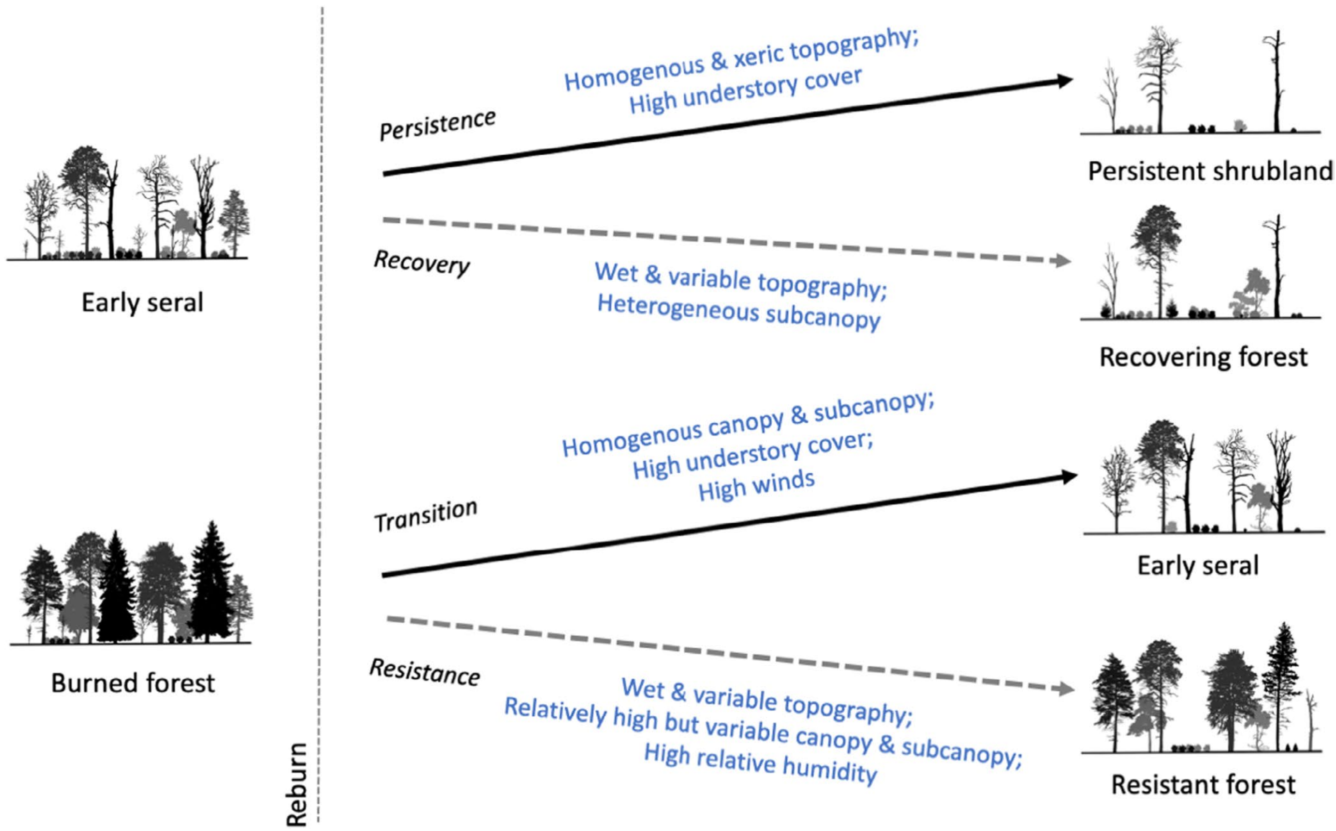

FIGURE 8 Vegetation trajectories following a wildfire in previously burned early seral or forest vegetation. Environmental characteristics associated with each pathway are annotated in blue

topography is fixed in ecological time-scales, these relationships can be used to identify fire refugia, which may be less sensitive to changes in vegetation structure and climate (Krawchuk et al., 2016; Wilkin et al., 2016). Because fire weather will be influenced by future changes in climate, we may see the rate of transition from forest to early seral vegetation grow following reburns as aridity increases (Pausas & Fernández-Muñoz, 2012; Williams et al., 2019), especially if fires continue to occur more often during high wind events (Keeley & Syphard, 2019).

Spatial variability in vegetative cover promoted resistance to high-severity fire, although this effect varied by vertical strata (Figure 8). Heterogeneity in both the canopy and subcanopy helped forests resist high-severity reburn, while heterogeneity in the subcanopy had a similar affect for early seral vegetation. Variability in stand structure can moderate fire behaviour by disrupting vegetation continuity (Parsons et al., 2017; Ziegler et al., 2020). In the understorey, higher cover was associated with greater probability of high-severity fire. The relationship between more extreme fire behaviour and effects and surface and ladder fuel loads (vegetation mass) is well established (Agee & Skinner, 2005). First-entry fires often reduce surface fuel loads (Stephens et al., 2009), which could provide insulation from intense fire behaviour in the short term. Ladder fuels, which would fall within our understorey and subcanopy height strata and can help carry fire into the forest canopy, are often associated with increased risk of high-severity fire (Stephens et al., 2009). Thus, our finding that subcanopy cover was negatively associated with high-severity is surprising and suggests that this established relationship may be most relevant to fire-excluded forests. Our once-burned forests had lower canopy and subcanopy cover and were more heterogeneous than unburned forests. Where forests survive a first-entry wildfire, they likely benefit from some restoration if fire-sensitive species (e.g. firs) and individuals (e.g. with small diameters) have been selected against and the remaining subcanopy is dominated by trees characterized by fire-resistant traits such as thick bark and elevated crown base height (Collins et al., 2018; Kane et al., 2019).

If considering the full variation of burned and unburned forest, the relationship between subcanopy density and fire hazard may be more U-shaped. This hypothesis suggests maximum resistance to high-severity fire may be achieved in burned forests characterized by moderate levels of cover and heterogeneous canopy and subcanopy, made up of fire-resistant tree species and a sparse understorey. Plausible mechanisms for this dynamic include suppression of understorey growth due to the moderately dense overstorey, reduction in surface-level airflow due to the presence of subcanopy vegetation and promotion of higher fuel moisture at the forest floor due to shading from the overstorey and subcanopy (Bigelow & North, 2012; Estes et al., 2012; Ziegler et al., 2020).

4.2 | Forest recovery

Two lines of evidence suggest forest recovery occurred in some areas following transition to early seral vegetation and a subsequent reburn. First, potentially recovering areas that reburned at low/moderate-severity had different structure on average than areas that reburned at high-severity and are likely to persist as shrubland. The potentially recovering class was characterized by greater and more variable subcanopy and canopy cover, consistent with young tree growth. Second, while field data from the persistent shrubland group showed zero conifer regeneration, a minority (9%) of the plots in the recovering forest class contained conifer trees. Both groups showed some regrowth of hardwood species indicating that while forest recovery is possible, often tree species composition is likely to diverge from the original conifer-dominated community. These observations are consistent with other studies conducted in the area that suggest recovering areas support a diverse mixture of shrub species in the understorey and re-sprouting black oak and some conifers in the subcanopy (Hammett et al., 2017; Nemens et al., 2018). Unlike black oak, which can resprout vigorously following repeat high-severity fire, the presence of conifer saplings in the subcanopy layer is largely dependent on the proximity of live seed trees after initial high-severity fire (Welch et al., 2016) as well as seedling survival during subsequent burns.

Establishment of oak-dominated forests or woodlands in previously conifer-dominated areas would represent a shift in forest type but would recover some ecosystem structure and function similar to the pre-fire vegetation community. Prior to Euromerican colonization, oaks were promoted as part of indigenous forest management making this alternative trajectory consistent with the historic landscape (Anderson, 2013). The ability of many oak species to resprout following fire, in combination with their general drought tolerance, suggests that a shift towards oak-dominated forests may become more common in a region like California, where conditions are projected to be warmer and more fire-prone (McIntyre et al., 2015).

4.3 | Regional shifts in vegetation composition

The dual processes of fire and succession create a dynamic mix of vegetation communities in fire-adapted regions. Reduced resistance to high-severity fire or declines in post-fire forest recovery will shift the landscape mosaic towards more early seral communities adapted to frequent high-severity fire at the expense of forests adapted to frequent low-severity fire. In the Sierra Nevada, both types of changes are likely occurring. A century of fire suppression has reduced the total area burned, increased landscape homogeneity and shifted forest composition towards shade-tolerant fire-sensitive tree species (Lydersen & Collins, 2018; Mallek et al., 2013). These changes, combined with longer fire seasons and more extreme fire weather, have decreased resistance to high-severity fire across much of the region (Westerling, 2016; Williams et al., 2019), a tendency that may play out in fire-prone ecosystems globally (Seidl et al., 2011). Furthermore, lower forest recovery rates from wildfire through slower or failed conifer regeneration may also be reducing broad-scale ecological resilience. Regeneration of non-serotinous conifers is challenged by increasing high-severity patch sizes and consequently reduced seed rain and dispersal (Shive et al., 2018; Steel et al., 2018; Stevens et al., 2017; Welch et al., 2016), as well as potential failure in tree recruitment due to a warmer and drier climate (Davis et al., 2019).

Some shift in the regional mix in vegetation may be inevitable without rapid climate change mitigation, but reintroduction of mixed severity fire dominated by low/moderate-severity in fire-adapted systems would help moderate the rate and magnitude of such changes (North et al., 2012). The use of prescribed fire and managed wildfire is critical for restoring forest resilience, especially considering current limitations on mechanical treatment (North et al., 2015). However, given the significant structural and compositional changes brought about by anthropogenic legacies such as long-established fire suppression and past timber harvest, we cannot assume that areas burned at low/moderate-severity are 'restored' after one fire. It is likely that repeated low/moderate-severity fire is needed to fully restore community composition and structure and maximize ecosystem resilience (Collins et al., 2018; Hessburg et al., 2015). By historical standards, both the Storrie and Chips fires burned at elevated levels of severity when they constituted the first-entry wildfire.

This study indicates that reforestation efforts to assist succession from early seral vegetation towards a forested state may be most successful when focused on areas where early seral communities are less likely to burn again at high-severity. Specifically, targeting reforestation in rough and mesic terrain in the middle of large high-severity patches where conifer seed rain is limited (Shive et al., 2018) may prove the best use of resources (North et al., 2019). Furthermore, incorporating spatial variability into planting patterns and applying fire early in stand development can promote resilience to future fire and drought (North et al., 2019). Beyond managing for forest cover, promoting spatial variability either through planting or maintaining fire-created heterogeneity (pyrodiversity; Steel, Collins, et al., 2021) can benefit other management objectives such as maintenance of wildlife habitat (Steel et al., 2019) and water provisioning (Boisramé et al., 2017). Ultimately, large uncharacteristically severe wildfires create both challenges and opportunities for conserving fire-prone ecosystems in an age of changing climate and disturbance regimes.

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CONFLICT OF INTEREST

The authors have no conflicts of interest.

AUTHORS' CONTRIBUTIONS

Z.L.S., D.F., M.C., S.L.S. and B.M.C. conceived the ideas and designed methodology; M.C., A.P., S.H.M. and K.M. facilitated data acquisition; Z.L.S., D.F. and J.M.L. analysed the data; Z.L.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Model code and data used in analysis can be accessed at https://doi.org/10.5281/zenodo.5181822 (Steel, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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