

What Burns and What Returns: Multi-Scale Consequences of
Unprecedented Fire Regimes in the Sierra Nevada

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Abstract

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Environmental and Forest Sciences

Unprecedented wildfire and climate change are altering landscapes in the Sierra Nevada at rates and extents that challenge the capacity of both ecosystems and communities to recover. Increasingly large and severe wildfires are pushing vegetation and inhabited communities beyond sustainable thresholds, raising concerns about managing these systems under more extreme future conditions. High uncertainty associated with changing fire regimes presents substantial challenges for land managers and community planners. This dissertation addresses three scales where uncertainty is greatest.

In my first chapter, I synthesize literature to analyze broad vegetation transitions across conifer, oak, shrub, meadow, and grassland communities in the Sierra Nevada. Limited research on non-coniferous ecosystems has created a bias in which vegetation types more readily adapted to unprece-

mented fire and climate are often overlooked. In the second chapter, I focus on lesser studied systems of oaks and shrubs alongside conifers, where I use airborne lidar datasets to map their post-fire extents in Yosemite National Park. The resulting maps show where each type is establishing long-term following high severity fire and reveal how novel fire regimes and climate patterns are driving compositional reorganization away from conifer dominance. In my final chapter, I move into the realm of human infrastructure, where extreme fires are causing significant housing loss in the wildland urban interface. I use lidar to measure parcel-scale fuel cover and how it interacts with multiple confounding variables to determine the survival or destruction of homes in the wildland urban interface. This interdisciplinary approach to measuring the effects of extreme fire was driven by a unifying question across all three scales: what burns and what returns?

Table of Contents

Acknowledgements	1
Introduction	3
Dissertation Overview	6
References	9
1 Chapter 1: From Past Patterns to Future Frameworks: Understanding Vegetation Transitions in the Sierra Nevada	14
1.1 Abstract	14
1.2 Introduction	15
1.3 Background	17
1.4 Synthesis: Analysis of Pathways of Vegetation Change in the Sierra Nevada	34
1.5 Management Implications	47
1.6 Conclusion	49
1.7 References	50
Appendix	66
2 Chapter 2: Mapping conifer, oak, and shrub regeneration following high-severity wildfire in Yosemite National Park, CA	73
2.1 Abstract	73
2.2 Introduction	74
2.3 Materials	76
2.4 Methods	81
2.5 Results	92
2.6 Discussion	99
2.7 Conclusion	108
2.8 References	109
Appendix	116
3 Chapter 3: WUI housing loss in the 2020 Creek Fire: fire behavior stage moderates the role of lidar-derived fuel structure	119
3.1 Abstract	119
3.2 Introduction	120
3.3 Study Area	122
3.4 Datasets	124
3.5 Methods	127
3.6 Results	136

3.7	Discussion	141
3.8	Conclusions	148
3.9	References	149
Conclusion		153
	What Burns	153
	What Returns	155
	Broader Implications	156

List of Figures

1.1	Vegetation land cover classes from CALFIRE Fire and Resource Assessment Program (FRAP) of the low-mid elevation Sierra Nevada EPA ecoregions. B: Percent area each land cover class occupies of the study area. The major vegetation types in this study correspond with the FVEG vegetation as follows: Conifer = Conifer, Oak = Hardwood, Shrub = Shrub, Herbaceous = Grassland/ Meadow. Hardwoods and Conifers make up the majority of vegetation types in the Sierra, with herbaceous and shrubland together occupying about a quarter of the area.	19
1.2	Frequency of which vegetation types found in literature on the Sierra Nevada and surrounding areas. Conifers highly dominate this topic, showing the need for more research in lesser studied ecosystems in the Sierra.	34
1.3	State and Transition Model for mesic ecosystems in the Sierra. The color of the transition represents the severity of fire disturbance (Low = Blue, Moderate = Orange, or High = Red) and whether that disturbance has been interrupted due to fire- fire-intolerant species encroachment (Interrupted Low Severity = Yellow and Interrupted Moderate Severity = Purple). The dashed lines represent temporal mechanisms of transition. Each pathway citation can be found in Appendix S2.	35
1.4	State and Transition Model for xeric ecosystems in the Sierra. The color of the transition represents the severity of fire disturbance (Low = Blue, Moderate = Orange, or High = Red) and whether that disturbance has been interrupted due to fire-intolerant species encroachment (Interrupted Low Severity = Yellow and Interrupted Moderate Severity = Purple). The dashed lines represent temporal mechanisms of transition or oak presence. Each pathway citation can be found in Appendix S3.	36
2.1	Yosemite fire perimeters from 1950-2019 overlaid with the classified high severity patches.	77
2.2	Plot layout adapted from Pokswinski et al. 2021. The figure shows the important parts of the plot layout (north-south transect, point intercept sample locations for shrub cover, and the plot center where the BLK scanned the plot). It also includes potential vegetation covers. This plot would be classified as low conifer cover (three occurrences), low oak cover (two occurrences), and low shrub cover (35% - seven point-intercept sample locations divided by 20).	78
2.3	Spectral resampling method for plot imagery calculation. The shaded areas are subsampled 10-m cells from Sentinel 2 imagery that are used to calculate the spectral metric mean in each plot.	81

2.4	Examples of vegetation compositions for different covers. It is important to note that individual tree and shrubs height varies regardless of type and cover- i.e. height alone cannot distinguish cover or type.	82
2.5	Height percentile dividing the canopy morphology by varying heights. The percentiles represent different parts of the understory and are structurally different depending on the amount, height, and type of vegetation. Height percentile bins are inclusive and overlapping. Points in the 90th-99th percentile (upper understory, brown) also appear in lower percentile bins but are shown only in their highest category for visual clarity. .	83
2.6	A) Simplified flow chart only showing the basic steps to provide an overview of methods. B) Flowchart of the full workflow Colors identify how steps correspond between the flow charts.	88
2.7	Distribution of field plots by elevation, time since fire, and vegetation type. Point size indicates plot count or percentage. Sampling captured structural diversity across the chrono sequence with variable temporal coverage.	93
2.8	Number of plots (left y-axis) compared to the total area burned at high severity (black line, right y-axis).	94
2.9	Geometric and spectral signatures of post-fire vegetation types with predictor variables shaded by height percentile. Point clouds and field composition (top) show representative plots. Geometric metrics from three lidar height strata (rows 2-4) and dual-season spectral indices (bottom) distinguish vegetation types. Each radar plot shows a distinct structural signal emitted from the selected plots.	96
2.10	Maps of the vegetation cover across three resultant high severity patches with different fire histories. Patch 1: The Illilouette Basin, some of the patches burned at high severity in the Illilouette Fire in 1991 and some burned in the Managed Meadow Fire in 2004. Patch 2: Lower Big Oak Flat Road, burned at high severity in the 1990 A-Rock Fire and again during the 2010 Big Meadow Fire. Patch 3: Hetch Hetchy: Burned in 2013 as part of the Rim Fire. All models have a probability raster which measures confidence in predictions. For visualization purposes, the probability rasters are averaged across the models.	100
2.11	Photo of a plot in a resultant high severity patch in the Rim Fire footprint with manzanita, California black oak, and a burned conifer snag in the foreground looking toward the patch edge in the background where surviving conifer forest either burned at low severity or did not burn. There are no conifer seedlings present.	105
3.1	Creek Fire Burn Severity Map. Calculated using the Composite Burn Index (CBI) two years post-fire.	123
3.2	Locations of structures within the Creek Fire perimeter, classified by damage status from the CAL FIRE Damage Inspection (DIS) database. Points show structures that were destroyed (>50% damage, red) or undamaged (blue) following the 2020 Creek Fire in the southern Sierra Nevada, California. Most structures were concentrated in the southern portion of the fire near the communities of Pineridge and Shaver Lake. .	125

3.3	Example lidar point cloud centered on a single structure footprint in the Creek Fire study area, with the structure removed and points classified into six height strata. Fuel metrics were calculated within each height class across three defensible space zones surrounding each structure. Point classification: gray (< 1 m), blue (1 to 2 m), green (2 to 4 m), pale yellow (4 to 8 m), gold (8 to 16 m), and orange (> 16 m).	127
3.4	Receiver Operating Characteristic (ROC) curves comparing four full-extent spatial GAMs with different predictor combinations, evaluated using 5-fold cross-validation. All four models produced nearly identical performance (CV AUC = 0.882 to 0.889), with overlapping curves indicating that the spatial smooth drove most of the predictive performance regardless of whether fuel variables, housing density, or both were included. The dashed diagonal represents the no-discrimination line (AUC = 0.5). . .	131
3.5	Despite the spatial smooth's strong predictive contribution, residual spatial autocorrelation remained. Moran's I calculated on the raw binary damage outcome was 0.559, confirming that spatial clustering was present in the response. After fitting the full-extent spatial GAM, the residual Moran's I was 0.254, showing that the spatial smooth reduced autocorrelation but did not eliminate it.	132
3.6	Map of the fire stages overlayed with house locations. The Fire Stages were delineated using NIROPS data from flown daily fire perimeters.	134
3.7	Housing loss by day in the Creek Fire, in 2020, in the southern Sierra Nevada, California, USA. The first plot examines total housing loss counts, the second plot looks at the proportion of housing loss per day.	136
3.8	Distribution of fuel variables, vegetation over home, and housing density across the three fire behavior stages (Blowup, Rapid Expansion, Flanking/Containment). Fuel variables are shown by height class (1-2 m, 2-8 m, 8-16 m, 16-100 m) within three defensible space zones (0-2 m, 2-10 m, 10-30 m from each structure).	139
3.9	Model performance by stage of models with different inputs. A 0.5 AUC represents random guessing, while values near one indicate high predictive power. The spatial models have the highest AUC of all models.	141
3.10	SHAP values for fuel and housing density variables across the three fire behavior stages and all stages combined. Points are colored by feature value (blue = low, red = high). Positive values indicate the observations pushed the model toward predicting destruction and negative values toward survival. Wider spreads indicate higher variable importance. Spatial coordinates were fixed at their median values.	142

List of Tables

1.1	Post-fire regeneration strategies across Sierra Nevada vegetation communities. All records are from the Fire Effects Information System (FEIS) unless noted otherwise.	25
1.2	Drought response strategies, key traits, and drought vulnerability across Sierra Nevada vegetation communities. All records are from the Fire Effects Information System (FEIS) unless noted otherwise.	32
2.1	Summary of vegetation structure metrics derived from lidar and Sentinel-2 imagery. .	86
2.2	Classified vegetation cover parameters. Each vegetation type had a different class depending on the sample size to create balanced classes for the ordinal logistic regression model.	87
2.3	Selected predictor variables and standardized coefficients for binary logistic regression (BLR) and ordinal logistic regression (OLR) models by vegetation type.	97
2.4	Conifer, oak, and shrub BLR confusion matrices and test statistics.	98
2.5	Conifer, oak, and shrub OLR confusion matrices and accuracy statistics.	99
3.1	Record of available days and fire stages. The total number of destroyed homes which met the building classification criteria was 511 and the total number of homes which survived was 1,375.	137
3.2	Kruskal-Wallis and coefficient of variation (Coef. of Var.) test results, sorted by coefficient of variation to show the magnitude of differences across variables.	140

List of Supplementary Figures and Tables

S1	Web of Science Search Query	66
S2	Citation Table for Figure 1.3	67
S3	Citation Table for Figure 1.4	69
S1	Model performance metrics for binary (logistic) and ordinal logistic regression models by vegetation type.	116
S1	Understory segmentation workflow steps using the Yosemite site as an example. The workflow starts with tall tree segmentation, then calculates understory p99 heights, then filters individual tree vegetation, and finally segments snags.	118

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Introduction

Anthropogenic climate change and changing fire regimes are rapidly transforming ecosystems beyond their historical and paleoecological ranges (Coop et al., 2020; Hoecker et al., 2023; Oliveira and Martins, 2026). Fire-prone ecosystems fall at the forefront of this change, as fire acts as a catalyst of change for systems pushed beyond their thresholds of resilience (Donato, Harvey, and Turner, 2016; Johnstone et al., 2016; Davis et al., 2019; Coop et al., 2020). Contemporary wildfires are burning at greater size, frequency, and severity (Anthony L. Westerling, 2016; Miller et al., 2012; Williams et al., 2023). They also are more frequently burning into built environments where they threaten human lives and property (Radeloff et al., 2018; Carlson et al., 2025; Kumar et al., 2025). In places such as Australia, the American West, and Mediterranean Europe, the effects of these unprecedented fire regimes and climate change are perpetuating uncertainty around their long-term effects on ecosystems and inhabited communities (Bowman, 2018; Clark-Wolf et al., 2025).

The Sierra Nevada region of California, USA is considered at high risk for rapid state changes (A. M. Young et al., 2017; Stevens-Rumann et al., 2018; Steel, Koontz, and Safford, 2018; Fettig et al., 2019; Safford and J. A. E. Stewart, 2026) and has one of the fastest growing wildland urban interface (WUI) populations, where built communities interact with wildland vegetation (S. I. Stewart et al., 2007; Radeloff et al., 2018). This region has been extensively studied due to its ecological and recreational value (Wallen, Kyle, and van Riper, 2015; Dugstad et al., 2024). For these reasons, I found the Sierra to be an ideal case study to analyze how ecosystems and people respond when faced with novel change.

Humans have played a significant part in influencing ecosystems for millenia (Pyne, 1997; Burney and Flannery, 2005; Bliege Bird et al., 2008). In California, an estimated 5.6 million to 13 million acres of land were burned each year through a combination of Indigenous burning practices and lightning-ignited wildfires (Martin and Sapsis, 1992; Van Wagtendonk and Lutz, 2007). Prior to settler colonialism, cultural burning by Indigenous tribes mitigated wildfire risk, supported ungulate forage and hunting, and maintained culturally important plant species for medicine, food, and materials (An-

derson, 2005). This sacred practice not only allowed Indigenous peoples to create livable, sustainable systems, but was an important part of social and spiritual identities among the tribes (Norgaard, 2014).

Settler colonialism caused precipitous losses in Indigenous populations through the introduction of diseases, forced displacement from ancestral homelands, and acts of genocide. Following loss or severe curtailment of Indigenous cultural burning practices, active fire suppression policies began in the late 1800s. Euro-centric management perceived fire as a destructive force and sought to suppress all fires and increase timber production across the Sierra (DuBois, 1914; Benedict, 1930; Van Wagtendonk and Lutz, 2007). It is now widely recognized that this was detrimental to fire-dependent ecosystems, and the mounting hazard created by fire suppression and exclusion has become apparent in uncharacteristically large and severe fires (Agee and Skinner, 2005; Lydersen et al., 2013; Hagmann et al., 2021). The further disconnect between Euro-centric management and TEK impedes our ability to create livable ecosystems which need to be adapted to fire rather than threatened by it (Eriksen, 2013; Vázquez-Varela, Martínez-Navarro, and Abad-González, 2022).

Contemporary, large high-severity fire patches in the Sierra Nevada are a product of the underlying disconnect between humans and fire and are generating novel outcomes for vegetation in fire-prone systems. Larger, more contiguous patches of stand-replacing fire produce homogeneous post-fire vegetation structure and composition (Cansler and McKenzie, 2014; Cova et al., 2023). The greater distance to living seed source from patch edge further constrains recolonization for species reliant on propagule dispersal (Welch, Safford, and T. P. Young, 2016; Shive et al., 2018), driving vegetation type conversion to favor vegetation which germinates from fire-activated soil seed banks (Zammit and Zedler, 1988; Davis et al., 2019; Jones et al., 2023) or resprouting mechanisms (Cocking, Varner, and Knapp, 2014; Nemens et al., 2022). These post-fire vegetation covers may differ substantially from pre-fire vegetation structure, composition, and function, experiencing a process known as type-conversion (Coop et al., 2020; Paudel et al., 2022).

Climate change further impacts the capacity of forest and non-forest ecosystems to recover from frequent high-severity fire. Moisture stress in pre-fire vegetation increases fire ignition risk through drier, desiccated fuels and drought induced mortality (A. L. Westerling et al., 2006; Allen

et al., 2010). Climate and localized fire weather anomalies further lengthen the window which fuel aridity is conducive to ignitions and increase the frequency of extreme weather conditions, such as heatwaves and foehn winds, to create more intense fire spread and intensity (Abatzoglou et al., 2025; Oliveira and Martins, 2026). In post-fire sites, climate affects regeneration potential, with elevated vapor pressure deficit (VPD) limiting establishment of drought-intolerant vegetation (Davis et al., 2019; Stevens-Rumann et al., 2018; J. A. E. Stewart et al., 2021).

Novel fire regimes are also causing increased risk to WUI communities. In California, the number of residents living among wildland vegetation has increased over the past few decades, putting more people and homes at risk of wildfire-induced loss (Radeloff et al., 2018; Kumar et al., 2025). Lengthening wildfire seasons further compounds this risk, with destructive wildfires now occurring in seasons previously considered low risk (Bowman, 2018), exemplified outside the Sierra by the January 2025 Palisades fire, in which 12 people lost their lives and roughly 6,800 homes were destroyed. Smoke from these fires also degrades air quality across rural and urban communities, with documented consequences for human health (Reid et al., 2016).

Due to these contemporary challenges, managers and communities must prepare communities and their surrounding vegetation for rapid transformations. This shift requires the development of socioecological adaptive capacity (Smit et al., 2001; Paveglio et al., 2009) and flexible management strategies (Kolden and Henson, 2019a; Crausbay et al., 2022). Although adaptive strategies are crucial for long-term resilience, they depend on developing methods and analyses that can characterize how vegetation and communities respond to larger and more frequent high-severity fire (Clark-Wolf et al., 2025). Remote sensing tools such as airborne lidar offer spatial coverage and structural detail needed to assess fuels and vegetation structure at scales relevant to management (reviewed in (Abdollahi and Yebra, 2025)), bridging the gap between field studies and landscape scale analyses.

My interest in these transformations is rooted in formative experiences across three fire-shaped landscapes. I grew up in Kansas, where annual spring burning maintains prairie function and limits woody encroachment. I saw firsthand how prairie ecosystems have been heavily degraded due to livestock grazing and invasive species encroachment, transforming diverse native prairies into miles

of invasive old-world bluestem (*Bothriochloa ischaemum*), brome (*Bromus* spp.), and fescue (*Lolium arundinaceum*). Working at Tall Timbers Research Station in Florida expanded my view of fire into forested systems, where pine-dominated stands depend on regular burning to maintain open stand structure and understory diversity for fire-adapted plants such as saw palmetto (*Serenoa repens*), gallberry (*Ilex glabra*), and wiregrass (*Aristida stricta*). These experiences shaped my view of fire as a process that maintains overall ecological function and diversity rather than one that alters it. When I moved to the western US and focused much of my research in California, I found a larger problem taking place in the Sierra Nevada, where fire was seen as a destructive force, degrading vegetation and livelihoods rather than supporting them. While this perspective among residents and land managers has changed significantly in the five years I spent developing this dissertation, I still see biases around the framing of non-coniferous vegetation as an obstacle to recovery rather than an integral component of fire-adapted landscapes. This disconnect motivated my dissertation research which, through a holistic view, examines post-fire vegetation dynamics across the full mosaic of Sierra Nevada vegetation types and the human communities that interact with them.

Dissertation Overview

In this dissertation, I analyzed ecosystem types and built environments at varying scales for a better understanding of fire ecology in altered systems. I was guided by a central question: How does wildfire maintain or change vegetation compositions and inhabited landscapes? Each chapter addresses this question through varying methods and scales across the Sierra Nevada:

- Chapter 2: I review the traits and mechanisms which drive vegetation type transitions;
- Chapter 3: I present a method which uses airborne lidar and satellite imagery to map post-high severity fire vegetation across large extents; and
- Chapter 4: I pivot to using lidar to characterize fuel structure in the WUI and how varying fire behaviors and vegetation covers contribute to housing loss.

Each chapter presents novel frameworks and methods to analyze systems experiencing novel fire regimes and climate change.

Chapter 2 is a literature review which compiles research on life-history traits, pathways of change, and projects trajectories of vegetation transitions based on a future where climate change and novel regimes create no-analogue conditions for vegetation. This chapter uses evidence across vegetation types to build a trait-based framework for understanding vegetation transitions as mechanistic processes operating within the bounds of their resilience. I examine multiple vegetation types and their traits and community adaptations of conifer, oak, chaparral, meadow, and grassland ecosystems. Research on type transitions in the Sierra Nevada is often centered around conifer-dominated ecosystems, where post-fire regeneration delays or failures are serious concerns (Coop et al., 2020; Tubbesing et al., 2020). This conifer-focused framing involves two related biases. First, it frames vegetation change as inherently undesirable rather than as a directional response to traits misaligned with contemporary conditions. Second, it overlooks the dynamics of non-conifer systems that play essential roles in fire regimes and ecosystem function. For example, shrublands are sometimes characterized as drivers of short-interval, high-severity reburns, when in fact increased fire return intervals would lead to a decline in shrubland composition and function, ultimately degrading the system and interrupting feedbacks (Nagel and Taylor, 2005; Paudel et al., 2022).

In Chapter 3, I address how wildlands revegetate following high-severity fire. To do so, I present a novel method which uses airborne lidar and satellite imagery to model post-fire vegetation cover for three major vegetation types: regenerating conifers, oaks, and shrubs. Post-fire field studies are typically conducted in small plots, projected over large extents, and only study vegetation less than 10 years post-fire (Welch, Safford, and T. P. Young, 2016; J. A. E. Stewart et al., 2021; D. J. N. Young et al., 2019). These constraints can produce inaccurate predictions of post-fire vegetation recovery, as ecosystem recovery operates on temporal scales which exceed typical field study designs (Coop et al., 2020; Tubbesing et al., 2020). The method presented in this chapter bridges the gap between plot-scale field observations and remote sensing vegetation classification by combining airborne lidar with field data collected across diverse post-fire vegetation structures in Yosemite National Park.

Finally, Chapter 4 pivots from a sole vegetation focus to how vegetation impacts human-inhabited systems. Housing loss in the wildland urban interface (WUI) is driven by many factors including home hardening (Syphard and Keeley, 2019), fuel management (Escobedo et al., 2025; Zamianlaei et al., 2025), fire behavior (Syphard, Rustigian-Romsos, and Keeley, 2021), housing density (Knapp et al., 2021), firefighting efforts (Cohen, 2000), WUI-adjacent fuel treatments (Smith et al., 2016; Bowman, 2018), and community preparedness (Kolden and Henson, 2019b). While many of these drivers operate beyond the control of an individual resident, managing vegetation around built structures is one of the primary mitigation strategies to create defensible space against wildfire-driven housing loss (Cohen, 2000; Syphard, Brennan, and Keeley, 2014). Whether residents implement defensible space depends on their risk perception of threat of wildfire (Meldrum et al., 2019; Larsen et al., 2025). In this chapter, I use lidar as a tool to analyze how property-scale fuels contribute to housing loss to accurately quantify parcel-level wildfire risk for residents faced with important decisions on defensible space mitigation.

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Chapter 1: From Past Patterns to Future Frameworks: Understanding Vegetation Transitions in the Sierra Nevada

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1.1 Abstract

Vegetation type transitions have shaped the Sierra Nevada for millennia, but anthropogenic climate change, fire exclusion, and novel fire regimes are now accelerating the rate at which they occur. Departures in fire severity, frequency, size, and patch size from historical conditions are pushing systems past thresholds of resilience, altering essential ecosystem services and limiting our ability to predict future vegetation types for effective management. These transitions are difficult to characterize because the concepts used to define them, such as type conversion, state-and-transition models, and alternative stable states, are applied inconsistently across studies. We present a literature review that synthesizes life history traits and contemporary patterns of change to analyze potential vegetation trajectories across five dominant vegetation types: conifers, oak woodlands, chaparral and shrubland, meadows, and grasslands. We found that the transitions studied are often subjective, defined by the temporal and spatial scales of observation, and biased toward conifers. This limits our understanding of less-studied vegetation types that may be more resilient to future climate and fire regimes, such as oak woodlands, which demonstrate resilience to high-severity fire. Acknowledging these vegetation mosaics is important to holistic management strategies, where frameworks such as the Resist, Accept, and Direct (RAD) framework can be applied across diverse vegetation types to improve community resilience to wildfire and build more livable landscapes.

1.2 Introduction

Contemporary wildfires are burning at higher severity, with increased magnitude and frequency (Cova et al., 2023; J. N. Williams et al., 2023; Oliveira and Martins, 2026). This is the result of over a century of wildfire suppression and exclusion (Hessburg, C. L. Miller, et al., 2019; Haggmann et al., 2021; Kreider et al., 2024) compounded by anthropogenic climate change (Abatzoglou and A. P. Williams, 2016; Seidl et al., 2017). Altered climate and wildfire regimes are transforming key ecological processes, including hydrology, nutrient cycling, carbon storage, and wildlife habitat (Thom and Seidl, 2016; Turner, 2010). Consequently, ecosystems are experiencing higher risk of type change from known historical compositions, leading to uncertainty about future trajectories (B. M. Rogers et al., 2020; Clark-Wolf et al., 2025).

Changing fire regimes can produce self-reinforcing conditions that constrain post-fire recovery (Coppoletta, Merriam, and Brandon M. Collins, 2016; Airey Lauvaux, Skinner, and Alan H. Taylor, 2016; Harris and Alan H. Taylor, 2017; Nemens, Kidd, et al., 2022; Paudel, Coppoletta, et al., 2022), affecting the stability, functional capacity, and resilience of emerging ecosystem states (Johnstone et al., 2016; Seidl et al., 2017). As increased fuel loads interact with extreme fire weather, fires are burning with larger, more contiguous patches at high severity, which in turn produces more homogeneous post-fire vegetation structure and composition (Cansler and McKenzie, 2014; Cova et al., 2023). As climate change creates warmer, drier conditions across the Sierra Nevada, it thus not only exacerbates fire behavior (Abatzoglou, Kolden, et al., 2025; Oliveira and Martins, 2026), but also creates more challenging conditions for post-fire vegetation establishment and recovery (K. T. Davis, Dobrowski, et al., 2019; Huesca et al., 2021; Hoecker, K. T. Davis, et al., 2026). These interacting mechanisms drive post-fire vegetation dynamics and the ability for certain compositions to persist or reorganize under different scenarios.

The Sierra Nevada is a well-documented region suited for examining the fire-climate-vegetation relationship. This region supports a diverse mosaic of vegetation types – ranging from foothill oak woodlands and chaparral through mixed conifer forests and subalpine meadows. Most contemporary

research in this area focuses on conifer forests, where high-severity fire is driving regeneration failure and shrub field conversion (Coppoletta, Merriam, and Brandon M. Collins, 2016; Welch, H. D. Safford, and T. P. Young, 2016; Brandon M. Collins, Stevens, et al., 2017; Stevens-Rumann and Morgan, 2019; Stevens-Rumann and Morgan, 2019). However, conifer dominance across these landscapes was amplified by a century of fire suppression and may itself represent a departure from longer-term vegetation patterns (White and Long, 2019; Jonathan D Coop et al., 2020; Scott L. Stephens, Hall, et al., 2023).

Palaeoecological evidence from lake sediments and tree ring records in the Sierra Nevada has documented major shifts in vegetation cover over millennia. On the western slope, montane and subalpine zones shifted from sagebrush-dominated landscapes of the early Holocene to mixed conifer forests of the late Holocene (Millar, Barbour, et al., 1996; R. S. Anderson, Smith, and Koehler, 1997), while lower elevation foothill zones likely maintained oak woodland and chaparral communities throughout much of this period. Contemporary vegetation formed only around 500 years ago, coinciding with a cooler, wetter time known as the Little Ice Age (Klimaszewski-Patterson and Mensing, 2016). Across millennial time scales, fire regimes have been influenced by a combination of climate and Indigenous burning. Contemporary vegetation represents a transient expression of ecological succession, reflecting life-history traits and ecological memory that capture past disturbance patterns (Peterson, 2002; Millar and Stephenson, 2015; Johnstone et al., 2016; Hastings et al., 2018).

Contemporary type transitions in the Sierra Nevada are occurring quicker and at higher frequencies than those documented in palaeoecological records (Tubbesing et al., 2020; Knight et al., 2022; Stephenson et al., 2024). A disequilibrium between climate and disturbance magnitude creates a lagged response where a discrete disturbance, such as fire, can act as a catalyst of type change (Turner, 2010; Svenning and Sandel, 2013; K. T. Davis, Higuera, and Sala, 2018). As climate change continues to push post-disturbance ecosystem recovery past critical thresholds, vegetation can lack the time and capacity to track suitable climate or adapt to rapidly changing conditions (Tepley et al., 2017; K. T. Davis, Dobrowski, et al., 2019). This effect is seen most often in trailing edge ecosystems, or ecosystems that exist on the boundaries of their adapted niches (Parks et al., 2019; Hoecker, K. T. Davis, et al., 2026).

Thus, predicting post-fire recovery trajectories requires analytical frameworks capable of addressing both the temporal constraints of available data and the novel conditions created by contemporary fire regimes (Clark-Wolf et al., 2025).

Quantitative techniques that predict future vegetation compositions are constrained by several limitations. These predictive models are typically developed with vegetation and climate scenarios based off of past analogues, which limit their ability to extrapolate to no-analogue conditions (J. W. Williams and Jackson, 2007; Mahony et al., 2017). These simulations are often deterministic and lack nuances of vegetation niche overlap (Broennimann et al., 2012; Parks et al., 2019; Hoecker, K. T. Davis, et al., 2026). Furthermore, the modeled pathways fail to capture the inherent complexity of type transitions, as transitional states are often overlooked for more stable, end vegetation states, subjecting predictions to oversimplified trajectories (Magness et al., 2022; Clark-Wolf et al., 2025).

The goal of this synthesis was to inform current understanding of post-fire vegetation transitions by comparing historical transitions to potential future transitions. Building on the background, the synthesis section moves from how communities adapt to fire toward how species composition may shift as novel climate and fire regimes may exceed thresholds to species adaptations. We organize the synthesis around four questions: (1) How did historical fire regimes interact with climate to maintain stable vegetation states? (2) How are vegetation transition pathways altered when fire-climate-vegetation feedbacks are disrupted? (3) Can disrupted trajectories be restored? (4) What does the future hold for climate-fire trajectories? These questions chronologically represent how vegetation adapted to fire and climate over glacial cycles, how it is currently responding to increased fire severity and climate change, and how projected trajectories may shape future management.

1.3 Background

1.3.1 Major vegetation types of the Sierra Nevada

The Sierra Nevada Ecoregion is one of the most biodiverse regions in North America, hosting a wide range of plant communities that often overlap due to the complex geography of the region

and its variety of microsite conditions (Millar, Barbour, et al., 1996). Here, we focus on five dominant vegetation communities found in the low-to-mid elevation band of the western slope: conifer, oak, shrub, grassland, and meadow (Figure 1.1).

Mixed-conifer forest ecosystems comprise a large majority of the mid-elevation band of the Sierra Nevada and can further be divided into Dry Mixed Conifer (DMC) at the lowest elevation, Moist Mixed Conifer (MMC), Red Fir (RF) in higher elevations, and Lodgepole Pine (LP) in the subalpine zone. DMC forests historically consisted of species such as ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), incensecedar (*Calocedrus decurrens*), California black oak (*Quercus kelloggii*), and occasional white fir (*Abies concolor*). MMC forests occupy a slightly higher elevation, often found on northern aspects and near riparian areas with a greater component of white fir than DMC. Many of the species found in drier forests overlap here, such as sugar pine, white fir, and incense cedar; however, oaks are limited in this ecosystem. Other species found here include Jeffrey pine (*Pinus jeffreyi*), Douglas-fir (*Pseudotsuga menziesii*) primarily in the northern latitudes, and giant sequoia (*Sequoiadendron giganteum*). RF forests are dominated primarily by red fir (*Abies magnifica*) often co-occurring with white fir. LP forests are at the highest elevation and include lodgepole pine (*Pinus contorta*), red fir and intermittent western white pine (*Pinus monticola*) and whitebark pine (*Pinus albicaulis*). Since they occupy an elevational zone that differs substantially from the low- to mid-elevation ecosystems in the Sierra Nevada, we decided to exclude LP forests from this analysis.

Oak woodlands are common throughout low and mid elevations in the Sierra Nevada. Lower elevation oak woodlands consist of blue oak (*Quercus douglasii*), California black oak, and interior live oak (*Quercus wislizeni*) with scattered oaks dominating sparse overstories and annual grasses dominating the understory (Barbour, Keeler-Wolf, and Schoenherr, 2007). Oak species such as black oak and canyon live oak (*Quercus chrysolepis*) intermingle with conifers in montane areas.

Chaparral ecosystems contain the most diverse vegetation type in the Sierra Nevada and can be split into two categories based off their permeance on the landscape: mixed/ montane chaparral and episodic chaparral. Mixed and montane chaparral exists in a more stable state, and is dominated by chamise (*Adenostoma* spp.), whitethorn (*Ceanothus* spp.), and manzanita (*Arctostaphylos* spp.). Episodic

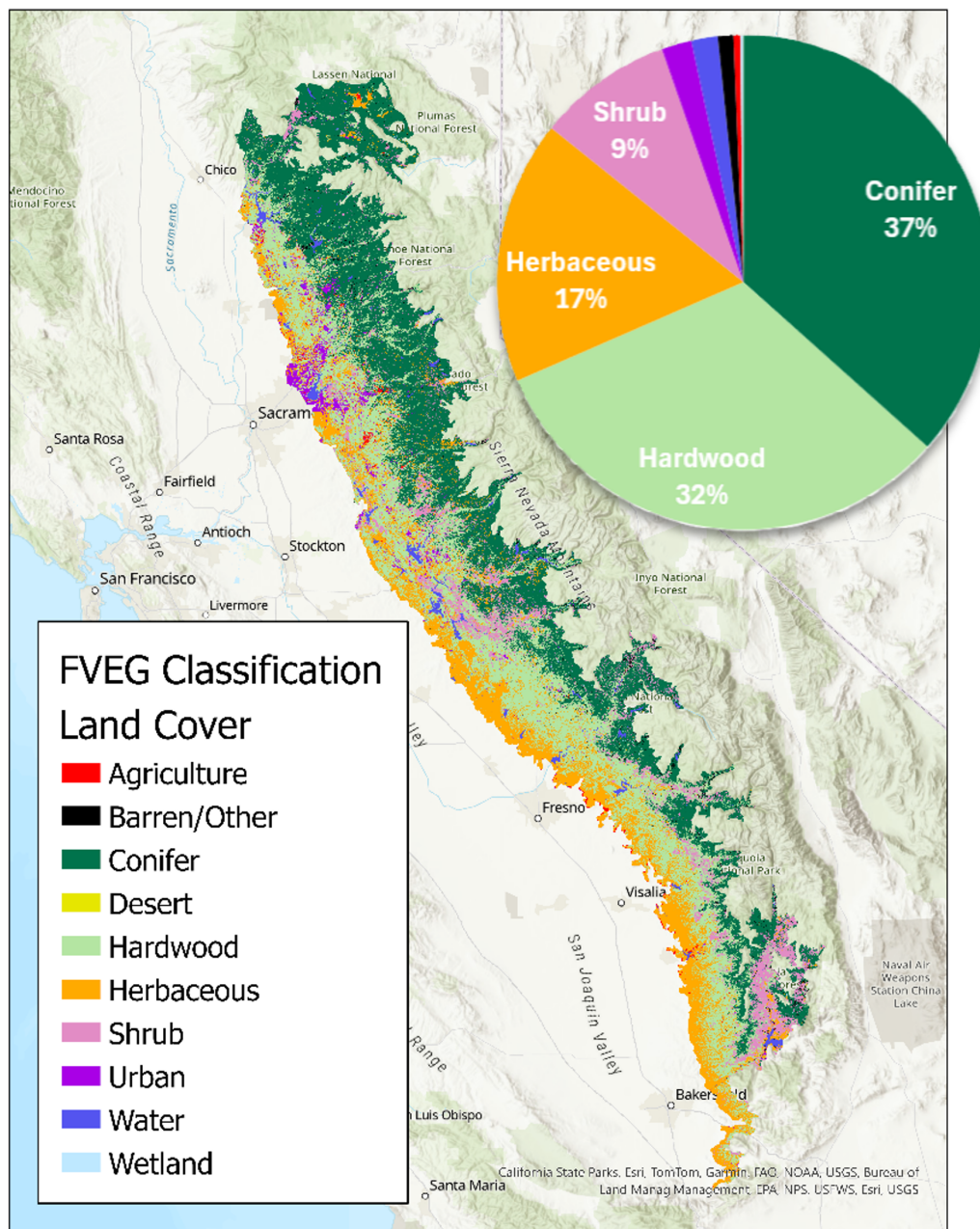


Figure 1.1: Vegetation land cover classes from CALFIRE Fire and Resource Assessment Program (FRAP) of the low-mid elevation Sierra Nevada EPA ecoregions. B: Percent area each land cover class occupies of the study area. The major vegetation types in this study correspond with the FVEG vegetation as follows: Conifer = Conifer, Oak = Hardwood, Shrub = Shrub, Herbaceous = Grassland/Meadow. Hardwoods and Conifers make up the majority of vegetation types in the Sierra, with herbaceous and shrubland together occupying about a quarter of the area.

chaparral is characterized by vegetation that recolonizes after stand-replacing fire in a different ecosystem type, such as mixed-conifer forests (Finegan, 1984; Kauffman and Martin, 1990; Keeley, 1991; Halpern et al., 2010; Swanson et al., 2011; Knapp et al., 2013). Episodic chaparral is a transient reorganization rather than a stable state, representing the initial step of forest succession after wildfire.

Annual grassland habitat occurs at lower elevations in the Sierra Nevada foothill zone. Historically dominated by native perennial bunchgrasses such as purple needlegrass (*Nassella pulchra*) and *Melica* species, these native, perennial grasslands have been largely converted into annual grasslands dominated by non-native species. Invasive grasses such as cheatgrass (*Bromus tectorum*) and medusa-head (*Elymus caput-medusae*) were introduced during Euro-American settlement and subsequent livestock grazing (Bartolome and Gemmill, 1981). This conversion represents one of the most extensive vegetation type changes in California, with an estimated 98% of native grassland lost to invasive annual grasses (Stromberg et al., 2007).

Meadows support a large diversity of habitat for plants and animals, act as carbon sinks, and are critical to the hydrologic cycle of water in the Sierra Nevada. Meadows are found throughout higher elevation mountain sites and can be perennially wet (“wet meadows”) or ephemerally wet (“dry meadows”). They are diverse in the number of plant species, including grasses, forbs such as lupines (*Lupinus* spp.) and asters (*Symphyotrichum* spp.), and woody shrubs such as willows (*Salix* spp.) and alders (*Alnus* spp.). However, their habitat is heavily degraded due to past cattle and sheep grazing practices (Ratliff, 1985; Kinney, 1996; Belsky, Matzke, and Uselman, 1999), decreased beaver populations (Pilliod, Welty, and Toevs, 2017; Fairfax and Whittle, 2020), forest encroachment through fire exclusion and suppression (Helms and Ratliff, 1987), and groundwater diversions from human activities such as road building (Kattelman and Embury, 1996). As a result, meadow habitat extent is severely underestimated and there may be up to three times more potential wet meadow sites than what are currently identified (Cummings, Pope, and Mak, 2023).

Even with such a large diversity of vegetation types in the Sierra Nevada, there is a significant focus on conifer forests in post-high-severity fire regeneration research. Given the historical dominance of conifer forests expanded through logging and fire suppression and exclusion (Lydersen, M. P.

North, et al., 2013; Knapp et al., 2013) and the economic and recreational value of conifers, they often dominate ecological literature. Discussions about type transitions to non-conifer forests are growing, specifically considering the mounting concern that rapid changes in disturbances are leading to a lack of conifer regeneration after stand-replacing fires across much of the American west (Stevens-Rumann and Morgan, 2019; Hessburg, C. L. Miller, et al., 2019; Jonathan D. Coop et al., 2019; Hagmann et al., 2021) and in the Sierra Nevada (Brandon M. Collins and Roller, 2013; Shive et al., 2018; K. T. Davis, Dobrowski, et al., 2019; Steel, Foster, et al., 2021). While the focus on conifer regeneration is valuable for understanding post-fire recovery in these historically conifer-dominated landscapes, it may not capture how diverse vegetation types respond to high-severity fires (White and Long, 2019). The historic landscape included a diversity of forests and non-forest vegetation, suggesting that other vegetation types also play crucial roles in ecosystem dynamics (Whitlock, Shafer, and Marlon, 2003; G. Boisramé et al., 2017; Ladwig, Damschen, and D. A. Rogers, 2018; White and Long, 2019; Hessburg, C. L. Miller, et al., 2019).

1.3.2 Comparisons of post-fire establishment and regeneration potential across major vegetation types

Vegetation composition, which consist of a variety of plant species that comprise a particular ecosystem or community, changes over time and space in response to disturbances (van der Maarel, 2005). Life-history traits of individual species reflect evolutionary responses to past climates and processes, indicating conditions that favor or limit certain species. Fire regimes are also heavily affected by climate-vegetation feedbacks, in which fuel availability, vegetation composition, and weather patterns interact on multiple spatial and temporal scales (Loudermilk et al., 2022). The recent change in fire frequency and intensity in the Sierra Nevada influences the composition and distribution of vegetation, favoring species with specific adaptations like fire-triggered seed release (i.e., serotiny) or rapid post-fire regeneration. Thus, fire-vegetation feedbacks play a critical role in determining the resilience of ecosystems, the succession of plant communities, and landscape heterogeneity.

Post-fire regeneration in Sierra Nevada ecosystems relies on two primary strategies, including

obligate seeding and resprouting. Obligate seeders are killed by fire and regenerate entirely from seed, relying on persistent soil seed banks or fire-stimulated germination (Lamont, Connell, and Bergl, 1991; Pausas and Keeley, 2014). Resprouters survive fire as established individuals and regenerate from belowground tissues such as root crowns, lignotubers, and rhizomes (Bond and Midgley, 2001; Clarke et al., 2013). Under contemporary fire regimes, short-interval (i.e. fire return interval under 50 years) and higher fire severities favor resprouters and seed-banking species over obligate seeders, which require longer recovery periods to rebuild reproductive capacity (Paudel, Coppoletta, et al., 2022).

All conifer species in the Sierra Nevada are obligate seeders and use masting to synchronize large seed crops at irregular intervals, which satiates seed predation and increases dispersal into burned areas (Fletcher et al., 2010; Wang et al., 2017). The establishment of conifer seedlings, especially pines, is more prevalent in years with above-normal precipitation and reduced during drought years (Paudel, Coppoletta, et al., 2022; Stewart et al., 2021). This dependence on favorable climatic windows makes conifer regeneration vulnerable to post-fire drought and chronic soil water deficits.

Chaparral species display the widest range of regeneration strategies of any Sierra Nevada community. Obligate seeders such as *Ceanothus* and *Arctostaphylos* maintain dormant seed banks that can persist for over 150 years until fire and moisture trigger germination (Zammit and Zedler, 1988; Jones et al., 2023). Frequent fires (give range) can negatively impact obligate seeder species by limiting the time available for seed bank accumulation, thereby impeding their ability to germinate following a disturbance and leading to a reduced function chaparral state which is dominated by resprouting and invasive species (Jones et al., 2023). Obligate resprouters, such as *Rhamnus* species, regenerate from belowground structures without relying on seed banks or propagule dispersal.

Episodic chaparral plays a transitional role in post-fire conifer forests. Shrubs provide nutrients to the soil, such as nitrogen, that facilitate recruitment of a new cohort of conifers that eventually overtop and shade out the shrubs (Busse, Cochran, and Barrett, 1996; Bellingham, Walker, and Wardle, 2001; Oakley, M. P. North, and Franklin, 2006). Some studies suggest that episodic shrub communities facilitate conifer growth through nutrient cycling, solar radiation protection, and increasing relative humidity and soil water availability (Castro et al., 2002; Crockett and Matthew D. Hurteau, 2022; Good-

win and Matthew D Hurteau, 2024). In contrast, other studies have found shrub presence to impede conifer growth, specifically pine, due to its shade intolerance (Tubbesing et al., 2020; Ursell and H. D. Safford, 2022; Brodie, Stewart, et al., 2023; Greene, Lindley, and Kane, 2024).

Oaks can persist through coppicing and shrub-like vegetation states (Cocking, Varner, and Knapp, 2014; Nemens, Varner, et al., 2018), but historical accounts and ecological evidence suggest that oak woodlands in the Sierra Nevada were maintained as mature groves of large, well-spaced trees through Indigenous burning practices (K. Anderson, 2005; Scott L. Stephens, Hall, et al., 2023). Most oak species only produce acorns in large quantities until roughly 100 years of age (Plumb, 1980; Huber and McDonald, 1992), reflecting the substantial time required for productive acorn harvests. European accounts corroborate this oak woodland structure, describing these woodlands as “orchards” (William Linn Jepson, 1923) with trunks reaching seven feet in diameter (quoted in THOMPSON (1961)). California black oak and other Sierra Nevada oaks rely on two primary regeneration strategies: resprouting from root crowns and lignotubers, and recruitment from acorns dispersed by corvids such as acorn woodpeckers and Steller’s jays. Resprouting is the dominant post-fire response across a wide range of fire severities, as belowground carbohydrate reserves allow rapid aboveground recovery even following crown kill (Cocking, Varner, and Knapp, 2014; Hammett, Ritchie, and Berrill, 2017). Acorn-based recruitment is more episodic, depending on mast years, disperser activity, and site conditions. Oaks are broadly resilient to even repeated high-severity fire as individuals, and repeated burning can reinforce oak dominance by suppressing conifer regeneration (Nemens, Varner, et al., 2018; Nemens, Kidd, et al., 2022).

Native bunchgrasses and invasive annual grasses employ markedly different reproductive strategies. Native bunchgrasses are long-lived perennials that invest in deep root systems and rely on vegetative resprouting after fire (Bartolome and Gemmill, 1981; Dyer, 2002). Invasive annual grasses maintain persistent soil seed banks that readily germinate after fire, allowing rapid colonization of burned areas (Brooks et al., 2004).

As with native bunchgrasses assemblages, meadow vegetation recovers from fire primarily through deep root systems. Graminoids in these communities survive fire through rhizomes and

protected basal meristems, with shallow burning typically producing only short-term reductions in aboveground biomass before resprouting (Soulard et al., 2016; Pausas and Keeley, 2014). Forbs in these systems persist through belowground organs such as bulbs, corms, and root crowns that buffer meristems from heat damage (Clarke et al., 2013). However, fire-driven recovery dynamics in Sierra Nevada meadows remain poorly characterized relative to adjacent forest types, particularly under high-severity fire regimes.

Across Sierra Nevada vegetation types, post-fire regeneration reflects a contrast between generalist species with broad regeneration niches and specialists with narrow trait-based requirements. Generalists, including most resprouting oaks, chaparral shrubs like *Rhamnus*, and meadow graminoids, recover across a wide range of fire severities and intervals through belowground roots and other plant structures that buffer them from variation in fire behavior. Specialists are adapted to narrower conditions. Conifers require post-fire climate windows suitable for seedling establishment and obligate-seeding chaparral like *Ceanothus* and *Arctostaphylos* require inter-fire intervals long enough to rebuild seed banks. Under contemporary fire regimes, shorter intervals and higher severities favor generalists over specialists, since specialists cannot complete their reproductive cycles within the temporal windows imposed by altered fire activity.

Table 1.1: Post-fire regeneration strategies across Sierra Nevada vegetation communities. All records are from the Fire Effects Information System (FEIS) unless noted otherwise.

Community / Species Group	Regeneration Mode	Seed Production / Timing	Key Mechanism	Limiting Factors
Ponderosa pine	Obligate seeder	Masting every 2–5 yrs; begins producing at 10–20 yrs	Wind and animal dispersal; rodent/nutcracker caching improves establishment; best germination on mineral soil or ash	Heavy seed predation; short seed viability; first-year moisture critical; establishment requires open canopy
Jeffrey pine	Obligate seeder	Strong masting every 2–4 yrs; cones common after ~20 yrs	Heavy seeds dispersed by gravity, wind, and animal caching; best emergence on burned mineral soil and ash; cached seeds far more successful than surface seeds	Regeneration “not rapid or reliable”; near-complete seed removal by rodents; high seedling mortality from summer desiccation
Sugar pine	Obligate seeder	Good production after ~30” DBH / ~150 yrs old; heavy crops produce 67–99% sound seed; up to 150 seeds/cone	Large seeds, wind dispersal (80% within 100 ft of source); bird and mammal dispersal	Low drought tolerance; slow early growth; poor development under shade or brush enclosure
White fir	Obligate seeder	Heavy crops every 3–9 yrs; best producers 12–35” DBH; begins bearing at 40 yrs	Shade-tolerant establishment even under closed canopy; germinates after snowmelt; endures decades of suppression then responds to release	Low seed viability; seeds not viable beyond 1 year; seedlings very sensitive to soil drying and heating; susceptible to spring frost and deer browse

(Table continued from previous page)

Community / Species Group	Regeneration Mode	Seed Production / Timing	Key Mechanism	Limiting Factors
Douglas fir	Obligate seeder	Heavy crops every 5–7 yrs; seeds wind-dispersed, most within 100 m	Wind and Clark's nutcracker dispersal; best germination on mineral soil; first-year seedlings need partial shade, then full sun	Low seed viability; seeds viable only 1–2 years; requires mineral soil seedbed; frost sensitive
Incense cedar	Obligate seeder	Abundant crops every 3–6 yrs	Shade-tolerant establishment in litter, brush, or mineral soil; well-developed root system in first year; light wind-dispersed seed carried long distances	Very slow seedling growth; high first-year mortality from cutworms and drought; growth suppressed by low light and deer browsing
Giant sequoia	Obligate seeder (seroti- nous)	Prolific; large crops after trees reach ~150–200 yrs; cones retained green on tree for decades as aerial seed bank	Fire-triggered seed release from serotinous cones; seeds dispersed onto fire-exposed mineral soil; rapid early growth overtops associates	Low field germination; extremely high seedling mortality from desiccation; seeds lose viability within weeks once dispersed; require canopy gaps and mineral soil
Red fir	Obligate seeder	Good crops every 2–6 yrs; min seed-bearing age 35–45 yrs; wind dispersal ~1–1.5 tree heights	Moderately shade tolerant; gap-phase regeneration in openings from fire, wind, or tree death; responds to release from suppression after age 10	Slow initial growth; frost, pocket gophers, deer browsing; competition from shrubs and grasses
Oaks	Resprouter + seeder	Acorns in large quantities after ~100 yrs of age (Plumb 1980; Lawson 1993)	Basal/root resprouting; coppicing	Slow juvenile growth; depends on reaching maturity within low-severity fire regime (Bond et al. 2001)

(Table continued from previous page)

Community / Species Group	Regeneration Mode	Seed Production / Timing	Key Mechanism	Limiting Factors
Chaparral – obligate seeders (<i>Ceanothus cuneatus</i> ; <i>Ceanothus leucodermis</i> ; <i>Arctostaphylos manzanita</i>)	Obligate seeder	Dormant seed banks lasting 150+ yrs (Zammit and Zedler 1988; Jones et al. 2023); highly variable year to year, peaking after high-precipitation years	Killed by fire and recovers entirely from a heat-cued seed bank; high temperatures during burning crack the impermeable seedcoat, producing a dense even-aged cohort germinating the first post-fire spring; little to no recruitment between fires	Short-interval reburns deplete seed banks (Zammit and Zedler 1988); high first-year seedling mortality from summer drought and herbaceous competition
Chaparral – facultative seeders (<i>Adenostoma fasciculatum</i> ; <i>Arctostaphylos patula</i>)	Resprouter + seeder	Variable; long-persistent soil seed banks	Lignotubers resprouting after fire combined with recruitment from a fire-cued seed bank; impermeable or hard seedcoats require heat scarification to break dormancy and trigger germination in the first post-fire rainy season	Sprouting trades off against seed output; high first-year drought mortality; minimal recruitment under intact canopy
Chaparral – obligate resprouters (<i>Rhamnus</i> spp.; <i>Cercocarpus betuloides</i> ; <i>Frangula californica</i>)	Resprouter	Seed production can be abundant but variable year to year; seedcoats are thin or short-lived; no dormant seed bank required (Jones et al. 2023)	Vigorous resprouting from root crowns, lignotubers, and rhizomes after fire or stem removal; does not depend on a dormant seed bank for postfire recovery	Seedling establishment rare in early postfire years and largely restricted to mature, long-unburned stands during high-moisture years; little to no fire-cued recruitment; severe or repeated top-kill can exhaust reserves
Native bunchgrasses	Resprouter	Long-lived perennials with deep roots (Dyer 2002; Bartolome and Gemmill 1981)	Vegetative resprouting from basal meristems	Competition from invasive annuals

(Table continued from previous page)

Community / Species Group	Regeneration Mode	Seed Production / Timing	Key Mechanism	Limiting Factors
Invasive annual grasses (<i>Bromus</i> spp.)	Seed bank	Persistent soil seed bank, high seed production (Brooks et al. 2004)	Rapid post-fire colonization; completes life cycle quickly	Few; competitive advantages increase with disturbance and fire frequency
Meadow species	Resprouter	Variable across graminoids, forbs, and shrubs	Resprouting from belowground structures (rhizomes, root crowns, bulbs); high fuel moisture limits fire exposure	Conifer encroachment under fire exclusion; degradation from grazing, beaver loss, hydrologic alteration

1.3.3 Implications of drought tolerance and water relations for species adaptations to a warmer, drier climate

The Sierra Nevada is classified as a Mediterranean climate with most precipitation falling between October and May. This winter snowpack is a critical reserve for Sierra Nevada ecosystems, releasing water as temperatures increase (y; Lubetkin, Anthony LeRoy Westerling, and Kueppers, 2017). Subsequently, warming spring temperatures trigger a flush of plant growth with abundant light and water availability. As water reserves diminish, the summer months are drier, which increases the amount of combustible biomass and wildfire risk (Scott L Stephens, Brandon M Collins, et al., 2018; Keyser and A. LeRoy Westerling, 2019).

These drought-tolerance strategies define the species likely to persist or decline under projected climate change in the Sierra Nevada. Resprouting species, including oaks and resprouting chaparral, are expected to maintain dominance through belowground reserves that buffer against warmer, drier post-fire microclimates (Liang, Matthew D. Hurteau, and Anthony LeRoy Westerling, 2017; Hoecker, Parks, et al., 2023). In contrast, conifers face increasing vulnerability across low to high elevations, with drought-avoiding species like sugar pine and Douglas-fir facing decline as cool, wet microsites are reduced, and even drought-tolerant pines susceptible to widespread mortality under sustained water deficit and bark beetle pressure (Restaino et al., 2019; Fettig et al., 2019).

All vegetation types have thresholds of desiccation under extreme conditions. Hydraulic failure is present at all systems under different thresholds, particularly at low-elevation or trialing edge ecosystems where moisture limitation is more evident, and fire regimes are changing at an accelerated pace (Parks et al., 2019). Furthermore, invasive annual grasses often outcompete native vegetation types due to their seasonal seeding. Increases in invasive annual grasses have profound implications for fire regimes in ecosystems at risk of further encroachment. Invasive annual grasses produce continuous fine fuels that cure earlier in the season and carry fire more readily than native vegetation, while their early life-cycle completion allows rapid recovery after fire to occupy space and resources before native species can re-establish (Brooks et al., 2004; Keeley and McGinnis, 2007).

Empirical studies have shown that climate change is altering the site conditions which these

conifers depend on. K. T. Davis, Dobrowski, et al. (2019) found that ponderosa pine is vulnerable to changes in water availability, particularly in the first year of germination. They also found that Douglas-fir was buffered due to its occupancy of cooler, wetter microsites that sustain spring moisture, although these refugia themselves may shrink under continued warming (K. T. Davis, Dobrowski, et al., 2019). D. J. N. Young et al. (2019) and (Stewart et al., 2021) found that white fir was dependent on higher levels of post-fire precipitation, which aligns with its limited drought tolerance strategies (Kris Zouhar, 2001). In contrast, (Oakley, M. P. North, and Franklin, 2006) and Goodwin and Matthew D Hurteau (2024) have shown that white fir was not limited to sites with above average precipitation. While these studies provide important insight into climatic drivers of conifer regeneration, their short post-fire windows (5–10 years) and limited spatial extents constrain inference about longer-term, landscape-scale dynamics of post-fire conifer establishment.

Oaks share several physiological traits with drought-tolerant conifers, including stomatal control and deep tap roots (Fryer, 2007). They can also enter drought-induced dormancy and reallocate resources to root growth during water scarcity (Fryer, 2007). Post-fire resprouting is even less affected by drought conditions, as the resprouting oaks already have deep root systems and carbohydrate reserves, which facilitate resprouting even under dry conditions. These strategies allow them to persist under especially dry conditions; however, they are not immune to drought-induced mortality. During the 2011-2016 California drought, which caused large numbers of conifer mortality, Huesca et al. (2021) observed widespread blue oak mortality across low-elevation oak woodlands.

Chaparral species employ the most specialized drought adaptations, including sclerophyllous leaves that minimize transpiration and C3 photosynthesis that decouples carbon fixation from daytime water loss (Jacobsen et al., 2007; Pratt et al., 2014). Like oak and conifer species, these physiological traits can be overridden with high-intensity or sustained low-intensity drought, leading to hydraulic failure (S. D. Davis et al., 2002; Pratt et al., 2014; Venturas et al., 2016).

Grassland species employ various drought adaptation strategies depending on their native or invasive status. Native perennial bunchgrasses persist through drought through complex root systems that access belowground moisture, dormancy during summer water deficit, and resource allocation

strategies that prioritize root growth more than shoot growth (Holmes and Rice, 1996). In contrast, invasive annual grasses avoid drought by completing their life cycles within the brief window of spring moisture availability, then setting seed and drying before peak summer water deficit (Bradford and Lauenroth, 2006). Because both groups are primarily C3 cool-season grasses, the difference reflects adaptation and rooting strategies rather than differences in photosynthetic pathways.

While meadows comprise a low percentage of the Sierra Nevada study area, they are critical for water storage. Meadows depend on groundwater reserves and fluctuate based on water table dynamics (Allen-Diaz, 1991; Loheide II and Gorelick, 2007; Hammersmark et al., 2010). Meadow species are dependent upon seasonal to persistent site moisture. Their water content also restricts their fire interactions specifically to drought years, allowing meadows to act as a fire break during periods of inundation.

Table 1.2: Drought response strategies, key traits, and drought vulnerability across Sierra Nevada vegetation communities. All records are from the Fire Effects Information System (FEIS) unless noted otherwise.

Community / Species Group	Primary Drought Strategy	Key Traits	Drought Vulnerability
Ponderosa pine	Tolerance	Rapid deep taproot development; more drought-tolerant than associated conifers; persists on dry south/west slopes	Growth suppressed by prior-year drought; regeneration tied to wet years; climate warming may limit future establishment
Jeffrey pine	Tolerance	Highly drought-tolerant; highly cold hardy; completes growth cycle early in season; occupies dry infertile sites	Not flood-tolerant; highest mortality at low-elevation sites
Sugar pine	Mesic preference	Deep taproot; not susceptible to windthrow; best growth at 4,500–6,000 ft in central Sierra Nevada	Low drought tolerance; struggles in serpentine soils
White fir	Avoidance (wet niche)	Highly shade tolerant; saplings endure decades of suppression; grows best in full sun once established; root development best in mineral soil	Very sensitive to soil drying and heating; no strong taproot; susceptible to windthrow; thin bark increases fire mortality
Douglas fir	Avoidance (cool niche)	More shade tolerant than pines but less than white fir; grows best on well-aerated deep soils; more common in northern Sierra Nevada	Frost sensitive; grows poorly on nutrient-poor soils; seral to shade-tolerant species without disturbance
Incense cedar	Tolerance	Drought tolerant; adapts to wide range of soil types; shade tolerant; root growth responds to moisture availability	Shoot growth slows rapidly with water stress; very slow growth on dry sites or in dense shade

(Table continued from previous page)

Community / Species Group	Primary Drought Strategy	Key Traits	Drought Vulnerability
Red fir	Avoidance (snowpack- dependent)	High frost tolerance; dependent on deep snowpack and short growing season; grows on well-drained moist soils	Low drought tolerance; vulnerable to snowpack decline under climate change; fire restores structure but does not alleviate drought vulnerability (Meyer et al. 2019; Meyer and North 2019)
Oaks	Tolerance + avoidance	Deep tap roots, stomatal control, drought-induced dormancy, increased root allocation during water scarcity (van Wagtendonk et al. 2018)	Extreme multiyear drought drives substantial mortality, concentrated in the hottest, driest foothill positions. Frost-sensitive depending on species
Chaparral	Structural + physiological	Sclerophyllous leaves reduce transpiration; CAM photosynthesis (Ha et al. 2022); stomata closed during day	Hydraulic failure under extreme drought (Davis et al. 2002; Venturas et al. 2016)
Native bunchgrasses	Tolerance	Deep root systems (Dyer 2002)	Combined fire and drought increases mortality; invasive annuals reduce seedling establishment (Dyer and Rice 1997)
Invasive annual grasses	Avoidance (phenological)	Completes life cycle and senescens before summer drought (Rice and Mack 1991; D'Antonio and Vitousek 1992)	Dependent on sufficient winter moisture for germination
Wet meadows	Moisture dependence	Perennial water availability; hydrologic buffering	Degraded by grazing, beaver loss, forest encroachment, road building

1.4 Synthesis: Analysis of Pathways of Vegetation Change in the Sierra Nevada

1.4.1 Scope

An initial literature search identified over 800 papers addressing post-fire vegetation responses, fire ecology, climate change impacts, and ecosystem transitions in the Sierra Nevada (for search terms see Appendix S1). Once studies were filtered based on geography, study focus, and vegetation type, the resulting 517 studies offered a representation of contemporary research topics (Figure 1.2). Conifer vegetation types dominated the literature, with more studies for conifers (420 total) than all other vegetation types combined. Oaks had 74 total studies, and then chaparral/ shrub followed as the next highest vegetation type with 47 studies due to their association with conifers and post-fire regeneration dynamics. Meadow, grassland, and invasive vegetation types were researched the least, likely due to their limited extent in contemporary Sierra landscapes.

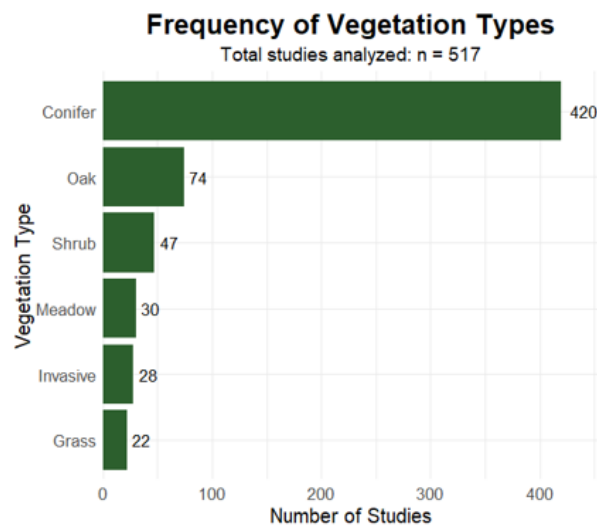


Figure 1.2: Frequency of which vegetation types found in literature on the Sierra Nevada and surrounding areas. Conifers highly dominate this topic, showing the need for more research in lesser studied ecosystems in the Sierra.

We derived state-transition models (STMs) from selected studies which represent post-fire trajectories across the five main ecosystem types comprising the Sierra Nevada vegetation mosaic, divided

by mesic (wet; Figure 1.3) and xeric (dry; Figure 1.4) climate. These ecosystems are further split into functional groups, with “young” representing a successional stage and “mature” representing a stable stage moderated by fire feedbacks. Other non-stable states include fire-intolerant species composition and episodic chaparral, which are temporary states that experience rapid change. The STMs use fire severity to delineate potential pathways, where high severity correlates to high mortality and low severity to low mortality. This definition of severity is purposefully nuanced, as severity can be defined at different scales for different vegetation types and is often used in many contexts to support study and management goals (Hagmann et al., 2021). When examined at the individual scale, severity may affect a single organism while community composition remains largely unchanged. For clarity, we use severity at the stand scale to define pathways to different dominant cover types.

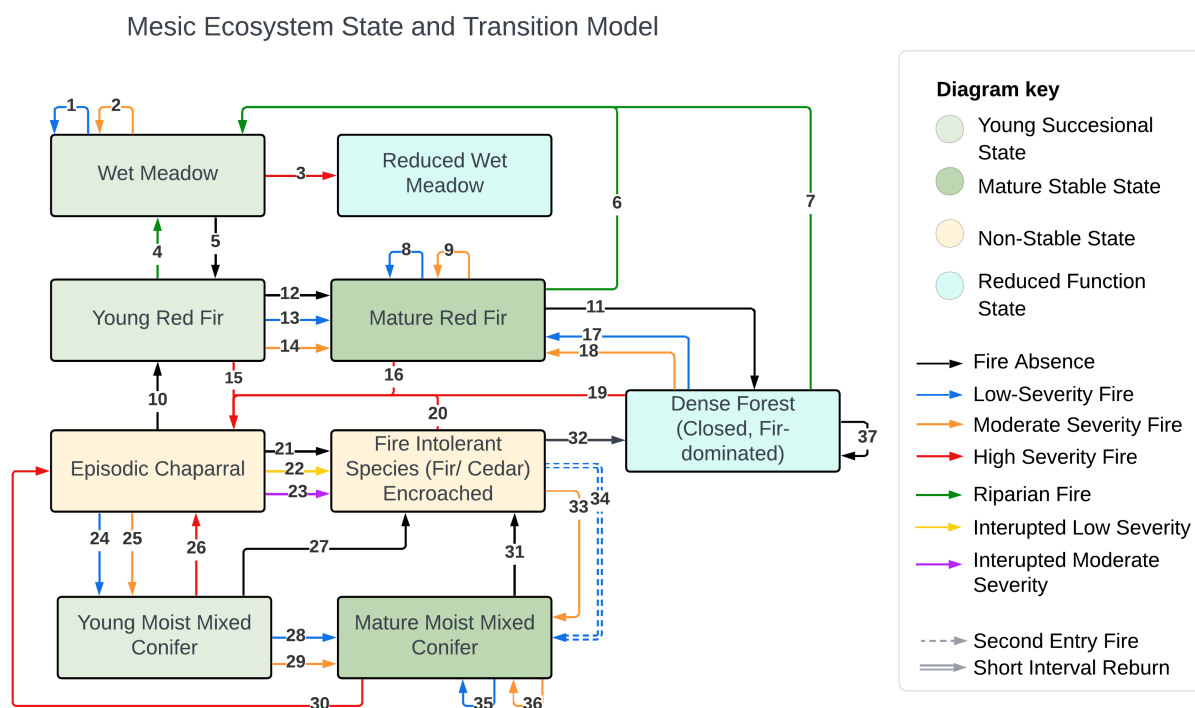


Figure 1.3: State and Transition Model for mesic ecosystems in the Sierra. The color of the transition represents the severity of fire disturbance (Low = Blue, Moderate = Orange, or High = Red) and whether that disturbance has been interrupted due to fire- fire-intolerant species encroachment (Interrupted Low Severity = Yellow and Interrupted Moderate Severity = Purple). The dashed lines represent temporal mechanisms of transition. Each pathway citation can be found in Appendix S2.

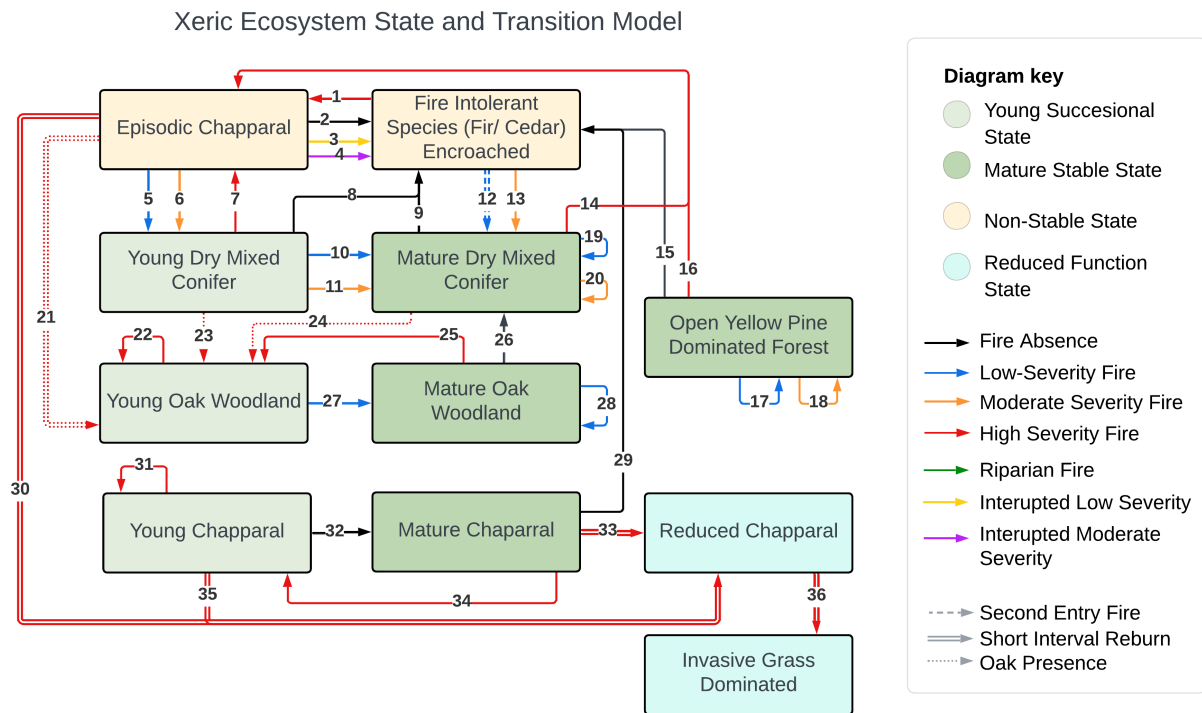


Figure 1.4: State and Transition Model for xeric ecosystems in the Sierra. The color of the transition represents the severity of fire disturbance (Low = Blue, Moderate = Orange, or High = Red) and whether that disturbance has been interrupted due to fire-intolerant species encroachment (Interrupted Low Severity = Yellow and Interrupted Moderate Severity = Purple). The dashed lines represent temporal mechanisms of transition or oak presence. Each pathway citation can be found in Appendix S3.

1.4.2 Question 1: How did historical fire regimes interact with climate to maintain stable vegetation states?

Historically, vegetation types in the Sierra Nevada operated within a broad envelope of resilience maintained by the coupling of climate and fire regimes (Hessburg, C. L. Miller, et al., 2019; Steel, Foster, et al., 2021). Over millennial time scales, climate oscillations shifted the extent and elevational range of these compositions, but the underlying disturbance-succession feedbacks persisted, allowing vegetation mosaics to reorganize rather than collapse (Millar and Woolfenden, 1999; Woolfenden, 1996; R. S. Anderson, Smith, and Koehler, 1997). These systems were never static, as communities overlapped across elevations and niches, but they were stable in the sense that fire regimes reinforced the conditions under which each vegetation type could persist (Hessburg, Prichard, et al., 2021).

Mesic ecosystems in the Sierra Nevada, including red fir and moist mixed conifer forests, historically experienced low to moderate fire severity. Higher precipitation and greater persistent snowpack reduced fuel desiccation and limit fire season length in these ecosystems (van Wagtendonk, Sugihara, et al., 2018; M. D. Meyer et al., 2019). Characteristics of the dominant conifers in these systems, such as the short densely packed needles of red and white fir, also enhance fuel moisture retention in the litter layer, despite higher fuel loads typical of productive mesic sites (M. Meyer and M. North, 2019). These biophysical mechanisms enable mesic forested ecosystems to self-regulate through feedback loops that perpetuate low- to moderate-severity surface fire regimes, regardless of increased densities that come with longer FRIs (Figure 1.3: Pathways 8, 9, 35, 36). These same fire regimes also maintain successional pathways by reducing competition from fire-intolerant species and shrubs, allowing young red fir and moist mixed conifer stands to mature (Figure 1.4: Pathways 12 13, 14, 28, 29).

Wet meadows are sustained by shallow water tables that keep soil and vegetation saturated for much of the year, restricting fire interactions to drought periods when water tables recede. High soil moisture limits fire intensity even during drought years, maintaining low to moderate severity fire regimes within meadow systems (Figure 1.3: Pathways 1, 2). During inundated periods, meadows function as natural fire breaks within the broader landscape. When fire is carried through meadow vegetation, it creates heterogeneous patches that maintain meadow extent and limit conifer encroach-

ment.

Forested xeric ecosystems in the Sierra Nevada, including dry mixed conifer, yellow pine-dominated forests, and oak woodlands, are also maintained by low to moderate fire severity. Climatic conditions such as higher temperatures and lower precipitation are more common in xeric ecosystems and create conditions where dry fuels spread fire more readily (Anthony L. Westerling, 2016; Kennedy et al., 2021). Frequent fire return intervals ($\sim 17 - 25$ years) further influence feedback mechanisms, as greater fuel consumption limits future fire spread, allowing frequent, low to moderate severity fire regimes to maintain open stand structures and regulate fuel accumulation (Figure 1.4: Pathways 17, 18, 19, 20, 28). Low- to moderate severity fires also maintain regeneration of fire-tolerant pines and oaks by maintaining open canopy conditions through which young stands could reach maturity (Figure 1.4: Pathways 10, 11, 27).

By definition, episodic chaparral was historically maintained in small patches within xeric and mesic mixed-conifer forests. Small patches of high severity fire remove individual or small groups of mature trees, creating open, full-light conditions where shrub species rapidly colonized (Figure 1.3: Pathways 15, 16; Figure 1.4: Pathways 7, 14). However, these small patches are transient, as conifers have historically overtopped and outcompeted shrubs, returning the site to full forest cover (Figure 1.3: Pathways 10, 24, 25; Figure 1.4: Pathways 2, 3, 4).

Mixed and montane chaparral ecosystems are moderated by infrequent, high-severity fire (Nagel and Alan H. Taylor, 2005). The timing of moist-season lightning historically decoupled ignition from fuel aridity on steep xeric slopes, constraining fire to limited periods when dry conditions and ignition aligned (van Wagtendonk and Cayan, 2008; Keeley and Syphard, 2018). Longer fire return intervals allow sufficient time for shrub species to mature and establish viable seed banks between fire events (Figure 1.4: Pathway 32). Following stand-replacing fire, young shrubs rapidly colonize and transition to mature chaparral during the subsequent fire-free interval (Figure 1.4: Pathways 31, 34).

1.4.3 Question 2: How are vegetation transition pathways altered when fire-climate-vegetation feedbacks are disrupted?

Climate change and a lack of fire in the Sierra Nevada have disrupted fire-vegetation-climate feedbacks driving unprecedented transitions across the region. These transitions are occurring at a more rapid temporal scale than historical shifts, with consequences for ecosystem processes including nutrient cycling, wildlife habitat, water storage, and carbon storage. Although they now occur at an accelerated pace, the underlying feedbacks have been degrading for decades, with the resulting state changes manifesting through a process of resilience debt, in which ecosystems accumulate risk expressed through disturbance events (Johnstone et al., 2016). As fires grow in size and severity, they alter the heterogeneous mosaics fire once maintained. As a result, the disrupted feedbacks shift them toward novel trajectories with reduced potential for return to pre-fire conditions.

Without the moderating process of fire, densification and tree encroachment alter the resilience of mesic ecosystem types. As stand density increases in red fir forests, competition for water and nutrients intensifies drought stress on individual trees, increasing forest susceptibility to bark beetle attacks and mortality from high-severity fire (Figure 1.3: Pathway 11). In moist mixed conifer forests, densification is compounded by the encroachment of fire-intolerant species such as white fir and incense cedar, which establish in the understory during fire-free intervals and gradually shift the stand composition away from fire-adapted species (Figure 1.3: Pathways 27, 31). Without the reintroduction of low to moderate severity fire, this compositional shift can culminate in a dense, closed-canopy forest state with reduced ecological function (Figure 1.3: Pathway 32). Due to increased water deficits and increased fuel loads of denser stands, moist mixed conifer and red fir forests are at greater risk of extensive landscape-scale transitions to non-forest type following high-severity fire (Figure 1.3: Pathways 19, 20).

The absence of fire has enabled widespread encroachment of fire-intolerant species in xeric ecosystems, particularly white fir and incense cedar, altering species' resilience to disturbance. Like mesic forests, dry mixed conifer and yellow pine-dominated forests have experienced an increase in stand densities due to the lack of fire and encroachment of shade-tolerant, fire intolerant species (Figure

1.4: Pathways 8, 9, 15). Meanwhile, oak woodlands have declined across the landscape due to fire exclusion and forest encroachment (Figure 1.4: Pathway 26). As denser stands experience increasing drought stress from declining snowpack and rising temperatures, they become more susceptible to drought-induced mortality and/or high-severity fire (Figure 1.4: Pathway 1).

The increased presence of white fir in mixed conifer forests has altered post-fire seed source composition, particularly in high-severity patches where episodic chaparrals are established. White fir now dominates the seed rain in these patches, which limits successional pathways from young mixed conifer back to mature mixed conifer (H. S. J. Zald, Gray, et al., 2008; Paudel, Coppoletta, et al., 2022). Pathways in moist mixed conifer forests have shifted to a cycle that sustains fire-intolerant species encroachment, regardless of whether intact low to moderate severity fire regimes are reintroduced (Figure 1.3: Pathways 21, 22, 23). Similarly, in dry mixed conifer and yellow pine systems, white fir now serves as the primary seed source for post-fire regeneration, perpetuating compositional shifts away from historical pine dominance (Figure 1.4: Pathways 2, 3). Whereas episodic chaparral historically functioned as a necessary but ephemeral successional stage in conifer-dominated systems, contemporary large-patch high-severity fires limit seed source availability for pines while promoting shade-tolerant fir establishment.

Climate change is also altering fire dynamics within shrub-dominated systems. Declining precipitation and increasing vapor pressure deficit reduce fuel moisture in chaparral ecosystems, narrowing the window of fire resistance that historically allowed these systems to recover between burns. These dynamics are amplified in lower-elevation xeric ecosystems compared to mesic systems because xeric chaparral experiences greater seasonal moisture limitation and drives fuel desiccation earlier in the year (Cinoğlu et al., 2021; Greene, Lindley, and Kane, 2024). In episodic chaparral in xeric ecosystems, short interval reburns prevent shrub recovery and push stands toward a reduced chaparral state (Figure 1.4: Pathway 30). Mixed and montane chaparral systems are experiencing similar dynamics, as shortened fire return intervals less than ~50 years fall below the reproductive thresholds of obligate seeding species (Figure 1.4: Pathways 33, 35). Where reburns occur in systems already disturbed by invasive grass establishment, grass-fire cycles can lock the system into an invasive-dominated state from

which recovery is unlikely without active intervention (Figure 1.4: Pathway 36).

In wet meadows, the absence of fire encourages conifer encroachment, reducing meadow extent across the Sierra Nevada (Figure 1.3: Pathway 5). Climate change, in the form of declining snowpack and precipitation, lowers water tables and reduces the saturated conditions that historically limited fire severity within meadows. When fire burns meadows under dry conditions long-duration burning can reduce soil permeability, further degrading hydrologic function and limiting recovery potential (Figure 1.3: Pathway 3).

1.4.4 Question 3: Can disrupted trajectories be restored?

Whether a disrupted trajectory can be restored depends largely on the ecosystem in question and the degree to which it has departed from its reference condition. Some pathways are reversible, while others have crossed thresholds into alternative stable states maintained by self-reinforcing feedbacks that requires more intentional management to change. Restoration potential therefore varies across Sierra Nevada systems, shaped by both the fire dynamics that can move these systems back toward prior states and the compounding factors that influence the pace and extent of recovery. Certain pathways from more mature, fire-intolerant, encroached forests back to mature moist conifer forests have been identified (Figure 1.3: Pathways 33, 34; Figure 1.4: Pathways 12, 13). Chamberlain, Bartl-Geller, et al. (2024) found that second-entry low- to moderate-severity fires restored forest structure in mixed conifer forests from unstable, increasingly dense states, with fire effects most strongly tied to pre-fire forest structure rather than fire weather alone. Active-fire landscapes that have experienced multiple low- to moderate-severity fires demonstrate increased structural resistance to subsequent fire and drought, suggesting these pathways can be self-reinforcing once initiated (Chamberlain, Wagten-donk, et al., 2026). Long-term studies in Sierra Nevada mixed-conifer forests show that repeated prescribed and managed fire reduces tree density, increases representation of large-diameter trees, and shifts species composition back toward fire-adapted species over decades (Webster and Halpern, 2010; Lutz et al., 2020). Similar patterns have been documented in red fir forests, where reestablished fire regimes restore stand structure through reduced tree densities and a greater proportion of

large-diameter trees (Figure 1.3: Pathways 17, 18; Merriam et al. (2022)). These findings suggest that restoration pathways depend on cumulative fire exposure rather than single fire events, and that the success of these pathways is constrained by the degree of departure from historical conditions prior to the first fire entry.

However, the capacity for fire alone to shift highly departed contemporary forests toward reference conditions remains uncertain, as the structural and compositional changes required may exceed what a single fire entry can accomplish (Jasperse et al., 2025). While first entry moderate severity fire and repeat low severity fire restore mixed-conifer forest structure, it is limited in shifting the species composition from fir encroached to yellow pine mixed conifer forest. Further management may be required in the form of planting and selective species removal to ultimately change the current states of fir-encroached forests.

Conifer encroachment into oak woodlands (Figure 1.4: Pathway 26) has substantially reduced oak dominance across mid-elevation Sierra Nevada ecosystems (Engber et al., 2011; Matasci et al., 2018; Scott L. Stephens, Hall, et al., 2023). The pathway in which encroached oak systems return to oak dominant systems is becoming increasingly common, as oaks are generalist species resilient to stand-replacing fire when residual rootstocks remain on the landscape. Even where conifers have overtopped historical oak habitat, oaks can persist in reduced states within conifer forests, often occupying small canopy gaps where light availability supports their shade-intolerant regeneration (Cocking, Varner, and Sherriff, 2012). Where oaks remain present as residual rootstocks, high-severity fire that removes dominant conifers allows most oaks (such as black oak, canyon live oak, and interior live oak) to resprout vigorously and re-establish dominance through belowground carbohydrate reserves that buffer them from crown kill (Figure 1.4: Pathways 23, 24). When chaparral seed banks are also present, as is common in mixed conifer forests, episodic chaparral will dominate immediate post-fire conditions alongside oak resprouts (Figure 1.4: Pathways 7, 14). While oaks may not initially outcompete shrubs, short-interval reburns offer an indirect pathway to oak dominance through the following trajectory: conifers encroach on oak woodland habitat (Figure 1.4: Pathway 26), encroaching conifers burn at high severity (Figure 1.4: Pathways 7, 14), episodic chaparral establishes alongside oak resprouts and reburns

before chaparral seed-bank maturity reset the shrub component, while oaks continue to resprout from belowground reserves (Figure 1.4: Pathway 21), ultimately favoring oak-dominated stands.

When fire occurs in conifer-encroached meadow areas, it can have restorative effects for meadow vegetation (Figure 1.3: Pathways 4, 6, 7). The Illilouette Creek Basin in Yosemite, where managed wildfire has been allowed to burn since the 1970s, demonstrates that recurrent low- to moderate-severity fire actively expands meadow extent by killing encroaching conifers and maintaining open hydrologic conditions (G. Boisramé et al., 2017; Scott L Stephens, S. Thompson, et al., 2021). Similar dynamics have been documented along forest-meadow ecosystems in the southern Cascades, where the historical fire regime-maintained meadow boundaries and fire absence have driven conifer encroachment into former meadow habitat (Norman and Alan H. Taylor, 2005). Post-fire meadow recovery is rapid where pre-fire meadow vegetation persists, with herbaceous cover returning within several years following wildfire (Soulard et al., 2016). However, fire is only one of several disturbances that have altered Sierra Nevada meadow extent and composition. Livestock grazing and road construction fragment meadow systems and disrupt the groundwater regimes that sustain them (Berlow, D'Antonio, and Reynolds, 2002; Cummings, Pope, and Mak, 2023). These compounding disturbances mean that fire-driven restoration pathways may be insufficient on their own where hydrologic function has been degraded, and meadow recovery often requires concurrent restoration of groundwater regimes and grazing management.

Restoring mixed/montane chaparral after type conversion is more difficult than restoring conifer or oak systems because the mechanisms that contributed to original conversion continue to feedback towards degraded states (Figure 1.4: Pathways 30, 35, 33). Once short-interval reburns depleted the soil seed banks of obligate-seeding *Ceanothus* and *Arctostaphylos*, recovery of these ecosystems requires fire-free intervals long enough for both rootstocks and seed banks to rebuild (Jones et al., 2023). Where invasive annual grasses colonize, they produce continuous fine fuels that increase ignition probability and shorten fire intervals, perpetuating the system into a grass-fire cycle that prevents recovery (Keeley, Lubin, and Fotheringham, 2003; Brooks et al., 2004; Keeley and McGinnis, 2007). Restoration therefore requires interventions beyond fire management alone,

including invasive grass control, native seed augmentation, and protection of long fire-free intervals (Birch et al., 2026). Even with active intervention, the climatic and fuel conditions that favor invasive grasses persist, and some converted landscapes may represent persistent alternative states.

1.4.5 Question 4: What does the future hold for climate-fire trajectories?

Climate change is projected to drive substantial vegetation transitions across Sierra Nevada ecosystems through both direct climate effects and altered fire regimes. Post-fire establishment, regulated through top-down climatic controls and bottom-up disturbance controls, determines the resulting ecosystem composition through seed production, germination, survival, and competition (Welch, H. D. Safford, and T. P. Young, 2016; Bolstad, Elliott, and Miniati, 2018; Dey et al., 2019). When vegetation cannot adapt to novel conditions, its current extent is expected to shrink to sites known as refugia, where microsite conditions allow it to persist (Rodman et al., 2023). In this section, we explore these potential transitions under more extreme and variable climatic conditions, as well as increased frequency and severity of wildfire.

Fire regimes are projected to continue shifting under increased warming and decreased precipitation (Abatzoglou and A. P. Williams, 2016). When accounting for fuel consumption feedbacks by fires, under the most optimistic scenario where prior fires will also limit subsequent fuel availability, many studies found large increases in burned area and vegetation impacted by unprecedented fire regimes (Matthew D. Hurteau et al., 2019; Hoecker, Parks, et al., 2023; Turco et al., 2023). Turco et al. (2023) estimated that burned area will increase by 53 percent, while Hoecker, Parks, et al. (2023) found that 65 percent of conifer forests in the western United States will face exposure to fire-regime change under 2 °C of warming, a threshold at which scientists and policy makers estimate as the critical point where climate will pose greater risk of ecological destabilization (*Climate Change 2021* 2021). With fuel consumption feedbacks failing to reverse increases in burned area, fire regimes pose significant risk to vegetation adapted to less extreme conditions.

The underlying change in forest density and composition, specifically through white fir encroachment, due to fire suppression and exclusion leads to profound effects in mixed conifer forests.

M. Hurteau, H. Zald, and M. North (2007) documented species-specific responses to climate variability in upper-elevation mixed-conifer forests, with shade-tolerant white fir strongly tracking annual climate fluctuations and shade-intolerant Jeffrey pine with a lagged response. White fir exhibits shorter mast-ing intervals and greater seed rain than co-occurring pines (Fletcher et al., 2010; Wang et al., 2017), and its shade tolerance allows establishment beneath shrub canopies that filter out shade-intolerant pines (H. S. J. Zald, Gray, et al., 2008; Paudel, Coppoletta, et al., 2022). Species-specific adaptations of white fir, such as fire-intolerance as a young age and drought intolerance, indicate that their increased presence is likely to increase stand-level fire risk, perpetuating a cycle of densification and high-severity fire that limits both mixed-conifer regeneration and obligate-seeding chaparral recovery.

Dense, fire-excluded conifer forests are more likely to experience drought mortality and subse-quent high-severity fire (Allen et al., 2010; Coppoletta, Merriam, and Brandon M. Collins, 2016; Scott L. Stephens, Brandon M Collins, et al., 2018) and subsequent type transition due to increased distances to seed sources (Welch, H. D. Safford, and T. P. Young, 2016; Shive et al., 2018). However, most empirical studies which measure conifer regeneration are conducted over short temporal windows following fire, typically within five years. Variable mast-ing strategies among Sierra Nevada conifers suggest that this window may not be sufficient for new cohorts to establish (Fowells and Schubert, 1956; Paudel, Cop-poletta, et al., 2022). As a result, while suitable site conditions for conifer establishment will occur less frequently than in the past (Mallek et al., 2013; K. T. Davis, Dobrowski, et al., 2019; Buonanduci et al., 2024), they are likely to still happen at different temporal scales and may permit episodic recruitment within refugia (Rodman et al., 2023). This refugia, defined as areas that are buffered from changing climates or disturbances, is expected to be small, with only around 6% of forested area suitable for refugia under extreme climate scenarios (Rodman et al., 2023).

In addition to changes in species composition, forest cover will likely shift in extent as climate changes across elevations and latitudes. Hoecker, K. T. Davis, et al. (2026) predict that dry forests will shift their extents upslope into present subalpine ecosystems to continue to persist in their climate niche. This will reduce subalpine forest extent, as conifers adapted to drier conditions will outcompete mesic-adapted conifers during extended drought periods.

With the reduction of conifer forestlands across the Sierra Nevada, our analysis identifies potential alternative states which are more adapted to changing climates and fire regimes. Liang, Matthew D. Hurteau, and Anthony LeRoy Westerling (2017) modeled species-specific responses to projected climate-wildfire interactions across the Sierra Nevada and predicts that post-disturbance recruitment composition is likely to be the driver of future alternative states. They found that regeneration of drought-tolerant species will be favored over less drought-tolerant species, particularly at mid-elevations. These projections align with the findings of this synthesis. Oaks and shrubs are more resilient than mesic conifers under extreme drought conditions (Cocking, Varner, and Knapp, 2014; Hammett, Ritchie, and Berrill, 2017) and may represent an alternative stable state where conifer regeneration fails (Coppoletta, Merriam, and Brandon M. Collins, 2016; M. P. North et al., 2019; Jonathan D Coop et al., 2020; Tubbesing et al., 2020). A transition from conifer to oak or shrub-dominated states would reduce aboveground carbon storage, creating a feedback to climate change that warrants consideration when evaluating which transitional pathways to manage (Liang, Matthew D. Hurteau, and Anthony LeRoy Westerling, 2017).

One lesser studied pathway that may benefit from increased fire activity is meadow restoration. High-severity fire that removes encroaching conifers can restore meadows to their pre-suppression extent or beyond, with implications for water storage capacity across the Sierra Nevada (G. Boisramé et al., 2017; Scott L Stephens, S. Thompson, et al., 2021). This hypothesis is based on a small body of work and warrants further investigation as a potential management pathway, particularly given the role of meadows in regulating water flow during the increasingly long dry season (Cummings, Pope, and Mak, 2023).

The simulation studies that inform future vegetation projections are limited in predictive power under contemporary conditions because they were calibrated against past climate and fire conditions (J. W. Williams and Jackson, 2007; Mahony et al., 2017). Uncertainty in ecological responses to climate change arises not only from uncertainty in future climate itself, but from path dependency, non-stationarity, and stochastic processes such as masting or disturbance sequences that shape how ecosystems respond to changing conditions (Clark-Wolf et al., 2025). As a result, the vegetation tra-

jectories described in this review represent plausible central tendencies rather than the full range of outcomes that may unfold across the Sierra Nevada. Broader spatial and temporal scales of investigation are needed to determine how fire-tolerant conifers regenerate under novel conditions and how they exploit microsite variation across the Sierra Nevada.

1.5 Management Implications

The future is uncertain, but we know from recent changes in Sierra Nevada landscapes and past changes in the paleo record, that multiple trajectories are inevitable. This synthesis directly addresses the accept and direct parts of the RAD framework, identifying which transitions are climatically inevitable and how those transitions can be directed toward resilient future ecosystem states. Traditional frameworks of management developed under less severe climate and fire conditions for landscape restoration and thus are difficult to apply to rapidly changing ecosystems. To address such rapid changes in vegetation and fire dynamics, we need an adaptation strategy. A recent framework which addresses these challenges is the Resist-Accept-Direct (RAD) framework, which allows for not just resisting change (R), as has been the standard in the past, but also accepting (A) changes, and even using the changes to direct (D) the restoration to new, preferred conditions (G. Schuurman et al., 2020; G. W. Schuurman et al., 2022). While all three strategies are relevant to Sierra Nevada management, operationalizing the accept and direct pathways requires an integrated understanding of transition mechanisms across the full vegetation mosaic (Hoecker, K. T. Davis, et al., 2026).

The accept strategy applies where contemporary fire and climate conditions are pushing landscapes toward vegetation compositions that resemble pre-suppression states. Historical accounts indicate that pre-suppression Sierra Nevada landscapes supported greater chaparral cover and more extensive oak woodland than current conifer-dominated forests, (K. Anderson, 2005; Klimaszewski-Patterson and Mensing, 2016; Long, M. K. Anderson, et al., 2016; Scott L. Stephens, Hall, et al., 2023). Where contemporary high-severity fire is converting fire-suppressed conifer forests back to chaparral-dominated and oak-dominated states at low- to mid- elevations, this represents a return to climatically supported conditions rather than degradation. Accepting these transitions, and managing the resulting

vegetation for ecosystem function, redirects investment away from restoring conditions that the climate no longer supports and toward sustaining the compositions that contemporary fire regimes are producing.

The direct strategy applies where managers can use altered fire regimes to push vegetation toward states that are more climate-resilient than the current trajectory. Here, we identified several pathways that support directing intervention strategies towards a different, yet still sustainable, vegetation composition. Direct intervention requires alignment of fire frequency and severity to favor the trait combinations that produce climate-resilient outcomes such as reduced density conifer forests or pushing management toward oak woodlands. Prescribed and managed fire applied at intervals that suppress fire-intolerant ingrowth before it establishes dominance or favor resprouters over obligate seeders, can shape trajectories at landscape scales (Webster and Halpern, 2010; Lutz et al., 2020; Chamberlain, Bartl-Geller, et al., 2024). Proactive meadow restoration through managed wildfire also allows fire to return systems toward herbaceous states that store carbon and water more effectively than conifer-encroached conditions (G. Boisramé et al., 2017; Scott L. Stephens, S. Thompson, et al., 2021). Direct strategies require accepting that target conditions are not strictly historical but rather functional under contemporary climate, and they require managers to identify which transitions are climatically supported before committing to direction.

Due to a relative lack of studies in non-conifer ecosystems, the accept and direct strategies require further research to guide adaptation work. The bias in the literature towards conifer forests is partly motivated by the social and economic values of conifer forests (REFS). These values may lead managers to focus on the resist pathway to preserve ecosystems that lack adaptations to increasingly dry and warm climate conditions. To be more resilient to future climate and fire conditions, mixed conifer forests will likely need to transition from dense, fir encroached forests to open stands consisting of fire-intolerant species through the pathways identified here.

1.6 Conclusion

Through this synthesis, we analyzed adaptive life-history traits and transitional pathways to assess potential trajectories of change across five dominant vegetation types on the west slope of the Sierra Nevada. Across all vegetation types, post-fire outcomes are trait-mediated and directional, reflecting which species can complete their reproductive cycles within the intervals defined by contemporary fire regimes. The pathway-based analysis presented here distinguishes transitions that remain reversible from those heading toward persistent alternative states and identifies where accept and direct strategies are climatically supported. Contemporary Sierra Nevada landscapes are moving through a period of rapid trajectory change, and effective management requires understanding which vegetation types are better suited for future conditions rather than past ones.

1.7 References

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Appendix

Table S1: Web of Science Search Query

(TS=(“Sierra Nevada” OR “southern Cascade*” OR “southern Cascades Range” OR
“Klamath-Siskiyou” OR “Lassen” OR “Yosemite” OR “Sequoia” OR
“Kings Canyon” OR “Stanislaus” OR “Tahoe” OR “Plumas” OR
“Eldorado National Forest” OR “Sierra National Forest”))

AND

(TS=(“fire regime*” OR “fire history” OR “fire frequency” OR “fire severity” OR
“fire return interval” OR “burn severity” OR “megafire*” OR
“high-severity fire” OR “mixed-severity fire” OR “reburn*” OR
“fire refugia” OR “fire-climate” OR “fire weather” OR “wildfire activity”)

OR

TS=(“climate adaptation” OR “climate change” OR “climate-driven” OR
“drought mortality” OR “hotter drought” OR “vapor pressure deficit” OR
“VPD” OR “climatic water deficit” OR “climate refugia” OR
“thermophilization” OR “range shift*” OR “elevational shift*” OR
“climate resilience” OR “RAD framework” OR “resist-accept-direct” OR
“novel ecosystem*” OR “state and transition”)

OR

TS=(“type conversion” OR “vegetation conversion” OR “vegetation transition*” OR
“vegetation change” OR “regeneration failure” OR “conifer regeneration” OR
“post-fire regeneration” OR “post-fire recovery” OR “shrub conversion” OR
“alternative stable state*” OR “vegetation mosaic” OR “trait-mediated” OR
“functional trait*” OR “fire-adapted”))

AND

(TS=(“mixed conifer” OR “ponderosa pine” OR “Pinus ponderosa” OR “Jeffrey pine” OR
“Pinus jeffreyi” OR “white fir” OR “Abies concolor” OR “red fir” OR
“Abies magnifica” OR “sugar pine” OR “Pinus lambertiana” OR
“incense cedar” OR “Calocedrus” OR “Douglas-fir” OR “Pseudotsuga” OR
“giant sequoia” OR “Sequoiadendron”)

OR

TS=(“Quercus” OR “oak woodland*” OR “black oak” OR “canyon live oak” OR
“blue oak” OR “Quercus kelloggii” OR “Quercus chrysolepis” OR
“Quercus douglasii” OR “hardwood*” OR “oak regeneration” OR
“sprouting” OR “resprout”)

OR

TS=(“chaparral” OR “shrubland*” OR “montane chaparral” OR “Ceanothus” OR
“Arctostaphylos” OR “manzanita” OR “deer brush” OR “whitethorn” OR
“obligate seeder*” OR “facultative seeder*” OR “shrub-dominated” OR
“shrub expansion”)

OR

TS=(“wet meadow*” OR “dry meadow*” OR “montane meadow*” OR “subalpine meadow*” OR
“meadow encroachment” OR “conifer encroachment” OR “meadow hydrology”)

OR

TS=(“grassland*” OR “annual grass*” OR “invasive grass*” OR “Bromus tectorum” OR
“cheatgrass” OR “medusahead” OR “Taeniatherum” OR “Ventenata” OR
“grass-fire cycle” OR “fine fuel*” OR “non-native grass*”))

NOT TS=(“Spain” OR “Spanish” OR “Iberian” OR “Andalusia”)

Table S2: Citation Table for Figure 1.3

Path	Pathway	Severity	Studies
1	Young wet meadow feedback	Low Severity	Ratliff (1985); DeBenedetti and Parsons (1984); Soulard et al. (2016); G. F. S. Boisramé, S. E. Thompson, Tague, et al. (2019)
2	Young wet meadow feedback	Moderate Severity	Ratliff (1985); @; Soulard et al. (2016); G. Boisramé et al. (2017)
3	Young wet meadow to Reduced Wet Meadow	High Severity	Ratliff (1985)
4	Young Red Fir to Wet Meadow	Riparian Fire	G. F. S. Boisramé, S. E. Thompson, Kelly, et al. (2017); Soulard et al. (2016); G. F. S. Boisramé, S. E. Thompson, Tague, et al. (2019)
5	Wet meadow to Young Red Fir	Fire Absence	Norman and Alan H. Taylor (2005); Kobziar and J. R. McBride (2006)
6	Mature Red Fir to Wet Meadow	Riparian Fire	G. F. S. Boisramé, S. E. Thompson, Kelly, et al. (2017); Soulard et al. (2016); G. Boisramé et al. (2017)
7	Dense Forest to Wet Meadow	Riparian Fire	G. Boisramé et al. (2017); Soulard et al. (2016); G. Boisramé et al. (2017)
8	Mature Red Fir Feedback	Low Severity	Chappell and Agee (1996); Scholl and Alan H. Taylor (2006); M. D. Meyer et al. (2019); Merriam et al. (2022)
9	Mature Red Fir Feedback	Moderate Severity	Chappell and Agee (1996); Scholl and Alan H. Taylor (2006); M. D. Meyer et al. (2019); Merriam et al. (2022)
10	Episodic Chaparral to Young Red Fir	Fire Absence	Bekker and Alan H. Taylor (2001); Airey Lauvaux, Skinner, and Alan H. Taylor (2016); M. D. Meyer et al. (2019); Merriam et al. (2022)
11	Mature Red Fir to Dense Forest	Fire Absence	Vankat and Major (1978); Dolanc et al. (2014); Mortenson, Gray, and Shaw (2015); M. D. Meyer et al. (2019); M. Meyer and M. North (2019); Merriam et al. (2022)
12	Young Red Fir to Mature Red Fir	Fire Absence	Pitcher (1987); Scholl and Alan H. Taylor (2006)
13	Young Red Fir to Mature Red Fir	Low Severity	Alan H. Taylor and Halpern (1991); Alan H. Taylor (1993); Scholl and Alan H. Taylor (2006); M. D. Meyer et al. (2019)
14	Young Red Fir to Mature Red Fir	Moderate Severity	Chappell and Agee (1996); Bekker and Alan H. Taylor (2010);
15	Young Red Fir to Episodic Chaparral	High Severity	Meng et al. (2015); Airey Lauvaux, Skinner, and Alan H. Taylor (2016)
16	Mature Red Fir to Episodic Chaparral	High Severity	Meng et al. (2015); Airey Lauvaux, Skinner, and Alan H. Taylor (2016); Stevens et al. (2017)
17	Dense Forest to Mature Red Fir	Low Severity	Becker and Lutz (2016); M. D. Meyer et al. (2019); Merriam et al. (2022)
18	Dense Forest to Mature Red Fir	Moderate Severity	Becker and Lutz (2016); M. D. Meyer et al. (2019); Merriam et al. (2022)

19	Dense Forest to Episodic Chaparral	High Severity	Russell, J. McBride, and Rowntree (1998); Brandon M. Collins and Roller (2013)
20	Fire Intolerant to Episodic Chaparral	High Severity	Russell, J. McBride, and Rowntree (1998); Brandon M. Collins and Roller (2013)
21	Episodic Chaparral to Fire Intolerant	Fire Absence	A. H. Taylor (2000); Nagel and Alan H. Taylor (2005); Scholl and Alan H. Taylor (2010); Airey Lauvaux, Skinner, and Alan H. Taylor (2016)
22	Episodic Chaparral to Fire Intolerant	Fire Intolerant Interrupted, Low Severity	Nagel and Alan H. Taylor (2005); Becker and Lutz (2016); J. D. Miller and H. D. Safford (2017)
23	Episodic Chaparral to Fire Intolerant	Fire Intolerant Interrupted, Moderate Severity	Nagel and Alan H. Taylor (2005); Bekker and Alan H. Taylor (2010); Becker and Lutz (2016); Hessburg, Spies, et al. (2016)
24	Episodic Chaparral to Young Moist Mixed Conifer	Low Severity	M. North et al. (2005); Crockett and Matthew D. Hurteau (2022); Goodwin and Matthew D Hurteau (2024)
25	Episodic Chaparral to Young Moist Mixed Conifer	Moderate Severity	Meng et al. (2015); Cinoğlu et al. (2021); Crockett and Matthew D. Hurteau (2022)
26	Young Moist Mixed Conifer to Episodic Chaparral	High Severity	Coppoletta, Merriam, and Brandon M. Collins (2016); Welch, H. D. Safford, and T. P. Young (2016); Tubbesing et al. (2020); Jonathan D Coop et al. (2020); K. T. Davis, Dobrowski, et al. (2019); Paudel and Markwith (2023)
27	Young Moist Mixed Conifer to Fir Encroached	Fire Absence	Oakley, M. P. North, and Franklin (2006); Welch, H. D. Safford, and T. P. Young (2016); Tubbesing et al. (2020); H. S. J. Zald, May, et al. (2024)
28	Young Moist Mixed Conifer to Mature Moist Mixed Conifer	Low Severity	Beaty and Alan H. Taylor (2008); H. S. J. Zald, Gray, et al. (2008); Scholl and Alan H. Taylor (2010); Krasnow, Fry, and Scott L. Stephens (2017)
29	Young Moist Mixed Conifer to Mature Moist Mixed Conifer	Moderate Severity	Bekker and Alan H. Taylor (2010); Cocking, Varner, and Knapp (2014); Becker and Lutz (2016); Merschel et al. (2024)
30	Mature Moist Mixed Conifer to Episodic Chaparral	High Severity	Welch, H. D. Safford, and T. P. Young (2016); Coppoletta, Merriam, and Brandon M. Collins (2016); G. F. S. Boisramé, S. E. Thompson, Kelly, et al. (2017)

31	Mature Moist Mixed Conifer to Fire Intolerant	Fire Absence	Dolanc et al. (2014); Scott L Stephens, Brandon M Collins, et al. (2018)
32	Fire Intolerant to Dense Forest	Fire Absence	Dolanc et al. (2014); Scott L Stephens, Brandon M Collins, et al. (2018); Paudel, Coppoletta, et al. (2022)
33	Fire Intolerant to Mature Moist Mixed Conifer	Moderate Severity	Lydersen, Brandon M. Collins, et al. (2016); Brandon M. Collins, Lydersen, et al. (2018); Welch, H. D. Safford, and T. P. Young (2016)
34	Fire Intolerant to Mature Moist Mixed Conifer	Second Entry, Low Severity	Becker and Lutz (2016); Chamberlain, Bartl-Geller, et al. (2024)
35	Mature Moist Mixed Conifer Feedback	Low Severity	Brandon M. Collins, J. D. Miller, et al. (2009); Mallek et al. (2013); Hagmann et al. (2021)
36	Mature Moist Mixed Conifer Feedback	Moderate Severity	Brandon M. Collins, J. D. Miller, et al. (2009); Mallek et al. (2013); Hagmann et al. (2021)
37	Dense Forest Feedback	Fire Absence	Dolanc et al. (2014); M. D. Meyer et al. (2019); Coppoletta, Knapp, et al. (2024)

Table S3: Citation Table for Figure 1.4

Path	Pathway	Severity	Studies
1	Fire Intolerant to Episodic Chaparral	High Severity	Russell, J. McBride, and Rowntree (1998); Brandon M. Collins and Roller (2013)
2	Episodic Chaparral to Fire Intolerant	Fire Absence	A. H. Taylor (2000); Nagel and Alan H. Taylor (2005); Scholl and Alan H. Taylor (2010); Airey Lauvaux, Skinner, and Alan H. Taylor (2016)
3	Episodic Chaparral to Fire Intolerant	Fire Intolerant Interrupted, Low Severity	Nagel and Alan H. Taylor (2005); Becker and Lutz (2016); J. D. Miller and H. D. Safford (2017)
4	Episodic Chaparral to Fire Intolerant	Fire Intolerant Interrupted, Moderate Severity	Nagel and Alan H. Taylor (2005); Bekker and Alan H. Taylor (2010); Becker and Lutz (2016); Hessburg, Spies, et al. (2016)
5	Episodic Chaparral to Young Dry Mixed Conifer	Low Severity	M. North et al. (2005); J. D. Miller and H. D. Safford (2017); Crockett and Matthew D. Hurteau (2022); Goodwin and Matthew D Hurteau (2024)
6	Episodic Chaparral to Young Dry Mixed Conifer	Moderate Severity	Meng et al. (2015); Richter et al. (2019); Cinoğlu et al. (2021)

7	Young Dry Mixed Conifer to Episodic Chaparral	High Severity	Coppoletta, Merriam, and Brandon M. Collins (2016); Welch, H. D. Safford, and T. P. Young (2016); Steel, Koontz, and H. D. Safford (2018); Jonathan D Coop et al. (2020); Tubbesing et al. (2020);
8	Young Dry Mixed Conifer to Fire Intolerant	Fire Absence	Knapp et al. (2013); H. S. J. Zald, Gray, et al. (2008); Welch, H. D. Safford, and T. P. Young (2016); Brodie, Knapp, et al. (2023); H. S. J. Zald, May, et al. (2024)
9	Mature Dry Mixed Conifer to Fire Intolerant	Fire Absence	Brandon M. Collins, Everett, and Scott L. Stephens (2011); Lydersen, M. P. North, et al. (2013); Knapp et al. (2013); Dolanc et al. (2014); Levine et al. (2016)
10	Young Dry Mixed Conifer to Mature Dry Mixed Conifer	Low Severity	Alan H. Taylor and Skinner (2003); A. H. Taylor (2000); Scholl and Alan H. Taylor (2010); J. D. Miller and H. D. Safford (2017)
11	Young Dry Mixed Conifer to Mature Dry Mixed Conifer	Moderate Severity	Beaty and Alan H. Taylor (2001); Alan H. Taylor and Skinner (2003); Richter et al. (2019); Norman and Alan H. Taylor (2005)
12	Fire Intolerant to Mature Dry Mixed Conifer	Second Entry, Low Severity	Becker and Lutz (2016); Chamberlain, Bartl-Geller, et al. (2024)
13	Fire Intolerant to Mature Dry Mixed Conifer	Moderate Severity	Lydersen, Brandon M. Collins, et al. (2016); Brandon M. Collins, Stevens, et al. (2017); Welch, H. D. Safford, and T. P. Young (2016)
14	Mature Dry Mixed Conifer to Episodic Chaparral	High Severity	Scott L. Stephens, Lydersen, et al. (2015); Welch, H. D. Safford, and T. P. Young (2016); J. D. Miller and H. D. Safford (2017)
15	Yellow Pine to Fire Intolerant	Fire Absence	Scholl and Alan H. Taylor (2010); Dunbar-Irwin and H. Safford (2016); J. D. Miller and H. D. Safford (2017)
16	Yellow Pine to Episodic Chaparral	High Severity	Scott L. Stephens, Lydersen, et al. (2015); Welch, H. D. Safford, and T. P. Young (2016); J. D. Miller and H. D. Safford (2017)
17	Yellow Pine Feedback	Low Severity	Alan H. Taylor and Skinner (2003); Scholl and Alan H. Taylor (2010); J. D. Miller and H. D. Safford (2017); Chamberlain, Bartl-Geller, et al. (2024)
18	Yellow Pine Feedback	Moderate Severity	Beaty and Alan H. Taylor (2001); Norman and Alan H. Taylor (2005); Fry and Scott L. Stephens (2006); Richter et al. (2019)
19	Mature Dry Mixed Conifer feedback	Low Severity	Brandon M. Collins, J. D. Miller, et al. (2009); Mallek et al. (2013); Hagmann et al. (2021)
20	Mature Dry Mixed Conifer feedback	Moderate Severity	Brandon M. Collins, J. D. Miller, et al. (2009); Mallek et al. (2013); Hagmann et al. (2021)

21	Episodic Chaparral to Oak Woodland	Short Interval High-Severity Reburns (With Oak Presence)	Cocking, Varner, and Sherriff (2012); Cocking, Varner, and Knapp (2014); Hammett, Ritchie, and Berrill (2017); Scott L. Stephens, Hall, et al. (2023)
22	Young Oak Woodland feedback	High Severity	Nemens, Varner, et al. (2018)
23	Young Dry Mixed Conifer to Young Oak Woodland	High Severity (With Oak Presence)	Cocking, Varner, and Knapp (2014); Nemens, Kidd, et al. (2022); Scott L. Stephens, Hall, et al. (2023)
24	Mature Dry Mixed Conifer to Young Oak Woodland	High Severity (With Oak Presence)	Cocking, Varner, and Knapp (2014); Nemens, Kidd, et al. (2022); Scott L. Stephens, Hall, et al. (2023)
25	Mature Oak Woodland to Young Oak Woodland	High Severity	Cocking, Varner, and Knapp (2014); Nemens, Kidd, et al. (2022); Scott L. Stephens, Hall, et al. (2023)
26	Mature Oak Woodland to Mature Dry Mixed Conifer	Fire Absence	Cocking, Varner, and Sherriff (2012); O’Gorman et al. (2022)
27	Young Oak Woodland to Mature Oak Woodland	Low Severity	Skinner, Alan H. Taylor, and Agee (2006); Long, Quinn-Davidson, et al. (2015)
28	Mature Oak Woodland Feedback	Low Severity	Skinner, Alan H. Taylor, and Agee (2006); Long, Quinn-Davidson, et al. (2015)
29	Mature Chaparral to Fire Intolerant	Fire Absence	Airey Lauvaux, Skinner, and Alan H. Taylor (2016)
30	Episodic Chaparral to Reduced Chaparral	Short Interval High-Severity Reburns	Biswell (1974); Nagel and Alan H. Taylor (2005)
31	Young Chapparral Feedback	High Severity	Nagel and Alan H. Taylor (2005); Airey Lauvaux, Skinner, and Alan H. Taylor (2016)
32	Young Chaparral to Mature Chaparral	Fire Absence	Nagel and Alan H. Taylor (2005); Airey Lauvaux, Skinner, and Alan H. Taylor (2016);
33	Mature Chaparral to Reduced Chapparral	Short Interval High-Severity Reburns	Keeley, Lubin, and Fotheringham (2003); Nagel and Alan H. Taylor (2005)

34	Mature Chaparral to Young Chaparral	High Severity	Nagel and Alan H. Taylor (2005)
35	Young Chaparral to Reduced Chaparral	Short Interval High-Severity Reburns	Keeley, Lubin, and Fotheringham (2003)
36	Reduced Chaparral to Invasive Grass	Short Interval High-Severity Reburns	Keeley, Lubin, and Fotheringham (2003); Keeley and McGinnis (2007); Guiterman et al. (2022); Paudel, Chen, et al. (2024)

Chapter 2: Mapping conifer, oak, and shrub regeneration following high-severity wildfire in Yosemite National Park, CA

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2.1 Abstract

The increase in size and frequency of high-severity fire patches in the Sierra Nevada is altering how vegetation responds to fire. As these patches grow, managers face uncertainty about whether conifers can regenerate across their interiors or whether alternative communities will persist. Characterizing regeneration in these patches is challenging, as the rugged terrain and the spatial extent of high-severity fire limit the utility of conventional field-based monitoring. We developed a method combining high-resolution airborne lidar with multispectral satellite imagery to map dominant vegetation communities of conifers, oaks, and shrubs across Yosemite National Park, CA, validated through two summers of fieldwork. Our approach uses a two-stage hurdle model through a binary logistic regression to model vegetation presence or absence, followed by a penalized ordinal logistic regression to model low, medium, and high cover. We applied eigenvalue-based geometric features to classify post-fire vegetation, a novel approach that captures the structural properties distinguishing each community in post-fire conditions. The models achieved classification accuracies of 71.6% for conifers, 62.1% for oaks, and 64.0% for shrubs, and predictions across the landscape were consistent with the known ecological adaptations of each community. We mapped post-fire vegetation at spatial scales not previously and can be used to identify large scale biophysical drivers of each vegetation type. These results give managers a way to anticipate where conifer regeneration is likely to persist and where transitions toward oak- or shrub-dominated states are most probable, helping direct reforestation, fuel treatment, and monitoring across large post-fire landscapes.

2.2 Introduction

Globally, wildfires are increasing in size and severity as ecosystems change in response to anthropogenic climate change (Jolly et al., 2015; Abatzoglou and A. P. Williams, 2016; Turco, Abatzoglou, et al., 2023) and a legacy of fire suppression and exclusion (C. D. Allen et al., 2002; Haggmann et al., 2021). Where wildfires burn as large, high severity fires, they can homogenize vegetation cover and structure across areas that were historically maintained as diverse mosaics by frequent, low- to moderate-severity fires (Cansler and McKenzie, 2014; Cova et al., 2023; J. N. Williams et al., 2023). Dry, mixed conifer forests in the California, USA are experiencing changes in fire and vegetation dynamics an accelerated pace, with many large fires (fires greater than 5000 ha) becoming increasingly common in the past several decades with increased area burned at high severity (Cova et al., 2023; McFarland et al., 2025). This problem, however, is not isolated to California; it also impacts ecosystems across North America dry forests (Singleton et al., 2019) and worldwide in places such as in Australia (Canadell et al., 2021) and the European Mediterranean (San-Miguel-Ayanz, Moreno, and Camia, 2013; Turco, Jerez, et al., 2019; Ruffault et al., 2020).

Disturbance severity, such as uncharacteristically large, severe fires, influences succession and recruitment patterns of post-fire vegetation (Johnstone et al., 2016). Post-fire vegetation establishment and recovery determine future structure, composition, and successional trajectory (Collins and Roller, 2013). Post-fire vegetation is generally composed of low-stature vegetation including shrubs, forbs, graminoids, conifer seedlings and saplings, resprouting oaks, and dead leaf and wood biomass.

Trajectories of post-fire vegetation regeneration ultimately determine whether ecosystems maintain their pre-fire composition or undergo conversion to alternative states (Holling, 1973; Falk et al., 2022). In California's mixed-conifer forests, conifer seedlings and saplings establish through masting and wind and herbivory seed dispersal strategies (Fowells and Schubert, 1956; Paudel et al., 2022), oaks resprout vigorously from surviving root crowns (McDonald, 1969; Stephens et al., 2023), and shrub species regenerate through both soil seed banks and resprouting (Kauffman and Martin, 1990; Zammit and Zedler, 1988). Diverse regeneration strategies create spatially heterogeneous

patterns of recovery influenced by fire severity, seed source availability, and post-fire climate (Mallek et al., 2013). Thus, characterizing the distribution and abundance of these vegetation types across post-fire landscapes is essential for understanding their resilience.

There are significant methodological challenges to characterizing post-fire vegetation communities at landscape scales. Field surveys are labor-intensive, spatially limited, and constrained by terrain accessibility. Multispectral satellite imagery covers extensive areas, but lacks sufficient spatial resolution to detect individual seedlings or distinguish between structurally similar low-stature vegetation types (Degbelo and Kuhn, 2018; Vanderhoof et al., 2021). Airborne lidar scanning (ALS) is effective at measuring forest structure in mature stands (Lefsky et al., 2002; Kane, Bakker, et al., 2010; Kane, North, et al., 2014) and seedling density in logged, managed sites (Buters, Belton, and Cross, 2019; Rana et al., 2023; Du and Pang, 2024). However, its application for post-fire regeneration remains limited, particularly where point/return density is insufficient to resolve understory vegetation beneath remnant canopy or within dense shrub layers (Campbell et al., 2018; Jarron et al., 2020). The spatial heterogeneity and structural complexity of post-fire vegetation further complicate detection compared to mature forest or managed forest mapping. With improvements in technology, more sufficient ALS coverage, better computational processing power, remote sensing studies increasingly able to examine understory dynamics (Gavilan-Acuna et al., 2025).

The central goal of this study was to examine the ability of remote sensing to identify the presence of different regenerating vegetation types following high severity fire in mixed forests and shrublands of Yosemite National Park to ultimately expand the predictions over the western Sierra. Our specific objectives were to 1) derive understory structure metrics from airborne lidar and spectral imagery that distinguish conifer, oak, and shrub vegetation types in post-fire landscapes; 2) develop and validate predictive models for presence/absence and relative abundance of each vegetation type using field observations; and 3) apply models to model vegetation composition 6-36 years post-fire across high-severity fire patches in Yosemite National Park.

2.3 Materials

2.3.1 Study Area

The west slope of the Sierra Nevada is characterized by specific climate and vegetation types. It has a Mediterranean climate with warm, dry summers and cool wet winters (Critchfield, 1975). The region is dominated by mixed conifer/yellow pine forests, including species such as ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), California black oak (*Quercus kelloggii*), and some higher elevation species such as red fir (*Abies magnifica*) and lodgepole pine (*Pinus contorta*). Post-fire successional communities are diverse mosaics of vegetation including increased shrub covers of Greenleaf manzanita (*Arctostaphylos patula*), whitethorn ceonothus (*Ceanothus cordulatus*), resprouting black oak, canyon live oak (*Quercus chrysolepis*), and regenerating conifers.

The diversity of post-fire vegetation structures in Yosemite National Park offers the opportunity to study the complex structures of regeneration. Post-fire vegetation types in Yosemite exhibit distinct structural and spectral signatures that can be measured through integrated remote sensing approaches. Individual conifers are characterized by vertical heterogeneity with excurrent branching patterns that create characteristic three-dimensional (3D) structures in lidar point clouds (Raumonen et al., 2013; Åkerblom et al., 2017). Resprouting oaks develop multi-stemmed architectures with spreading canopies and where they are dominated by broadleaf deciduous species, can have pronounced seasonal spectral variation between growing season, senescence, and dormant seasons (Vanderhoof et al., 2021; Enayetullah et al., 2022; Bohlin, Wallerman, and Fransson, 2016). Shrublands often have dense, broad-sclerophyll canopies with evergreen foliage that maintain distinct seasonal reflectance properties (Joiner et al., 2018). Combining lidar-derived structural metrics with multispectral indices that capture structural and phenological differences offers potential for distinguishing these vegetation types across diverse post-fire landscapes.

To capture these vegetation structures, our study focused on all high-severity fire patches greater than 650 m² on the west slope/side of Yosemite National Park (YOSE) that occurred more

than six years prior to the 2019 Yosemite lidar acquisition (Figure 2.1). Fire severity was derived from modeled Composite Burn Index (CBI) derived from remotely sensed spectral indices following the methods outlined in Parks et al. (2019). We define high-severity fire as CBI values above 2.25, which is correlated with the conventional definition of 95% or greater cover loss (Miller et al., 2009; Parks et al., 2019). To distinguish objects in the high-severity patches, we chose the threshold of six years as a minimum time for regenerating vegetation to become tall enough post-fire. This also allowed the inclusion of high severity patches from the large 2013 Rim Fire, which was the largest fire in YOSE as of 2019. These patches have not yet undergone any post-fire management such as planting or vegetation control.

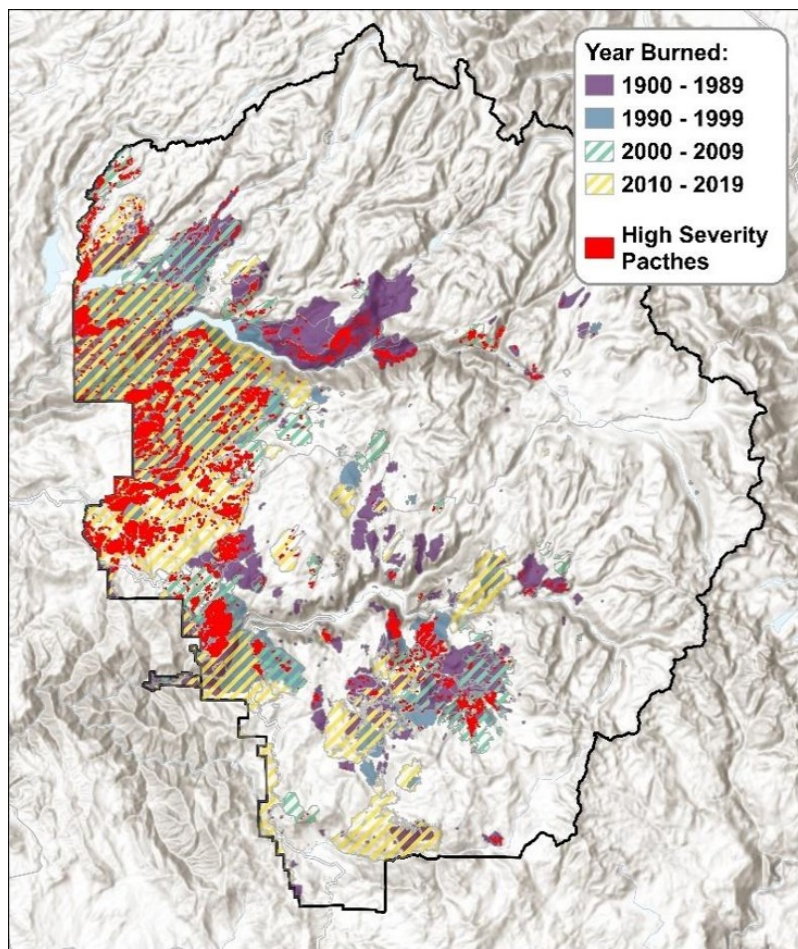


Figure 2.1: Yosemite fire perimeters from 1950-2019 overlaid with the classified high severity patches.

2.3.2 Field Sampling

Field sampling was conducted to ground-truth vegetation cover during the summers of 2022 and 2023. A total of 123 plots were recorded representing 16 different fires, a range of 6-36 years since fire, and elevations from 1,280 to 2,400 m. We captured a range of understory responses, from initial shrub colonization post-fire to conifer regeneration that was over 30 years old.

We used stratified random sampling to select plot locations that were both accessible and structurally diverse. Sampling was restricted to areas within one mile of access points and on slopes less than 45 degrees for safety and efficiency. Within accessible areas, we used stratified random sampling to select plots based on a stratified random sample of traditional lidar metrics representing ecosystem structure, such as number of lidar-identified overstory trees, dominant canopy height (P95), canopy base height (P25), number of snags, and canopy cover of the 2-4m height strata.

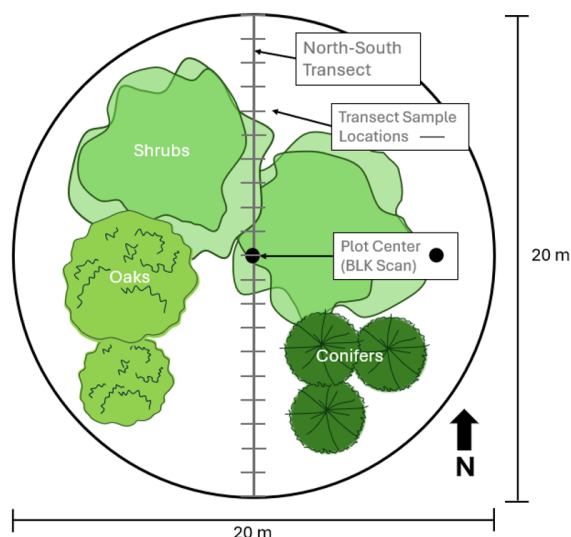


Figure 2.2: Plot layout adapted from Pokwinski et al. 2021. The figure shows the important parts of the plot layout (north-south transect, point intercept sample locations for shrub cover, and the plot center where the BLK scanned the plot). It also includes potential vegetation covers. This plot would be classified as low conifer cover (three occurrences), low oak cover (two occurrences), and low shrub cover (35% - seven point-intercept sample locations divided by 20).

The sampling framework (Figure 2.2) was adapted from Pokwinski et al. (2021) to measure vegetation compositions for validation from TLS and ALS scans. We scanned each plot with a Leica BLK 360 terrestrial lidar scanner (TLS) at the center of a 20-m diameter plot with a target 12m north of

the plot center. Following scanning, we recorded oak tree and conifer tree species, height, and count each quadrant of the plot. Regenerating trees were recorded if they were emergent (i.e., extending above the surrounding shrub canopy height) from the shrub cover by at least 0.5 m because ALS would not be able to differentiate the vegetation structure of an object below the shrub canopy. We only selected emergent trees over two meters in height to account for the time difference between the lidar acquisition (2019) and the field sampling (2022/23), as trees would be shorter in the older ALS acquisition. Furthermore, emergent conifers were recorded only if they were non-cone bearing, indicating their juvenile tree status.

Since shrub vegetation is less easily distinguished as individual objects due to dense, overlapping shrub canopies, we measured shrub percent cover rather than individual counts. We recorded point intercept samples of vegetation types (woody shrub, graminoid, litter, etc.) 1 m apart on the north-south transect (Figure 2.2) to obtain percent cover of shrubs (Pokwinski et al., 2021; Loudermilk et al., 2023).

A JAVAD GNSS receiver was placed at plot center location with sub-meter accuracy for a minimum of 30 minutes to optimize position accuracy. However, most JAVAD coordinates did not achieve a sufficient accuracy threshold for our modeling objectives, with a significantly higher error (RMSE = 2.1 m) than the ALS horizontal accuracy (RMSE = 0.13 m). To resolve the accuracy mismatch, we registered the TLS scans to the ALS structure to get exact locations of our field plots.

2.3.3 Remote Sensing Datasets

We used ALS data to measure the structure of low-stature vegetation to identify distinct community structure of different vegetation types and then map their cover. The Yosemite ALS collected in October 2019 as part of the USGS 3DEP program (Survey, 2019) covers approximately 803,000 acres within and adjacent to Yosemite National Park using a Riegl VQ-1560i laser scanner. The acquisition achieved an average point density of ~ 23 pts/m² across the project area (Survey, 2019). The survey and its processing meet USGS 3DEP Quality Level 1 standards with sufficient point cloud densities for detecting post-fire vegetation structure.

Based on preliminary analysis, we found that moderate resolution (10 m) cloud-off 2019 Sentinel-2 satellite imagery from Google Earth Engine (Gorelick et al., 2017) contained spectral information that helped classify vegetation cover. Specifically spectral signals vary among vegetation types that can be used as a complement to ALS data for distinguishing structurally similar species or vegetation types (e.g., evergreen shrubs vs. regenerating broadleaf deciduous oaks; (Martín-Alcón et al., 2015)). For our analysis, we employed dual-season vegetation indices to capture differences in phenology between the growing season (June) and senescence (October) (Vanderhoof et al., 2021). The indices include the Normalized Difference Vegetation Index (NDVI) and Normalized Difference Infrared Index (NDII). NDVI measures vegetation “greenness” and NDII measures vegetation water content (Joiner et al., 2018).

2.3.4 Pre-Processing

Prior to modeling vegetation types, ALS point clouds were filtered to isolate low-stature vegetation. Standard tree segmentation removes all points in the vertical columns beneath tree crowns, including understory vegetation, while setting height thresholds retains tree boles and snags that influence understory metrics. To address this, we used methods introduced in Redford et al. (in prep) to iteratively segment overstory trees and snags while retaining understory vegetation. This process is necessary to ensure that structural metrics reflect low-stature regeneration rather than remnant overstory structure. First, overstory vegetation was delineated using identification and segmentation using a local maxima filter after Silva et al. (2016). However, this tree segmentation algorithm segments the entire vertical column of vegetation beneath each tree crown, eliminating the understory layer directly beneath the tree canopies (Hamraz, Contreras, and Zhang, 2017). To retain the understory, this method calculates the 99th percentile on surrounding vegetation and clips the point cloud at this height, then calculates the 95th percentile of vegetation on the clipped tree column to remove any residual tree boles. Finally, the method segments and removes standing dead trees (snags) using a height to canopy width ratio to produce the final understory point cloud representing live post-fire regeneration (full workflow in Appendix S1).

To capture specific spectral signals of post-fire vegetation types, we calculated the NDVI and the NDII from Sentinel 2 imagery (10m resolution) (Joiner et al., 2018; Enayetullah et al., 2022). The cells of the 10-m resolution imagery were spatially misaligned with the plot locations, so we resampled the Sentinel 2 imagery to 1-m and calculated the mean of the resampled cell values within each plot (Figure 2.3). Seasonal difference metrics were then calculated by subtracting October index values from June values, capturing changes in vegetation greenness and canopy moisture between early growing season and senescence (Vanderhoof et al., 2021). These spectral metrics complemented the lidar structural data by providing information on phenological dynamics and vegetation conditions not captured by 3D structural measurements alone.

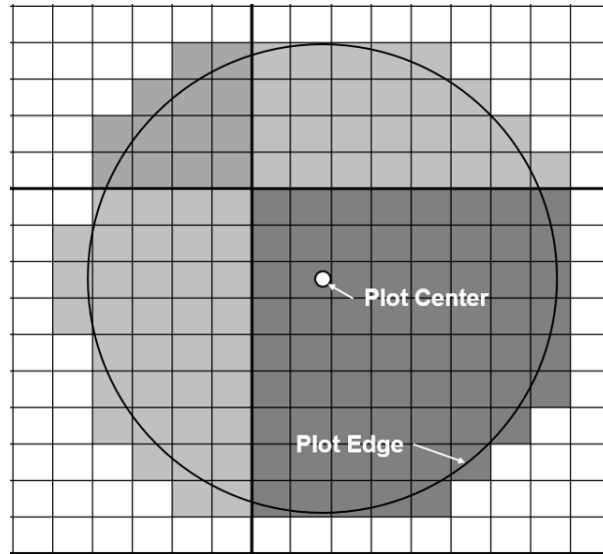


Figure 2.3: Spectral resampling method for plot imagery calculation. The shaded areas are subsampled 10-m cells from Sentinel 2 imagery that are used to calculate the spectral metric mean in each plot.

2.4 Methods

2.4.1 Deriving Understory Structure Metrics

Modeling understory structure with traditional remote sensing techniques is distinctly more challenging than that of overstory forest structure due to larger variations in understory canopy morphology and potential canopy occlusion where overstory trees are present. Overstory structure exhibits

more predictable allometric relationships and spatial patterns (Lefsky et al., 2002), while understory vegetation is composed of greater size diversity, species mixing, and growth stage variability. Canopy occlusion was not a serious limitation in this study due to the lack of tall tree canopy in resultant high-severity patches.

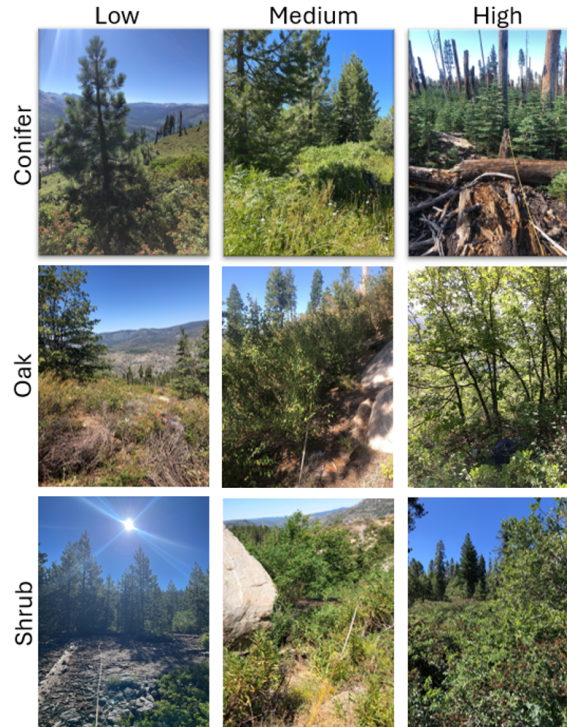


Figure 2.4: Examples of vegetation compositions for different covers. It is important to note that individual tree and shrubs height varies regardless of type and cover- i.e. height alone cannot distinguish cover or type.

While the stratified random sample successfully generated a dataset representative of understory vegetation, it also created challenges in evaluating potential metrics across such a wide diversity of structures. Structural metrics are typically computed within height strata at fixed vertical bins (i.e. 0.5-1, 1-2, 2-4 m) that isolate specific canopy layers for analysis. Across this dataset, point clouds varied widely in absolute height, horizontal structure, and the objects present in each plot (Figure 2.4). The same cover type had different heights across plots, and any fixed height bin captured different cover types depending on the plot. Thus, metrics computed within static strata were not capturing specific canopy information in our plots.

To extract specific understory canopy positions across such a wide range of vegetation heights, we used height percentiles rather than static height strata. We modified methods from McGaughey et al. (2024), which delineated conifer types in the western Cascades based on their upper canopy structure. The study differentiated western hemlock (*Tsuga heterophylla*) from Douglas-fir (*Pseudotsuga menziesii*) due to its significantly different upper crown morphology. (McGaughey et al., 2024). Adapting this methodology, we defined three functional understory height strata in the filtered point cloud to delineate understory canopy morphology: P55-P85 (mid-layer understory canopy), P85-P95 (upper understory canopy), and P90-P99 (emergent understory objects). This percentile-based approach ensured that structural metrics captured structurally relevant vegetation layers regardless of absolute height (Figure 2.5).

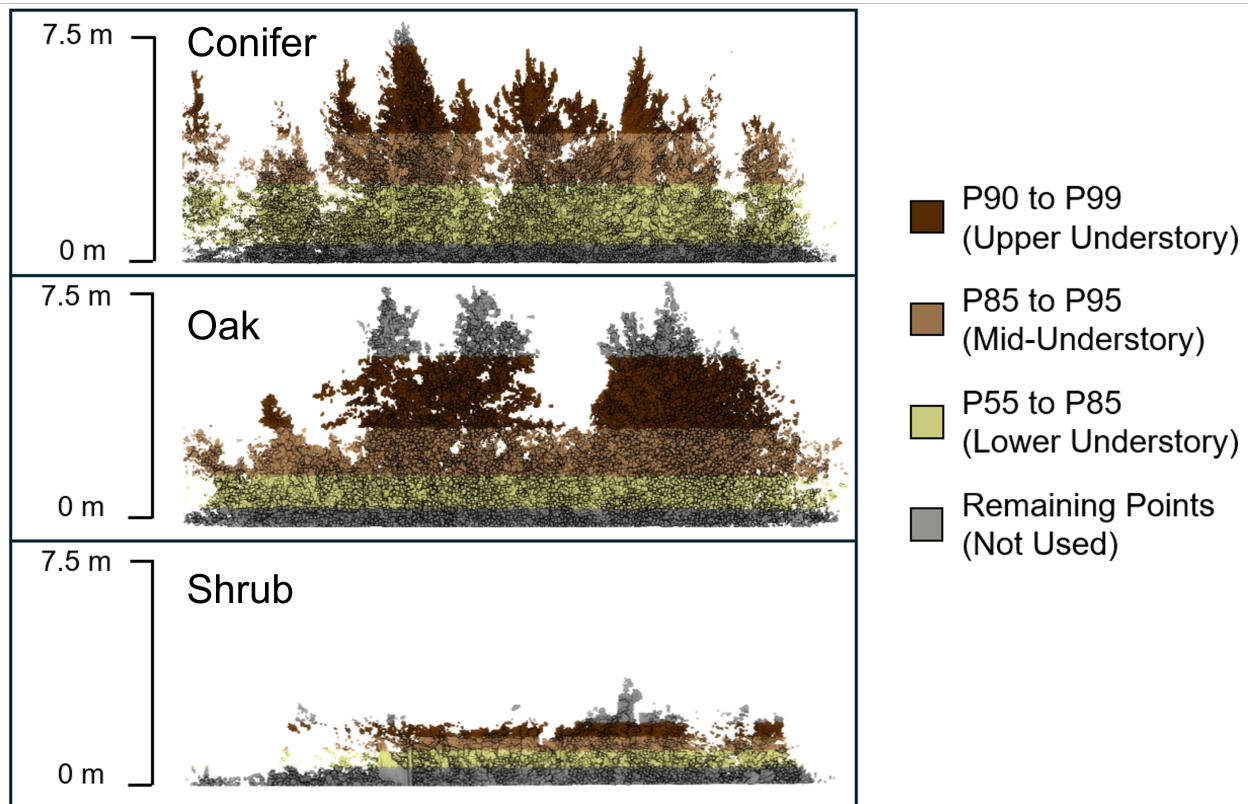


Figure 2.5: Height percentile dividing the canopy morphology by varying heights. The percentiles represent different parts of the understory and are structurally different depending on the amount, height, and type of vegetation. Height percentile bins are inclusive and overlapping. Points in the 90th-99th percentile (upper understory, brown) also appear in lower percentile bins but are shown only in their highest category for visual clarity.

We initially calculated commonly used lidar metrics in each height percentile for measuring understory vegetation structure, including complexity (rumple), canopy cover, standard deviation of height, skewness, kurtosis, and dominant canopy height (P95) that correlate with overstory field-based measurements (Kane, Bartl-Geller, et al., 2019; Jeronimo et al., 2018). However, this initial exploration showed that these metrics performed poorly in identifying regenerating tree and shrub covers. Therefore, we turned to structural metrics that reflect finer distinctions in the canopies of our filtered point clouds

Structural metrics characterizing 3D vegetation geometry have proven effective for vegetation classification. Brodu and Lague (2012) developed a multi-scale dimensionality approach using eigenvalue-based geometric features (linearity, planarity, sphericity) calculated at multiple neighborhood scales to classify complex natural scenes from urban objects using terrestrial lidar. Y. Wang et al. (2017) and Zhou et al. (2019) used a suite of neighborhood-based point metrics to characterize leaf points and wood points. These metrics are also used in a variety of machine learning capacities to distinguish individual object shapes (Y. Wang et al., 2017; Lucas et al., 2019; Tarsha Kurdi et al., 2023).

We expanded the application of these neighborhood-based structural metrics beyond previous studies by exploring their effectiveness in unmanaged post-fire ecosystems. We stratified the metrics across height percentiles within the understory layer to distinguish how post-fire regeneration covers (conifer, oak, shrub) differ in their 3D architecture (Table 2.1; (Lucas et al., 2019)). Metrics used include planarity (flatness of point distributions), linearity (one-dimensional structure), anisotropy (directional variation), curvature (surface smoothness), and sphericity (volumetric uniformity). Additionally, we applied a metric (minimum eigenvalue) describing the relative contribution of vertical versus horizontal vegetation structure from principal component analysis of the point distribution. We omitted the maximum and medium eigenvalues as they emphasize point density which is highly variable in ALS acquisitions due to overlapping flight paths.

The point ALS point density for the understory layer was too low to identify individual plants. We therefore chose to classify the vegetation cover in 20m pixels (the size of the field plots) across resultant high-severity patches. Using coarse vegetation structure allows for pattern-based classification,

where the overall classification remains accurate despite lidar occasionally missing individual objects. The structural metrics were calculated for each plot and across the entire understory point cloud at 20m cell sizes using a k -neighborhood of $n=50$ points with the `point_metrics` function in the `lidR` package (Lucas et al., 2019; Roussel et al., 2020).

Table 2.1: Summary of vegetation structure metrics derived from lidar and Sentinel-2 imagery.

Metric	Category		Mathematical Meaning	Ecological Interpretation
EV ₃ (smallest eigenvalue)	Eigenvalue metrics	point	Variance along minor axis (normal vector direction)	Layer thickness; very small EV ₃ = flat surfaces (leaves, shrub canopy); larger EV ₃ = diffuse/volumetric fill
$(EV_1 - EV_2) / EV_1$ (Linearity)	Eigenvalue metrics	point	Alignment of points along a single dominant axis	Stem- or branch-like elements (snags, taller objects)
$(EV_2 - EV_3) / EV_1$ (Planarity)	Eigenvalue metrics	point	Concentration of points in a planar configuration	Flat layers (shrub canopies, understory foliage mats)
EV ₃ / EV ₁ (Sphericity)	Eigenvalue metrics	point	Ratio of minimum to maximum variance	Bushy shrubs, tangled regrowth, volumetric clumps
$(EV_1 - EV_3) / EV_1$ (Anisotropy)	Eigenvalue metrics	point	Difference between maximum and minimum variance directions	Structural organization of vegetation (organized directional patterns or stochastic forms)
EV ₃ / (EV ₁ +EV ₂ +EV ₃) (Curvature)	Eigenvalue metrics	point	Variation in the surface normal direction relative to total variance	Boundary sharpness; distinguishes open gaps vs solid vegetation
Rumple	Calculated metrics	lidar	Ratio of canopy surface area to ground area	Vegetation structure roughness
Interquartile Range	Calculated metrics	lidar	P25 subtracted from P95	Difference in height to live crown and dominant canopy height
Standard Deviation of Height	Calculated metrics	lidar	Vertical heterogeneity	Variability of vegetation structure
NDVI (June, Growing Season)	Spectral (Sentinel-2)		Normalized (NIR – Red) / (NIR + Red): greenness proxy in June	Leaf-on vigor; higher values indicate greener, photosynthetically active understory/low canopy in June
NDVI (October, Senescence)	Spectral (Sentinel-2)		Normalized (NIR – Red) / (NIR + Red): greenness proxy in October	Leaf-off/aging foliage; lower values reflect senescence and reduced greenness in October
NDVI Difference (June – October)	Spectral (Sentinel-2)		Difference in NDVI: June minus October	Seasonality of greenness; larger positive = much greener in June (deciduous signal), near-zero = evergreen/persistent cover or non-veg
NDII (June, Growing Season)	Spectral (Sentinel-2)		Normalized (NIR – SWIR) / (NIR + SWIR): canopy water/structure proxy in June	Higher canopy water content/denser foliage signals in June

2.4.2 Modelling Understory Vegetation

To map post-fire landscape-scale regeneration, we used a hurdle model which handles zero-inflated data and coarse classification. Due to a limited sample size ($n=123$) and class imbalance, which resulted in zero-inflated data, a single-stage model was not possible. Hurdle models work in two stages to account for zeros: first determining if an event occurs (“passing the hurdle”), then determining how often it occurs (Preisser et al., 2016). To model vegetation presence/absence in the first stage, we used a binary logistic regression (BLR) model. For the second stage, to model vegetation cover in ranked classes (low $\rightarrow$ medium $\rightarrow$ high density), we used an ordinal logistic regression (OLR) model.

Low, medium, and high vegetation classes were determined using field plot vegetation counts (conifer and oaks) or cover proportion (shrubs) to create balanced classes (Table 2.2). This method avoids model bias towards the dominant class, as OLR models tend to misclassify minority classes when distributions are imbalanced. All analyses were conducted in R version 4.3.0 (Team, 2023) using the ordinalNet package (Wurm, Rathouz, and Hanlon, 2021) for penalized ordinal regression, base glm (Team, 2023) for binomial models, and terra (Hijmans, 2023) for spatial raster processing and predictions.

Table 2.2: Classified vegetation cover parameters. Each vegetation type had a different class depending on the sample size to create balanced classes for the ordinal logistic regression model.

Vegetation Type	Response Type	Class Thresholds (cover/plot)			n
		Low	Med	High	
Conifer	Count	1–4	5–19	20+	79
Oak	Count	1–4	4–8	9+	29
Shrub	Proportion	0.01–0.39	0.4–0.69	0.7+	91

To model conifer, oak, and shrub cover across high-severity patches in Yosemite, we used the same model framework for all three vegetation types (Figure 2.6). We first evaluated the metrics across all vegetation types (Figure 2.6B.b, Figure 2.6B.e, Figure 2.6B.g). To ensure comparable coefficient estimates and consistent model fitting across features with different measurement scales, we then standardized the metrics prior to modeling (mean = 0, SD = 1) (Figure 2.6B.i and Figure 2.6B.o). Distinct

subsets of these metrics identified different vegetation covers (Figure 2.6B.j, 6B.p).

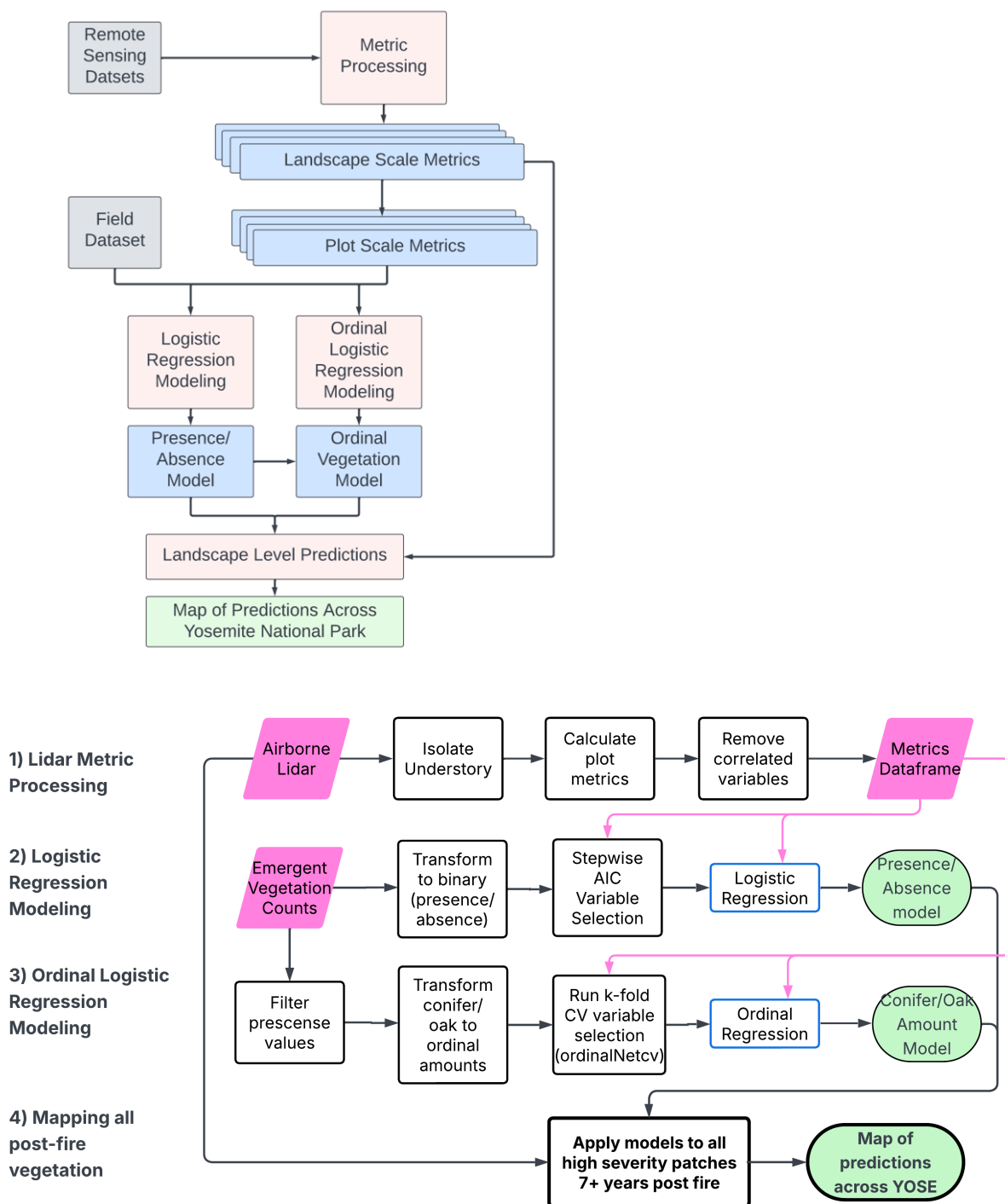


Figure 2.6: A) Simplified flow chart only showing the basic steps to provide an overview of methods. B) Flowchart of the full workflow Colors identify how steps correspond between the flow charts.

2.4.2.1 Presence/ Absence Modeling - Binary Logistic Regression

To model vegetation presence/absence at the first stage of the hurdle model, we used a BLR model of the form:

$$\log\left(\frac{p}{1-p}\right) = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_p X_p \quad (2.1)$$

which predicts the probability of response presence/absence based on independent variables (D. A. Walker and Smith, 2020). A BLR allows for a straightforward interpretation of predictor variables' influence on the likelihood of vegetation presence. This model identifies probability of presence and determines whether areas require further modeling to quantify vegetation cover or lack the specific vegetation composition (absent). Data must pass this “hurdle” before the OLR model assesses conifer, oak, and shrub cover.

To reduce dimensionality among the 45 total metrics, we used a pairwise comparison that reduces multicollinearity and overfitting in the metric selection to obtain noncorrelated structural metrics (Figure 2.6B.i). Pairwise correlation calculates the correlations between all pairs of metrics and keeps the metric with a stronger correlation to the response data. For each pair above a threshold (here 0.7), we discard the metric with a lower correlation to the response data to obtain an independent set of predictors. We also removed all height metrics and metrics that were correlated with height metrics including P95, P25, and P50 (*i.e.*, mean height) to avoid capturing height-related effects to make the models more applicable across fire ages. This reduced the dataset to 12 total predictors.

To identify the best set of variables for each model, we tested all permutations of the remaining metrics to identify the group that performed the best using the Akaike Information Criterion (AIC) (Figure 2.6B.j). We assessed all combinations of the variables (up to 5 variables per combination to avoid overfitting) to find the best fit for each vegetation cover.

2.4.2.2 Regeneration Cover Modeling - Ordinal Logistic Regression

To model conifer, oak, and shrub regeneration cover as a ranked, ordinal response, we used cumulative link models with a logit link function for locations where each vegetation type was modeled as present (Figure 2.6B.m). Unlike standard linear models, which assume a continuous response, OLR accommodates the sequential ordering in the cover categories without assuming equal spacing between them. Regeneration cover was ranked into three ordered categories (low, medium, high) based on field-measured emergent objects for oaks and conifers and proportional area coverage for shrubs (Figure 2.6B.m). We used proportional area measurements for shrubs due to the difficulty in determining individual counts with their complex growth patterns. Individual shrub crowns are often overlapping and difficult to distinguish, which required the additional step of measuring proportion cover rather than counts.

To address smaller sample sizes and model overfitting, we implemented penalized ordinal regression using elastic net regularization ($\alpha = 0.5$) which improves prediction accuracy and selects variables (Wurm, Rathouz, and Hanlon, 2021). The function minimizes the negative log-likelihood normalized by the number of observations in each vegetation class (N_+), measuring how well the model fits the data while applying regularization penalties to prevent overfitting. The elastic net combines L1 (lasso) and L2 (ridge) penalties. The L1 component forces weak coefficients to zero, creating sparse models, while the L2 component shrinks remaining coefficients without eliminating them. The regularization parameter (λ) controls model complexity by penalizing large coefficients (Hesterberg et al., 2008; Sun, J. Wang, and Fang, 2013). We selected λ via 5-fold cross-validation, evaluating 20 λ values and selecting the maximized cross-validated accuracy, where high λ (out of 20) signifies overfitting while a low λ over penalizes the model (Figure 2.6B.p). Models included both parallel and non-parallel terms (also known as a “semi-parallel” model) to allow threshold-specific effects (i.e. low to medium and medium to high) when warranted by the data st

Semi-Parallel OLR Model Function (Wurm, Rathouz, and Hanlon, 2021):

$$M(c, b, B; \alpha, \lambda, \rho) = -\frac{1}{N_+} l(c, b, B) + \lambda \left(\rho \sum_{j=1}^P \left(\alpha |b_j| + \frac{1}{2} (1 - \alpha) b_j^2 \right) + \sum_{j=1}^P \sum_{k=1}^K \left(\alpha |B_{jk}| + \frac{1}{2} (1 - \alpha) B_{jk}^2 \right) \right) \quad (2.2)$$

2.4.3 Threshold Selection and Model Validation

To assess the accuracy of the BLR models, we used the F1-score from a leave one out cross validation to determine the classification thresholds to balance precision (potential positive values) and sensitivity (true positive values) (Figure 2.6B.k). The F1-score provides a balanced measure of model performance that is particularly important when both false positives (predicting presence where vegetation is absent) and false negatives (missing true regeneration) carry ecological significance. We evaluated model performance at these thresholds using leave one out cross validation on the training data, with metrics including overall accuracy, sensitivity (recall), specificity, Cohen’s kappa, and F1-score (Appendix S1).

For OLR models, we used overall classification accuracy and class-specific accuracies to evaluate model performance (Figure 2.6B.q). Final models used selected λ indices for the vegetation types, retaining 5-8 non-zero predictors per model. The optimal lambda (λ) values chosen by the model were 10, 4, and 12 for the conifer, oak, and shrub models, respectively. We evaluated performance using k-fold cross validated accuracy values and weighted Cohen’s kappa. We used a quadratic weighted Cohen’s kappa because it accounts for the magnitude of disagreement among ordinal ranks (Li, Gao, and Yu, 2023). For example, a “low” prediction receives greater penalty than a “medium” prediction when actual cover was “high” (Appendix Table 2). We used the irr R package to calculate the weighted kappa scores (Gamer et al., 2019).

2.4.4 Landscape Level Predictions

To handle extrapolation in the spatial prediction stage, we constrained landscape-scale metric raster values to the training data range before scaling to prevent extrapolation beyond observed con-

ditions (Figure 2.6B.s). This approach, termed clamping, limits predictor values that fall outside the training data range to the minimum or maximum observed values, ensuring model predictions rely only on predictor combinations the training data represents (Elith et al., 2020; Valavi et al., 2023). Species distribution modeling uses this method when predicting to novel environmental conditions (Elith et al., 2020; Valavi et al., 2023). Without clamping, extreme metric values in unsampled areas, such as very high rumple in complex topography or very low linearity in sparse vegetation, could produce unreliable predictions because these conditions did not appear in the training data. The resulting landscape-scale rasters represent the scaled and clamped metrics across all high-severity patches.

To predict vegetation cover across landscape scales, we applied the hurdle models on landscape-scale rasters of each metric. First, the BLR models predicted where each vegetation type was present or absent (Figure 2.6B.t). Subsequently, we applied the OLR models only to locations predicted as present to classify vegetation cover as low, medium, or high (Figure 2.6B.u). This two-stage process resulted in individual rasters for conifers, oaks, and shrubs, with four classes per vegetation type: absent, low cover, moderate cover, and high cover.

We chose three distinct areas with different fire histories and elevations to focus on to visualize overall patterns of vegetation cover in Yosemite. Illouette Basin represents the highest elevation area with the most diverse fire history. The Lower Big Oak Flat Road was selected to represent a mid-elevation ecosystem that experienced two high-severity fires within 30 years, also known as a short interval high-severity reburn. Finally, the Hetch Hetchy site was chosen as our lowest elevation site and represents a large patch of high severity fire.

2.5 Results

2.5.1 Field Data

The field dataset captures substantial heterogeneity in post-fire vegetation cover across the study area, with conifer, shrub, oak, and grass components co-occurring in varying proportions across fires of different ages and elevations (Figure 2.7). Plot selection prioritized capturing this structural

diversity over balancing plots by elevation, time since fire, or high-severity patch characteristics. Based on what was accessible for sampling in our study area, plot representation varied with time since fire with fewer plots in the 20-to-30-year bin than the 5-to-10-year and 30+ year bins. Although this temporal gap exists in field sampling during the 6-to-36-year period, the structural diversity captured by stratified random sampling still enables prediction of plot structure across the full time since fire sequence.



Figure 2.7: Distribution of field plots by elevation, time since fire, and vegetation type. Point size indicates plot count or percentage. Sampling captured structural diversity across the chrono sequence with variable temporal coverage.

Field observations revealed distinct spatial and temporal patterns in post-fire vegetation regeneration across 113 plots (Figure 2.7, 2.8). Conifer regeneration was densest at higher elevations (2125-2500m) and in sites 15-35 years post-fire. Lower elevation sites supported less dense conifer regeneration (typically less than 40 individuals), occurring primarily in sites < 15 years post-fire. Oak regeneration spanned the broadest elevational range (1300-2500m) but reached greatest abundance at mid-elevations (1600-2200m), with establishment occurring across all fire ages sampled. Oaks regenerated at lower densities than conifers, with most plots containing fewer than twenty individuals. Shrubs dominated low- to mid-elevation sites (1300-2375m) and declined noticeably to elevations greater than 2375m. Shrub cover persisted even in older fires (25-35 years), demonstrating persistent shrub dominance across the study area.

Vegetation composition varied with time since fire (TSF) across plots, accounting for the total

area burned in each time since fire bin (Figure 2.8). Shrubs dominated younger fires (5-10 years TSF), representing a narrow 5-year window, with substantial conifer and oak recruitment in half of the plots. The 10–20-year TSF category had the largest sample size (82 plots) and total burned area. While shrubs also dominated this TSF category, conifers and oaks were often present and represented a considerable portion of post-fire vegetation. Recruitment patterns mirrored earlier TSF categories. The 30+ year TSF category showed presence of both conifer and shrub types, with limited oak presence in plots.

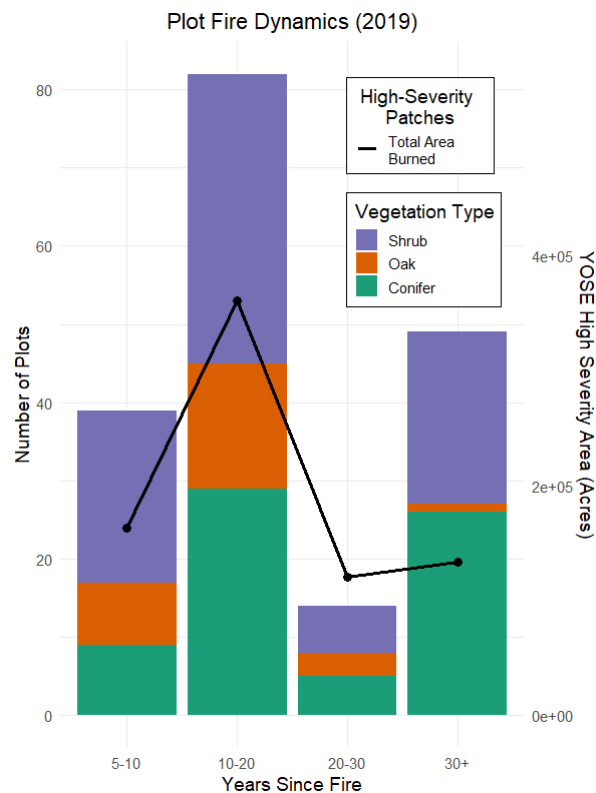


Figure 2.8: Number of plots (left y-axis) compared to the total area burned at high severity (black line, right y-axis).

2.5.2 Deriving Understory Metrics

Within geometric and spectral metrics, different subsets of metrics correlated with the presence and cover of each vegetation type. Given the novel application of these structural metrics to post-fire vegetation, we assessed whether the metrics captured distinct aspects of the understory canopy. Lidar-derived metrics and spectral indices captured structural and phenological signatures of different post

high severity fire vegetation structures (Figure 2.9). The final predictive models excluded metrics based on multicollinearity among related variables. For example, anisotropy and linearity are both eigenvalue-based metrics describing similar aspects of point cloud geometry and were highly correlated, however the models only retained linearity. The complete suite of selected metrics shows unique fingerprints across height percentiles and vegetation types, highlighting their effectiveness.

The variables selected for each model represent vegetation-specific structural and spectral features (Table 2.3). The conifer models selected for linearity (Lin.) across multiple vertical strata (P55-85, P90-99), Interquartile Range (IQR) in the mid-understory (P85-95) and eigenvalue minimum (Emin) in of the upper-understory (P90-99), reflecting the columnar architecture and vertical structure of regenerating conifers. Oak models selected linearity at low- and mid-understory heights (P55-85, P85-95), and rumple (Rump.) and IQR of the upper-understory (P90-99) to reflect branching, bushy structures, and vertical variability. Shrub models selected linearity in the low-understory (P55-85), IQR and planarity (Plan.) in the mid-understory (P85-95), and eigenvalue minimum of the upper-understory (P90-99) to capture dense, uniform structure with limited vertical extent characteristic of shrub vegetation.

Spectral indices revealed distinct phenological patterns among vegetation types (Table 2.3). Conifer models selected June NDVI (jNDVI), October NDII (oNDII), and seasonal NDVI difference (sdNDVI), capturing the evergreen spectral signature with minimal seasonal variation. Oak models selected the same three metrics plus October NDVI (oNDVI), with the stronger seasonal NDVI contrast reflecting deciduous leaf senescence.

June NDII (jNDII), October NDII (oNDII), and seasonal NDVI difference (sdNDVI) strongly influenced shrub ordinal logistic regression patterns, with June NDII (jNDII) and seasonal NDVI (sdNDVI) difference showing consistent negative relationships across density thresholds (Table 2.3). Higher shrub densities corresponded to lower vegetation water content and reduced seasonal variation, which reflects the physiological adaptations of evergreen shrubs to dry summer conditions.

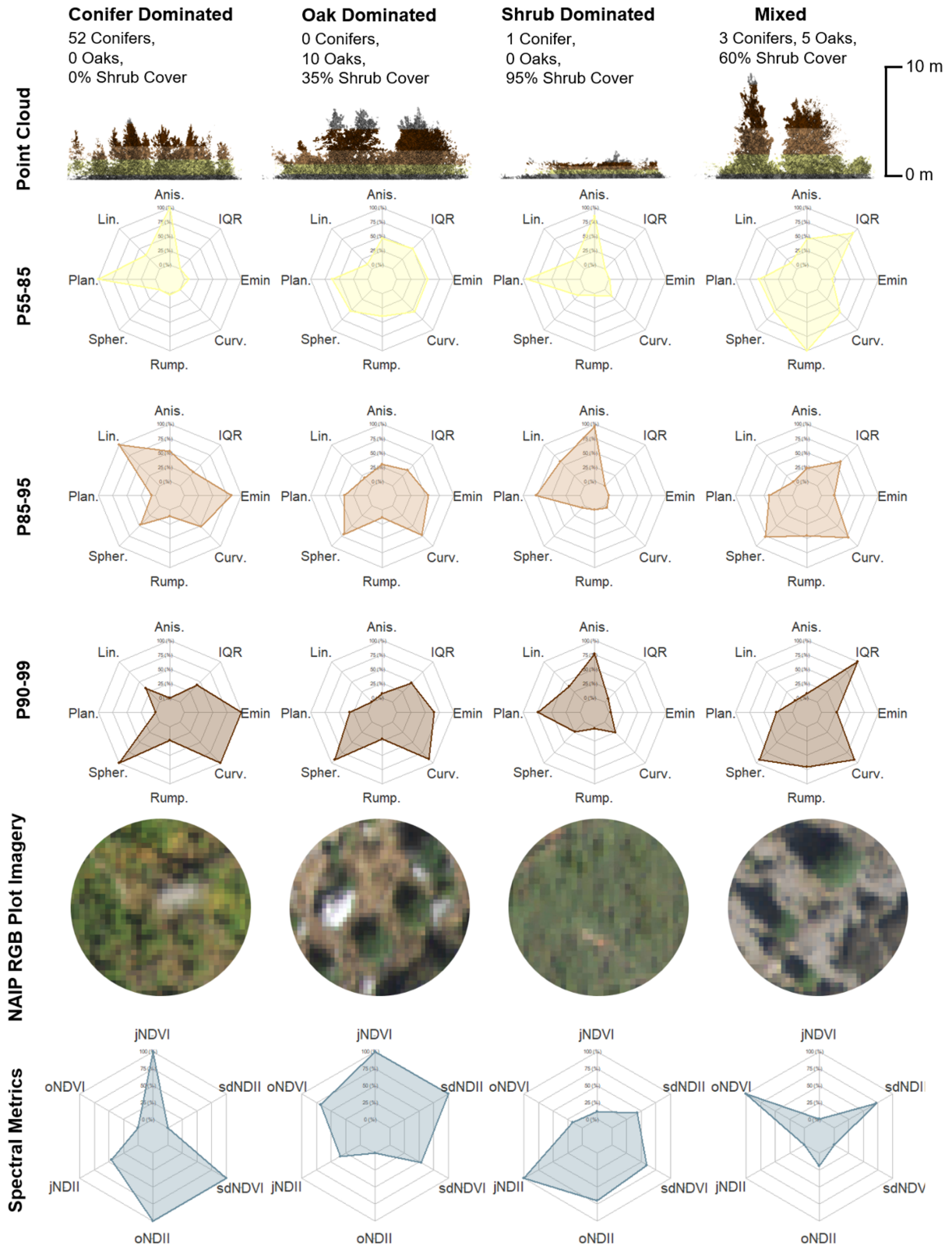


Figure 2.9: Geometric and spectral signatures of post-fire vegetation types with predictor variables shaded by height percentile. Point clouds and field composition (top) show representative plots. Geometric metrics from three lidar height strata (rows 2-4) and dual-season spectral indices (bottom) distinguish vegetation types. Each radar plot shows a distinct structural signal emitted from the selected plots.

Table 2.3: Selected predictor variables and standardized coefficients for binary logistic regression (BLR) and ordinal logistic regression (OLR) models by vegetation type.

Vegetation Type	BLR Variables	OLR Variables
Conifer	90th to 99th percentile eigen minimum ($\beta = 0.687$) 55th to 85th percentile linearity ($\beta = 0.876$) June NDVI ($\beta = 1.288$) October NDII ($\beta = 2.258$) NDVI seasonal difference ($\beta = -2.712$)	90th to 99th percentile eigen minimum ($\tau_1 = -0.103, \tau_2 = -0.68$) Eigen minimum of objects ($\tau_1 = -0.183, \tau_2 = -0.652$) NDVI seasonal difference ($\tau_1 = 0.637, \tau_2 = 0.703$) 85th to 95th percentile interquartile range ($\tau_1 = 0, \tau_2 = 0.202$) June NDII ($\tau_1 = 0.053, \tau_2 = -0.114$) 90th to 99th percentile linearity ($\tau_1 = -0.3, \tau_2 = -0.217$) October NDII ($\tau_1 = -0.062, \tau_2 = 0$)
Oak	55th to 85th percentile linearity ($\beta = 0.699$) 85th to 95th percentile rumple ($\beta = 0.922$) June NDVI ($\beta = -1.06$) October NDII ($\beta = -2.997$) NDVI seasonal difference ($\beta = 1.592$)	90th to 99th percentile rumple ($\tau_1 = -0.239, \tau_2 = -0.136$) 90th to 99th percentile interquartile range ($\tau_1 = -0.194, \tau_2 = -0.136$) 85th to 95th percentile planarity ($\tau_1 = -0.358, \tau_2 = 0.086$) 85th to 95th percentile linearity ($\tau_1 = 0.197, \tau_2 = 0.197$) 85th to 95th percentile eigen minimum ($\tau_1 = 0, \tau_2 = 0.007$) October NDII ($\tau_1 = 0, \tau_2 = -0.009$)
Shrub	55th to 85th percentile linearity ($\beta = 0.405$) June NDVI ($\beta = 1.01$) October NDII ($\beta = -1.687$) NDVI seasonal difference ($\beta = 1.485$)	June NDII ($\tau_1 = -0.614, \tau_2 = -0.613$) NDVI seasonal difference ($\tau_1 = -0.327, \tau_2 = -0.327$) 90th to 99th eigen minimum ($\tau_1 = 0.197, \tau_2 = 0.197$)

2.5.3 Model Performance

2.5.3.1 Binary Logic Regression (Presence/ Absence of Vegetation)

BLR models accurately predicted the presence/absence of conifer, oak, and shrub with 74.3%, 77.2%, and 74.3% balanced accuracy, respectively (Table 2.4). Leave-one-out cross-validation yielded F1 scores of 0.794 (conifer), 0.667 (oak), and 0.72 (shrub), confirming robust model performance and balanced accuracy across all vegetation covers. We balanced sensitivity and specificity using the F1 threshold for each vegetation cover (0.5 for all). All three models had Cohen's kappa scores above 0.5, which is an acceptable, moderate agreement according to Landis and Koch (1977) and Altman (1991) kappa benchmarks.

Table 2.4: Conifer, oak, and shrub BLR confusion matrices and test statistics.

	Conifer BLR		Oak BLR		Shrub BLR	
	Absent	Present	Absent	Present	Absent	Present
Absent	31	15	72	10	17	10
Present	12	52	9	19	11	72
Overall Accuracy	0.755		0.827		0.81	
Bal. Accuracy	0.743		0.772		0.743	
F1 Score	0.794		0.667		0.72	
F1 Threshold	0.5		0.5		0.5	
Unweighted Kappa	0.542		0.579		0.533	
Sensitivity	0.813		0.655		0.607	
Specificity	0.674		0.889		0.878	

2.5.3.2 Ordinal Logistic Regression (Proportion of Vegetation Cover)

We developed separate ordinal logistic regression models for each vegetation cover that predicted ranked amounts (low, medium, and high). The OLR models performed well, with high accuracy and weighted kappa test statistics. Overall model accuracy for the conifer, oak, and shrub OLR models was 71.6%, 62.1%, and 64% respectively (Table 2.5). The weighted kappa statistics showed good to

substantial agreement across the ordinal models, achieving 0.65 – 0.73 agreement, according to Landis and Koch (1977) and Altman (1991) kappa benchmarks. The models distinguished high and low classes well from each other yet struggled most to predict the difference between low-medium and high-medium classes. The weighted kappa accounts for this ranked disagreement, weighting classes further from each other less than classes near each other.

Table 2.5: Conifer, oak, and shrub OLR confusion matrices and accuracy statistics.

	Conifer OLR				Oak OLR				Shrub OLR			
	Low	Med	High	Bal. Acc.	Low	Med	High	Bal. Acc.	Low	Med	High	Bal. Acc.
Low	17	2	1	0.872	8	2	1	0.821	23	9	2	0.776
Medium	3	11	5	0.69	0	4	3	0.647	7	16	7	0.637
High	1	7	20	0.787	2	3	6	0.668	1	6	18	0.777
Overall Accuracy	0.716 (71.6%)				0.621 (62.1%)				0.64 (64%)			
Weighted Kappa	0.733				0.65				0.723			

2.5.4 Landscape Level Predictions

The resulting landscape level predictions show where our models detected conifer, oak, and shrub cover across our three sites (Figure 2.10). When paired with the model probability, we can identify where the models were confident in predicting vegetation cover versus where they are not. Conifers had the highest modeled cover in the fire patch edges of Illilouette basin, with shrubs having high probability in the interiors of the patch. Oaks had the greatest cover in the Big Oak Flat site and were dispersed throughout the Hetch Hetchy site, often co-occurring with low to moderate shrub covers. Shrubs were present across most areas, with the highest cover in the Hetch Hetchy site where oaks and conifers were absent.

2.6 Discussion

2.6.1 Post-Fire Vegetation Mapping Methods

We found that airborne lidar metrics combined with multispectral indices can effectively distinguish conifer, oak, and shrub regeneration in high-severity fire patches. Recent advances in ALS

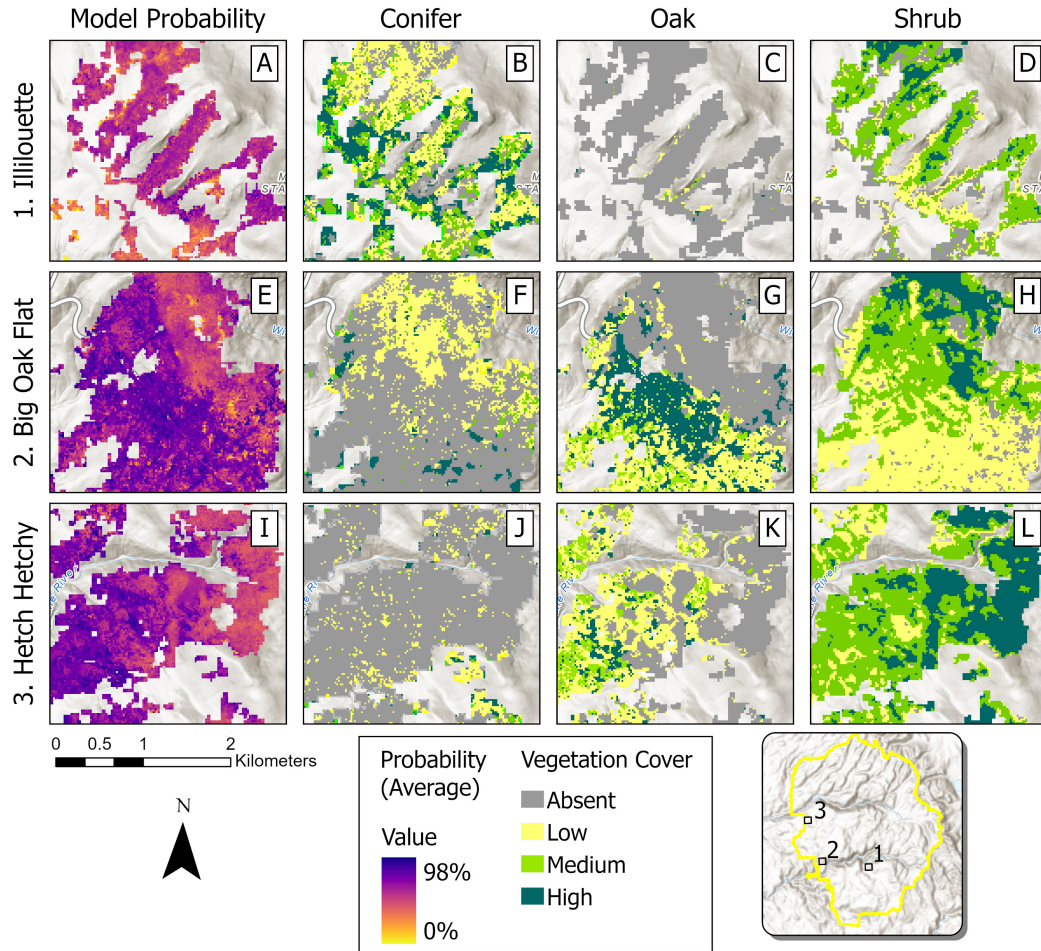


Figure 2.10: Maps of the vegetation cover across three resultant high severity patches with different fire histories. Patch 1: The Illilouette Basin, some of the patches burned at high severity in the Illilouette Fire in 1991 and some burned in the Managed Meadow Fire in 2004. Patch 2: Lower Big Oak Flat Road, burned at high severity in the 1990 A-Rock Fire and again during the 2010 Big Meadow Fire. Patch 3: Hetch Hetchy: Burned in 2013 as part of the Rim Fire. All models have a probability raster which measures confidence in predictions. For visualization purposes, the probability rasters are averaged across the models.

technology enable detailed characterization of low-stature vegetation (Gavilan-Acuna et al., 2025), particularly in high severity patches with few instances of canopy occlusion. Our models, which employ a novel application of eigenvalue-based geometric features for classifying post-fire vegetation, successfully differentiated not only presence/absence but also cover density classes across all three vegetation types. This method has the potential to help researchers and managers to monitor post-fire vegetation patterns and identify where cover type transitions may be occurring.

The top performing geometric variables for the binary logistic regression models are ones that capture key structural characteristics of vegetation covers. For example, linearity, represents stem- and branch-like objects in the lower to mid-canopy, was important across all models (conifer, oak, and shrub). Its significance across all vegetation types indicates it is an important metric for distinguishing vegetation cover from non-vegetation cover (i.e. boulder fields, bare ground) found throughout the study area. Other important metrics varied by vegetation type. Vertical complexity in the upper canopies of regenerating conifers (90-99th percentile eigen minimum) and surface roughness in the mid to upper canopy of oaks (85th to 95th percentile rumple) were both important, reflecting the different morphological structures of these two vegetation types. The observed spectral responses of the models reflect physiological adaptations of different vegetation types, including phenological changes and timing of productivity (Joiner et al., 2018).

With limited sample sizes, model testing was essential to prevent overfitting and build robust models. Cohen's kappa scores suggest moderate to strong agreement across predictions, while reducing collinearity, cross-validation, and lambda parameter optimization minimizes the risk of overfitting. This predictive accuracy shows promising results; however, we were limited to the plot data available from the study and don't have the mapped vegetation types over large scales as a validation. Thus, maps detailing model error and confidence are essential to use alongside predictive maps to determine confidence in modeled prediction (Figure 2.10).

2.6.1.1 Conifer regeneration models

The variables selected for the conifer binary logistic regression model represented important morphological and phenological characteristics of this structurally emergent, evergreen vegetation type. The high vertical complexity of the upper canopy (90th to 99th percentile eigen minimum) associated with conifer presence captured the volumetric structure of the emergent vegetation. Conifer presence was also associated with stable photosynthetic activity across multiple seasons (low, negative NDVI Seasonal Difference), consistent with evergreen adaptations.

The conifer ordinal logistic regression model found that upper understory structural complexity metrics (90th-99th percentile eigen minimum and linearity) were important structural predictors. Interestingly, while conifer presence associated with greater upper-understory volumetric complexity (eigen minimum), conifer cover was positively associated with flatter, more planar upper understory structure (lower eigen minimum values) and reduced vertical stem complexity (lower linearity values). This suggests that while conifers are present in structurally complex sites, dense conifer regeneration occurs where the upper understory forms a more uniform canopy rather than scattered tall stems at lower densities. Spectral metrics also had strong coefficients in the conifer model, particularly the positive relationship between conifer cover and seasonal NDVI difference. Contrary to expectations for evergreen species, this relationship may reflect underlying site productivity differences, where dense conifer regeneration occurs on sites capable of supporting a seasonal herbaceous or graminoid understory, though this pattern requires further investigation.

2.6.1.2 Oak regeneration models

The binary logistic regression model characterized oak presence through high surface roughness in the mid to upper canopy (85th to 95th percentile rumple). This highlights the complex crown structures of regenerating oaks, which make them stand out among other vegetation types, as oak was the only type where rumple was a significant metric. Oak regeneration also corresponded to sites with increased seasonal variation (high, positive NDVI Seasonal Difference) and lower peak productivity (low June NDVI), patterns observed in other spectral oak mapping studies and attributed to their

deciduous physiology (Bohlin, Wallerman, and Fransson, 2016; Enayetullah et al., 2022).

The primary predictors of oak regeneration in the oak ordinal logistic regression model cover included rumple and interquartile range of the upper-understory (90th to 99th percentile) and planarity in the mid-understory (85th-95th percentile). These metrics emphasize the importance of canopy heterogeneity patterns of oak recruitment. Established oaks tend to have more developed crowns from adaptations such as crown resprouting, complex canopy architecture, and coppicing (Fry, 2008), all of which present as higher density of oak regeneration in our models.

2.6.1.3 Shrub regeneration models

The shrub binary logistic regression model variables demonstrated a phenological pattern consistent with vegetation water content, combining early-season productivity (high June NDVI) with a lack of late-season water retention (low, negative October NDII). This is a distinct feature of sclerophyllous vegetation, which has thick leaves adapted to survive in hot, dry climates, particularly in Mediterranean regions. Like the other two vegetation types, sites where shrubs were present were characterized by high linearity; however, no other structural metrics were selected in this model.

The ordinal logistic regression model variables followed a similar pattern, with more emphasis on spectral than structural metrics. The most important variable was early-season productivity (June NDVI), which decreased with greater shrub cover. This pattern is likely due to shrubs establishing in lower-productivity sites, ultimately filling a niche where conifers and oaks struggle.

2.6.2 Post Fire Regeneration Patterns

Using examples of each vegetation type, our methods highlight structural differences resulting from different fire behaviors, fire histories, and site conditions. While it is necessary to gather more information about pre-fire vegetation composition and landscape mosaics to effectively analyze type transitions, we can infer pre-fire site compositions from burned conifer snags and oak resprouting presence.

The Illilouette Basin has an active fire regime, supplemented by a prescribed burning program

that was established in the 1960s (Van Wagtendonk and James A. Lutz, 2007; Boisramé et al., 2017). This higher elevation site is characterized by cooler, wetter climate – conditions known to support conifer regeneration (Davis et al., 2019). The conifer model captured this phenomenon (Figure 2.10B), with higher amounts of conifer regeneration found in patches at this site compared to lower elevation, drier sites such as Lower Big Oak Flat Road and Hetch Hetchy. Oaks existed in small amounts in the Illilouette site with no identifiable pattern (Figure 2.10C). Shrubs were common here, and their cover increased with distance to patch edge (Figure 2.10D) and were associated with areas of lower conifer cover as has been observed by other studies in this region (Collins and Roller, 2013; Stewart et al., 2021).

Lower Big Oak Flat Road is a dry, south-facing slope that experienced a short-interval, high-severity reburn in 2012. Short-interval reburns can limit or delay conifer regeneration (Coppoletta, Merriam, and Collins, 2016) and obligate-seeding shrubs that require long fire return intervals (i.e. greater than 50 years) to develop seed banks (Nagel and Taylor, 2005; Van de Water and Safford, 2011). Conifers were absent across the patch (Figure 2.10F), suggesting delays in conifer regeneration following the high severity reburn. Oaks dominated the patch center with high cover (Figure 2.10G), while shrubs showed only low to moderate cover in these areas (Figure 2.10H), demonstrating oak resilience to compound disturbances and frequent, higher severity fire regimes (Cocking, Varner, and Knapp, 2014; Nemens et al., 2022). The dry, high-insolation site favors drought-tolerant oaks (M. F. Allen, 2015) and shade-intolerant shrubs (Zailaa, Scoffoni, and Brodersen, 2024).

The 2013 Rim Fire remains the largest fire recorded in Yosemite National Park. The specific Hetch Hetchy patch we examined is situated at one of the lowest elevations in the park and, as a result, faces the greatest risk of post-fire conversion from conifer forest to non-forest type (Donato, Harvey, and Turner, 2016; Parks et al., 2019). While the pre-fire vegetation varied, mixed conifer forest primarily dominated the area prior to the 2013 Rim fire (Figure 2.11). Our models show isolated patches of low conifer recruitment and an oak/shrub dominated landscape at six years post fire. The small pockets of low conifer regeneration throughout the patch (Figure 3-10J) indicate potential refugia for conifers to increase establishment density over time (A. M. Young et al., 2017) or maintain a more open spatial

pattern (Larson et al., 2013; R. Walker et al., 2019). Oaks were present at various covers, with low oak cover dominating the western part of the patch with pockets of intermittent high cover (Figure 2.10K). Shrubs were present in low to medium covers where oaks were present, and at high covers where oaks and conifers were low or absent (Figure 2.10L). As such, whether managers classify this patch as “type conversion” depends on the spatial and temporal scales at which they analyze it, as well as specific management goals for the site.



Figure 2.11: Photo of a plot in a resultant high severity patch in the Rim Fire footprint with manzanita, California black oak, and a burned conifer snag in the foreground looking toward the patch edge in the background where surviving conifer forest either burned at low severity or did not burn. There are no conifer seedlings present.

2.6.3 Management Implications

Land managers currently lack the tools to systematically assess post-fire vegetation across burned landscapes. The inability to comprehensively assess tree regeneration across large, burned ar-

feasibility constrains restoration efforts and forces managers to extrapolate from limited field plots or make assumptions based on coarse-scale maps of burn severity. The methods developed in this study represent a potential shift in post-fire management capability by providing comprehensive modeled maps of conifer, oak, and shrub regeneration across resultant high-severity fire patches using publicly available lidar and multispectral imagery. These detection methods allow managers to prioritize potential restoration locations based on actual regeneration status rather than relying on burn severity maps or limited field surveys.

Wildfire-driven conversion of conifer forests is a serious concern raised by land managers and scientists who are worried that large, high-severity patches will not support conifer regeneration due to a lack of a seed source and warming climate conditions (Coppoletta, Merriam, and Collins, 2016; Davis et al., 2019; Stevens-Rumann et al., 2022). One solution to this is conducting post-fire planting in sites which support conifer establishment but may be too far from a seed source requiring intervention (Donato, Harvey, and Turner, 2016; North et al., 2019). Success in post-fire planting depends on site conditions conducive to conifer survival, and plantings can fail when seedlings are placed in sites with unsuitable microclimate or heavy shrub competition (North et al., 2019). Our methods can delineate specific areas within high-severity patches that lack conifer establishment or have minimal conifer establishment, which could identify where planting could be targeted.

Oak restoration treatments are becoming an increasingly common topic among Sierra Nevada managers, driven by recognition of the ecological value of oak ecosystems and their decline due to fire exclusion and conifer encroachment (North et al., 2019; Stephens et al., 2023). The methods developed in this study offer novel opportunities for identifying and monitoring resprouting oak populations following wildfire, which offer critical wildlife habitat and cultural importance (Long et al., 2016; Hankins, n.d.). Specifically, managers could use post-fire vegetation mapping to prioritize post-fire environments where oaks have successfully resprouted for treatments that promote oak dominance, such as reducing conifer competition through selective thinning or prescribed fire. Conversely, maps could target areas lacking oak regeneration for planting or protection of remnant individuals (North et al., 2019). The ability to map oak distribution at landscape scales allows managers to assess the ef-

fectiveness of different post-fire management strategies on oak recovery, comparing outcomes across fires with different severities, time since fire, and management histories.

2.6.4 Spatial Modeling Advantages and Limitations

Earlier remote sensing techniques, including lower-resolution satellite imagery and airborne methods, struggled to detect understory vegetation with sufficient detail to characterize regeneration patterns (Dash et al., 2019; Gavilan-Acuna et al., 2025). Our use of high-resolution ALS dataset addresses these limitations by enabling landscape-scale assessment of regeneration cover while maintaining sufficient resolution to distinguish understory structures.

Despite the robust performance of these classification models, there are errors inherent to any predictive framework. A number of factors contribute to uncertainty in model predictions, including our plot sample size, the time lag between lidar acquisition and field work, and where plots were accessible by roads or trail in our study area. Areas of high model uncertainty may not be reliable for strategic planting and other post-fire management actions. Furthermore, for this method to be applied to new fires or forest types beyond our study area, validation datasets would be needed to assess transferability and recalibrate uncertainty thresholds. Incorporating uncertainty into operational workflows transforms model outputs from simple classification maps into decision-support tools that communicate prediction reliability, allowing managers to make informed choices about where remote sensing alone suffices and where they need additional data collection.

Finally, our methods do not identify which species of conifer, oak, and shrubs are regenerating. For example, species-specific information is important to understand conifer regeneration, with an increase of white fir into previously fire-adapted, pine-dominated systems altering ecosystem function and fire resilience (J. A. Lutz, van Wagtendonk, and Franklin, 2009; Collins, Lydersen, et al., 2018). While we were unable to differentiate between conifer species, inferences can be made about their regeneration patterns, with red fir, white fir, and lodgepole pine establishing in larger densities than Jeffery or ponderosa pine (Welch, Safford, and T. P. Young, 2016). However, vegetation type maps or local field surveys could be used as additional validation to complement our models when extrapolating

to other areas in the Sierra Nevada.

2.7 Conclusion

This study introduces innovative methods for identifying regeneration among conifer, oak, and shrub vegetation after high severity fire using high-resolution ALS datasets. While developed in Sierra Nevada mixed-conifer forests, our framework is potentially transferable to other fire-prone ecosystems where post-fire regeneration dynamics drive forest recovery trajectories. This approach is particularly valuable given the diversity of vegetation responses to fire; while conifer regeneration failures often dominate management concerns, understanding spatial patterns in oak woodland and shrubland regeneration is equally critical, as these ecosystems provide essential wildlife habitats, erosion control, and fire-resilient vegetation that may represent stable alternative states in a warming climate.

Furthermore, this study sets the stage for evaluating the biophysical drivers of regeneration using variables such as climate, topography, and distance to seed source. This forthcoming research (Redford et al. *in prep*) can be used to predict future vegetation trajectories under different climate scenarios, assess carbon sequestration potential across regenerating landscapes, and develop monitoring protocols as remote sensing data becomes more accessible. As high-severity fires become more common and resources for active restoration remain limited, predictive models of post-fire regeneration offer a foundation for adaptive management decisions that acknowledge the ecological value of post-fire communities.

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Appendix

Table S1: Model performance metrics for binary (logistic) and ordinal logistic regression models by vegetation type.

Vegetation Type	Model Type	Variables	Metric Category	Metric	Value
Conifer	Logistic Regression	emin_90to99, linear_55to85, octndii	Overall	Accuracy	0.700
			Overall	Kappa	0.400
			Binary Metrics	Sensitivity	0.667
			Binary Metrics	Specificity	0.733
			Binary Metrics	Precision	0.688
			Binary Metrics	Recall	0.733
			Binary Metrics	F1 Score	0.710
Oak	Logistic Regression	emin_90to99, iqr_85to95, linear_55to85, rumple_85to95, octndii	Overall	Accuracy	0.765
			Overall	Kappa	0.529
			Binary Metrics	Sensitivity	0.765
			Binary Metrics	Specificity	0.765
			Binary Metrics	Precision	0.765
			Binary Metrics	Recall	0.765
			Binary Metrics	F1 Score	0.765
Shrub	Logistic Regression	emin_90to99, junendvi, octndii	Overall	Accuracy	0.821
			Overall	Kappa	0.643
			Binary Metrics	Sensitivity	0.821
			Binary Metrics	Specificity	0.821
			Binary Metrics	Precision	0.821
			Binary Metrics	Recall	0.821
			Binary Metrics	F1 Score	0.821

Vegetation Type	Model Type	Variables	Metric Category	Metric	Value
Conifer	Ordinal Logistic Regression	emin_90to99, seasDiff_ndvi, taos_90to99, iqr95_90to99, junendii, linear_55to85, linear_90to99	Overall	Accuracy	0.727
			Overall	Kappa	0.590
			Low Class	Sensitivity	0.750
			Low Class	Specificity	0.925
			Medium Class	Sensitivity	0.667
			Medium Class	Specificity	0.820
			High Class	Sensitivity	0.769
			High Class	Specificity	0.843
Oak	Ordinal Logistic Regression	rumple_90to99, iqr95_90to99, planar_85to95, linear_85to95, taos_90to99, emin_85to95	Overall	Accuracy	0.621
			Overall	Kappa	0.428
			Low Class	Sensitivity	0.800
			Low Class	Specificity	0.842
			Medium Class	Sensitivity	0.444
			Medium Class	Specificity	0.850
			High Class	Sensitivity	0.600
			High Class	Specificity	0.737
Shrub	Ordinal Logistic Regression	junendvi, linear_55to85, octndvi, planar_85to95, taos_55to85, linear_85to95	Overall	Accuracy	0.663
			Overall	Kappa	0.495
			Low Class	Sensitivity	0.759
			Low Class	Specificity	0.850
			Medium Class	Sensitivity	0.484
			Medium Class	Specificity	0.810
			High Class	Sensitivity	0.759
			High Class	Specificity	0.833

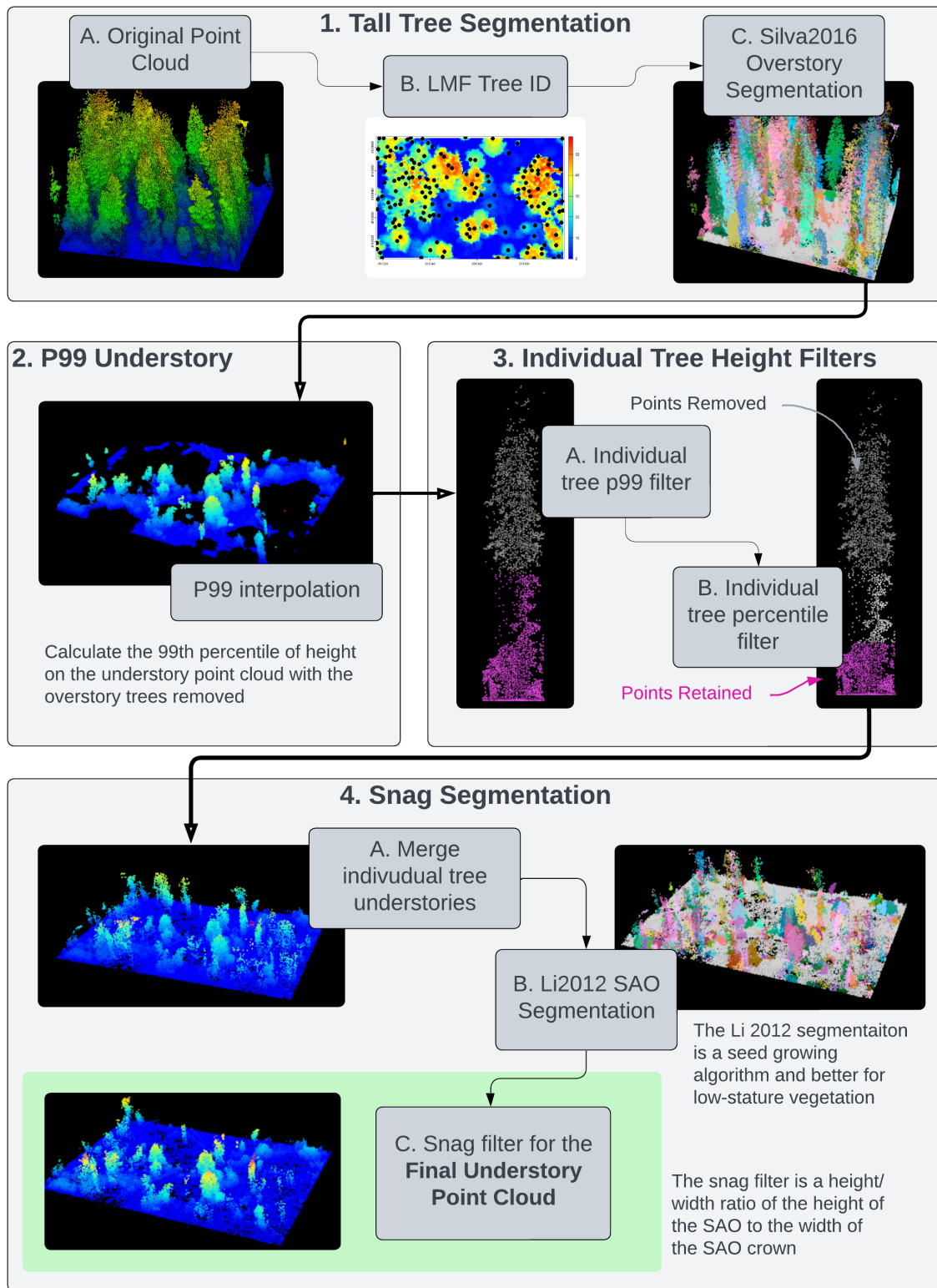


Figure S1: Understory segmentation workflow steps using the Yosemite site as an example. The workflow starts with tall tree segmentation, then calculates understory p99 heights, then filters individual tree vegetation, and finally segments snags.

Chapter 3: WUI housing loss in the 2020 Creek Fire: fire behavior stage moderates the role of lidar-derived fuel structure

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3.1 Abstract

Wildfire-driven housing loss increasingly affects residents of the wildland urban interface (WUI), where built communities intersect with wildland vegetation. Disentangling the drivers of this loss is challenging because numerous factors govern whether a structure survives or is destroyed. Among these, defensible space mitigation is particularly important because it falls under the direct control of the resident, yet it remains difficult to monitor and measure at scale. We used the 2020 Creek Fire as a case study, drawing on high-resolution lidar acquired two months prior to the event to measure defensible space fuels across three home ignition zones and assess their influence on housing loss. To account for unmeasured variables in our dataset, including community type, firefighting effects, and fire behavior, we stratified the fire into three stages: Blowup (the most extreme fire behavior), Rapid Expansion (a shift in fire behavior as the fire moved into different communities), and Flanking and Containment (the mildest fire behavior). By examining the drivers within each stage, we found that fuels measurements varied across the progression of the fire according to community archetypes. Fuels exerted the greatest influence during the most extreme stages. Housing density emerged as the dominant factor during the mildest stage, where increased density led to increased probability of survival, likely due to firefighting activities at the later stages of the fire. These results indicate that no single variable fully predicts housing loss, even within a single event. This finding suggests that the drivers of housing loss will likely differ from fire to fire, and that high-resolution fuel measurements are essential to capturing this variation. Our methods can inform residents of their

vulnerability to wildfire by providing a probability of destruction rather than a definitive outcome.

3.2 Introduction

Globally, wildfires have increased in area burned and severity over the past several decades (Jones et al., 2022; Cunningham, Williamson, and D. M. J. S. Bowman, 2024), contributing to widespread structure loss in wildland-urban interface (WUI) zones (Radeloff et al., 2018; Schug et al., 2023). Increasingly long and severe wildfire seasons are driven by a combination of anthropogenic climate change, prolonged drought, and legacy fuel accumulation (Keeley and Syphard, 2016; Westerling, 2016; Abatzoglou and Williams, 2016), while continued expansion of development into fire prone areas places more homes and residents at risk (Radeloff et al., 2018). As fire behavior becomes more extreme, a growing number of residential structures are exposed to high-intensity fire under short response windows (Higuera et al., 2023; Balch et al., 2024; Carlson et al., 2025; Kumar et al., 2025).

Housing loss in the WUI can be attributed to a range of causes. Factors including distance to nearest burned structure (Knapp et al., 2021), spatial arrangement of homes (Alexandre et al., 2016; Syphard, Rustigian-Romsos, and Keeley, 2021), home hardening (Syphard and Keeley, 2019), WUI-adjacent fuel treatments (A. M. Smith et al., 2016; D. Bowman, 2018), community fuel networks (Kolden and Henson, 2019), and property-level fuels (Escobedo et al., 2025; Zamanialaei et al., 2025) have all been found to contribute to housing loss across different fires and scales. Because outcomes are influenced by the interaction of all factors, the relative importance of any single factor, particularly defensible space, varies across studies, scales, and fire events (Syphard, Rustigian-Romsos, and Keeley, 2021). However, the ability of any single resident to implement these mitigations depends on a variety of socio-economic filters. Home hardening is expensive, spatial arrangement is decided at subdivision, and landscape-scale treatments happen on public lands through expensive, agency-led efforts. Defensible space is an intervention residents can act on, and it is the main target of property-scale wildfire policy.

Resident fuel mitigation decisions depend not only on measured hazards but also on threat ap-

praisal and response efficacy, both of which are shaped by information residents receive about their own risk (Wilson, McCaffrey, and Toman, 2017; Dupey and J. W. Smith, 2019; Meldrum et al., 2019; Larsen et al., 2025). Parcel-level studies have shown that perceived vulnerability often diverges from measured hazards driving housing loss (Paveglio, Edgeley, and Stasiewicz, 2018; Meldrum et al., 2019; Larsen et al., 2025). In California, defensible space compliance is assessed through ground-based inspections conducted by CAL FIRE on State Responsibility Area lands (CA Public Resources Code 4291) and by local agencies on Local Responsibility Area lands within designated Very High Fire Hazard Severity Zones (CA Code 51182; CAL FIRE, 2024). These inspections tend to inaccurately characterize defensible space mitigations (Wilkin, Benterou, and Stasiewicz, 2025), limiting the information residents and agencies use to appraise risk. The disconnect between perceived threat and actual threat indicates that better frameworks are necessary for measuring and integrating risk when studying the drivers of housing loss.

Wildfire management has historically operated under a simple risk framework, in which top-down, expert-driven fuel reduction strategies are applied to complex social-ecological systems (Essen et al., 2023; Larsen et al., 2025). In contrast, complex risk framing treats wildfire outcomes as a result of interactions across scales, actors, and conditions that cannot be fully captured by any single management activity (Essen et al., 2023). Applying a complex risk framework requires fuel measurements that account for fine-scale fuel variability which can more accurately and consistently inform residents of their wildfire risk. This is a step in bridging the gap between perceived threat and actual threat in WUI communities.

Fine-scale fuel structure around homes is one dimension of the inherent complexity present in WUI communities that remains difficult to measure. Efforts to link defensible space to structure outcomes are constrained by the spatial resolution and dimensionality of available fuel data. Past studies have relied on coarse, remotely sensed vegetation measurements at ~30-m resolution (Alexandre et al., 2016; Syphard, Rustigian-Romsos, and Keeley, 2021), at which scale spatial arrangement of homes and topography consistently outranked fuel composition as predictors of housing loss. More recent work has incorporated lidar and high-resolution imagery, but fine-scale fuel information is often aggregated

into simplified, one-dimensional metrics. Zamanialaei et al. (2025) derived Vegetation Separation Distance (VSD) from lidar to measure horizontal distance from fuels to the home and found VSD ranked lower in variable importance than home hardening and spatial arrangement, though simulated vegetation mitigation reduced structure destruction. Post-fire studies have also relied on homeowner self-reports and simple distance-based buffers, none of which capture the vertical and horizontal complexity of vegetation structure around homes. This lack of fine-scale, three-dimensional fuel data makes it difficult to isolate the components of fuel structure that contribute to ignition.

In this study, we introduce the use of high-resolution airborne lidar to measure fuel compositions as they relate to parcel-level defensible space. Lidar penetrates forest canopy and resolves sub-canopy fuel structure, providing a more complete characterization of fuels across defensible space zones than imagery or ground-based inspections alone (Wing et al., 2012; Venier et al., 2019). By linking fine-scale, three-dimensional (3D) fuel measurements with fire behavior and housing density across communities and fire stages, we account for the multi-scale interactions that shape wildfire risk at the parcel level. Our objectives are to: (1) use airborne lidar to measure property-scale fuel structure across defensible space zones using high-resolution fuel measurements; (2) assess how the relationship between fuel structure and structure loss changes across different fire behavior conditions and communities within a single fire; and (3) compare the relative contributions of vegetation structure and housing density to structure outcomes across fire behavior stages.

3.3 Study Area

The 2020 Creek fire burned primarily in the San Joaquin Watershed in the Southern Sierra Nevada Mountains, ranging from low-elevation chaparral and oak woodlands to high-elevation and cold forest alpine environments. Across the study area, individual homes and communities of homes are classified as Wildland Urban Interface, representing both low to high housing density were present before the fire. In this study, we define the wildland-urban interface (WUI) as areas with more than one housing unit per 40 acres that meet one of two vegetation criteria (Stewart et al., 2007): interface WUI, where wildland vegetation covers more than 50% of the immediate land area, or intermix WUI,

where wildland vegetation covers less than 50% locally but more than 75% of the surrounding 1.5-mile area.

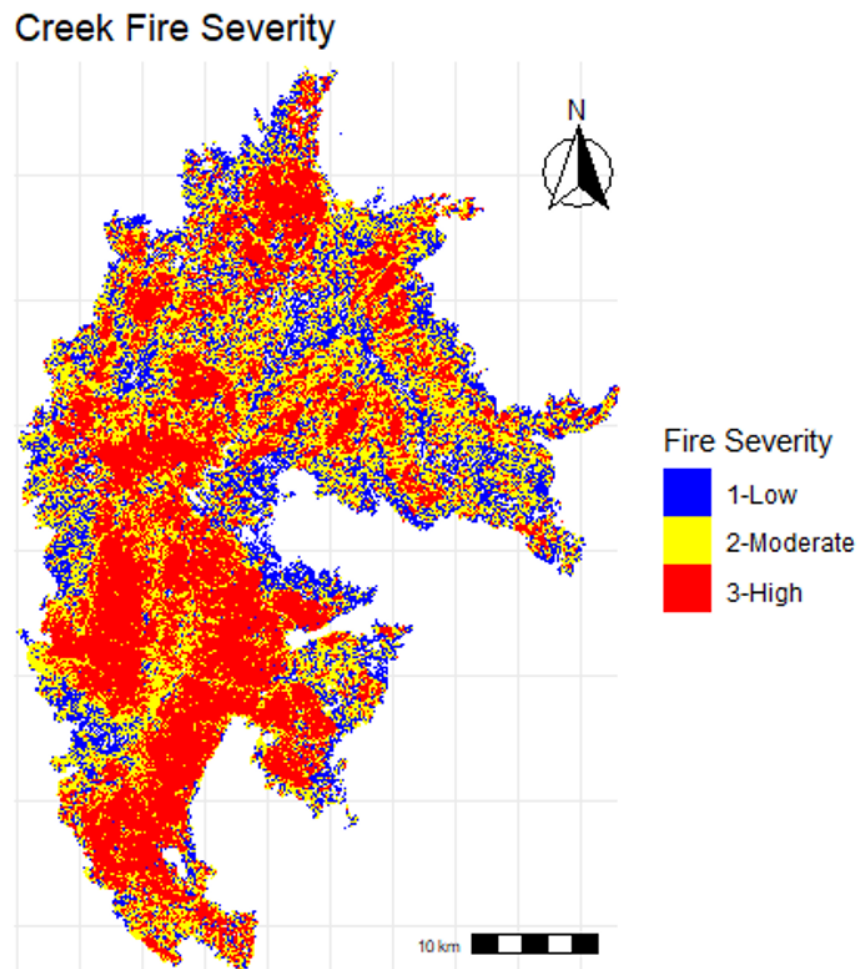


Figure 3.1: Creek Fire Burn Severity Map. Calculated using the Composite Burn Index (CBI) two years post-fire.

The fire began on September 4, 2020 as a suspected lightning ignition during an extended period of hot, dry conditions and rapidly escalated into one of the largest and most severe wildfires in California history (Figure 3.1). Fueled by extreme drought, record-setting temperatures, and dense, overstocked forests with high fuel loads, the fire exhibited rapid growth, including a 24 km run in a single burn period during its first 24 hours (Stephens, Bernal, et al., 2022). It ultimately burned 153,738 hectares across the Sierra National Forest and surrounding communities (CAL FIRE, 2020), with intense fire behavior characterized by frequent crown fire, long-range spotting, and pyrocumulus

development (Stephens, Bernal, et al., 2022; J. M. Lee et al., 2023). The Creek Fire destroyed 856 structures, including single-family residences, schools, utility buildings, and businesses.

The Creek Fire impacted communities with attributes distinct from those typically represented in WUI fire analyses. In an exploratory analysis, we found that the structures impacted by the Creek Fire were primarily built prior to the 2000s, when construction began implementing more fire-resistant building materials and methods (Syphard, Brennan, and Keeley, 2017; Knapp et al., 2021). Furthermore, housing densities averaged 0.8 units per acre, with over 90% of homes at distances greater than 30 m from destroyed homes. We used these differences to guide our analysis through an approach which accounts for the differences in structural and spatial characteristics conducive to more rural, recreational communities in the Sierra Nevada.

3.4 Datasets

3.4.1 DIS Database

The home structure data used to conduct this analysis was derived from the CALFIRE Damage Inspection (DIS) database (obtained from CAL FIRE 09/13/ 2022). The DIS is a program that records damage and destroyed structures because of wildfire in California since 2013. The database includes structural information about the affected buildings such as building type, home hardening properties, and the damage status in the fire. There were few records for individual structures in this database that provided complete information on the building and home hardening properties, so for this analysis that metric was excluded. The records were filtered to only include single family units and multi-family units. The resulting layer was a point shapefile that included the location and status of each building (Figure 3.2).

3.4.2 Lidar Acquisition

Two months prior to the ignition of the Creek Fire, airborne laser scanning was conducted across 1,921 square miles of the southern Sierra Nevada, which captured a large portion of what was to become the fire footprint (SSARR, 2019). The dataset is classified as United States Geological



Figure 3.2: Locations of structures within the Creek Fire perimeter, classified by damage status from the CAL FIRE Damage Inspection (DIS) database. Points show structures that were destroyed ($>50\%$ damage, red) or undamaged (blue) following the 2020 Creek Fire in the southern Sierra Nevada, California. Most structures were concentrated in the southern portion of the fire near the communities of Pineridge and Shaver Lake.

Survey (USGS) 3D Elevation Program (3DEP) Quality Level 1 data at 9.4 pulses per m² with 55% side overlap, providing a dataset suitable for high-resolution mapping of fuels within the WUI.

Buildings were classified as ASPRS (American Society for Photogrammetry and Remote Sensing) Class 6 by the vendor as part of the USGS 3DEP lidar acquisition, following the LAS specification (ASPRS, 2013) and the USGS Lidar Base Specification (Heidemann, 2018). We filtered the point cloud to include only classified structures with a corresponding DIS record and added a 0.25 m buffer around each home to capture points that may have been missing (e.g., walls, building points obscured by vegetation). We also removed any records that had an unclassified structure within 30-m, identified using the DIS Database structures, as these points would influence fuel measurements within the defensible space zones. The resulting point clouds contained only correctly classified, buffered structures, which were then removed prior to calculating fuel measurements.

Home Ignition Zones (HIZs) were divided into three zones based on distance from a structure and recommended fuel management practices from CalFire. Zone 0, the immediate zone, encompasses the first 2 meters of a structure, where recommendations state all combustible materials should be cleared. Zone 1, the intermediate zone, extends from 2 to 10 meters and focuses on removing dead fuels and promoting fuel separation. Zone 2, the furthest zone from the building, covers 10 to 30 meters, where the emphasis shifts to fuel spacing among larger trees rather than low-stature shrubs and fine fuels due to the greater distance from the structure. To delineate defensible space HIZs, we buffered each zone sequentially, starting with Zone 0 at 2 m, Zone 1 at 10 m from the Zone 0 boundary, and Zone 2 at 30 m from the Zone 1 boundary.

To measure fuel loads surrounding the structures, we calculated lidar-based canopy cover in the 1-2, 2-4, 4-8, 8-16, and >16 m height strata within each HIZ (Figure 3.3). The thresholds are used in lidar forest structure assessments (Kane et al., 2014) and in understory mapping (Redford et al., *in prep*). Points under 1 m were omitted in this analysis as it is difficult to differentiate ground points from fuel points in this stratum. The 1-2 and 2-4 m height strata represent low-stature shrub fuels, often smaller regenerating trees or shrubs. The 4-8 and 8-16 m strata are conducive to ladder fuels, which carry fire into the canopy of forest vegetation. Fuels >16 m are generally considered as individual tree

crowns. We also added a vegetation metric that measured the vegetation over the highest point of the classified structure, vegetation over home.

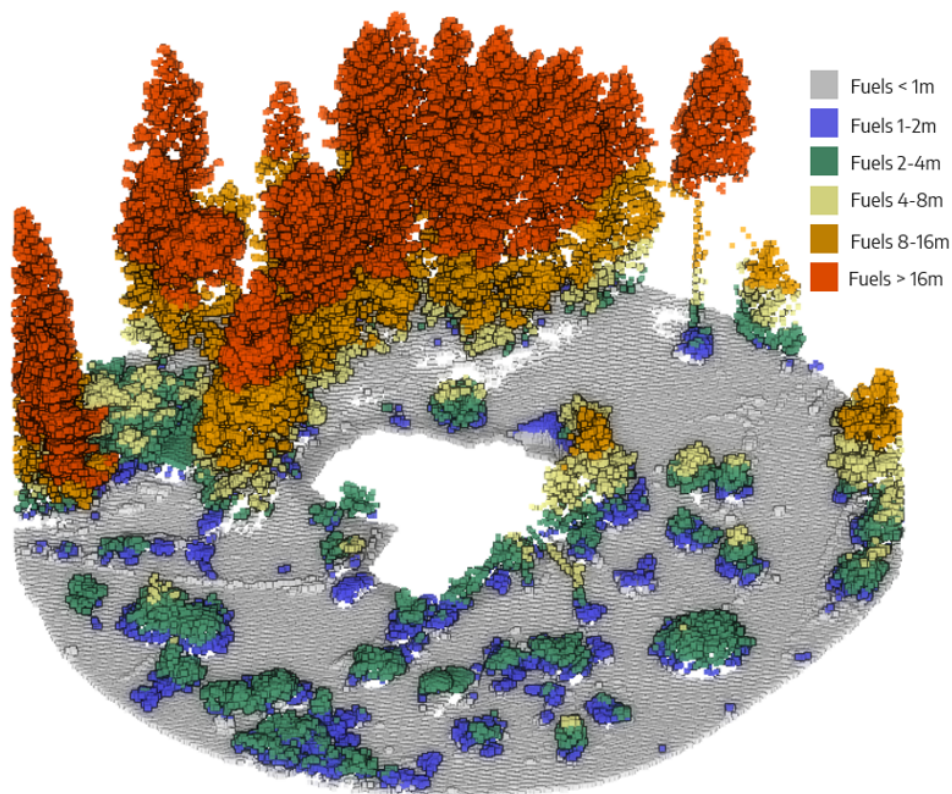


Figure 3.3: Example lidar point cloud centered on a single structure footprint in the Creek Fire study area, with the structure removed and points classified into six height strata. Fuel metrics were calculated within each height class across three defensible space zones surrounding each structure. Point classification: gray (< 1 m), blue (1 to 2 m), green (2 to 4 m), pale yellow (4 to 8 m), gold (8 to 16 m), and orange (> 16 m).

3.5 Methods

The goal of these methods was to quantify how fine-scale fuel structure within home ignition zones influenced housing loss during the Creek Fire, given that variables such as firefighting efforts, fire behavior, and building material were unavailable as explicit predictors. First, we derived canopy cover across five height strata within three home ignition zones along with housing density, providing a parcel-scale set of predictors describing the fuel arrangement and community spatial patterns. To

address the influence of the unmeasured variables, we split the fire into three stages based on fire behavior and timing, which accounted for unexplained variance in the full-extent model. Within these three stages, we compared the coefficient of variation (CV) of our variables, model fit (AUC), and SHAP-based contributions.

3.5.1 Spatial Modeling

For each structure, we calculated a suite of lidar fuel metrics and housing density values. At each defensible space zone (Zone 0, Zone1, Zone 2) we measured canopy cover across five height strata (1-2, 2-4, 4-8, 8-16, and >16 m) to account for fuel distribution of both distance from the structure and vegetation height. Points below 1 m were excluded as ground returns are difficult to separate in this stratum (). The 1-2 m stratum captured low-stature shrub fuels and regenerating trees; the 2-4 and 4-8 m strata captured ladder fuels capable of carrying fire into the canopy; and fuels 8-16 and > 16 m correspond to canopy fuels. Housing density was calculated as structures per acre within a 200 m radius of each home, using the housing-units-per-acre framework that CAL FIRE's Fire and Resource Assessment Program (FRAP) uses for wildland-urban interface and community wildfire risk classification (CAL FIRE, 2018).

Because housing loss in the Creek Fire is spatially autocorrelated, meaning structures near other structures tended to share similar destruction or survival outcomes, our dataset violated the assumption of independent residuals. To assess the amount of spatial autocorrelation in our datasets, we calculated Moran's I on both the response variable and the residuals of the data (Moran, 2021). We defined a weighted distance using a 200 m threshold based on a semivariogram of the response variable where the sill plateaued around 700 m. Moran's I was first calculated on the raw binary damage outcome to confirm that spatial clustering was present, then on deviance residuals from the full spatial model to assess whether the spatial smooth adequately addressed it. All calculations used the "spdep" package in R (Bivand and Wong, 2018).

Accounting for the spatial autocorrelation of the structure dataset also required a model capable of handling spatial effects. We used spatial Generalized Additive Models (GAMs) to identify fuel

structure variables which contributed to housing loss and survival. Prior studies have favored GAMs when studying non-linear relationships of housing loss with fire variables (Syphard, Keeley, Massada, et al., 2012; Ager et al., 2021; Raveendran et al., 2025). To capture the spatial relationships in the data, the GAM uses a spatial term, $s(x, y)$ to model spatially varying risk across the fire extent as a Duchon spline smooth of geographic coordinates. This term accounts for spatially structured processes not captured by the fuel variables alone, such as fire progression patterns, local weather effects, neighborhood characteristics, and firefighter access.

Variables were selected for each model through the Marra and Wood double-penalty approach (Marra and Wood, 2011). This method fits each candidate covariate as a penalized smooth term using thin plate regression splines with an additional shrinkage penalty that allows the smooth to be penalized to exactly zero (Equation 1). Variables with effective degrees of freedom (EDF) greater than 0.5 were retained in the full spatial GAM model (Equation 2), while variables penalized below this threshold were considered effectively removed from the model. We calculated the GAMs and their variable selection using the gam package in R.

Equation 1: Marra and Wood Double Penalty (Marra and Wood, 2011)

$$\text{logit}(E(Y_i)) = \beta_0 + \sum_{j=1}^P f_{j(z_{ji})} + s(x_i, y_i) \quad (3.1)$$

where:

- i = each individual structure
- p = the number of candidate fuel and density covariates
- $\text{logit}(E(Y_i))$ = the log-odds of the expected probability of housing loss for structure i
- β_0 = intercept
- $f_{j(z_{ji})}$ = penalized thin plate regression spline with double-penalty shrinkage for covariate j . Variables with $\text{EDF} > 0.5$ are retained; variables penalized to zero are removed.
- $s(x_i, y_i)$ = 2D Duchon spline smooth of spatial coordinates for structure i

Equation 2: Logistic GAM with Duchon Spline (Wood, 2017)

$$\text{logit}(E(Y_i)) = \beta_0 + \beta_1 z_{1i} + \cdots + \beta_p z_{pi} + s(x_i, y_i) \quad (3.2)$$

where:

- i = each individual structure
- p = the number of variables retained during variable selection
- $\text{logit}(E(Y_i))$ = the log-odds of the expected probability of housing loss for structure i
- β_0 = the intercept
- $\beta_1 z_{1i} + \cdots + \beta_p z_{pi}$ = linear fuel and density covariates retained by Marra and Wood double penalty method
- $s(x_i, y_i)$ = 2d Duchon spline smooth of spatial coordinates for structure i

Although the spatial approach is essential to this analysis, we also wanted to account for and understand larger-scale differences in community structure and fire behavior that may contribute differently to housing loss. Therefore, we conducted a nested analysis, beginning with a full-extent model that explores overall interactions of the explanatory variables across the entire fire (Full-Extent Analysis – Section 4.4.2), followed by a second modeling phase, where we split the data reflecting three temporal stages of burning during the fire (Stage-Stratification – Section 4.4.3), to better account for potential differences in fire behavior, community structure, and fuel configurations. The models in the full extent and stage stratification use the same modeling framework.

3.5.2 Preliminary Full-Extent Analysis and Justification for Stage Stratification

Most WUI studies estimating the drivers of housing loss analyze the entire fire extent to identify the most important predictors. We began with this approach to establish a baseline understanding of housing loss across the Creek Fire and to assess whether fuel structure and housing density identified distinct signals when modeled together. The full extent analysis was also important for evaluating whether a single model could adequately quantify housing loss across a diverse study area, or whether residual spatial autocorrelation reflected unexplained variance that warranted further stratification into

fire stages.

To analyze the drivers of housing loss across the entire study area, we tested iterations of variables with four spatial GAMs for the full-extent analysis: housing density, fuels, housing density and fuels, and only the spatial term. We compared cross-validated ($k=5$) ROC curves of each model to determine if there was any difference in modeling the housing density separate from the fuel variables.

AUC scores were closely clustered (0.882 to 0.889), and the ROC curves followed nearly identical trajectories regardless of whether fuel variables, housing density, or both were included alongside the spatial smooth (Figure 3.4). This indicates that the spatial term is driving most of the predictive performance in the full-extent model, with fuel and density variables contributing only marginal improvement.

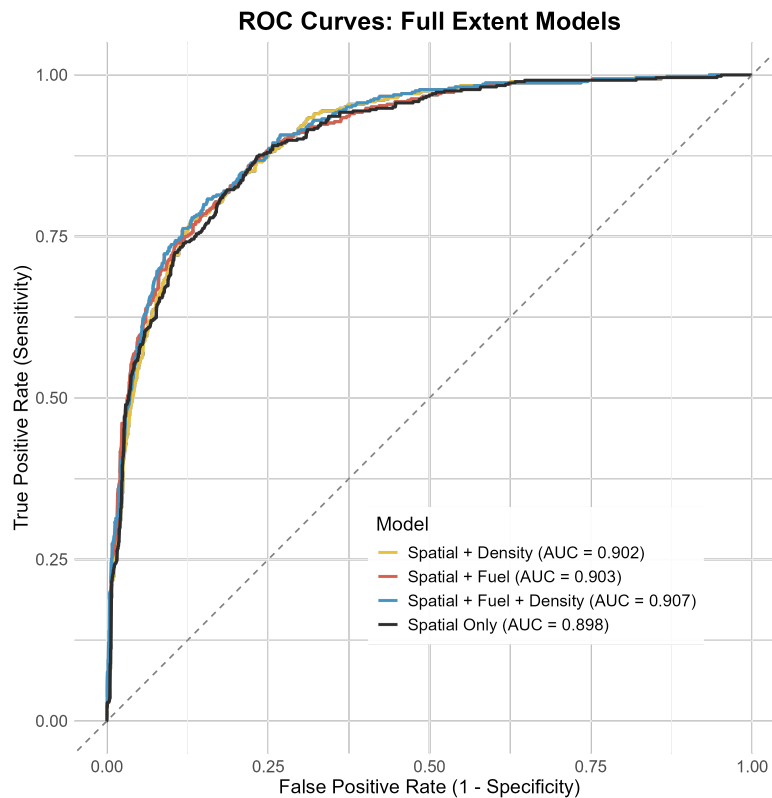


Figure 3.4: Receiver Operating Characteristic (ROC) curves comparing four full-extent spatial GAMs with different predictor combinations, evaluated using 5-fold cross-validation. All four models produced nearly identical performance (CV AUC = 0.882 to 0.889), with overlapping curves indicating that the spatial smooth drove most of the predictive performance regardless of whether fuel variables, housing density, or both were included. The dashed diagonal represents the no-discrimination line (AUC = 0.5).

After fitting the model, we investigated whether the spatial smooth was capturing some aspect of fire behavior. Modeled fire behavior products would introduce additional error due to coarse spatial resolution and uncertainty in input parameters, so we instead used satellite-derived fire severity as a proxy for fire behavior. Relativized Burn Ratio (RBR) provides an empirical measure of fire effects on the landscape and correlates with fire intensity and rate of spread. We ran a Spearman's correlation between the estimated spatial effect and RBR values to determine if a meaningful relationship existed between the two. The correlation between the spatial effect and fire severity was 0.53 (Figure 3.5). This relationship suggests that the spatial smooth is at least partially tracking variation in fire severity across the landscape.

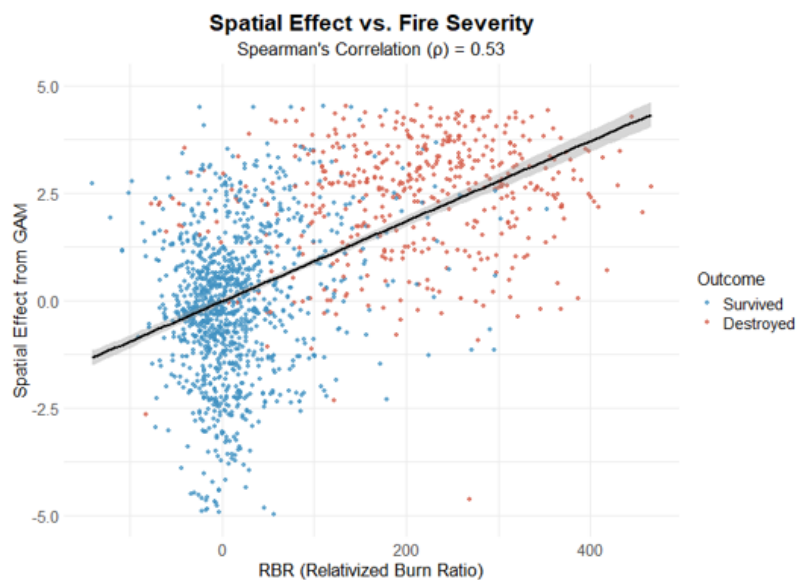


Figure 3.5: Despite the spatial smooth's strong predictive contribution, residual spatial autocorrelation remained. Moran's I calculated on the raw binary damage outcome was 0.559, confirming that spatial clustering was present in the response. After fitting the full-extent spatial GAM, the residual Moran's I was 0.254, showing that the spatial smooth reduced autocorrelation but did not eliminate it.

In addition to capturing fuel effects across the fire, we also wanted to account for larger-scale differences in community structure and fire behavior that may contribute differently to housing loss across the fire's progression. The full-extent preliminary analysis reinforced this approach statistically. The relationship between the spatial smooth and RBR indicated that fire behavior was a major driver of the spatial effect, and including fire severity directly as a predictor would overwhelm fuel signals

given its relationship with housing loss. Splitting the data by fire behavior stage allowed us to account for fire behavior differences, firefighting effects, and community structure while isolating the effects of fuels on housing loss.

3.5.3 Stage Specific Models: Extracting Fuel Drivers

3.5.3.1 Stage Stratification

After the response matrix was split according to fire stage, we tested the Morans I of houses in each fire stage to assess spatial autocorrelation of the stratification. The Morans I of the Blowup stage was 0.39, Rapid Expansion was 0.62, and Flanking/ Containment was 0.52 indicating high spatial autocorrelation of the data. The residuals of the fuel + density + spatial models had Morans I values of -0.09, 0.18, and 0.08 respectively, indicating that the spatial GAM model greatly reduced autocorrelation of the data compared to the full extent model.

Results from the full-extent model indicated that the spatial smooth largely captured variation attributable to fire behavior, though residual spatial autocorrelation remained. To isolate the effects of fuels on housing loss under different fire conditions and further address spatial structure in the data, we split the data into three stages corresponding to major fire behavior events: Blowup, Rapid Expansion, and Flanking/Containment (Figure 3.6). This stratification allows fuel-housing relationships to be evaluated regardless of confounding variables such as fire behavior and community attributes while limiting the spatial extent of autocorrelation.

We adopted an approach that categorized fire behavior at a multi-day scale to address data limitations and improve analytical consistency. Daily National Infrared Operations perimeters (NIROPS, USDA Forest Service, 2020), expert interpretation, and the DIS database revealed substantial variability in fire spread and intensity across days. Some days experienced rapid fire spread and large-scale housing loss, while others had low or inconsistent impacts on housing outcomes (Figure 3.7). However, the number of days that contained over 100 single-family home records was too small to support robust modeling at a daily scale. Therefore, we grouped the fire into three stages that captured major transitions in fire behavior and progression.

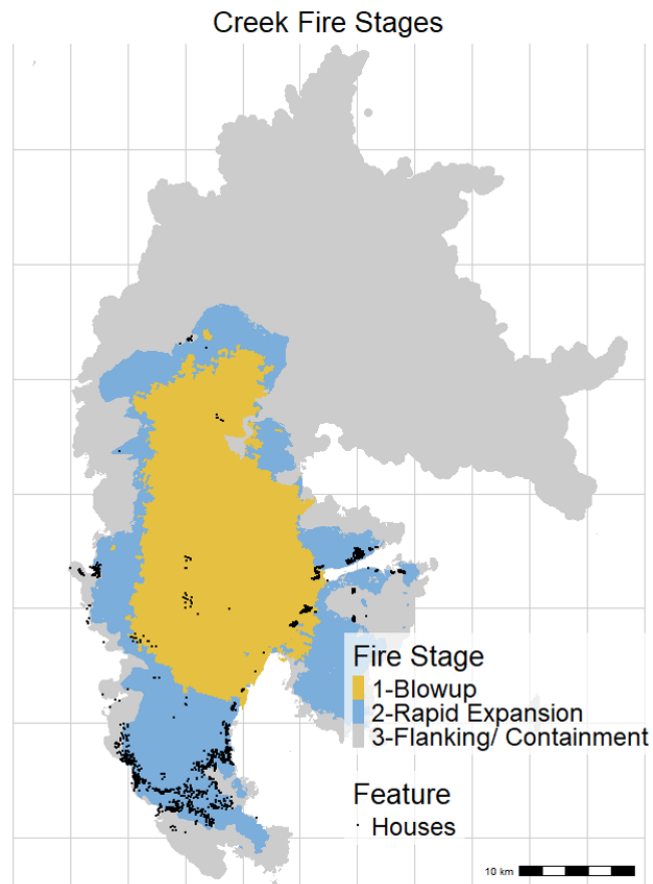


Figure 3.6: Map of the fire stages overlayed with house locations. The Fire Stages were delineated using NIROPS data from flown daily fire perimeters.

3.5.3.2 Statistical Differences Across Stages

When splitting data across temporal boundaries, there is a risk that each fire stage captures different vegetation conditions rather than different fire behavior contexts. For example, homes in the Blowup stage may be situated in denser communities with less surrounding vegetation, meaning the model could be detecting differences in community fuel structure rather than isolating how fuels interact with fire behavior. To test this, we ran Kruskal-Wallis tests on each fuel variable across the three stages to determine whether vegetation cover differed significantly. Subsequently, we calculated the coefficient of variation to quantify the magnitude of any differences.

We used 5-fold cross validation to evaluate model prediction accuracy for each fire stage. For each fold, the model was trained on 80% of the data and predictions were generated for the held out 20%. We compared cross-validated AUC values across spatial only, nonspatial fuel-only, nonspatial density-only, and spatial-fuel-density models to assess how much predictive performance each component contributed within each stage.

3.5.3.3 Variable Importance

To interpret the relative influence of explanatory variables on housing loss predictions within each stage-specific model, we used SHapley Additive exPlanations (SHAP; (Lundberg and S.-I. Lee, 2017)). SHAP values quantify the marginal contribution of each variable to a given prediction by computing the average change in the predicted outcome when a variable is included versus excluded across all possible combinations of variables. This produces a per-observation, per-variable measure of contribution that accounts for interactions and nonlinearities, which makes it well suited for interpreting GAMs where smooth terms can make it difficult to tease apart individual variable importance. We calculated SHAP values for fuel and housing density variables in each stage-specific model using permutation-based estimation via the “fastshap” package with 50 simulations (Greenwell, n.d.). To isolate the effects of these variables, we fixed spatial coordinates to their median values during SHAP computation, holding the spatial component constant so that the resulting values reflect only fuel and density contributions.

3.6 Results

3.6.1 Stage Stratification

The Creek Fire ignited on the night of September 4, 2020, in rugged terrain near the Big Creek community in the Sierra National Forest. On September 5th, the fire transitioned into an extreme event, producing a pyrocumulonimbus cloud that towered nearly 16-km into the atmosphere (J. M. Lee et al., 2023). The plume-driven firestorm generated its own winds, feeding the fire in nearly all directions and causing ember showers and spot fires miles ahead of the flaming front. From September 5 through 7, the fire rapidly accelerated north through the San Joaquin River Valley (NIROPS; Figure 3.7). During this initial stage, the fire exhibited aggressive crown fire behavior and extensive spotting, with embers igniting new fires more than half a mile ahead of the main front (Stephens, Bernal, et al., 2022). By September 7, the fire had grown to around 32,000-ha in size, prompting widespread evacuations in communities including Big Creek and Huntington Lake. Because much of the early fire burned through public land, the fire only encountered 120 houses during the initial stage (Table 3.1).

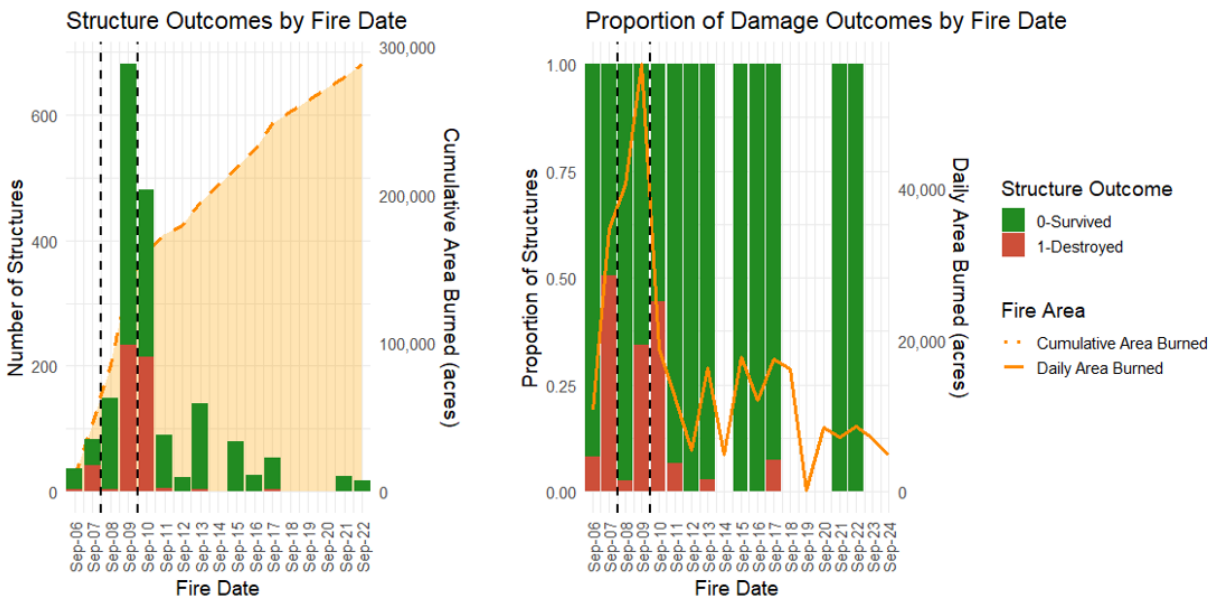


Figure 3.7: Housing loss by day in the Creek Fire, in 2020, in the southern Sierra Nevada, California, USA. The first plot examines total housing loss counts, the second plot looks at the proportion of housing loss per day.

On September 8, 2020, an offshore wind event shifted the Creek Fire’s behavior, driving it aggressively to the south (Stephens, Bernal, et al., 2022). The fire remained highly active and destructive, expanding into new terrain and threatening more populated and denser communities, including Pineridge and Shaver Lake, according to the daily flown NIROPS perimeters (NIROPS, 2020). The total acreage burned doubled in two days from roughly 32,000 to 66,000 ha (Figure 3.7). Spot fires and torching remained common, and suppression efforts were still limited due to safety concerns and the ability to organize crews within a few days of ignition. While not as explosive as the blowup period, this stage sustained high rates of spread and significant new growth on the southern flank, encountering a total of 830 homes (Table 3.1).

In the days following the rapid southern expansion, the Creek Fire entered a slower but still active phase from September 10-23, 2020. The fire was still progressing but had significantly slowed (Figure 3.7) due to higher relative humidity and cooler weather accompanying a Pacific disturbance (Service, 2020a) and dense smoke, which helped to keep the ignition component low (Service, 2020b). Suppression efforts focused primarily on the southern flank, where populated communities were threatened, while northern portions of the fire burned through subalpine and alpine vegetation within designated wilderness. This stage represented a shift from explosive plume-driven fire growth to a milder phase, though the fire continued to grow and increase in edge complexity, interacting with a total of 936 homes (Table 3.1).

Table 3.1: Record of available days and fire stages. The total number of destroyed homes which met the building classification criteria was 511 and the total number of homes which survived was 1,375.

	Destroyed (>50%)	No Damage
Stage 1 – Blowup (9/4–9/7)	45	75
Stage 2 – Rapid Expansion (9/8–9/9)	238	592
Stage 3 – Flanking/ Containment (9/10–9/23)	228	708

3.6.2 Differences in Fuels Across Fire Stages

Characteristics of the built environment and surrounding fuels differed across the three fire stages, in both the distribution of vegetation within the home ignition zones and local housing density (Figure 3.8). The most pronounced difference of fuel distributions within the home ignition zones, across fire stages occurred in the upper canopy strata (8-16 m, >16 m) and was more limited in the lower strata (1-2 m, 2-4 m). Meanwhile, housing density showed the clearest separation between stages (Figure 3.8). Vegetation cover was lowest in the 1-2 m height class across all zones and stages, with medians below 10% in most stage-zone combinations. In the 8-16 m and >16 m classes, the Rapid Expansion stage had higher median cover than the Blowup and Flanking/Containment stages in all three zones. Vegetation over home cover was similar across stages, with medians between 14% and 18%. Housing density also differed by stage. The Blowup stage had a median of approximately 1.0 units per acre, compared to approximately 0.3 units per acre in both the Rapid Expansion and Flanking/Containment stages.

Based on Kruskal-Wallis tests, 11 of 17 fuel and density variables significantly differed across fire behavior stages ($p < 0.05$; Table 3.2). The coefficient of variation across stage means varied considerably by variable. Housing density had the greatest difference across stages at 42.7%. Tall vegetation cover (>16 m) also had higher coefficients of variation, ranging from 19.7% in Zone 0 to 23.7% in Zone 2. Mid-height fuels (2-4 m, 4-8 m, 8-16 m) in Zones 1 and 2 were statistically significant but had lower coefficients of variation, ranging from 7.7% to 11.9%. Most Zone 0 variables were not significantly different across stages, with coefficients of variation below 6%. Vegetation over the home and Zone 1: 1-2 m fuels were also non-significant, with coefficients of variation of 6.2% and 6.3%, respectively.

We compared the predictive performance of non-spatial models (fuel-only and density-only) against spatial models across fire behavior stages using 5-fold cross-validated AUC (Figure 3.9). The Blowup stage showed the largest difference between models, where fuel-only and density-only models achieved AUCs of 0.60 and 0.51, respectively, compared to 0.92 for the spatial-only model. During

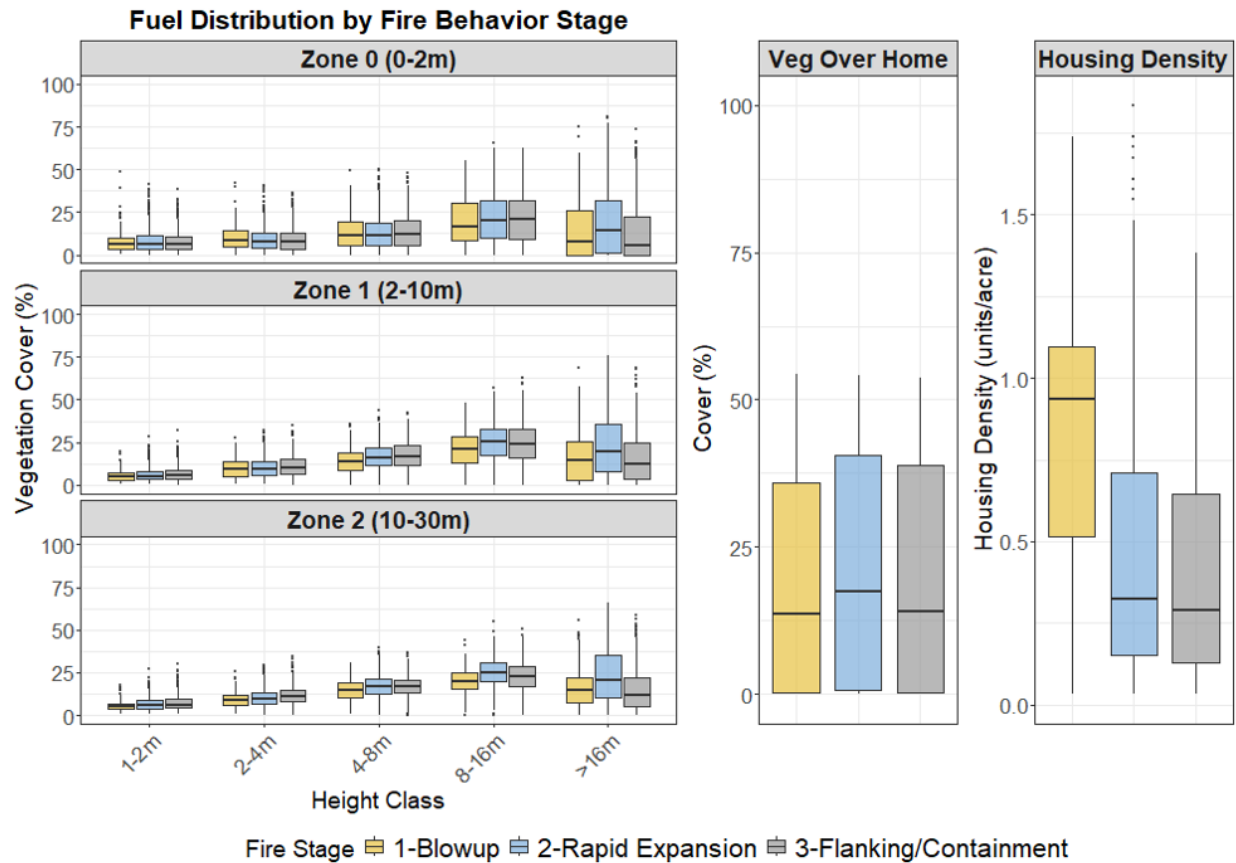


Figure 3.8: Distribution of fuel variables, vegetation over home, and housing density across the three fire behavior stages (Blowup, Rapid Expansion, Flanking/Containment). Fuel variables are shown by height class (1-2 m, 2-8 m, 8-16 m, 16-100 m) within three defensible space zones (0-2 m, 2-10 m, 10-30 m from each structure).

Table 3.2: Kruskal-Wallis and coefficient of variation (Coef. of Var.) test results, sorted by coefficient of variation to show the magnitude of differences across variables.

Variable	P-value	Significance	Coef. of Var.
Housing Density	1.03E-30	***	42.7
Veg Over Home	0.156867	ns	6.2
Zone 0: 1–2 m	0.436049	ns	3.8
Zone 0: 2–4 m	0.201638	ns	5.7
Zone 0: 4–8 m	0.776663	ns	1.7
Zone 0: 8–16 m	0.531176	ns	3.3
Zone 0: >16 m	4.58E-09	***	19.7
Zone 1: 1–2 m	0.074701	ns	6.3
Zone 1: 2–4 m	0.000197	***	7.7
Zone 1: 4–8 m	2.48E-05	***	9.6
Zone 1: 8–16 m	1.06E-05	***	11.2
Zone 1: >16 m	5.42E-14	***	21
Zone 2: 1–2 m	5.26E-06	***	11.7
Zone 2: 2–4 m	4.47E-11	***	11.9
Zone 2: 4–8 m	0.000473	***	7.7
Zone 2: 8–16 m	3.09E-11	***	10.2
Zone 2: >16 m	8.4E-24	***	23.7

Rapid Expansion, fuel-only and density-only models achieved AUCs of 0.57 and 0.75, while the spatial-only model reached 0.91. Flanking/Containment non-spatial AUCs were 0.67 and 0.62, compared to 0.90 for the spatial-only model. The combined Spatial + Fuel + Density model achieved AUCs of 0.92, 0.91, 0.91, and 0.89 for Blowup, Rapid Expansion, Flanking/Containment, and All Stages Combined, respectively.

3.6.3 Drivers of Housing Loss Across Stages

The variables selected by the Marra and Wood double-penalty method varied across stages, reflecting within-fire differences in the drivers of housing loss. Fuel variables had the largest effect during the Blowup stage, when fire behavior was most extreme. Fuels in the 2-4 m stratum in Zone 2 had the highest SHAP magnitude in both the Blowup and Rapid Expansion stages, while housing

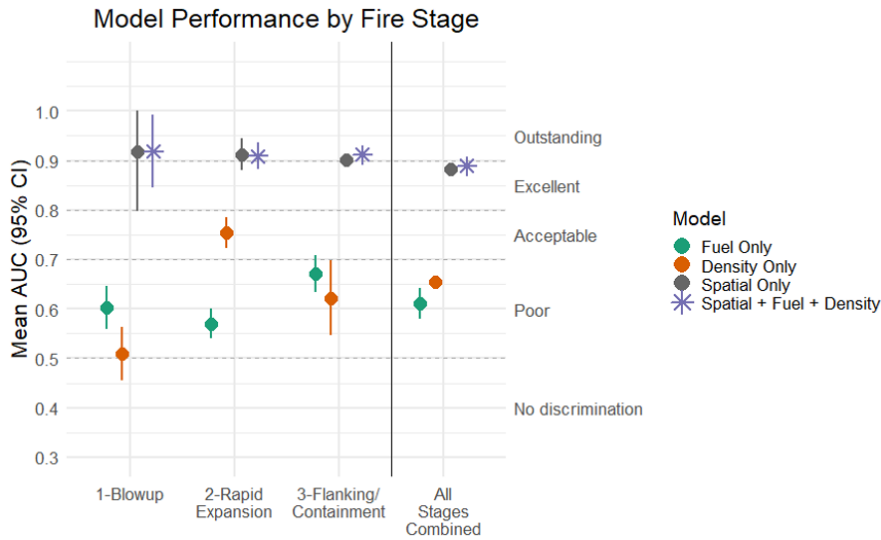


Figure 3.9: Model performance by stage of models with different inputs. A 0.5 AUC represents random guessing, while values near one indicate high predictive power. The spatial models have the highest AUC of all models.

density was the most important variable in the Flanking/Containment stage and the full-extent model (Figure 3.10).

The direction of SHAP values along the x axis indicates whether each variable pushed model predictions toward survival (negative SHAP value) or loss (positive SHAP value) (Figure 3.10). Housing density exhibited opposite effects depending on stage: higher density increased the predicted probability of destruction during Blowup but increased the predicted probability of survival in other stages. For most fuel variables, higher vegetation cover was associated with a higher predicted probability of housing loss. However, a few variables (Zone 2: 8-16 m, Zone 1: 4-8 m, Zone 1: 8-16 m) had the opposite pattern, where higher cover pushed predictions toward survival.

3.7 Discussion

We used high resolution airborne lidar to evaluate how fuel structure within defensible space zones related to structure outcomes of the 2020 Creek Fire. Fire weather, such as large scale wind patterns, and fire behavior strongly influenced where structures were lost, clustering housing outcomes

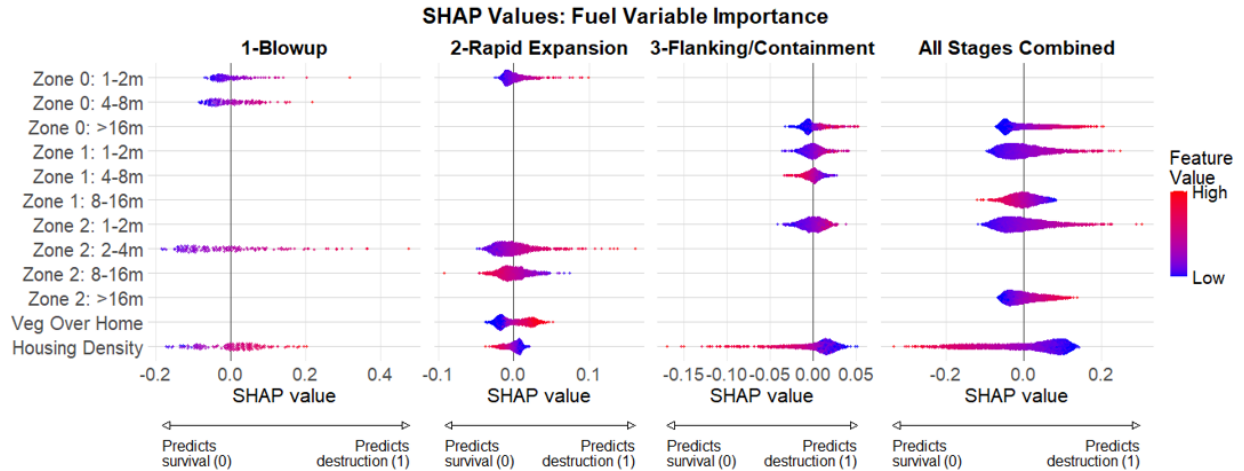


Figure 3.10: SHAP values for fuel and housing density variables across the three fire behavior stages and all stages combined. Points are colored by feature value (blue = low, red = high). Positive values indicate the observations pushed the model toward predicting destruction and negative values toward survival. Wider spreads indicate higher variable importance. Spatial coordinates were fixed at their median values.

to a degree that a single full-extent model could not separate from fuel effects. We therefore stratified the fire into three stages (Blowup, Rapid Expansion, and Flanking/ Containment) to identify how the drivers of housing loss varied within a single fire event. The spatial term in the GAM models dominated predictions across all stages, meaning structure location, which tracked fire severity (RBR), predicted housing loss more strongly than surrounding fuels. However, fuel structure and housing density variables still contributed to housing loss and survival depending on the fire stage, with AUCs of the non-spatial models ranging from 0.5 to 0.75. Because the variable responses differed across the stages, this analysis demonstrated that full-extent models can mask specific fuel effects under varied conditions. The drivers were also strongly spatially autocorrelated, which can lead to inflated significance for broad-scale variables, such as RBR, that override smaller-scale fuel effects.

3.7.1 Housing Density and Vegetation Cover Across Fire Stages

The Creek Fire footprint covered 379,895 acres and subsumed a sizeable elevational gradient from ~900 to 14,000 ft, encompassing heterogeneous landscape and fire conditions (Stephens, Bernal, et al., 2022). Across this extent, vegetation structure varied with topography, weather, and commu-

nity management strategies, each of which shaped fire behavior at broad scales. Treating the drivers of housing loss as uniform across these gradients limits a model's ability to resolve the finer-scale relationships. The stage stratification approach presented here was designed to accommodate this variance, and it revealed significant differences among stages that corresponded to distinct drivers of housing loss.

Through the coefficient of variation analysis, we found significant variation in tall vegetation (>16 m) cover and housing density across all stages. The significant differences in tall vegetation (19.7%-23.7% CV across HIZs) and housing density (42.7% CV) potentially reflect differences in community type and forest structure across the stages. For example, the Rapid Expansion stage (where cover was greatest in tall vegetation) was primarily composed of recreational communities such as Shaver Lake situated in denser forest settings, while the Blowup stage had the highest housing density and primarily interacted with communities such as Big Creek, a community built around a hydroelectric project, and rural inholdings with more year-round residents. These community patterns describe the community archetypes found in Paveglio, Moseley, et al. (2015) which classified WUI communities ranging from suburban, formal communities to rural, working communities based off their sociodemographic characteristics, field notes, and interview transcripts. Community archetypes in the WUI differ systematically in land use history, development patterns, and vegetation management (Paveglio, Moseley, et al., 2015; Evers et al., 2019), suggesting these factors may contribute to the patterns we observed across stages. Regardless of the specific community differences driving this pattern, the stage stratification was able to account for these differences while measuring how their fuels interact with housing loss.

The absence of significant differences in Zone 0 fuels below 16 m ($CV < 5.7\%$) across fire stages suggests that immediate defensible space conditions were relatively consistent regardless of where the structure was located. The area immediately surrounding structures is largely determined by homeowner landscaping and maintenance decisions rather than by landscape-level forest structure (Cohen, 2000). Zone 0 is known to accumulate embers, where buildings interrupt wind flow and create eddies that deposit embers against exterior walls, in reentrant corners, and at the base of the structure,

where they ignite combustible materials and spreading fire to the structure (Manzello and Quarles, 2017; Quarles et al., 2023). Our finding is consistent with recent Zone 0 regulations in California (AB 3074, 2020), which requires residents to clear all combustible materials within the 2 m zone directly near the structure. This result specifically addresses fuel differences across stages and does not suggest that Zone 0 clearance is insufficient, but rather most residents in our study area had relatively low Zone 0 fuel loads. Despite consistent Zone 0 fuels across the fire, housing loss rates varied substantially, indicating that Zone 0 conditions interact with other factors to shape structure outcomes.

Fuels <16 m in Zones 1 and 2 (1-2, 2-4, 4-8, 8-16 m) varied significantly across stages, though minimally with CVs ranging from 7.7-11.9% compared to fuels >16 m. The significant variation in Zones 1 and 2 suggests that vegetation structure in these outer zones is shaped more by landscape position and forest management history than by homeowner action in our study area (Stephens, Moghaddas, et al., 2009; J. Lydersen and North, 2012). This result reflects research on limitations of defensible space implementation, specifically where outer zones extend across property boundaries or onto adjacent wildland vegetation (Brenkert-Smith et al., 2017).

3.7.2 Within Fire Drivers of Housing Loss

The differences in fuels and housing density across the Creek Fire interact with variable fire behavior and firefighting effects to create various drivers of housing loss. For example, increased housing density in the Blowup stage increased the probability of housing loss, while increased housing density in the Rapid Expansion and Flanking/ Containment stages decreased the probability of housing loss. These contrasting patterns indicate that drivers of housing loss are unlikely to be uniform, even within a single event.

Fuels in Zone 2: 2-4m had the largest SHAP values during the Blowup and Rapid Expansion stages, when the fire was the most active and extreme. Fuel variables overall had larger SHAP values in the Blowup stage, indicating that during extreme fire behavior in the Creek Fire, low stature fuels further from the home were significant drivers of housing loss. Near-surface and ladder fuels have long been recognized as critical for fire propagation, serving as the pathway by which surface fires transi-

tion to crown fires (Agee and Skinner, 2005), and fuel treatments targeting these strata have moderated fire behavior even under extreme conditions (Stephens, Moghaddas, et al., 2009; J. M. Lydersen et al., 2017). The importance of low-stature fuels during the Blowup and Rapid Expansion stages is also consistent with the fuel-driven fire behavior documented in the Creek Fire. Widespread accumulation of dead surface and downed fuels from bark beetle-driven tree mortality contributed to sustained plume-dominated fire behavior and extreme rates of spread (Stephens, Bernal, et al., 2022).

Housing density showed contrasting effects across fire stages. During the Blowup stage, higher housing density was positively related to housing loss, consistent with studies finding that dense WUI communities can increase structure loss through structure-to-structure ember cast and ignition (Caton et al., 2017; Knapp et al., 2021; Syphard, Keeley, Massada, et al., 2012). By the Flanking/Containment stage, fuel variables had low SHAP values, and high housing density contributed as the primary driver of housing *survival*. This opposite effect may reflect the temporal effect of fire where residents and fire crews had more time to prepare communities for wildfire interaction, along with differences in how developments were planned and maintained (Kolden and Henson, 2019).

A few mid-canopy variables (Zone 1: 4-8 m, Zone 1: 8-16 m, Zone 2: 8-16 m), representing canopy cover of mid-sized trees, exhibited the opposite pattern in the Rapid Expansion and Flanking/Containment stages, where greater vegetation cover was associated with survival. However, the SHAP magnitudes of mid-canopy variables were small relative to the dominant predictors. These variables were not correlated with near-surface fuel cover or housing density, suggesting the pattern is not explained by understory clearing or neighborhood configuration. Further research on how mid-canopy structure interacts with ember trajectories under different fire conditions is needed to explain this pattern.

3.7.3 Drivers of Housing Loss Across Other Fire Events

Prior work has shown that drivers of housing loss differ across fires and regions (Syphard, Rustigian-Romsos, and Keeley, 2021). Results from various studies support these findings; fire behavior is driven by different factors (i.e., weather or fuel) and therefore drivers of housing loss also vary

by geography, fire weather, and characteristics of individual fire events. Housing density (Knapp et al., 2021), home hardening (Syphard and Keeley, 2019), and fuels near the home (Zamanialaei et al., 2025) were each identified as the most important driver of housing loss during various fires, yet all three studies used different inputs, measurements, and methods. Disagreement among studies indicates that the relative importance of housing loss drivers remains unresolved, particularly regarding the role of fine-scale fuel structure.

During the Creek Fire, fire behavior was strongly driven by fuel conditions, including accumulation of hazardous fuels and dry antecedent weather conditions (Stephens, Bernal, et al., 2022), which contrasts with study results from other fires in the region. Tree mortality due to compound disturbances including bark beetle attacks, drought, and fire suppression and exclusion created unique conditions for the fire to cause such high severity. These drivers vary widely between other large fires across California, such as the 2025 Palisades fire which was driven by a rare Santa Ana wind event (Guirguis et al., 2025). Furthermore, vegetation and community types vary significantly across fires. In investigating housing loss drivers, differences in larger scale biophysical and geographical drivers across fires are an important part of the story that is so often left out when aggregating multiple fires into a single model (Syphard, Keeley, Gough, et al., 2022) and are important for considering why homes are destroyed or survived.

3.7.4 Management Implications and Limitations

Our findings suggest that no single mitigation pathway can fully prevent structure loss in WUI communities. Rather, reducing housing loss requires a combination of mitigation decisions that address the heterogeneity of human decisions and the complexity of wildfire conditions. The Swiss cheese model of accident causation frames risk as a series of defensive layers, each with gaps, where negative outcomes occur when gaps across layers align (Reason, 1990). In the WUI context, these layers include home hardening, the immediate ember-resistant zone (Zone 0), the intermediate defensible space zones (Zones 1-2), community-scale fuel networks and development patterns, and landscape-scale fuel management. Our results show the importance of the fuels at the parcel level, particularly

Zones 1 and 2, while still addressing the community and landscape scale conditions that fall outside individual homeowner control.

Addressing the inherent complex risk in WUI communities threatened by fire is fundamentally a social challenge. Residents base mitigation decisions on threat appraisal and response efficacy, both of which are shaped by the information they receive about their own risk (Wilson, McCaffrey, and Toman, 2017; Dupey and J. W. Smith, 2019; Meldrum et al., 2019). When that information comes from inaccurate ground-based inspections (Wilkin, Benterou, and Stasiewicz, 2025) or perceptions that diverge from measured exposure (Paveglio, Edgeley, and Stasiewicz, 2018; Larsen et al., 2025), resident decisions become decoupled from their actual risk. Lidar-based fuel measurements can support decision-making within a complex risk framework by providing consistent, multi-zone characterizations of defensible space at the scales where social processes operate, from individual parcels to neighborhoods to entire communities. Combined with measures of perceived risk and response efficacy, these data can help align mitigation decisions across residents, agencies, and planners as fire severity, magnitude, and frequency continue to increase.

While our analysis provides broad conclusions about how to measure drivers of housing loss, a few limitations should be noted. The DINS data for home hardening practices and structure age were incomplete, rendering the sample size too small to include these variables. Additionally, by stratifying the fire into multiple stages, we are introducing assumptions into our analysis. Fire behavior varies widely depending on the scale at which it is characterized, and since most fire behavior variables are modeled rather than directly observed, it is difficult to determine exactly what the fire was doing at any given point in time. The Creek Fire had clear behavioral boundaries that were straightforward to classify; this method may not be applicable to fires with more complex progression patterns. Finally, data on firefighting activities during the fire were difficult to incorporate, and while we hypothesize that some of the patterns observed here were influenced by suppression efforts, further research is needed to disentangle these effects.

3.8 Conclusions

Overall, the results of this study are limited to a single fire event, and the within-fire variation we observed underscores the difficulty of generalizing fuel-housing loss relationships across fires and communities. The Creek Fire burned through WUI communities that are significantly less dense than many other fire-affected areas in California, and the surrounding fuel structure reflects the mixed-conifer forests of the southern Sierra Nevada, which may not represent conditions in other fire-prone regions. These findings suggest that effective fuel treatment and defensible space regulation may need to be more flexible and context-dependent, accounting for how fire behavior, community density, and fuel structure interact to shape housing loss outcomes. Future work could apply these methods across multiple fires with varying community densities, fuel types, and fire behavior to assess whether the stage-specific fuel effects observed here hold under different conditions.

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Conclusion

What Burns

Fire burns materials through combustion, a chemical reaction dependent upon the oxygen, available fuel, and an ignition source to complete its reaction. At the atomic level, this process is well understood and acts within the boundaries of our knowledge. When applying these principles at a larger scale, there are exponential variables which introduce increasingly complexity to the reaction. With current computational and technological abilities, we are limited in measuring these variables beyond their stochastic effects. At scales which ecology operates on, high temporal and spatial variability in fire effects contribute to great uncertainty about the interactions between fire and systems such as vegetation and wildland urban interface (WUI) communities. While we can't measure or predict how every single material will burn in a wildfire, we can infer why certain communities had destructive interactions with wildland fire, and what that means for moderating potentially drastic effects in the future. To answer this question, my second and fourth chapters explored drivers and interactions of fire, vegetation communities, and residential structures in the WUI.

In chapter 2, I examined which ecosystems face the greatest risk of type conversion under novel fire regimes and climate change. Type conversion, the shift from one dominant vegetation state to another, is often framed as loss because of its effects on ecosystem processes, but whether a given conversion is a loss or a correction depends on the historical baseline against which it is measured. Through a thematic review of empirical studies, incorporating a more holistic view of vegetation transitions allowed me to identify patterns of interaction among multiple vegetation types rather than defaulting to broad "forest to non-forest" framing. I reviewed over 800 abstracts to determine whether studies measured conifer, oak, shrub, meadow, grassland, or invasive vegetation, and found that conifer studies greatly outnumbered all other types. This bias shapes conversations around type transitions, where shrublands are often characterized negatively in relation to conifers without being fully understood

with prior literature. If type conversion is framed as a process rather than a failure, we can anticipate where fire will catalyze change and direct those transitions toward more resilient states.

The finding in chapter 2 that overly dense conifer stands carry high type conversion risk is not new. However, by comparing pathways of change through state and transition models, I found that current conifer extents represent an overrepresentation of historical cover, and that transitions to non-forest states are often a correction and represent a return to conditions that preceded fire suppression and exclusion. When a more holistic view of vegetation is incorporated beyond “forest to non-forest” type transitions, additional patterns emerge. Chaparral is among the most diverse and ecologically important systems in the Sierra Nevada, and it is also among the most vulnerable. Because chaparral depends on seedbanks for regeneration, frequent fire truncates its growth cycle and limits seed production before plants are killed. With increasing fuel dryness because of climate change, fire frequency is expected to increase. As a result, chaparral systems, which were once difficult to burn due to the decoupling of ignition timing, are more likely to degrade through reduced biodiversity and invasive grass encroachment.

In chapter 4, I examined residential structure loss during the 2020 Creek Fire, an uncharacteristically large fire on the western slope of the Sierra Nevada. Accounting for spatial autocorrelation and variable fire behavior, I divided the fire into three stages and fit spatial GAM models to each. The dominant spatial effect in these models had a meaningful correlation with fire severity, emphasizing that broad spatial patterns, not just local fuel conditions, drove housing loss during this event. Furthermore, the defensible space factors that led a home to burn down varied spatially and temporally across the fire, indicating that drivers of housing loss are different throughout the fire. With a single variable unable to explain destruction, more research into standardized methods and improved mapping capabilities is necessary to untangle the effects of fire in the wildland urban interface.

Across this dissertation, a central theme about what burns has emerged: timing matters. The timing and consistency of vegetation treatments determines whether systems can recover to historical densities. The historical scale at which vegetation is measured introduces biases into management decisions. The timing and frequency of fire can deplete the structural and compositional diversity

of chaparral. Also, the timing of a building's exposure relative to fire stage can determine whether it remains standing. Combustion at the atomic scale may be deterministic, but at the scale of landscapes and communities, it is timing and our ability to anticipate proactive interventions that shape outcomes.

What Returns

Resilience is the capacity of a system to absorb disturbance and recover its prior state (Holling 1973). Across the chapters of this dissertation, I found that resilience is not uniformly distributed across Sierra Nevada vegetation types or WUI communities, but rather it depends on adaptation, context, and the conditions under which recovery occurs.

In chapter 2, my synthesis of relevant literature in the Sierra Nevada Range identified pathways better suited to warmer, drier future conditions. Oaks demonstrated exceptional resilience to repeated high-severity fire and represent a plausible alternative stable state to conifers under projected climate trajectories. Meadows may function similarly, though research on the use of fire as a restoration tool in these systems remains limited. These ecosystems are worth prioritizing, as oaks provide a fire-resilient alternative to conifers, and meadows offer increased water storage capacity.

In chapter 3, I developed novel methods to map post-fire vegetation recovery 6 to 36 years after high-severity fire in Yosemite National Park. Using groundtruthed field data, this approach achieved model accuracies ranging from 0.62 R² to 0.72 R². Across three case study sites, the pathways to conifer, oak, and shrub dominance tracked the patterns identified in the literature review: oaks established dominance at a site that experienced a short-interval reburn, conifers retained dominance at a higher-elevation site with an intact fire regime, and shrubs colonized the interiors of high-severity burn patches at a lower-elevation site. These results reinforce a consistent conclusion at landscape scale: longer-term post-fire vegetation trajectories reflect species' adaptations to climate and fire, not simply proximity to seed sources or time since disturbance.

In chapter 4, I found that variables which driver housing loss depended on fire stage, ultimately suggesting that no single variable can predict housing loss in the wildland urban interface. However, certain trends emerge, with housing density and fuel cover in the 1 to 2 m height stratum within home

ignition zone 2 (10 to 30 m from the structure) having the greatest influence on structure survival across fire stages. Outcomes varied by stage: homes in the Blowup stage faced the highest probability of destruction, while dense communities during the Rapid Expansion stage showed higher survival likelihood. These findings suggest that the window for effective intervention is narrow and stage-dependent, and that managing near-structure fuels in the years before a fire, as well as during suppression, is where outcomes are shaped. The communities which were impacted by the Creek fire were primarily composed of older homes at low densities in comparison to other fire-impacted areas. This led to different results than studied across other fires, further indicating that drivers of housing loss are dependent on specific conditions and are not generalizable.

Broader Implications

Overall, this dissertation examines strategies to build systems which are adapted to fire to live with it rather than against it. Chapters 2 and 3 examined the vegetation specific strategies, while chapter 4 focused on built environment and how contemporary societies can better live with fire.

Humans have lived alongside wildland fire for thousands of years, and for most of that history, managed to live with fire rather than against it. Indigenous burning practices across the Sierra Nevada shaped the vegetation communities this dissertation examines, and the fire exclusion era represents a historically anomalous departure from that relationship. The consequences of that departure are the problems this dissertation has worked to characterize, including overstocked forests, altered perspectives, invasive vegetation, and communities unprepared for fire. Returning to landscapes which work with fire rather than against it requires respectful engagement with Indigenous and ecological knowledge, and necessitates coordinated action across managers, residents, and policymakers who share landscapes shaped by fire.

This dissertation contributes empirical and methodological grounding for addressing these challenges through a synthesis of post-fire vegetation dynamics across the Sierra Nevada, novel remote sensing methods for detecting long-term recovery, and a spatially explicit framework for understanding structure loss during an uncharacteristically large fire event. The central question of what burns and

what returns has no single answer. But the patterns described here show that vegetation transitions, post-fire recovery, and structure loss are not random. Identifying their drivers allows managers and communities to make better decisions in an era of larger and more frequent fire.