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Fostering landscape resilience and species conservation in frequent fire landscapes

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ABSTRACT

Restoration of dry forest landscapes of the Pacific Northwest often involves the removal of some closed-canopy forest that has expanded due to fire exclusion, but this can conflict with species conservation when species require closed-canopy forest as part of their habitat. Fire refugia—areas within fire perimeters that burn less severely or frequently—might provide a solution to this conflict. We used a species-specific approach to understanding fire refugia *for* northern spotted owls to model the post-fire persistence of nesting and roosting (NR) forest in the frequent fire landscapes of the eastern Washington Cascades and the Klamath province and parts of the southern Cascades. Persistent NR forest occurred in topographically sheltered locations and lower slope positions whereas less persistent NR forest occurred in topographically exposed locations. These patterns of persistence reflect historical vegetation patterns when complex interactions among topography, vegetation and weather maintained resilient landscapes. These vegetation patterns may also resemble higher quality heterogenous habitat for spotted owls. Our models can help managers achieve the dual objectives of maintaining viable populations of native species, including those that rely on closed-canopy forests, while also restoring resilient landscapes. In an era of rapid ecological change, we suggest that northern spotted owl conservation and fire-adapted landscape restoration are not opposing goals. By identifying the biophysical settings that promote persistent NR forest and acknowledging the role of heterogeneous landscapes for maintaining resilient ecosystems and high quality spotted owl habitat, the dual objectives of supporting long-term resilience for native species and ecosystems can be achieved.

1. Introduction

Many dry forest ecosystems across western North America were historically maintained by frequent fire (Agee, 1993; Reilly et al., 2021). Complex interactions among the region's climate, topography, and vegetation resulted in heterogenous patterns of burn severity that translated into a mosaic of vegetation types that served as habitats for diverse biological communities (Bowman et al., 2016; Perry et al., 2011). The complex interactions giving rise to these vegetation patterns conferred strong resistance (the propensity to resist disturbance-induced change) and resilience (the propensity of a disturbed landscape to recover the form and function equivalent to its pre-disturbance state; Holling, 1973). Nearly two centuries of fire exclusion and land use practices have altered dry forest ecosystems and these landscapes are now less resistant and resilient than their historical counterparts (Hessburg et al., 2005). Contemporary increases in wildfire activity coupled with reduced resilience is now a significant threat to native species persistence (Kelly et al., 2020) and ecosystem function. As a response, land managers and ecologists are now increasingly focused on restoring landscape resilience by returning landscape structure and composition to a condition that more closely resembles historical conditions (Hessburg et al., 2015; Keane et al., 2009). However, landscape

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restoration efforts can come into conflict with other management objectives when desired outcomes appear incompatible with other objectives such as native species persistence, creating what ecologists refer to as a conservation conflict (Redpath et al., 2013).

Prior to European settlement, vegetation patterns in frequent fire landscapes were maintained by repeated burning. The frequent nature of these fires created a self-reinforcing pattern wherein areas previously burned at lower severity (severity in this context refers to the degree of change in total organic matter loss resulting from fire; Keeley, 2009) tended to reburn at lower severity and areas previously burned at higher severity tended to reburn at higher severity (Harris and Taylor, 2017; Parks et al., 2015; Povak et al., 2020; Rodman et al., 2023; Tortorelli et al., 2024). Topography played a key role by modulating fire effects at the local scale with topographically sheltered locations along or near drainage bottoms often burning less frequently and/or at lower severity, supporting denser stands of closed-canopy, older coniferous forests (Beaty and Taylor, 2001; Taylor and Skinner, 1998). These dense, old forests were maintained by repeated, low severity fire—what Meddens et al. (2018) referred to as 'fire-tended' old growth. In these same landscapes, upper slope positions tended to burn more frequently and/or at higher severity (Beaty and Taylor, 2001; Taylor and Skinner, 1998) maintaining more open vegetation types including pine-oak woodlands, meadows and shrub fields (Odion et al., 2010; Taylor and Skinner, 2003). Frequent fire was the linchpin in this dynamic feedback process responsible for maintaining this heterogeneity.

Contemporary frequent fire landscapes are now significantly departed from their historical condition (Demeo et al., 2018; Haugo et al., 2015). Over a century of effective fire suppression and the exclusion of Indigenous fire stewardship has allowed dense, closed-canopy forests to expand outward from those topographically sheltered locations, shifted species composition from fire-tolerant to fire-intolerant species, and increased ladder fuel growth in remaining fire-tended old forests (Agee and Edmunds, 1992; Greenler et al., 2024; Hessburg et al., 2005). Meanwhile, historical logging practices removed large amounts of fire-tended old growth located on lower slope positions (Curtis et al., 2007). As a result, contemporary frequent fire landscapes now contain less fire-tended old growth, but in some cases, more closed-canopy forest in exposed locations compared to historical landscape composition (Hagmann et al., 2021; Knight et al., 2022). Today's landscapes are now less resilient and resistant to fire at a time when fire seasons are getting longer, hotter, and drier (Abatzoglou and Williams, 2016).

In frequent fire landscapes of the Pacific Northwest, northern spotted owls (*Strix occidentalis caurina*; hereafter spotted owl) are closely associated with closed-canopy, older coniferous forests for nesting and roosting (Forsman et al., 1984; Lahaye and Gutiérrez, 1999; Sovern et al., 2019). Spotted owls tend to nest and roost on the lower portions of slopes (Buchanan et al., 1995; Lahaye and Gutiérrez, 1999) in more topographically sheltered locations that are conducive to the development of fire-tended old growth. At the time of the spotted owl's listing as threatened in 1990, the U.S Fish and Wildlife Service cited the loss of old forests due to logging as the main cause of the owl's decline (U.S. Fish and Wildlife Service, 1990), and while logging of federally managed public lands has been greatly curtailed (Davis et al., 2022), the recruitment and retention of old forest often considered 'habitat' for the species has been a main focus of recovery (Lesmeister et al., 2018; U.S. Fish and Wildlife Service, 2011). More recently, increasing wildfire activity in the frequent fire portions of the spotted owl's range has become the largest source of old forest loss (Davis et al., 2022) and the most significant threat to old forests used by spotted owls (Davis et al., 2022). The increasing threat of fire-induced loss has placed an even greater emphasis on the retention of all older forests regardless of topographic context because the spotted owl is critically imperiled and at risk of being extirpated from large parts of its former range (Franklin et al., 2021).

Long-term monitoring of spotted owls began in the 1980s (Gutiérrez and Carey, 1985). At that time, land management agencies had been suppressing nearly all wildfires throughout much of the owl's range for nearly a century (Pyne, 1982), and these successes had unintended yet profound impacts in frequent fire landscapes (Everett et al., 1997; Hagmann et al., 2021; Halofsky et al., 2024; Hessburg et al., 2005; Knight et al., 2020). In the eastern Washington Cascades, contemporary estimates suggest there were about 50% more old forests considered suitable for spotted owl nesting and roosting (hereafter NR forest) on federally administered public lands in 1994 than either historical (1930s) or contemporary estimates indicate (Davis and Lint, 2005). Likewise, studies in frequent fire landscapes in northwestern California have noted that the extent of Douglas-fir forest, which is closely associated with NR forest in this region (Lahaye and Gutiérrez, 1999), has increased over 30% since the pre-settlement era (Knight et al., 2020; Taylor and Skinner, 2003). Hence, the onset of long-term monitoring, the spotted owl's listing as threatened (U.S. Fish and Wildlife Service, 1990), and the establishment of the Northwest Forest Plan (NWFP; U.S. Department of Agriculture, & U.S. Department of the Interior, 1994) all coincided with a period of effective fire suppression and land use practices that increased the availability of NR forest in more exposed locations and reduced the availability of NR forest in topographically sheltered locations. Yet while early fire suppression efforts initially reduced the threat of fire-induced NR forest loss, continued fire suppression was recognized early on as a potential threat to northern spotted owl conservation (Agee and Edmunds, 1992; Everett et al., 1997).

The conflicting relationship between short-term habitat gains and long-term forest resistance and resilience (Halofsky et al., 2024; Lee and Irwin, 2005) has come under increased scrutiny as wildfire is now considered the biggest threat to NR forest loss (Davis et al., 2022). As a result, managers now face a conservation conflict: retain all NR forest and risk future increased losses because of reduced landscape resilience or increase landscape resilience by removing and restoring stands of NR forest highly susceptible to fire to more closely resemble pre-European conditions, but in doing so reduce the amount of NR forest available to spotted owls (Stephens et al., 2019). A promising lens for resolving this conflict is the concept of fire refugia (Krawchuk et al., 2026; Lesmeister et al., 2025). Fire refugia are areas that burn less frequently or severely than surrounding locations (Krawchuk et al., 2016; Meddens et al., 2018) and as such, they serve as ecological anchors sustaining old forest structure through multiple fire events, sheltering sensitive species during fires, and providing post-fire seed sources to aid regeneration (Camp et al., 1997; Downing et al., 2021; Meddens et al., 2018; Rodman et al., 2023; Schwilk and Keeley, 2006). Where fire refugia occur is influenced by complex interactions between top-down (daily fire weather, climate) and bottom-up (local topography, pre-fire vegetation) drivers of fire severity (Collins et al., 2019; Downing et al., 2021; Krawchuk et al., 2016; Mcwethy et al., 2018; Meigs et al., 2020; Rodman et al., 2023) with local topography exerting strong influence on the occurrence of fire refugia (Downing et al., 2021). However, local controls such as topography can be overwhelmed during extreme fire weather conditions when top-down drivers dominate (Krawchuk et al., 2016; Meigs et al., 2020). The structure and composition of fire refugia can vary depending on geography and biophysical context (Downing et al., 2021; Krawchuk et al., 2026). Persistent, closed-canopy fire refugia occur in frequent fire forests occupied by spotted owls (Krawchuk et al., 2026). This refugia type tends to occur in topographically sheltered locations and north-facing slopes where microclimatic buffering and decoupling (Davis et al., 2019; Frey et al., 2016) creates cooler, moister conditions that dampen fire behavior (Pettit and Naiman, 2007; Pyne et al., 1996), adding an important source of heterogeneity to these landscapes.

The concept of fire refugia can be extended to examining the persistence of certain vegetation types when burned, including habitat components required by native species. For example, NR forest that developed within refugial locations should be more resistant to fire-induced loss because it developed through repeated low severity fire (i.e., fire refugia *for* spotted owls; sensu Meddens et al., 2018), in topographically sheltered locations conducive to cooler and moister microclimates: NR forest occurring in these locations should have a relatively high probability of persistence. Conversely, NR forest that developed outside fire refugia as a result of fire exclusion should be more susceptible to fire-induced loss because it developed in the absence of fire in uncharacteristic locations: NR forest occurring in these locations should have a relatively low probability of persistence.

Our research aims to address the conflict of spotted owl conservation in frequent fire landscapes in two ways. Our main aim was to identify the spatial patterns of NR forest persistence within the frequent fire portions of the northern spotted owl's range. Second, we were also interested in understanding how the drivers of fire behavior and severity (topography, pre-fire vegetation, and climate/weather) influence the persistence of NR forest so we could begin to understand the mechanisms that confer persistence. We addressed these objectives by extending the concept of fire refugia to examine the persistence of NR forest by linking species-specific models of NR forest (Davis et al., 2022) with concepts of fire behavior to model the post-fire persistence of NR forest and produce spatial predictions of where NR forest is more or less likely to persist when burned. Understanding where and why NR forest is more or less susceptible to fire-induced loss can provide guidance for fire and fuels management that supports both wildlife species conservation and landscape resilience and offer tools for successfully navigating this conservation conflict in fire-prone spotted owl landscapes.

2. Materials and methods

2.1. Study area

We focused our analysis on those portions of the northern spotted owl's range that are characterized by very frequent or frequent fire regimes (Spies et al., 2018). Two regions met these criteria; the eastern Cascades in Washington state ("north" modeling region; Fig. 1), and the Klamath province including portions of the south Cascades and the California coast ("south" modeling region; Fig. 1). The north modeling region was composed of mostly dry mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*), grand fir (*Abies grandis*), and ponderosa pine (*Pinus ponderosa*) in lower to mid-elevations, and moist mixed-conifer forest at higher elevations including Douglas-fir, grand fir, western larch (*Larix occidentalis*), ponderosa pine, lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*), and western hemlock (*Tsuga heterophylla)* (Franklin and Dyrness, 1973). Southern modeling region vegetation consisted mostly of mixed-conifer and mixed-evergreen forests. Mixed-conifer forests in the south modeling region were similar to lower elevation mixed-conifer forests in the north modeling region except white fir (*Abies concolor*) replaces grand fir. Mixed-evergreen forests in the south modeling region are composed of an emergent canopy of conifer species mostly consisting of Douglas-fir with a smaller component of incense cedar (*Calocedrus decurrens*), ponderosa pine, sugar pine (*Pinus lambertiana*) and Jeffrey pine (*Pinus jeffreyi*), and broadleaf trees such as tanoak (*Notholithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), big-leaf maple (*Acer macrophyllum*), canyon live oak (*Quercus chrysolepis*), California black oak (*Q. kelloggii*), and golden chinquapin (*Castanopsis chrysophylla*) occurring either in the understory or in some settings, as overstory components (Whittaker, 1960). Historically, vegetation structure and composition in both modeling regions was strongly influenced by topography with closed-canopy, coniferous forests occurring more frequently on north-facing slopes and more open forest types (e.g., ponderosa pine, pine-oak woodland) occurring more frequently on lower elevation, south-facing slopes (Taylor and Skinner, 2003). Land use practices including logging, livestock grazing, and fire suppression have altered this pattern to some degree with closed-canopy forests now occurring across large portions of both regions (Hessburg et al., 2005; Knight et al., 2022).

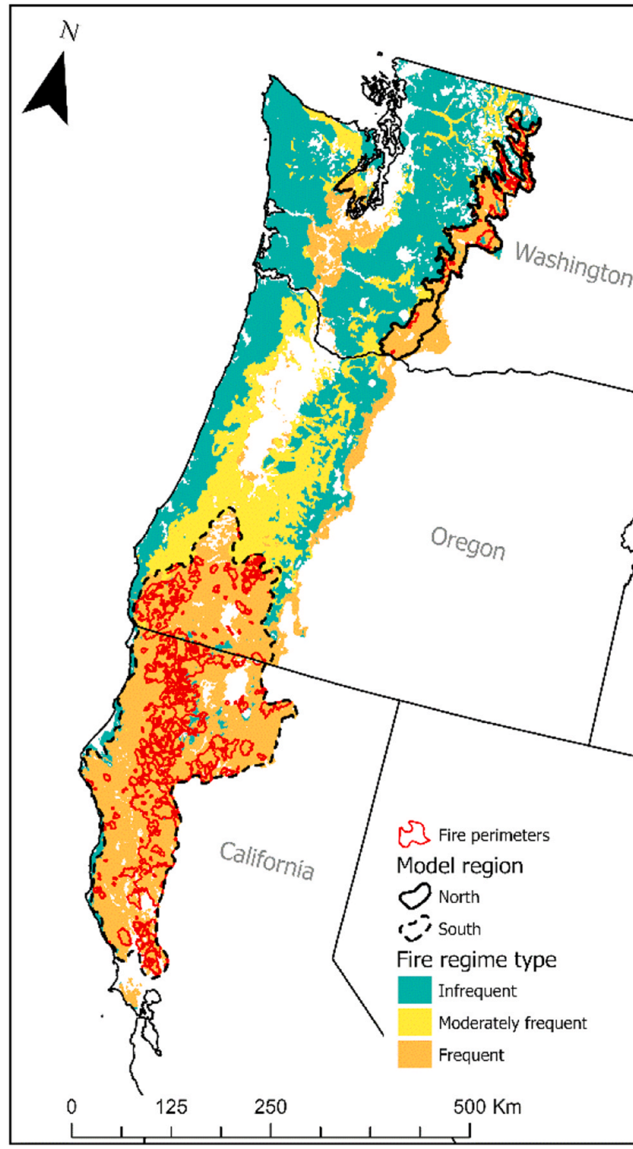

Fig. 1. Study area map showing our north and south modeling regions located within the frequent fire landscapes of the northwest forest plan footprint.

2.2. Modeling nesting/roosting (NR) forest persistence

We examined factors that confer persistence to NR forest across both modeling regions and for NR forest that burned multiple times using boosted regression trees. We defined persistence based on whether or not NR forest that was considered suitable NR forest one year before a fire remained suitable NR forest one year after fire. We created separate datasets for both regions and for areas of NR forest burned once, twice, and three times (e.g., north region, initial-burn; south region, twice-burned, etc.). We began by creating a systematic grid of sample points with a spacing of 210 m (every seventh pixel) to reduce the effect of spatial autocorrelation in our data. We then overlayed our sample grid with annual fire perimeters and excluded all points that: 1) fell outside existing fire perimeters, 2) did not fall on a pixel classified as suitable NR forest one year before a fire, and 3) were < 100 m from a fire perimeter edge. The remaining pixels represented our sample population. Next, we extracted our predictor and response variables from this reduced sample and fed these data into our boosted regression tree models. We repeated this process for each combination of modeling region and burn histories.

All spatial data manipulations were conducted using the terra package (Hijmans, 2024) in program R (R Core Team, 2024).

2.2.1. Wildfire data

We downloaded all fire perimeters from 1985 through 2022 cataloged by the Monitoring Trends in Burn Severity (MTBS) project (Eidenshink et al., 2007) from www.mtbs.gov. From this dataset, we selected fires categorized as wildfires that overlapped our modeling regions. We used these data to identify areas of NR forest that burned and to characterize the number of times an area burned and the time since previous fire for NR forest burned more than once. Using fire perimeters rather than a metric of fire severity to define our sample implicitly assumes that all NR forest within a fire perimeter experienced fire. However, fire refugia include places burned less severely as well as those burned less frequently (not burned but within a fire perimeter). Thus we think our use of fire perimeters accurately reflects fire refugia *for* northern spotted owls.

2.2.2. Response variable – nesting/roosting (NR) forest

Northern spotted owl NR forest has been monitored consistently since 1994 under the effectiveness monitoring program of the NWFP. As part of this monitoring effort, managers have created a set of annual maps going back to 1985 that classify forest-capable lands within the NWFP footprint as suitable or unsuitable NR forest (Davis et al., 2022). These maps were made by correlating a suite of forest structure and composition metrics with northern spotted owl nest and roost locations from 1993 using Maxent (Davis et al., 2022). The forest structure and composition metrics used to define suitable NR forest were in turn developed using gradient nearest neighbor imputation methods (GNN: Ohmann and Gregory, 2002, Bell et al., 2023) to correlate forest structure and composition metrics from ~11,000 forest inventory plots on federally administered public lands with a suite of predictor variables (satellite imagery, topography, etc.). We used these pre-existing maps to define our response variable.

Our response variable was the persistence of NR forest. We considered a pixel (30 m x 30 m) of NR forest to have persisted after being burned if it was classified as suitable one year before a fire and remained suitable one year after fire; these pixels were assigned a response value = 1. We considered a given pixel of NR forest to have not persisted (degraded habitat suitability) if it was classified as suitable one year before fire and not suitable one year after fire; these pixels were assigned a response value = 0. We defined persistence based on NR forest suitability rather than burn severity because suitability was closely associated with several forest structural elements (e.g., canopy cover of conifers, large conifer density; Davis et al., 2022) and any reduction in these components, regardless of burn severity could result in the loss NR forest suitability (Lesmeister et al., 2018). We assumed pixels of NR forest that did not persist (response = 0) was a direct result of fire. By only examining persistence one-year post-fire, we excluded any effects of post-fire delayed tree mortality. Additionally, while barred owls are known to displace spotted owls (Wiens et al., 2014), they were relatively rare in 1993 (Franklin et al., 2021; Yackulic et al., 2019). Thus, we believe spotted owl space use was not significantly affected by interactions with barred owls and these NR forest cover maps accurately reflected spotted owl use of NR forest.

2.2.3. Predictor variables

Fire behavior is driven by complex interactions that result in a mosaic of fire effects within the fire footprint. We incorporated a suite of bottom-up and top-down explanatory variables informed by the fire behavior triangle (topography, vegetation (fuels), climate/weather) that previous research has indicated are important for explaining fire behavior and severity (Chapman et al., 2020; Collins et al., 2019; Downing et al., 2021; Kane et al., 2015a; Krawchuk et al., 2016). In addition, we developed several new variables that attempted to describe how the spatial arrangement and structure of forest patches influence NR forest persistence (Table 1).

Our bottom-up variables included slope (SLOPE; %), aspect

Table 1
List of explanatory variables and their acronyms used to model the persistence of northern spotted owl nesting and roosting forest.

Explanatory Variable	Description	Source
Climate/Weather		
Palmer Drought Severity Index (PDSI)	Cumulative measure of long-term drought	Abatzoglou et al. (2018)
Climatic Water Deficit (CWD)	Measure of plant water stress, defined as the difference between actual and potential evapotranspiration	Abatzoglou et al. (2018)
Maximum daily temperature (TMAX)	Maximum daily temperature interpolated for each day of burn	Abatzoglou (2013)
Wind speed (WIND)	Maximum daily wind speed interpolated for each day of burn	Abatzoglou (2013)
Topography		
Topographic Position Index (TPI)	Measure of relative topographic exposure. Negative values represent topographic depressions; positive values represent exposed locations.	DEM
Slope (SLOPE)	Measure of terrain steepness (%)	DEM
Aspect (ASPECT)	Azimuth of slope	DEM
Heat Load Index (HLI)	Measure of potential incident solar insolation. It is a function of slope, aspect, and latitude	DEM, (McCune and Keon, 2002)
Catchment Slope (CSLOPE)	Measure of the overall slope of a catchment basin	DEM
Soil Wetness Index (SWI)	Measure of potential soil wetness	DEM
Topographic Convergence Index (TCI)	Measure of potential cold air pooling	DEM
Terrain dissectedness (DISSECT)	From Sappington et al. (2007) vector ruggedness measure. Used to characterize the degree of terrain complexity based on local slope and aspect.	Sappington et al. (2007)
Vegetation		
Relative Habitat Suitability (RHS)	Continuous version of NR forest suitability maps developed for the northwest forest plan.	(Davis et al., 2022)
Distance to patch edge (EDGE)	Distance from a pixel of NR forest to patch edge	(Davis et al., 2022)
Neighboring stand age (NS_AGE)	Average age of dominant trees of non-NR forest within 200 m of NR forest	Ohmann and Gregory (2002)
Neighboring stand height (NS_HEIGHT)	Average stand height of non-NR forest within 200 m of NR forest	Ohmann and Gregory (2002)
Neighboring stand canopy cover (NSCOVER)	Average canopy cover of non-NR forest within 200 m of NR forest	Ohmann and Gregory (2002)
Time since previous fire (TSF)*	Time (years) since previous fire	Eidenshink et al. (2007)

* Time since previous fire variable was only used in twice- and thrice-burned analyses.

(ASPECT; radians), topographic position index (TPI), heat load index (HLI; a measure of potential incident solar radiation based on slope and aspect), catchment slope (CSLOPE; a measure of the overall slope of a catchment basin), soil wetness index (SWI; a measure of potential soil wetness), and topographic convergence index (TCI; a measure of potential cold air pooling), We also included a variable we called terrain dissectedness (DISSECT), that was a scaled up version of the vector ruggedness measure developed to characterize the difficulty of local animal movements associated with local terrain ruggedness (Sappington et al., 2007; Figure S1).

Vegetation (fuel) comprises another side of the fire behavior triangle and has known influences on fire behavior and severity. Stands of suitable NR forest tend to be situated within the context of other forest types unsuitable for nesting and roosting (e.g., young forest), and it is possible the structure and composition of these forest neighborhoods could influence the persistence of NR forest stands by affecting how fire arrives at stands of NR forest. We created three variables to describe the structure of these forest neighborhoods within 200 m of suitable NR forest including: neighboring stand height (NS_HEIGHT), neighboring stand age (NS_AGE) and neighboring stand canopy cover (NS_COVER; Table 1). These variables were calculated using a moving window across all matrix forest lands (unsuitable NR forest) to summarize mean values of GNN variables for stand height, age, and canopy cover of conifers (Bell et al., 2023). Interior NR forest has been shown to burn less severely than NR forest edges (Lesmeister et al., 2021), so we created a variable to describe the distance of a given pixel of suitable NR forest from the edge of the patch (DIST). Finally, we created a variable characterizing relative habitat suitability (RHS) of each NR forest pixel because highly suitable NR forest with high levels of biomass may be more likely to persist through fire than marginally suitable NR forest (Meigs and Krawchuk, 2018).

Our top-down variables included a suite of climate and weather variables with demonstrated effects on fire behavior and severity in previous studies (Table 1). Antecedent climate is known to exert a strong influence on fire behavior and severity (Collins et al., 2021; Parks et al., 2018). Drought influences fire severity through a variety of mechanisms including the regulation of the accumulation of fine fuels, fuel moisture levels, and physiological stress (Clark et al., 2016; Kane et al., 2015b; Kolden et al., 2015). We used monthly estimates of Climatic Water Deficit (CWD) to characterize near-term drought, and mean values of 1-, 2-, and 3-year lags of monthly Palmer Drought Severity Index (PDSI) to characterize long-term drought. We assigned PDSI and CWD values to each pixel based on the ignition month for each fire. Daily fire weather is also a strong predictor of fire behavior and fire effects (Downing et al., 2021; Meigs et al., 2020; Parks et al., 2018, 2015) and we used maximum daily temperature (TMAX) and wind speed (WIND) estimated for each day of burn by interpolating MODIS hotspot detection point data across every burned pixel within a fire perimeter (Parks, 2014). We used GridMET data (Abatzoglou, 2013) to characterize TMAX and WIND, and TerraClimate data (Abatzoglou et al., 2018) to characterize PDSI and CWD.

2.2.4. Analysis

We evaluated the influence of top-down and bottom-up drivers on NR forest persistence using boosted regression trees. Boosted regression trees are useful for modeling complex, nonlinear relationships such as those expected to drive NR forest persistence (Elith et al., 2008; Friedman, 2001). Because our modeling regions have experienced numerous burns and reburns, we created separate datasets based on the number of times a pixel of NR forest burned following Downing et al. (2021) to determine if relationships between our predictor variables and NR forest persistence changed with each reburn. We created separate datasets for initially burned, twice-burned, and thrice-burned pixels of NR forest. Because MODIS hotspot detection data were only available beginning in 2002, but our MTBS fire perimeter data began in 1985, we only included pixels of NR forest that burned for the first time after 2001 in our initial burn dataset so we could model the influence of daily fire weather. We acknowledge that our definition of initially burned NR forest precludes fires prior to 1985, but this time point represents the beginning of accurate and reliable fire perimeter data (Eidenshink et al., 2007). As such, our initially burned dataset represents NR forest not burned since 1985 and burned first after 2001. We refer to this as 'initially burned' NR forest for simplicity. Our criteria for twice- and thrice-burned datasets were slightly different. We included all pixels that burned and persisted as NR forest as early as 1985 and subsequently reburned for the second time after 2001 in our twice-burned dataset, and all NR forest that burned and persisted through two fires since 1985 and reburned again for the third time after 2001 in our thrice-burned dataset. These criteria resulted in 5 separate datasets, once- ($n = 8612$) and twice-burned ($n = 507$) datasets for the north modeling region, and once- ($n = 155,666$), twice- ($n = 38,975$), and thrice-burned ($n = 5530$) datasets for the south modeling region. Initial modeling efforts for our twice-burned dataset in the north modeling region indicated an insufficient sample size so we do not discuss this dataset further. Correlation plots of predictor variables for initial-burn datasets are provided in supplemental figures (Figures S2 and S3).

We incorporated a nested cross-validation scheme consisting of five outer folds and four inner folds to help guard against biased model performance scores (Varma and Simon, 2006). To begin, we used data from outer folds 1–4 as training data and held fold five out for final testing. Within the training data (outer folds 1–4), we created another four distinct inner folds that we used to select the optimal set of tuning parameters with cross-validation. Next, a model was built using all the training data with the optimal set of tuning parameters and predictive performance was measured using fold five. We repeated this procedure five times with each outer fold being held out and used once as the test data set. We tested 250 different combinations of tuning parameters using a grid search approach (Bischl et al., 2023) across a range of learning rates (0.1–0.001), number of trees (1500–15,000) and tree complexities (3–5). To minimize lack of independence among training, validation, and test sets that may occur due to spatial autocorrelation, we used the blockCV package in R (Valavi et al., 2019) to create spatially separated blocks (folds) by generating empirical variograms for each predictor variable and using the median of the ranges of those variograms to inform block size.

We used the mean, cross-validated Area Under the receiver-operator characteristic Curve (AUC) scores across all 5 outer folds to assess model performance and evaluated the relative importance of each predictor variable and variables grouped by driver type (climate/weather, topography, vegetation) using permutation feature importance, a metric that measures the increase in classification error when each variable or group of variables is randomly permuted. Because this process is inherently variable, we permuted each variable or group of variables 100 times to generate an estimate of uncertainty associated with classification error increase. We visually assessed the relationships between our predictor variables and NR forest persistence using partial dependence plots and Shapley value plots (Povak et al., 2020; Sanna et al., 2025). Partial dependence plots represent the average predicted value of NR forest persistence across all observations while the variable of interest changes and are considered a measure of global variable influence. Shapley values are an extension of cooperative game theory where the objective is to apportion the contribution of each player to the outcome of a cooperative game. In a machine learning context, this is reinterpreted as evaluating the contribution of each predictor variable (player) to a model's predicted value (game outcome). Shapley values are calculated by evaluating the contribution of each predictor variable to the model's predicted value across all possible combinations of predictor variables and represent the log-odds contribution to the model's predicted value. This evaluation is done at the level of each observation (pixel) and can be considered a measure of local variable importance (Rozemberczki et al., 2022). Model analyses were performed using the mlr3 package (Lang et al., 2019) and model interpretations were performed using the mlr3 and iml (Molnar, 2018) packages in R (R Core Team, 2024).

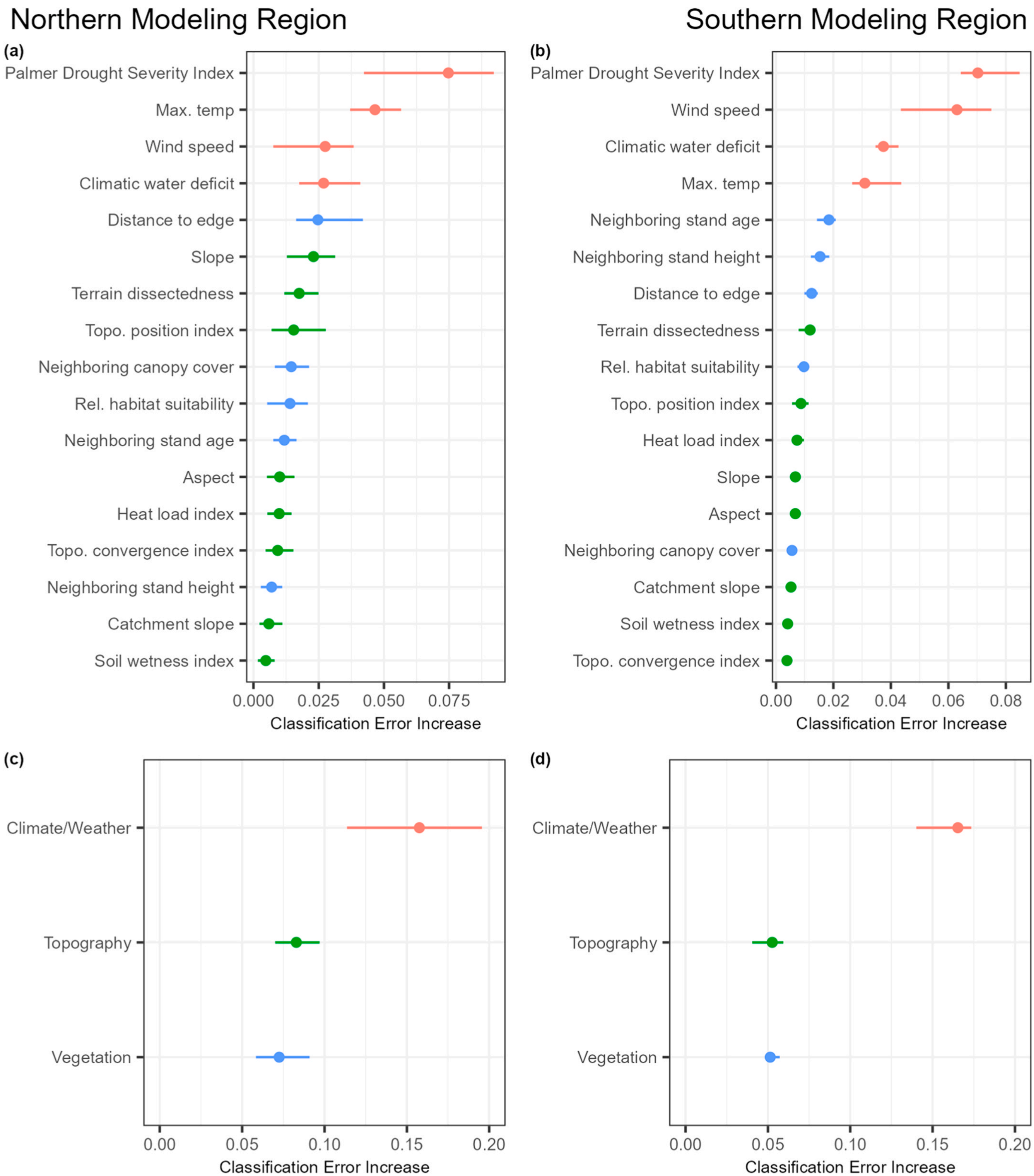

Fig. 2. Permutation feature importance scores of variables (a,b) and variables grouped by driver type (c,d) ranked by classification error increase used to analyze the post-fire persistence of northern spotted owl nesting and roosting forest in the north (a,c) and south (b,d) modeling regions. Classification error increase is the increase in classification error associated with randomly permuting each feature in a model. A list of variable names and acronyms can be found in Table 1. Colors for individual variables (a,b) match the associated driver types (c,d).

2.3. Mapping NR forest persistence

We used our models to predict the relative conditional probability of persistence of each 30 m x 30 m pixel of suitable NR forest in 2022 for both modeling regions given it burns under moderate or extreme fire weather conditions. We then mapped our predictions to identify any spatial patterns in the relative probability of NR forest persistence. We used vegetation conditions as of 2021 (one year pre-fire) because this was the most recent year of GNN data available. We defined two fire weather scenarios to represent fires burning under moderate fire weather conditions when bottom-up local controls are expected to drive fire severity, and extreme fire weather conditions when top-down drivers are expected to dominate (Krawchuk et al., 2016; Meigs et al., 2020). We defined moderate fire weather as the 50th percentile and extreme fire weather as the 90th percentile of daily estimates of TMAX and WIND during the fire season over the period 1991–2020. We defined the fire season start date as the date that included 90% of all ignitions in our dataset (i.e., 10th percentile of ignition dates) for each modeling region, and the end date as 30 September. We then calculated percentiles on a per-pixel basis to maintain the spatial variation in weather and assigned TMAX and WIND to every pixel of suitable NR forest. To ensure we were using reasonable combinations of TMAX and WIND we compared scatter plots of observed TMAX and WIND with our hypothetical combinations of TMAX and WIND to ensure point clouds for our hypothetical weather fell within the point cloud of observed weather conditions (Figure S2). Predictive maps for both modeling regions under

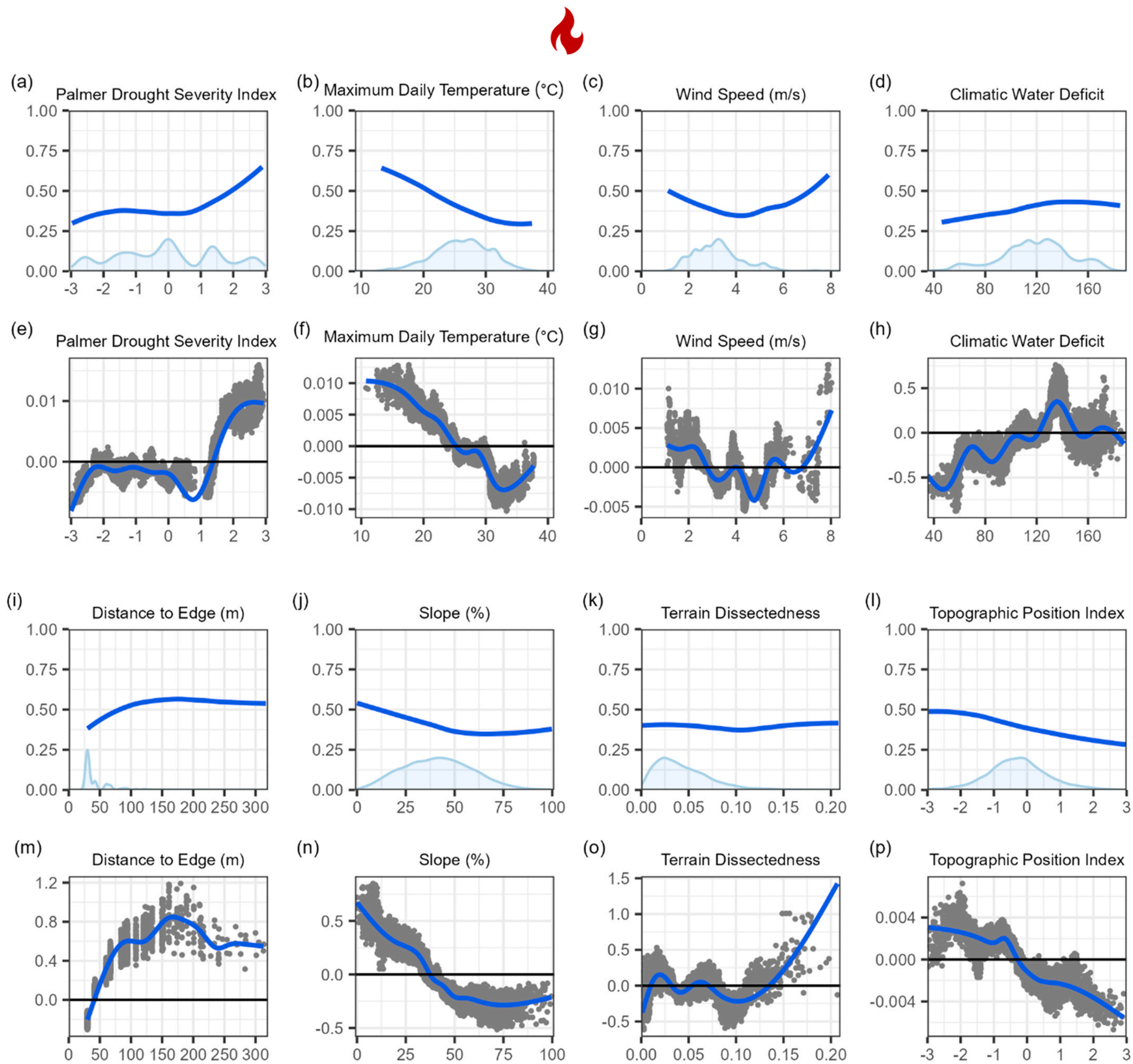

Fig. 3. North modeling region partial dependence plots (1st and 3rd rows) and Shapley plots (2nd and 4th rows) of the top 8 predictor variables arranged by classification error increase illustrating the relationships between the post-fire persistence of initially burned northern spotted owl nesting and roosting forest. Y-axes of partial dependence plots are relative probability of NR forest persistence and y-axes for Shapley plots are the increase or decrease in log-odds associated with each observation. Density plots in partial dependence plots show the distribution of data used to define observed relationships.

moderate and extreme fire weather scenarios are available for download from the fire refugia project website: https://firerefugia.forestry.oregonstate.edu/NSO-fire-refugia.

3. Results

3.1. Initially burned NR forest

Topography, vegetation, and climate/weather all influenced the persistence of initially burned NR forest in both modeling regions. Initial burn models performed similarly in both regions (south region mean AUC = 0.72; north region mean AUC = 0.71), suggesting reasonably good model performance. Climate and weather variables were the most important drivers of NR forest persistence, whereas topography and vegetation variables were relatively less important (Fig. 2a,b). This pattern of variable importance was also apparent when grouping variables by driver type, indicating climate and weather drivers were two to three times more important than topographic and vegetation drivers (Fig. 2c,d). Whereas the overall importance of driver types was similar across both modeling regions, the importance of individual variables changed from one region to the next. The persistence of NR forest in our north modeling region was positively associated with prolonged (2 yrs) wet conditions (i.e., PDSI > 0), increasing near-term (monthly) water deficit and for interior NR forest > 150 m from patch edge (Fig. 3). NR forest persistence was negatively associated with increasing daily temperatures during the fire, steeper slopes, and in more topographically exposed locations (i.e., TPI > 0; Fig. 3). Wind speed during the fire was negatively associated with NR forest persistence at moderate speeds

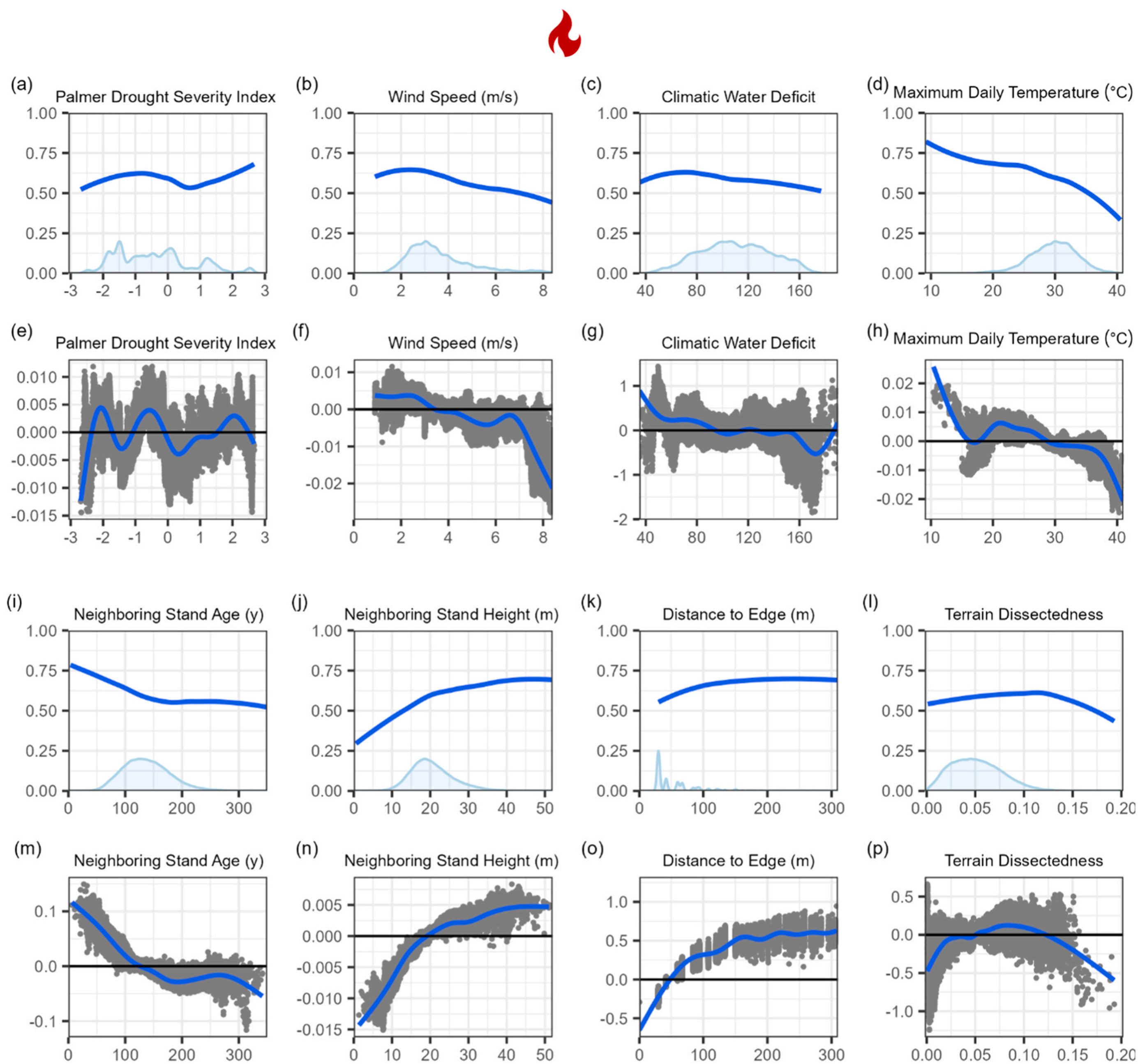

Fig. 4. South modeling region partial dependence plots (1st and 3rd rows) and Shapley plots (2nd and 4th rows) of the top 8 predictor variables arranged by classification error increase illustrating the relationships between the post-fire persistence of initially burned northern spotted owl nesting and roosting forest. Y-axes of partial dependence plots are relative probability of NR forest persistence and y-axes for Shapley plots are the increase or decrease in log-odds associated with each observation. Density plots in partial dependence plots show the distribution of data used to define observed relationships.

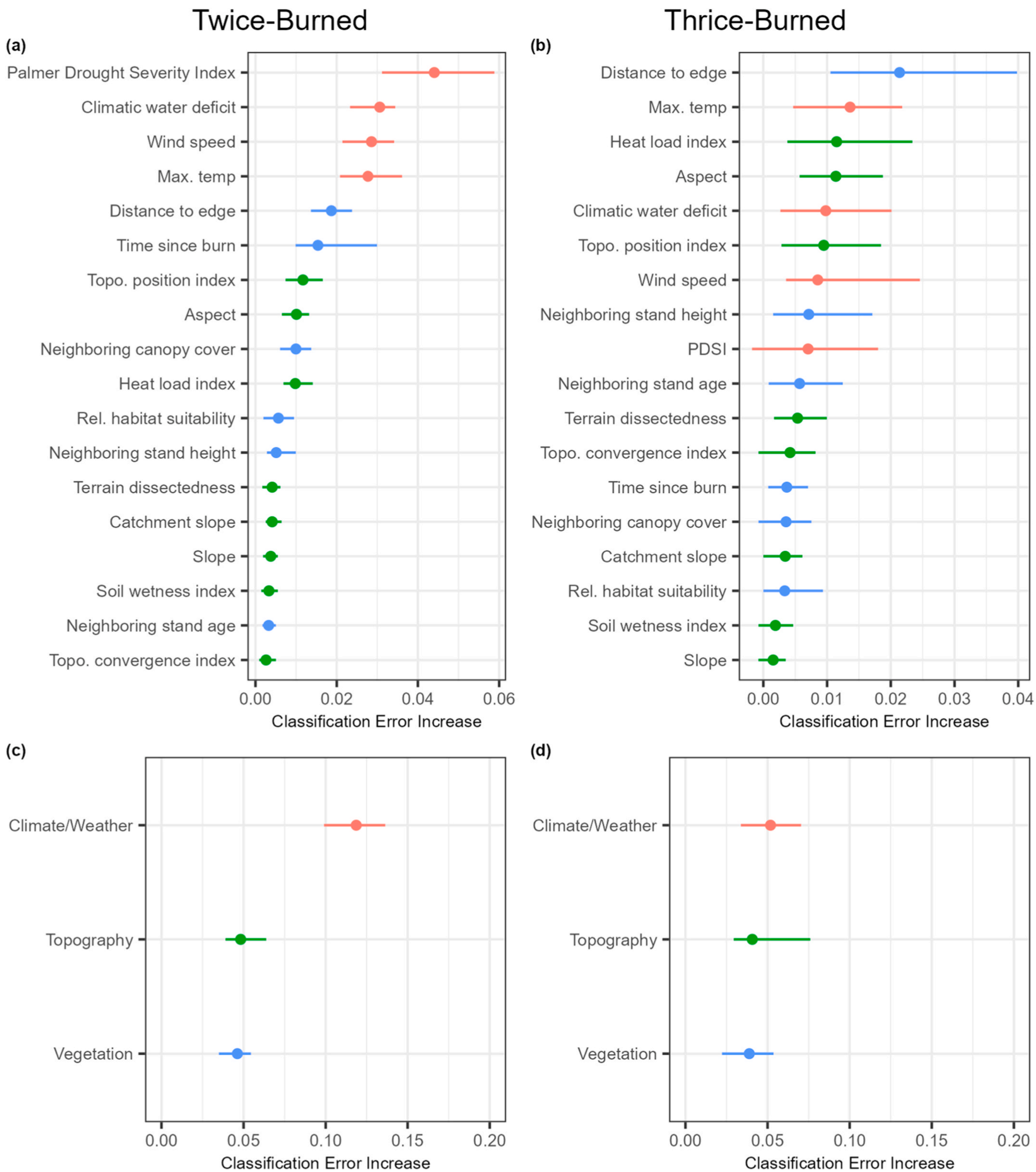

Fig. 5. Permutation feature importance scores of variables (a,b) and variables grouped by driver type (c,d) ranked by classification error increase used to analyze the post-fire persistence of twice-burned (a,c) and thrice-burned (b,d) northern spotted owl nesting and roosting forest for the south modeling region. Classification error increase is the increase in classification error associated with randomly permuting each feature in a model. Colors for individual variables (a,b) match the associated driver types (c,d).

(~1–5 m/s), but positively associated with persistence at the highest wind speeds (> 5 m/s) where data were sparse. In our south modeling region, NR forest persistence was positively associated with taller neighboring stands and increasing distance to patch edge (persistence was highest > 200 m from patch edge; Fig. 4). NR forest persistence was negatively associated with increasing daily temperature, near-term water deficit, wind speeds, and older neighboring stands (Fig. 4). Refer to Supplemental material for variable relationship plots of less influential variables.

3.2. Twice-burned NR forest

Model performance scores increased slightly between initial- and twice-burned datasets in our south modeling region (initial-burn AUC = 0.72; twice-burned AUC = 0.73). Climate and weather variables continued to be the most influential variables for predicting NR forest persistence through two fire events (Fig. 5a,c), however their importance decreased somewhat compared to our initial burn dataset. The importance of our topographic and vegetation drivers remained relatively unchanged (Fig. 5c). NR forest persistence for twice-burned patches of NR forest was positively associated with distance to edge (persistence was highest > 150 m from patch edge). NR forest persistence was also positively associated with prolonged wetter periods, and negatively associated with increasing daily temperatures and wind speeds during the fire, and in more topographically exposed locations. Time since previous fire had a variable effect on NR forest persistence. Shapley plots indicated that previous fires occurring < 10 years prior positively affected persistence whereas previous fires occurring > 10 years ago had a minimal or slight negative effect on predictions of NR forest persistence (Fig. 6n). Aspect also had a strong effect on NR forest persistence at the local level wherein west- and north-facing slopes had a positive effect on persistence, while east- and south-facing slopes had negative effects on persistence (Fig. 6p). In general, our models predicted NR forest that had previously burned once was more likely to persist through a second fire than NR forest not previously burned (Fig. 6; i.e., an overall increase in predicted persistence across all

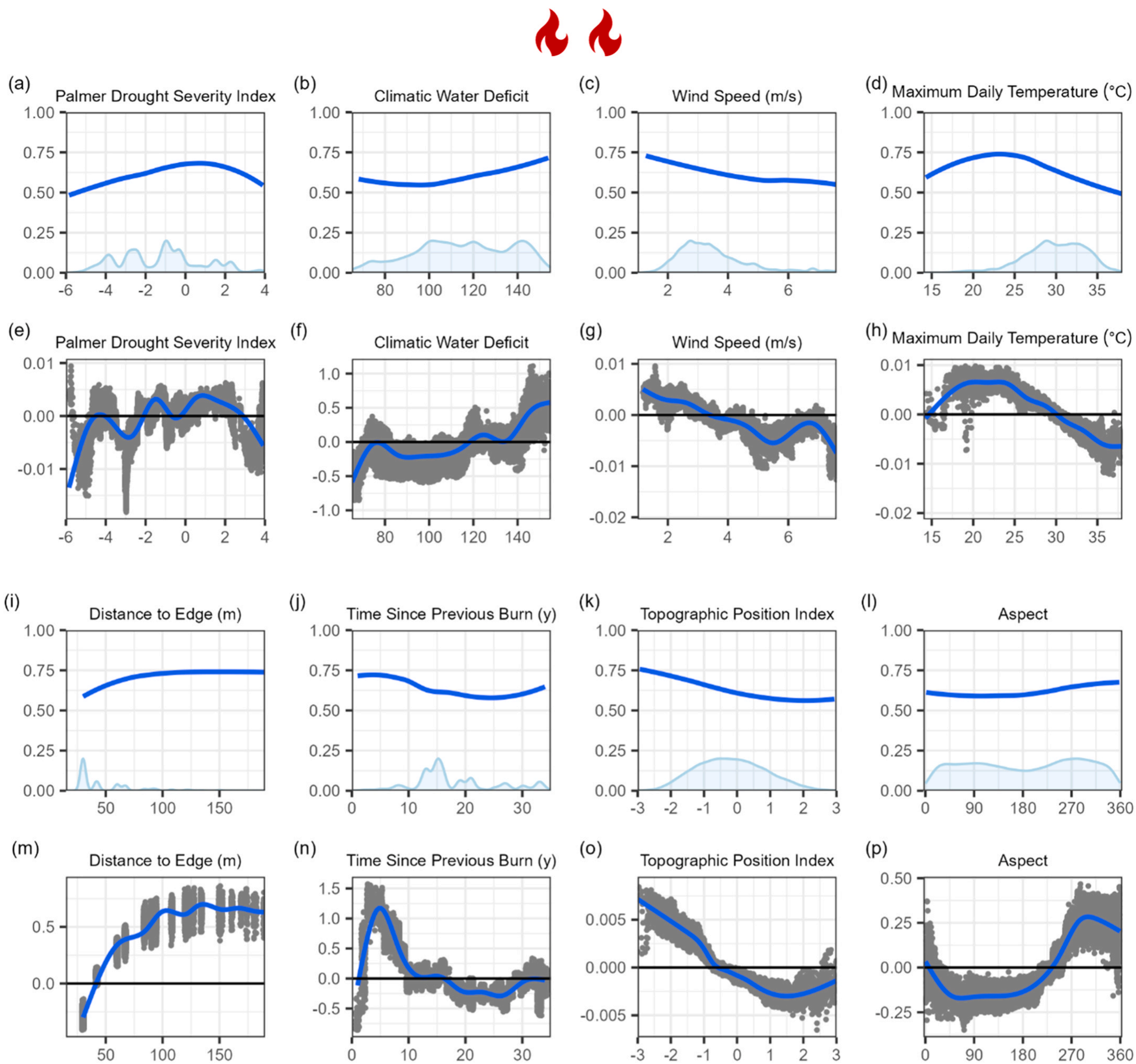

Fig. 6. South modeling region partial dependence plots (1st and 3rd rows) and Shapley plots (2nd and 4th rows) of the top 8 predictor variables arranged by classification error increase illustrating the relationships between the post-fire persistence of twice-burned northern spotted owl nesting and roosting forest. Y-axes of partial dependence plots are relative probability of NR forest persistence and y-axes for Shapley plots are the increase or decrease in log-odds associated with each observation. Density plots in partial dependence plots show the distribution of data used to define observed relationships.

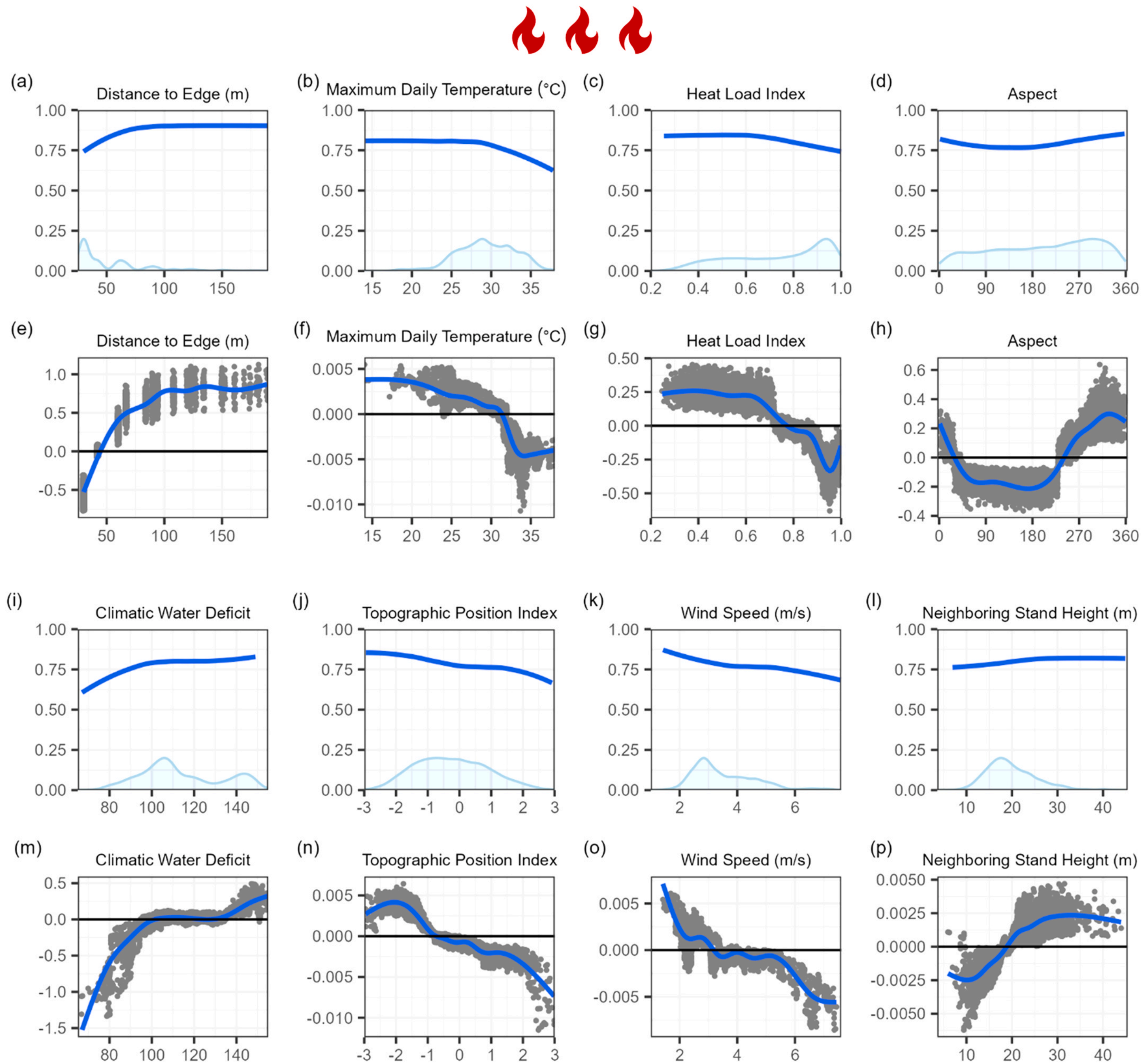

Fig. 7. South modeling region partial dependence plots (1st and 3rd rows) and Shapley plots (2nd and 4th rows) of the top 8 predictor variables arranged by classification error increase illustrating the relationships between the post-fire persistence of thrice-burned northern spotted owl nesting and roosting forest. Y-axes of partial dependence plots are relative probability of NR forest persistence and y-axes for Shapley plots are the increase or decrease in log-odds associated with each observation. Density plots in partial dependence plots show the distribution of data used to define observed relationships.

model variables compared to initially burned NR forest [Fig. 4]).

3.3. Thrice-burned NR forest

Model performance scores increased slightly between our twice- and thrice-burned datasets in our south modeling region (AUC = 0.76). Predictions of persistence for thrice-burned NR forest increased again compared to the twice-burned data suggesting that NR forest that persisted through two previous fires was more likely to persist through a third (Figs. 7, 8). The importance of climate and weather drivers decreased again from twice- to thrice-burned datasets, whereas the importance of topographic and vegetation drivers remained relatively consistent across all datasets. Thus, after NR forest burned three times, all three driver types were approximately equally important drivers of persistence (Fig. 5d). Furthermore, while all 4 of our climate and weather variables were the most important drivers for initial- and twice-burned datasets, 3 of the 4 top drivers for thrice-burned NR forest were topographic and vegetation variables (Fig. 5b). Persistence of thrice-burned NR forest was positively associated with distance from patch edge and was highest > 100 m from patch edge (Fig. 7a). NR forest persistence was also positively associated with increasing near-term water deficit (Fig. 7i) and taller neighboring stands (Fig. 7l). NR forest persistence was negatively associated with increasing daily temperatures (Fig. 7b) and wind speeds (Fig. 7k), on northeast- to southwest-facing slopes (Fig. 7d), with increased heat load (Fig. 7c) and in more topographically exposed locations (Fig. 7j). Shapley plots indicated strong threshold effects at the local scale for several explanatory variables. Maximum daily temperature exhibited a strong threshold effect

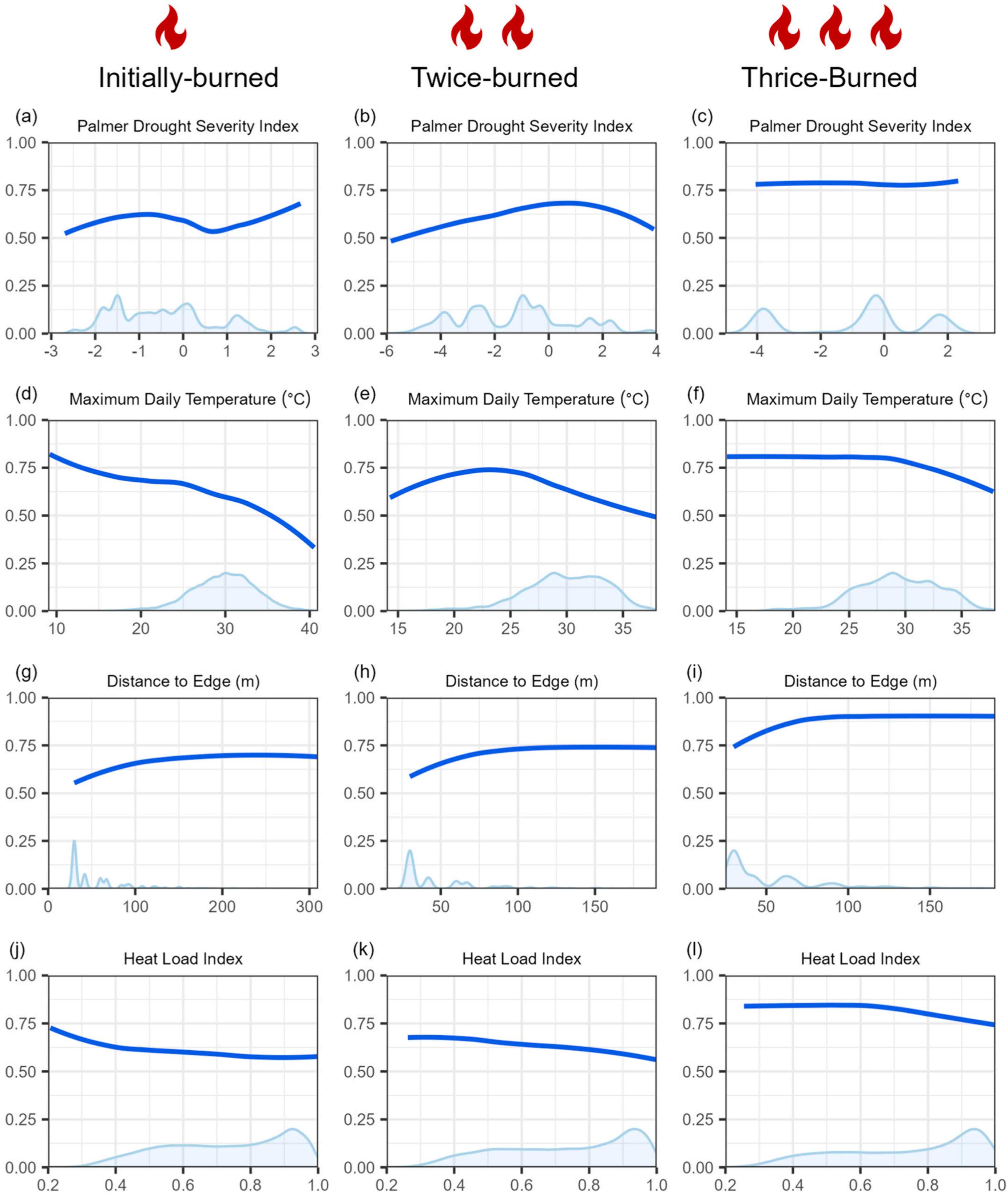

Fig. 8. Intercomparisons of partial dependence plots illustrating how driver influence changes for initially burned, twice-burned, and thrice-burned datasets for several variables. Plots are identical to those in Figs. 4, 6, and 7, but replicated here to facilitate comparison across datasets (columns). Y-axes represent the relative probability of NR forest persistence. Density plots in partial dependence plots show the distribution of data used to define observed relationships.

on NR forest persistence where moderate temperatures (< 30°C) had benign effects on persistence, but temperatures > 30°C had an increasingly negative effect (Fig. 7f). Similarly, wind speeds < 5 m/s had minimal effect on persistence, but wind speeds > 5 m/s had increasingly negative effects (Fig. 7o). Heat load index and aspect also exhibited threshold effects depending on the local setting. Local aspect positively influenced NR forest persistence where it occurred on southwest- to northeast-facing slopes, but negatively influenced persistence where it occurred on northeast- to southwest-facing slopes (Fig. 7h). Low heat load index values (< 0.7) positively influenced NR forest persistence, but values > 0.7 had strong negative effects (Fig. 7g).

3.4. Patterns of NR forest persistence

Patterns of NR forest persistence in both modeling regions were closely associated with local topography. NR forest persistence tended to be highest on north-facing slopes and in topographically sheltered locations (Figure S3; TPI < 0). In contrast, NR forest persistence was lowest in more topographically exposed locations such as ridgetops and south- southwest-facing slopes. Comparing predictions across both modeling regions and under moderate and extreme fire weather scenarios revealed differences in predictions of NR forest persistence. While the biophysical settings for persistent NR forest were similar for both regions (e.g., persistence was highest in topographically sheltered locations and lowest in topographically exposed locations), the north modeling region had generally lower probabilities of NR forest persistence under moderate fire weather conditions compared to the south modeling region (Fig. 10). Under moderate fire weather conditions, persistent NR forest in our south modeling region was more extensive and exhibited a well-connected dendritic pattern closely associated with the complex, dissected terrain of the region (Fig. 9). Persistence of NR forest in both modeling regions under extreme fire weather conditions declined (Fig. 10), likely resulting in increased losses of NR forest. Interestingly, our south modeling region appeared to endure relatively more NR forest loss than our north modeling region under extreme fire weather conditions. (Fig. 10).

4. Discussion

We used a species-specific approach to understanding fire refugia *for* northern spotted owls. By modeling the persistence of NR forest, we gained insight into the drivers of NR forest persistence and were able to assess where NR forest is most and least likely to persist through fire. The patterns of persistence predicted by our models closely resemble historical vegetation patterns and vegetation patterns consistent with high quality habitat for northern spotted owls (Dugger et al., 2005; Franklin et al., 2000; Kuntze et al., 2023; Olson et al., 2004; Zulla et al., 2022), which could be beneficial to spotted owl recovery efforts. Our results provide convincing evidence that the seemingly conflicting management goals of maintaining viable populations of northern spotted owls in frequent fire ecosystems and restoring landscape scale resistance and resilience are compatible.

4.1. Continued conflict or a path forward?

Our models indicated the persistence of NR forest was closely associated with local topography (Fig. 9), with the most persistent stands of NR forest occurring along drainage bottoms and topographically sheltered locations. These locations are also where the majority of spotted owl nest and roost locations occur (Forsman et al., 1984; Lahaye and Gutiérrez, 1999) and are referred to as core use areas because they represent areas of concentrated use (Berigan et al., 2012; Samuel et al., 1985). Past research in our south modeling region and throughout much of the frequent fire forests inhabited by California spotted owls (*S. o. occidentalis*) in the Sierra Nevada has shown that habitat heterogeneity benefits spotted owls (Dugger et al., 2005; Franklin et al., 2000; Kuntze et al., 2023; Zulla et al., 2023, 2022), but importantly *where* that heterogeneity occurs is critical. Spotted owl apparent survival is highest in territories with core use areas of mostly older, closed-canopy forest and more heterogenous conditions outside core use areas (Dugger et al., 2005) and spotted owls are more sensitive to the loss of NR forest inside their core use areas than outside core use areas (Rockweit et al., 2024). Restoration efforts that are guided by our maps of NR forest persistence could provide a way to navigate through this conflict. By maintaining areas of persistent NR forest where it occurs (in topographically sheltered locations) and restoring areas of susceptible NR forest to an appropriate historical analog, the resulting vegetation patterns (persistent NR forest in topographically sheltered locations and less persistent NR forest moving outward from topographically sheltered locations; Fig. 9), might be spatially similar to the vegetation patterns associated

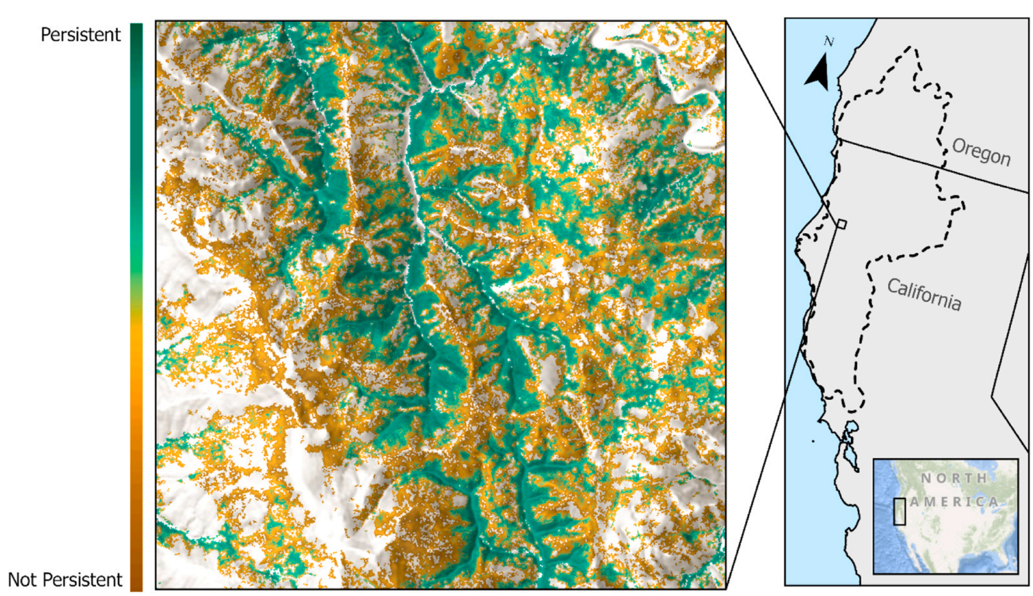

Fig. 9. Predictions of NR forest persistence for a representative area of our south modeling region showing spatial patterns in persistence. Persistent NR forest occurs along drainage bottoms and topographically sheltered locations, whereas less persistent NR forest occurs along upper slope positions and ridgetops in topographically exposed locations. Predictions are based on the initial-burn dataset.

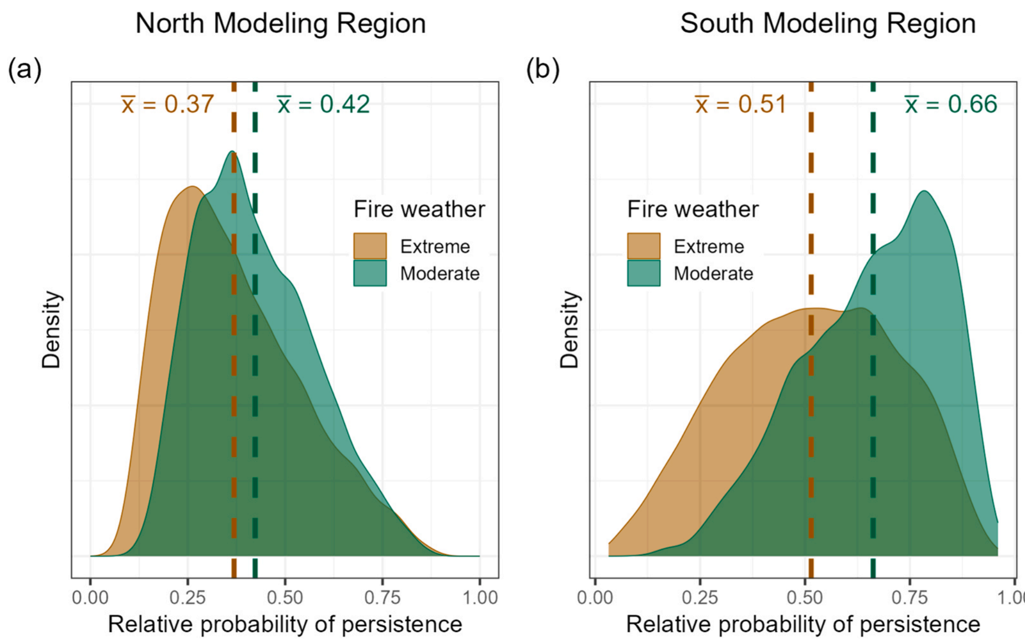

Fig. 10. Distributions of the relative probability of NR forest persistence for the north (a) and south (b) modeling region under a moderate (green) and extreme (brown) fire weather scenario. Vertical lines represent mean probabilities of persistence under moderate and extreme fire weather scenarios. Initial burn models indicate a smaller reduction in the relative probability of persistence as fire weather changes from moderate to extreme in our north modeling region compared to our south modeling region.

with high quality spotted owl habitat (core areas of mostly NR forest plus some heterogeneity outside core areas) because heterogenous territories may be higher quality territories (Dugger et al., 2005; Franklin et al., 2000) with more abundant prey (Kuntze et al., 2023) and increased prey delivery rates (Zulla et al., 2023, 2022), while also maintaining the important spatial component (Dugger et al., 2005; Rockweit et al., 2024). To advance this line of inquiry, we suggest experimental manipulation of vegetation within spotted owl territories using maps of NR forest persistence to more closely resemble historical conditions while monitoring subsequent impacts to spotted owl vital rates. This could help increase our understanding of the compatibility between spotted owl conservation and landscape restoration. We caution however, that these patterns have not been observed in other parts of the northern spotted owl's range including moister forest types or in our north modeling region, and it is unknown how our findings will apply to these other landscapes.

4.2. Patterns of NR forest persistence

Patterns of NR forest persistence in both modeling regions and across initial-, twice-, and thrice-burned datasets were similar revealing that persistence of NR forest was highest in topographically sheltered locations such as steep drainage bottoms, and lower portions of north-facing slopes—areas that historically tended to burn at lower severity and represent stands of persistent NR forest (Fig. 9; Taylor and Skinner, 2003, 1998). Conversely, persistence of NR forest was lowest where it occurred in more topographically exposed locations (TPI $>$ 0; Figure S3.). These areas likely represent stands that developed in the absence of fire and in uncharacteristic locations (Fig. 9). The spatial distribution of persistent NR forest we observed was similar to spatial patterns of fire refugia occurrence from other studies noting areas of high refugial potential tend to be located in topographically sheltered locations, whereas areas with low refugial potential tend to occur in topographically exposed locations (Camp et al., 1997; Downing et al., 2021; Krawchuk et al., 2016; Rodman et al., 2023).

While patterns of NR forest persistence between our north and south modeling regions were similar, there were notable differences that are reflective of regional differences in topography and historical landscape composition. Predictions of persistence based on our initial-burn models were generally lower overall for our north modeling region compared to the south region. These differences could be explained by differences in topography, climate, and tree species composition between these regions. Topography in the south modeling region was more complex and dissected, consisting of numerous deeply incised drainages that provide the optimal biophysical template for microclimatic buffering or decoupling (Betts et al., 2018; Davis et al., 2019; Frey et al., 2016) and provide suitable conditions for the development of persistent NR forest. Conversely, topography in the north modeling region generally consisted of broader, linear drainages shaped by recent glacial activity that may provide fewer opportunities for the development of persistent NR forest (Lillybridge et al., 1995; Montgomery, 1999). Our north modeling region also receives approximately half the annual precipitation as the south modeling region (National Oceanic and Atmospheric Administration, 2025), suggesting this region was historically composed of mostly dry, open forest types with limited opportunities to support persistent, closed-canopy NR forest (Agee and Edmunds, 1992; Halofsky et al., 2024; Hessburg et al., 2005; Irwin et al., 2004). Indeed, historical estimates suggest this region contained more NR forest cover on federally administered public lands around the time of the northern spotted owl's listing (1990) than in the 1930s (Halofsky et al., 2024; Hessburg et al., 2005; Spies et al., 2010). Tree species composition in the north modeling region may also be less fire resistant (Stevens et al., 2020) compared to the south modeling region, which could help explain overall lower probabilities of persistence in the north region.

Interestingly, predictions of NR forest persistence between moderate and extreme fire weather conditions also varied between regions. In the north modeling region, predictions from our initial-burn model indicated most NR forest had a relatively low probability of persistence under a moderate fire weather scenario, with only modest decreases in the probability of persistence under an extreme fire weather scenario (Fig. 10). This pattern was reversed in our south modeling region where our initial-burn model indicated that most NR forest had a relatively high probability of persistence under moderate fire weather, but under an extreme fire weather scenario, NR forest persistence declined more substantially (Fig. 10). The opposing patterns between these regions also suggest potentially important differences in historical and contemporary landscape composition. Davis and Lint, (2005) used historical forest survey maps from the 1930s and 1940s to estimate the amount of NR forest on federally administered public lands within the geographic range of the owl at the onset of effective fire suppression (Pyne, 1982). Their analysis suggested there was proportionately less forest capable of supporting spotted owls in the eastern Washington Cascades than in the Klamath Province—which encompasses most of the south modeling region. If more contemporary NR forest in the north modeling region is located in uncharacteristic locations as a result of fire exclusion (Hessburg et al., 2005), we might expect more substantial losses of this forest type under moderate fire weather conditions which could help explain these divergent patterns in NR forest persistence.

While NR forest in the south modeling region had relatively high probabilities of persistence under moderate fire weather conditions, this region is expected to experience the greatest increase in large wildfire activity over the coming decades (Davis et al., 2017). While our models predicted modest increases in NR forest persistence with each reburn (Figs. 4,6,7), fires are expected to operate under increasingly hotter and drier conditions (Parks et al., 2016; Parks and Abatzoglou, 2020; Westerling, 2016) that could overwhelm topographic controls (Meigs et al., 2020) resulting in substantial losses of NR forest. This could have dire consequences for spotted owls in the region because this region represents the last population stronghold for northern spotted owls (Franklin et al., 2021). Paradoxically, the immense conservation efforts focused on retaining and recruiting as much NR forest as possible may have contributed to the reduction in landscape resilience and may now be increasing the risk to remaining populations (Agee and Edmunds, 1992; Jones et al., 2025; Steel et al., 2023).

4.3. Changing drivers of fire effects

Our analyses in the south modeling region indicated that the relative importance of our top-down and bottom-up fire drivers changed as landscapes burned multiple times. While our top-down drivers were the most influential drivers of NR forest persistence for initial- and twice-burned datasets, the relative importance of our bottom-up drivers gradually increased with each burn such that bottom-up and top-down drivers were equally important influences on NR forest persistence by the third fire (Figs. 2 and 5). In particular, we observed an increase in the importance of some of our topographic drivers such as aspect, heat load index, and topographic position index (Figs. 2 and 5). Prior to European settlement, fire behavior and forest structure varied with local topography (Agee, 1991; Beaty and Taylor, 2001; Taylor and Skinner, 2003, 1998). Since then, fire exclusion and increased fuel loads (Agee and Skinner, 2005; Hessburg et al., 2005) have resulted in larger, more uncharacteristically severe fires that may override local topographic controls and dampen the role of local topography (Kuntzemann et al., 2025; Meigs et al., 2020). The gradual emergence of some of our topographic drivers as important drivers of fire behavior could indicate increased resilience compared to fire-excluded areas, provided fires burn under moderate weather conditions. This could help land managers better anticipate fire effects because bottom-up drivers are predictable, whereas top-down drivers are stochastic by nature. We note however, that the relationships observed in this study are based on observational data and thus are not causative, but instead represent correlational relationships between our fire drivers and NR forest persistence.

Our analyses indicated that after more than a century of fire exclusion, a return to an active fire pattern may help restore the roles of topography and vegetation in governing fire behavior to some degree, provided that previous fires burned under moderate weather conditions (Collins et al., 2019; Meigs et al., 2020). While this is encouraging and provides additional evidence of fire's restorative role (Pausas and Keeley, 2019), our models also indicated that NR forest persistence declined notably when maximum daily temperatures exceeded ~ 30 °C, a finding that was remarkably consistent across both modeling regions and initial and reburn datasets (Figs. 3–4,6–7). Thus, while our data suggest that leveraging wildfire's restorative role could yield significant ecosystem-wide benefits, longer, hotter and drier fire seasons (Parks and Abatzoglou, 2020; Westerling, 2016) suggest the time to leverage fire as an ecological service (McLauchlan et al., 2020) may be rapidly dwindling.

Vegetation structure was also an important driver of NR forest persistence across initial and reburn datasets, but apart from our distance to patch edge and relative habitat suitability metric, there was little consistency to its influence on NR forest persistence. Our distance to patch edge and relative habitat suitability variables had consistent influences on NR forest persistence across all initial and reburn datasets that indicated increased persistence for interior stands and for highly suitable NR forest (Figs. 3–7, Figures S5-S8). While these metrics described vegetation conditions, we suspect vegetation indirectly influenced NR forest persistence by modifying stand microclimate and by the increasing importance of local topography that reduced fire contagion. Interior old forest stands are associated with cooler, moister and less windy microclimates compared to old forest edges (Chen et al., 1999; Wolf et al., 2021), which could reduce fire intensity (Countryman, 1956) and increase NR forest persistence. While edge effects associated with microclimate may be partly responsible for the observed patterns, our analyses also revealed that edge effects shortened with each reburn (Fig. 8). This could indicate a gradual transition of pre-fire landscape vegetation patterns with each reburn to one that more closely resembles historical vegetation patterns and limits the contagious nature of fire (Povak et al., 2020) leading to increasingly resistant NR forest stands. In addition, high quality NR forest is characterized by dense, multi-layered forests with high biomass (Lahaye and Gutiérrez, 1999; Sovern et al., 2019; Davis et al., 2022) that have been found to be a good predictor of fire refugia (Lesmeister et al., 2021; Meigs et al., 2020). Thus, while distance to edge and relative habitat suitability were correlated with NR forest persistence, we believe these findings provide further evidence of the important role of old forest microclimate and landscape composition and structure in the development of persistent, closed-canopy forest (Betts et al., 2018; Krawchuk et al., 2026; Lydersen et al., 2013).

The neighboring stand structure metrics we developed to examine the role of nearby vegetation on NR forest persistence had less consistent effects and were relatively unimportant. In our north modeling region, our neighboring stand metrics were relatively unimportant for predicting NR forest persistence, whereas in our south modeling region, neighboring stand age and height were important for initially burned, but less so for reburned NR forest (Figs. 2, 5). The relationships between our neighboring stand structure metrics and NR forest persistence also varied across initial and reburned datasets, making inferences difficult. Our south modeling region included the Klamath physiographic province and portions of the southern Cascades and California coast range provinces, which have high levels of vegetation diversity (Whittaker, 1960; Franklin and Dyrness, 1988). One possible explanation for these results is that our metrics were confounded by variation in site productivity or species composition not accurately reflected in our neighboring stand variables. Indeed, a post-hoc examination of our neighboring stand age variable indicated significant additional variation attributable to different stand structures and compositions that may vary in their ability to carry fire into neighboring stands (Figure S4). It is also possible that the presence of numerous underlying interactions among our variables made drawing inferences from our variable relationship plots difficult. Thus, we suspect a combination of unobserved interactions and uncaptured variability contributed to uncertainty regarding the importance of neighboring vegetation structure.

Numerous underlying interactions may also be responsible for the interesting relationships we found with PDSI and CWD, and NR forest persistence. Both variables were highly important in our south modeling region, initial and twice-burned datasets (Figs. 2b and 5a), yet our plots indicated relatively flat relationships between these variables and NR forest persistence (Figs. 4 and 6). One explanation could be important, yet unaccounted for interactions between PDSI and CWD with other fire drivers not evident in our plots (e.g., Kane et al., 2015a). The slight positive relationship between CWD and NR forest persistence in all but our south modeling region, initial-burn dataset was also unexpected (Figs. 3,6, and 7). Climatic water deficit is both positively and negatively associated with fire severity depending on the degree to which varying constraints influence fire behavior (Krawchuk and Moritz, 2011; Parks et al., 2014). The positive relationship with CWD we observed could be a result of reduced fine fuels associated with near term drought that limited fire spread and severity in these dry forest types (Parks et al., 2014). Alternatively, the observed relationship could be due to a scale mismatch between the resolution of our climate data (~ 4 km) and the scale at which local topography influences CWD within persistent NR forest. If more NR forest burns as CWD increases, but our coarse scale CWD metric misses important fine scale variation that depresses CWD in topographically sheltered locations because of cooler, moister microclimates (Davis et al., 2019; De Frenne et al., 2021; Frey et al., 2016), the positive relationship with CWD observed in our data would be expected.

4.4. Management implications

There is a perceived conflict between conservation efforts geared towards maintaining viable populations of northern spotted owls and those efforts aimed at increasing forest resilience (Halofsky et al., 2024; Irwin et al., 2004). This conflict is more dire than ever because the remaining population stronghold of northern spotted owls exists in our southern modeling region (Franklin et al., 2021; Rockweit et al., 2023) where fire activity is projected to increase substantially (Davis et al., 2017). Fire refugia concepts such as those used in this study to identify fire refugia *for* northern spotted owls (sensu Meddens et al., 2018) could help resolve this conflict (Krawchuk et al., 2026; Lesmeister et al., 2025) because these refugia represent anchors of resistance in otherwise dynamic landscapes. The spatial patterns of persistence we observed could help target priority areas for management intervention and inform treatment objectives. Moreover, treatment objectives will be most effective at meeting desired conditions when they are guided by the processes responsible for creating the vegetation patterns that restoration attempts to emulate (Churchill et al., 2013; Hessburg et al., 2015; Jones et al., 2025). In areas of highly persistent NR forest, treatment objectives that mimic the effects of historically frequent, low severity fire using prescribed fire to reduce fuel loads might increase the resistance of already persistent NR forest. In areas where NR forest is unlikely to persist even during moderate fire weather, restoration activities that tailor treatment objectives (e.g., restoring oak stands, etc.) based on local topography and designed to mimic historical fire effects could be prioritized (Downing et al., 2021; Hessburg et al., 2015). This could include commercial removal of some stands of highly susceptible NR forest, especially if those stands are not being used for nesting and roosting. While we believe this approach holds much promise, there will nonetheless be some cases where this management approach is unfeasible and it may be necessary to retain some stands of susceptible NR forest particularly where occupied by spotted owls. In these cases, management activities designed to reduce the contagious nature of fire by restoring historical vegetation patterns outside currently occupied, but susceptible NR forest stands may increase stand resistance and hence the likelihood of spotted owl persistence. Similar work aimed at addressing this complex and nuanced issue has been conducted within the range of the California spotted owl and recent work there also indicates these seemingly conflicting goals may actually be more complementary than previously thought (McGinn et al., 2026; Peery et al., 2017). Our study adds to this growing body of research by identifying the spatial patterns of persistence of an important habitat component, thereby providing important spatial context to help guide forest restoration and spotted owl conservation.

CRediT authorship contribution statement

Meg A. Krawchuk: Writing – review & editing, Supervision, Methodology, Conceptualization. **Jeremy T. Rockweit:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Katie M. Dugger:** Writing – review & editing, Supervision, Resources, Funding acquisition. **David M. Bell:** Writing – review & editing, Conceptualization. **Damon B. Lesmeister:** Writing – review & editing, Resources, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123800.

Data availability

Maps of NR forest persistence are hosted online at: https://firerefugia.forestry.oregonstate.edu/NSO-fire-refugia.html

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