Mixed-severity wildfire and habitat of an old-forest obligate

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Abstract.   The frequency, extent, and severity of wildfire strongly influence the structure and function of ecosystems. Mixed-severity fire regimes are the most complex and least understood fire regimes, and variability of fire severity can occur at fine spatial and temporal scales, depending on previous disturbance history, topography, fuel continuity, vegetation type, and weather. During high fire weather in 2013, a complex of mixed-severity wildfires burned across multiple ownerships within the Klamath-Siskiyou ecoregion of southwestern Oregon where northern spotted owl (*Strix occidentalis caurina*) demographics were studied since 1990. A year prior to these wildfires, high-resolution, remotely sensed forest structural information derived from light detection and ranging (lidar) data was acquired for an area that fully covered the extent of these fires. To quantify wildfire impact on northern spotted owl nesting/roosting habitat, we fit a relative habitat suitability model based on pre-fire locations used for nesting and roosting, and forest structure variables developed from 2012 lidar data. Our pre-fire habitat suitability model predicted nesting/roosting locations well, and variable response functions followed known resource selection patterns. These forests had typical characteristics of old-growth forest, with high density of large live trees, high canopy cover, and complex structure in canopy height. We projected the pre-fire model onto lidar data collected two months post-fire to produce a post-fire suitability map, which indicated that >93% of pre-fire habitat that burned at high severity was no longer suitable forest for nesting and roosting. We also quantified the probability that pre-fire nesting/roosting habitat would burn at each severity class (unburned/low, low, moderate, high). Pre-fire nesting/roosting habitat had lower probability of burning at moderate or high severity compared to other forest types under high burning conditions. Our results indicate that northern spotted owl habitat can buffer the negative effects of climate change by enhancing biodiversity and resistance to high-severity fires, which are predicted to increase in frequency and extent with climate change. Within this region, protecting large blocks of old forests could be an integral component of management plans that successfully maintain variability of forests in this mixed-ownership and mixed-severity fire regime landscape and enhance conservation of many species.

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INTRODUCTION

Climate and land-use patterns are strong predictors of disturbance regimes that ultimately influence the structure and function of an ecosystem (Sousa 1984). Globally, forest ecosystems are at risk of large disturbance regime shifts (frequency and severity) and ultimately a range of possible alternative stable states due to climate change-induced drought and heat stress, and associated interactions with insect disease outbreaks and wildfire (Dale et al. 2001, Allen et al. 2010, Kitzberger et al. 2012). In the case of fire regimes, their frequency and severity are typically negatively correlated, such that frequent fires are of lower severity, and strongly influence community dynamics and successional pathways (Agee 2005). Fire regimes play a key role in species adaptations as well as community structure and distribution of ecosystems, including the availability of several key components of wildlife habitat (Bunnell 1995, Noss et al. 2006, Pausas and Keeley 2009). Persistence of native wildlife species that are adapted to historical fire regimes may be at risk given climate change and land management practices that alter patterns in fire frequency and intensity relative to historical patterns. For example, in many dry forests the extent of areas impacted by high-severity fire is increasing, with concern for sensitive wildlife species that rely on forest types altered by fire (Westerling et al. 2006, Miller et al. 2008, Miller and Safford 2012, Reilly et al. 2017, Rockweit et al. 2017).

The fire regime of an ecosystem is defined as the natural patterns of wildfire in a given area including fire frequency, seasonality, extent, severity, and synergistic effects with other disturbances (Agee 1993, Halofsky et al. 2011). Forest successional theory suggests that in most areas, the interval length between disturbances should influence outcomes of succession, such that early-seral stands, low stature, and open microclimates are common in ecosystems with short-interval fires, whereas those with long-interval fires generally are dominated by mature forests with relatively closed canopies (Donato et al. 2009, Halofsky et al. 2011). Low-severity regimes are most often associated with dry forest types which experience frequent and predominantly low-severity fires where loss of biomass due to fire is low, and <30% mortality of trees is typical (Agee 1993). This disturbance regime results in stands with open canopies and an understory dominated by sprouting and rhizomatous shrubs and herbaceous plants, which are described in historical accounts as open, parklike forests (Agee 2013). The extent of these forest types was often overrepresented in historical records due to the ease of traveling through them and the opportunities for pleasing photographs (Van Pelt 2008). In truth, these open, parklike forest conditions do not represent many forests in western North America (Odion et al. 2014). Forests in high-severity fire regimes experience infrequent (>200-yr return intervals) but high-severity fires. Large patches of total mortality occur within the fire events and overall mortality is high (>70%), though areas of low- and moderate-severity fire are also common (Agee 1993, Turner and Romme 1994). In western North America, these forest types associated with high-severity fire regimes are characteristic of high-elevation, lodgepole pine (*Pinus contorta*)-dominated stands, some spruce (*Picea* spp.)-dominated forests, and moist Douglas-fir (*Pseudotsuga menziesii*)/western hemlock (*Tsuga heterophylla*) forests of the Pacific Northwest (Agee 1993).

Within mixed-severity fires, 30–70% tree mortality is common; however, the mixed-severity regime is not simply intermediate between low- and high-severity fire regimes (Agee 1993, Perry et al. 2011). The resulting pattern of low-, moderate-, and high-severity fire patches within a given area is highly variable and difficult to predict (Agee 2005), although at a large enough spatial scale (e.g., watersheds), nearly all fires are mixed-severity (Turner and Romme 1994, Baker et al. 2007, Halofsky et al. 2011). This variability can occur at fine spatial and temporal scales dependent on previous fire history, topography, fuel continuity, vegetation type, and weather (Heyerdahl et al. 2001, Donato et al. 2009, Thompson and Spies 2009, Krawchuk et al. 2016). Because of the spatiotemporal variability across the landscape, mixed-severity fire regimes are the most complex and least understood fire regimes, unique in terms of patch metrics and the life history attributes of native species (Schoennagel et al. 2004, Agee 2005, Halofsky et al. 2011). Fire histories in mixed-severity regimes, in particular, are difficult to determine

because most fire history techniques have been developed to study either the low- or high-severity extremes in fire regimes (Agee 2005). Short-interval severe fires are an important characteristic of mixed-severity fire regimes and are typically considered extreme events and expected to be deleterious to forest succession and diversity (Donato et al. 2009). However, many native plants within these forests possess functional traits (e.g., persistent seed banks, vegetative sprouting, rapid maturation) lending to resilience to short-interval severe fires that result in distinct vegetation assemblages that enhance landscape heterogeneity inherent to mixed-severity fire regimes (Donato et al. 2009). Furthermore, high diversity of vegetation types, driven by short-interval repeat fires in a mixed-severity fire regime landscapes, plays an important role in conservation and the structure of avian communities (Fontaine et al. 2009).

Fire behavior is most strongly influenced by weather, topography, and fuels (i.e., above-ground vegetation biomass) interacting through multiple pathways and at multiple spatial scales (Agee 1993). Weather is perhaps the most important factor controlling fire behavior and severity, especially in mixed-severity regimes (Bessie and Johnson 1995, Collins et al. 2007, Thompson and Spies 2009, Bradstock et al. 2010). In moderate fire weather, topographical complexity and position (east- and south-facing, upper- and mid-slopes) have been shown to strongly influence fire intensity, with pre-fire vegetation condition and fire history also important predictors of severity (Estes et al. 2017). Under these conditions, shrubs and younger forests were more likely to burn at higher intensity than mature forests. In very high and severe fire weather, the amount (fuel loads), type (e.g., younger vs. older forest), and vertical and horizontal spatial arrangement of fuels (contiguous vs. unconnected) can be the primary driver of spatial patterns in mixed-severity fire (Zald and Dunn 2018). Furthermore, previous fires and post-fire management can set up the landscape for patterns of self-perpetuating high-severity fire in mixed-severity regimes (Donato et al. 2009, Thompson and Spies 2010). Even in drier forest types with high frequency of fire, certain topographic settings have lower fire frequencies where patches of dense, old forest can develop and persist as islands in a matrix of open, older forests (Camp et al. 1997, Krawchuk et al. 2016). With changing climates and land management practices, the size of patches of high-severity fire is increasing relative to historical patterns, with concern for sensitive species that rely on forests dramatically altered by fire (Westerling et al. 2006, Miller et al. 2008, Miller and Safford 2012, Reilly et al. 2017, Rockweit et al. 2017).

Northern spotted owls (*Strix occidentalis caurina*) are an obligate species of old forests in the Pacific Northwest of the United States and southwest Canada and typically nest in large old conifer trees (Wilk et al. 2018). The subspecies was listed as threatened under the U.S. Endangered Species Act because populations declined primarily as result of habitat loss due to large-scale harvest of late-successional forests (USFWS 1990). A variety of forest types are used by northern spotted owls for foraging, but nesting and roosting primarily occur in forests older than 125 yr of age. These older forests have average tree diameters above 50 cm and many trees exceed 75 cm diameter, canopy cover is usually >60%, and the forest has multiple canopy layers (Davis et al. 2016). The Northwest Forest Plan (NWFP) was designed to protect most remaining old forest and, after several decades, provide enough habitat on federal lands for viable populations of several old-forest species, primarily through a network of late-successional forest reserves (USDA and USDI 1994). On federal lands, loss of northern spotted owl habitat due to timber harvest has declined, but losses due to wildfires have increased in recent decades (Davis et al. 2016). Studies focused on the subspecies of northern spotted owls suggest that occupancy and survival generally decline after fire, especially if post-fire logging occurs (Clark et al. 2011, 2013, Rockweit et al. 2017). The effects of fire on individual northern spotted owls and habitat quality are complex and not fully understood (Lesmeister et al. 2018), but clearly suitability of forests for nesting and roosting decreases if canopy cover is reduced and with spatial aggregation of high-severity fire (Davis et al. 2016, Rockweit et al. 2017, Sovern et al. 2019).

Fire regimes within the range of northern spotted owls range from infrequent/high severity in the northern and coastal regions to frequent/low

severity in the eastern and southern regions (Spies et al. 2018). In between these two extremes is a broad area of mixed-severity regimes, including the Oregon Klamath, where recent wildfires have caused high rates of loss of old forests and threaten species associated with them (Spies et al. 2006, 2018). Wildfires within this regime are comprised of a mix of burn severities, with low-severity ranging from 45% to 54% of the burned area, moderate-severity from 24% to 36%, and high-severity fire from 23% to 26% (Reilly et al. 2017). While the frequency and extent of high-severity fire have been increasing due to a general increase in large wildfires within the owls range, there is no strong evidence that high-severity wildfire comprises a higher proportion of burned areas than it did historically (Miller and Safford 2012, Reilly et al. 2017).

Within the Klamath-Siskiyou ecoregion of southwestern Oregon, an area characterized as moderate-frequency, mixed-severity fire regime (Spies et al. 2018), northern spotted owl demographics have been studied on the Klamath demographic study area since 1990 (Dugger et al. 2016). In and near the study area, lightning from a thunderstorm on 26 July 2013 started 54 fires that burned under very high fire weather conditions and were managed as the Douglas Complex and Big Windy Fires (Zald and Dunn 2018). Most of the fires joined into several large fires that burned with mixed severity over an area of about 38,000 ha. Within the fire perimeter were large patches of high-severity fire and subsequent salvage logging, primarily on private lands and along roads on federal lands. The non-overlapping—but nearby—large mixed-severity wildfires burning simultaneously in a mixed-ownership and management landscape presented a unique landscape experiment to evaluate interactions between severity classes (unburned/low, low, moderate, and high) and vegetation condition (e.g., suitable or unsuitable forest for nesting and roosting by northern spotted owls). Further, the study area provided an exceptional opportunity to study responses of vegetation to fire because high-resolution remote sensing data of vegetation height provided by aerial light detection and ranging (lidar) were available pre- and post-fire, which provided an unprecedented ability to measure forest attributes before and immediately following the fires.

Our objectives were to (1) quantify the immediate impact of various wildfire severities on northern spotted owl nesting/roosting habitat, which has typical characteristics of old-growth forests in the Pacific Northwest; and (2) analyze the relative susceptibility of northern spotted owl nesting/roosting habitat to higher or lower severity fire. We hypothesized that northern spotted owl nesting/roosting habitat would be degraded as severity increased, but the relationship would be non-linear where habitat would not be degraded at low severity, only slightly degraded with moderate severity, and highly degraded with high severity. Because the area was in drought and fire weather was very high to severe, we expected the high fuel loading of northern spotted owl nesting/roosting habitat may cause these stands to burn at higher or equal severity than other forest types with less fuel (Weatherspoon et al. 1992). However, several lines of evidence suggest older forests with dense, multi-storied canopies are more resistant to high-severity wildfire during severe fire weather (e.g., Countryman 1955).

METHODS

Study site

The study was conducted in the Klamath-Siskiyou ecoregion, which extends from northwestern California into southwestern Oregon (Fig. 1). The Douglas Complex and Big Windy Fires burned mostly within the boundary of the Klamath northern spotted owl demography study area (1422 km^2; Fig. 1) with elevations ranging from 610 to 1680 m. Annual precipitation ranged from 1500 to 3000 mm over the study area (http://prism.oregonstate.edu/), with <15% falling from May to September. The region is among the top global hotspots of species rarity and richness, identified as a global center of biodiversity, a World Wildlife Fund globally outstanding ecoregion (www.worldwildlife.org/publications/global-200), and an IUCN area of global botanical significance (Olson and Dinerstein 1998, Noss 2000). The complexities of climate, topography, biogeographic patterns, geology, and mixed-severity fire regime in the Klamath and Siskiyou Mountains create one of the four richest temperate coniferous forests in the world with high endemism, species richness, and unique community assemblages (Noss et al. 1999, Vance-Borland

1999). Forests were dominated by Douglas-fir, ponderosa pine (*P. ponderosa*), sugar pine (*P. lambertiana*), and incense cedar (*Calocedrus decurrens*) and mixed with a variety of other conifers (*Pinus* spp. and grand fir *Abies grandis*) and hardwoods (e.g., Pacific madrone *Arbutus menziesii*, golden chinquapin *Castanopsis chrysophylla*, and oak *Quercus* spp.).

Within the Klamath-Siskiyou ecoregion, a complex and variable fire regime prevails, dominated by frequent mixed-severity and very frequent mixed-severity fires (Fig. 1; Spies et al. 2018). Historical fire severity varied in spatial scale, patchiness, and fire-return intervals (c. 5–75 yr), but overall exhibiting mixed severity over

time and space (Agee 1993, Taylor and Skinner 1998, Perry et al. 2011). When a stand-replacing fire occurs, rapid recovery of vegetation and fuel continuity, coupled with dry summers and frequent lightning, create the potential for recurrent high-severity fires over decadal timescales (Thompson et al. 2007). Thus, short-interval severe fires have likely been a component of the complex fire regime and a factor structuring vegetation in the region (Agee 1993, Donato et al. 2009).

Fire data

We used daily fire perimeter map data for the Douglas Complex Fires that burned with mixed
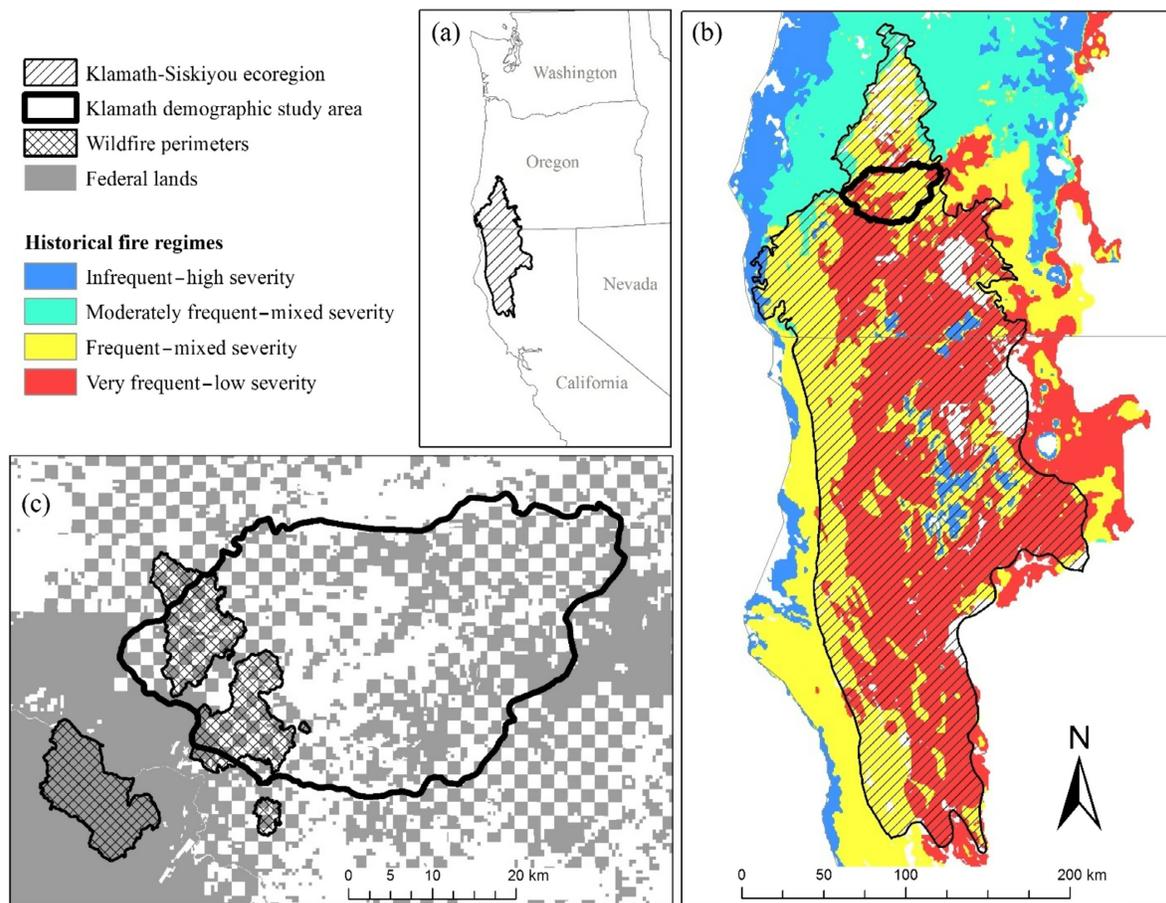

Fig. 1. Maps showing (a) the Klamath-Siskiyou ecoregion of California and Oregon, USA (hatched area); (b) historical fire regimes in the Klamath-Siskiyou ecoregion (Spies et al. 2018), Klamath northern spotted owl demography study area (1422 km^2; center = 123.315° W, 42.782° N, heavy black border); and (c) landownership (federal land, gray; private land, white) and the 2013 Douglas Complex and Big Windy Fires (cross-hatched area).

severity: Dads Creek (final perimeter = 9890 ha), Rabbit Mountain (9706 ha), and Brimstone (928 ha); and for the Big Windy Fire (10,799 ha; Fig. 2). Low precipitation in 2013 resulted in moderate-to-severe drought conditions in southern Oregon (NDMC 2018) and contributed to active fire behavior in the early burning period of these fires. Zald and Dunn (2018; and unpublished data) summarized weather data for the first 4 d of the Douglas and Big Windy Complexes (see Fig. 2 for fourth-day fire perimeters)

from three Remote Automatic Weather Stations near fires and found maximum temperature was 25–32°C, minimum relative humidity was 17–30%, and maximum wind speed was 19–29 kmh. After the fourth day of the fire, a temperature inversion developed—a common occurrence in this region (Estes et al. 2017)—which dramatically changed fire behavior and greatly improved the effectiveness of suppression efforts. Mean daily burning index (BI) for the first 4 d of the fire was 52–76, which was above the
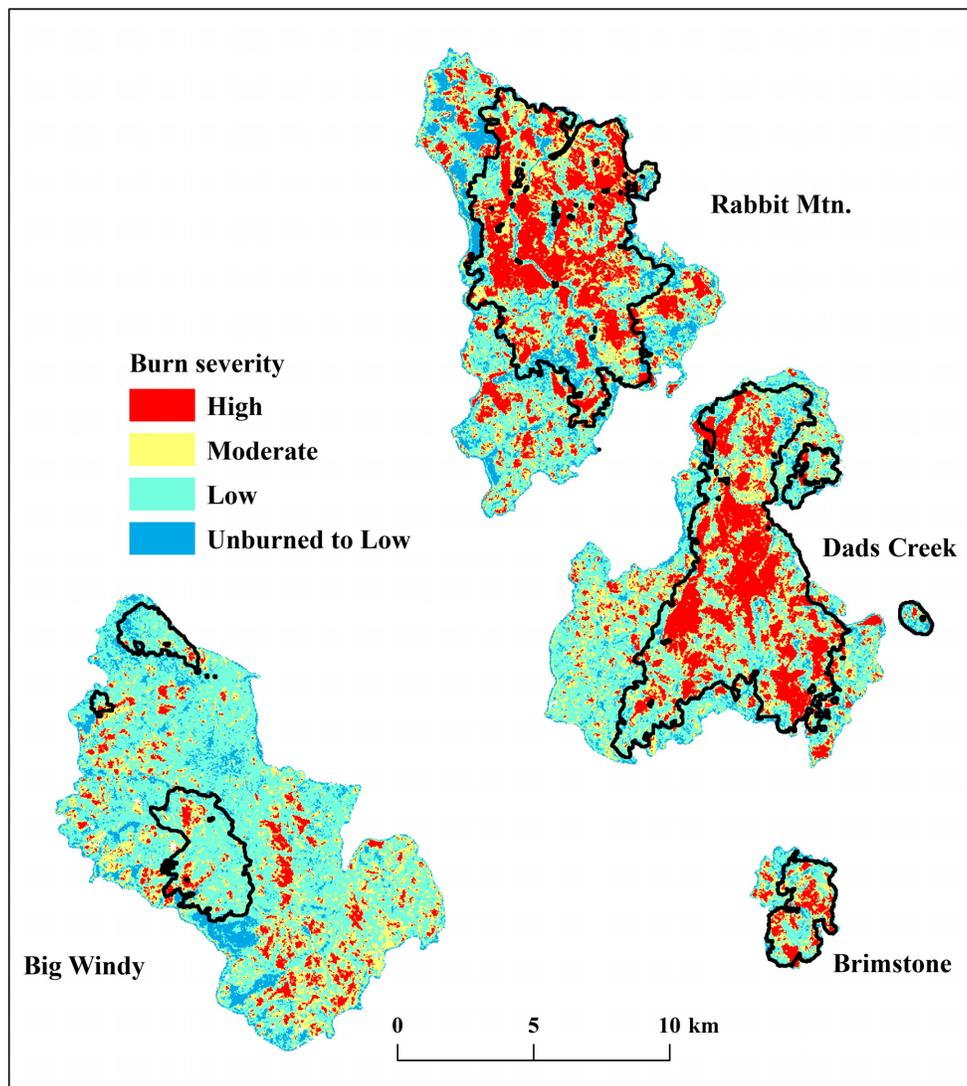

Fig. 2. Map of monitoring trends in burn severity (Eidenshink et al. 2007) data for the Big Windy and Douglas Complex Fires in southwest Oregon, USA, 2013. Severity is based on change in normalized burn ratio (dNBR) from Landsat-8 images from pre- and post-fire. The perimeter of the fires after the fourth day is outlined in black.

historic (1991–2017 1 June–30 September) 90th percentile for this period (Zald and Dunn 2018). Mean daily energy release component (ERC) values ranged from 49 to 67, also above the 90th percentile for this area (Dalton et al. 2015) for 3 of 4 d. Burning index is a fire behavior index proportional to flame length that incorporates wind speed estimates, and ERC is an index of fire energy that includes the cumulative drying effect of weather in the days prior to the estimate and measures live and dead fuel moisture (Bradshaw et al. 1983, Cohen and Deeming 1985). Post-fire logging occurred over much of the high-severity portions of the private lands, but most federal land was unlogged post-fire because the area was designated as a late-successional reserve under the NWFP. The areas of the Douglas Complex Fires were primarily composed of Oregon and California Railroad Lands with federal lands, managed by the U.S. Bureau of Land Management, in a checkerboard pattern with private lands (Fig. 1; Zald and Dunn 2018). The Big Windy Fire burned within an intact landscape of federally managed forest lands (Fig. 1).

Pre- and post-fire habitat suitability

We used program MaxEnt version 3.3.3k (Phillips et al. 2006) to produce a pre-fire relative nesting/roosting habitat suitability model of forests used by northern spotted owls and applied the model algorithm to post-fire forest conditions to map post-fire suitability. MaxEnt is based on the maximum information entropy theory and is widely used to develop resource selection functions through the use of machine learning applied to known species locations (i.e., model training data) and relevant environmental predictor variables (Harte and Newman 2014). Previous efforts also used machine learning to develop nesting/roosting cover type models in several northern spotted owl studies and monitoring reports (Davis et al. 2011, 2016, Glenn et al. 2017). We followed Ackers et al. (2015) by using lidar-derived forest structure variables to develop a model of suitable forest for northern spotted owl nesting and roosting.

We used site locations where northern spotted owls nested and roosted within the demographic study area as training and testing data for relative habitat suitability models. These location data were collected during long-term research of northern spotted owl demography, including survival rates, reproductive rates, and annual rate of population change. The protocol used to determine site occupancy, nesting, and reproductive status for this study followed the guidelines specified by monitoring effectiveness of the NWFP (Franklin et al. 1996, Dugger et al. 2016).

We derived our pre- and post-fire model predictor variables from multiple-return discrete lidar data acquired in 2012 (1 yr pre-fire) and 2013 (2 months post-fire) by Quantum Spatial (previously Watershed Sciences, Corvallis, Oregon, USA) using aircraft-mounted Leica ALS 50 and/or Leica ALS 60 sensors with an average point density of ≥10 points per square meter. The 2012 data were collected as part of the Oregon Lidar Consortium (OLC) Rogue River lidar acquisition, covering an area of ~567,000 ha. Within this OLC Rogue River collection area, ~50,000 ha of lidar data were acquired again in 2013 post-wildfire, encompassing the Douglas complex and Big Windy Fires. We processed all lidar metrics from delivered point clouds, creating 1-m-resolution models of highest (i.e., first) return and bare earth digital elevation models (DEMs) with FUSION/LDV software (McGaughey 2015).

Following Ackers et al. (2015), we derived four metrics from the lidar data known to be important drivers in northern spotted owl nesting and roosting ecology: percentage overstory canopy cover (CANOPY), mean overstory canopy height (HEIGHT), density of large live trees (LARGE TREES), and rumple index (RUMPLE; Parker et al. 2004). We calculated the percent CANOPY taller than 2 m and the mean vegetation height using only first returns at 30 m resolution. We calculated RUMPLE, a measure of stand structure diversity where higher values represent stands with more horizontal and vertical complexity, using a 3 × 3 window focal mean of the 1-m canopy height model (CHM; Ackers et al. 2015). We matched the resolution of the HEIGHT and CANOPY metrics using a cell multiplier of 30 and then derived RUMPLE from the surface area ratio output. We calculated LARGE TREES from point files representing large live tree (≥31 m tall) locations from the 1-m CHM and CanopyMaxima in FUSION/LDV (McGaughey 2015). The tree height threshold of 31 m was the average height of 80-yr-old trees based on a

height–age relationship of trees in forest inventory plots from the study area. To minimize the chance of having multiple points for the same tree, we created 10 m radius buffers around all points in ArcGIS 10.1 (ESRI, Redlands, California, USA), dissolved overlapping buffers, and then created a new point layer from the centers of the dissolved buffers. Any trees that were mapped only in the post-fire LARGE TREES map were added to the pre-fire model (with the assumption that large trees present after the fire were present prior to fires).

Northern spotted owl presence data for model training and testing were based on 107 nesting or roosting locations from 27 territories. Given that presence data originated from a long-term northern spotted owl study area, we were confident that we met sampling assumptions of minimal sampling bias and high probability of detecting owls when they were present. We followed standard procedures for presence-only modeling to avoid multi-collinearity between model variables by restricting modeling response functions that were overly complex, using stepwise calibration, and testing of bootstrapped model replicates (O'Brien 2007, Phillips and Elith 2013, Merow et al. 2014). We followed the model selection method used by Ackers et al. (2015) by using a random subset of our owl location data (75%) and 10,000 random modeling region locations to develop bootstrapped replicate models that related location data to random environmental conditions. We used the held-out 25% of northern spotted owl locations to test model predictions. We made stepwise adjustments to the model regularization multipliers that serve as a penalty parameter in machine learning by eliminating model coefficients and keeping only those that increase model gain, which relates to the likelihood ratio of an average species location to average background environmental conditions. Higher gains produce better differentiation of species locations from background conditions. The best model was based on balancing two criteria: (1) minimizing the difference between regularized training gain and test gain to avoid over-fitting the models, while (2) maximizing model test statistics (area under the curve [AUC] and Spearman rank correlation [Rs]). Once the best model was selected, we used the predicted vs. expected (P/E) curve to classify the model into a binary map of suitable and unsuitable nesting/roosting habitat (Hirzel et al. 2006).

Burn severity and change in suitability

We assumed most of the negative effects of wildfire on northern spotted owl nesting/roosting habitat would result from loss of canopy cover and mortality of large trees. To capture changes in the large, live tree component (LARGE TREES), we needed to estimate the proportion of LARGE TREES that suffered mortality by fire severity to adjust our post-fire LARGE TREES variable for the post-fire nesting/roosting habitat model. However, initial examination of the lidar data indicated that the post-fire lidar data could not differentiate live vs. dead trees ≥31 m height, leading to a bias in the lidar-based LARGE TREES variable. Previous research has indicated that lidar variables are better predictors for live and total basal area while multispectral imagery variables (e.g., Landsat data) are better predictors for dead and percent dead basal area (Bright et al. 2014). For example, changes in normalized burn ratio (NBR) are commonly used for mapping forest disturbance, especially timber harvest and wildfire (Miller and Thode 2007, Kennedy et al. 2010, 2012, Schroeder et al. 2011). In particular, changes in NBR have been widely used to assess fire severity (Miller et al. 2009, 2012, Cansler and McKenzie 2012, Lydersen et al. 2016). Furthermore, changes in NBR have been effectively related to changes in canopy cover (Miller et al. 2009) and basal area (Reilly et al. 2017). In this study, we used changes in satellite-based NBR from Landsat-8 to assess changes in canopy cover, and thus tree mortality, in live trees ≥31 m height to avoid biases produced by directly calculating changes in LARGE TREES from pre- and post-fire lidar data.

To assess canopy cover losses, and thus large live tree mortality associated with the fire, we acquired two spatial datasets to be used for mapping vegetation change within the fire perimeters: (1) We used Google Earth Engine (Google Earth Engine Team 2015, Gorelick et al. 2017) to collect 30-m-resolution Landsat-8 LaSRC imagery for the study area from 1 May to 1 August of 2013 and 2014 to generate pre- and post-fire NBR maps; and (2) we used post-fire high-resolution (7.62 cm) imagery acquired concurrently with lidar acquisition to estimate tree canopy

cover. For all 30 × 30 m (900 m^2) pixels in the study area, we calculated NBR in 2013 (pre-fire) and 2014 (post-fire) as the normalized differences between near-infrared and shortwave-infrared bands (bands 5 and 7, respectively; Li et al. 2013) for each Landsat-8 image. For our study area, no single image was optimal (e.g., cloud cover over part of the area on a given date), so we created a median composite image of NBR for each growing season (May–August; Kennedy et al. 2012). Large, live trees represented by LARGE TREES were only located in older forests; therefore, we measured live tree canopy cover visible in the high-resolution aerial photographs at 200 randomly generated 30 × 30 m (900 m^2) plots within older forests (95th percentile lidar return height ≥30.8 m) inside the study area snapped to the 2014 Landsat-8 pixel boundaries. Within each plot, 36 systematically distributed sampling points were established and tree canopy cover was measured as the proportion of sampling points where we observed live tree crowns in the high-resolution imagery. Plots co-located with roads, timber salvage, young plantations, or lacking clear imagery (e.g., steep slope in shadow) were excluded from our analysis, resulting in a final sample size of $n = 181$ that included post-fire canopy cover in forests experiencing a variety of fire severity conditions. Note that canopy cover measurements collected at these sample locations represent only live tree canopy cover and were independent from lidar-based canopy cover estimates that include both live and dead trees.

Statistical models relating NBR change and forest change (e.g., basal area mortality; Reilly et al. 2017) are available, but we did not have reliable measurements of canopy cover change based on both pre- and post-fire aerial photographs upon which we could parameterize a model. Pre-fire aerial imagery could not be used in conjunction with post-fire aerial imagery to calculate change in canopy cover directly because of the lower resolution images and differing parallax (i.e., an apparent shift in the position of objects as viewed from differing vantage points) between pre- and post-fire images. Therefore, an accurate assessment of cover change between photographs was unreliable. Additionally, published models were not parameterized for our landscape, but rather broad regional datasets for California (Miller et al. 2009) or Oregon and Washington (Reilly et al. 2017). Because only post-fire reference data for canopy cover (high-resolution aerial photographs) were available, we developed a mortality algorithm based on changes in forest canopy cover predicted from NBR data. The algorithm (1) predicted live canopy cover based on post-fire NBR and canopy cover measurements from aerial photography, (2) calculated the change in predicted canopy cover from the pre-fire to post-fire conditions, and (3) assigned mortality to LARGE TREES with probability proportional to the change in Landsat-based canopy cover.

Because tree canopy cover data were non-negative, we modeled tree canopy cover as a function of NBR with a zero-truncated regression model (Fig. 3). The model was fit to the 2014 NBR (post-fire) and tree canopy cover data in the R statistical environment version 3.3.1 (R Core Team 2016) with the function tobit (AER package; Kleiber and Zeileis 2009). For each 30-m Landsat pixel, tree canopy cover predictions for pre- and post-fire were generated by applying the fitted model to 2013 (before fire ignition) and
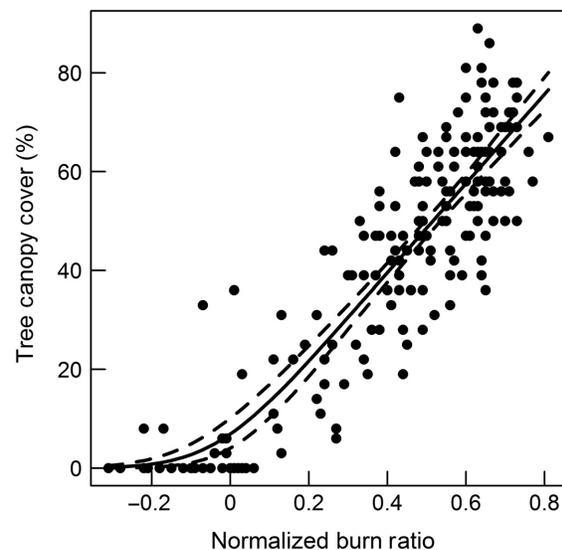

Fig. 3. Mean (solid line) and 95% confidence intervals (dashed lines) for predicted live tree canopy cover as a function of normalized burn ratio within the Douglas Complex and Big Windy Fires in southwest Oregon, USA, in 2013 based on the zero-truncated regression model.

2014 NBR data, respectively. To minimize differences between 2013 and 2014 canopy cover maps, we normalized the 2013 NBR data so that the differences between 2013 and 2014 NBR outside the fire perimeter were minimized. We transformed the 2013 NBR image by creating a mask of high NBR (stable forest, both 2013 and 2014 NBR were >0.75) outside the fire boundaries, and within the study area, which served as the population for creating a normalization between the two image dates. We then created a simple least-squares linear fit between NBR 2013 and NBR 2014 based on all pixels in the mask population, with a slope of 0.845 and intercept of 0.119 based on estimated coefficients. We created the transformed NBR 2013 by applying slope/intercept from linear fit, thereby transforming the 2013 image calibrated to the values in the 2014 image and quantified differences.

Pre- and post-fire predictions of canopy cover were differenced and divided by the predicted pre-fire canopy cover to calculate the proportional change in canopy cover (ΔC). The probability of mortality for a given 30-m pixel on the landscape was taken to be $1 - \Delta C$ (i.e., canopy cover-weighted tree mortality). Areas with canopy cover increases (i.e., $\Delta C > 0$) were assumed to have no tree mortality. We assessed the performance of the canopy cover-weighted mortality by comparing our predictions for each pixel with a large live tree with an independent basal area-weighted mortality prediction generated using existing models (Appendix S1; Reilly et al. 2017). We use these data for validation because the models produced by Reilly et al. (2017) predict basal area-weighted tree mortality from a regional forest inventory network based on RdNBR ($r^2 = 0.68$) and perform particularly well in identifying patches of forest experiencing basal area-weighted mortality >75% (classification accuracy = 82.8%).

Large tree mortality within each pixel was assigned proportional to $1 - \Delta C$. For a given pixel with n canopy dominant trees identified based on lidar imagery, a sample $n \times (1 - \Delta C)$ trees, rounded to the nearest integer, was taken and recorded as having died during the fire, with the remaining $n \times \Delta C$ trees surviving. This assumes that the number of trees dying during the fire was proportional to the canopy cover losses and that the identity of trees dying does not matter. For canopy dominant trees examined in this paper, such an assumption seems reasonable. We, therefore, used the mortality algorithm to modify our post-fire point file of tree stems to estimate which trees mapped by lidar suffered mortality. We then used the post-fire live tree point file to generate our post-fire LARGE TREES density variable for nesting/roosting habitat modeling.

We recognize that by leveraging multiple datasets and modeling techniques—lidar-based LARGE TREES and satellite-based canopy cover-weighted mortality—there is the opportunity to propagation of error from one step to another. For example, errors in estimating forest carbon stocks may arise from field data collection, allometric equations, and modeling errors (Clough et al. 2016). In the case of this study, errors associated with canopy cover modeling, the calculation of canopy cover-weighted mortality, and the application of that mortality to attribute tree death to individual trees all contribute to overall errors.

Pre-fire vegetation vs. fire severity analysis

Our main interest was to examine the relationship between fire severity and nesting/roosting habitat with limited confounding effects of fire suppression activities and differences in fire weather during the time the fire burned. Though it is difficult to separate the confounding effects of suppression efforts when analyzing almost all fires, we reasoned we could minimize this effect by examining the early days of the fire before more extensive backfiring occurred and suppression activities had limited effect. Thus, we used the spatial extent of daily fire growth (as mapped using aerial IR technology each night) throughout the first 4 d after ignition. Starting at approximately day 5 of the fire, changes in atmospheric temperature altered fire weather conditions and suppression efforts included igniting backfires in some areas (K. Kosel, *personal communication*; Fig. 2). Additionally, by focusing on these rapid fire growth days we believe there is little to no alteration of natural fire behavior or severity across the spectrum of northern spotted owl nesting/roosting habitat suitability. To quantify the odds of forest types burning in 1 of 4 severity types, we evaluated the ratios of the proportion of suitable and unsuitable nesting/roosting

habitat that burned (B) at each fire severity to what was available to burn (A). Fire severity types were taken from Monitoring Trends in Burn Severity (MTBS 2017) data, a map product based on changes in NBR commonly used by forest management agencies. The types include high severity, moderate severity, low severity, and unburned to low severity. By using the same fire severity classifications commonly used by land managers, communication and application of results from this research will be more straightforward. A value of B/A < 1 indicates that the forest type burned less than would have been expected by chance, and a ratio B/A > 1 indicates it burned more than would be expected by chance (Moreira et al. 2001, 2009, Manly et al. 2010). While the canopy cover-weighted mortality modeling we used to attribute large tree mortality depends on NBR and is thus likely related to the MTBS fire severity classes, we use the MTBS classes for summarizing across severity classes because of their widely accepted use in forest planning.

RESULTS

Pre- and post-fire habitat suitability

Our best model of nesting/roosting habitat suitability predicted nesting/roosting locations well with an AUC statistic of 0.89 and a P/E curve Spearman rank correlation of 0.92. The binary classification of the habitat model into suitable and unsuitable was based on P/E = 1 (0.32). Model variable response functions (Fig. 4) followed known resource selection patterns by owls (Ackers et al. 2015, Glenn et al. 2017).

Burn severity and change in suitability

Post-fire nesting/roosting habitat suitability decreased with increasing fire severity (Table 1),
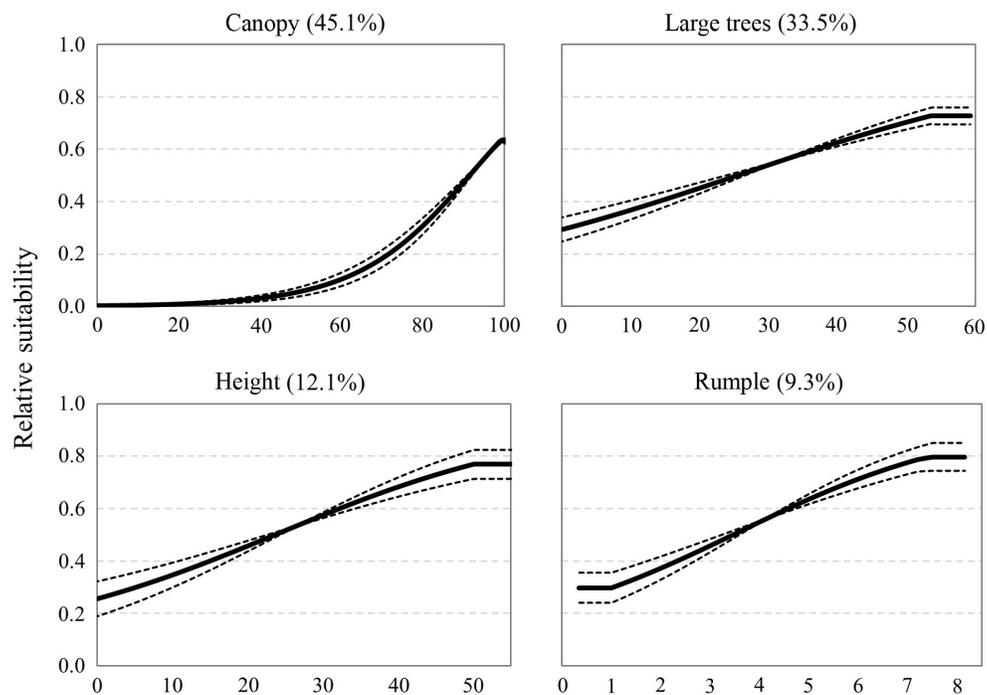

Fig. 4. Variable response functions with percent contribution (%) to pre-fire nesting/roosting habitat suitability model for northern spotted owls in the Klamath demographic study area in southwest Oregon, USA, where the Douglas Complex and Big Windy Fires burned in 2013. The solid line represents the mean, and the dashed lines represent 95% confidence intervals. Variables were derived from lidar data, and the variables included were CANOPY (percent canopy cover), LARGE TREES (large live trees per hectare), RUMPLE (rumple index), and HEIGHT (mean tree height [m]).

Table 1. Metrics within areas burned at four severity classes based on Monitoring Trends in Burn Severity (MTBS) measurements.

Fire severity	Pre-fire live trees	Trees killed	% Mort	Mean pre-fire NBR	Mean post-fire NBR	Δ Mean NBR (%)	Mean pre-fire suitability	Mean post-fire suitability	% Loss suitable habitat
Unburned to low	66,015	2830	4	0.75	0.68	−9.2	0.22	0.20	4.5
Low	251,356	49,413	20	0.74	0.56	−24.6	0.22	0.21	25.5
Moderate	71,826	40,038	56	0.72	0.30	−58.3	0.10	0.08	63.9
High	67,897	62,348	92	0.75	−0.04	−104.9	0.12	0.03	93.7

Notes: Reported are estimated number of large live trees pre-fire, estimated number large live trees killed during fire, percentage of large live trees killed, mean normalized burn ratio (NBR) pre (2013)- and post-fire (2014), percent change in NBR, pre (2012)- and post-fire (2013) mean nesting/roosting habitat suitability, and percent loss of suitable nesting/roosting habitat for northern spotted owls in the Douglas Complex and Big Windy wildfires in southwest Oregon during 2013.

mainly owing to fire-caused decreases in LARGE TREES and CANOPY. Low-severity fire had little effect on nesting/roosting habitat suitability. High-severity fire resulted in 75% decrease in mean suitability and >93% loss of suitable nesting/roosting habitat (Table 1) and commonly converted pre-fire suitable forests to conditions that were unsuitable for nesting and roosting (Fig. 5). Overall, most pre-fire habitat was lost if it burned at moderate severity (Table 1), but depending on the pre-fire suitability, moderate-severity fire produced mixed effects on nesting/roosting habitat suitability and did not consistently result in a loss of suitability. The forests that burned at unburned to low severities had pre-fire suitability values approximately two times higher than suitability of forests that burned at moderate or high severity (Table 1); thus, moderate- to high-severity fire had the greatest effect on pre-fire areas with low habitat suitability for northern spotted owls (Fig. 6).

Tree mortality and pre-fire vegetation vs fire severity

Canopy cover-weighted mortality (Appendix S1: Fig. S1) generated as the basis of attributing post-fire tree mortality for large trees exhibited a slight positive bias (mean error = 2.42% mortality) and root mean square deviation of 5.82% compared to an existing basal area-weighted mortality model based on regional forest inventory datasets co-located with large wildfires (Reilly et al. 2017). Despite these errors, our canopy cover-weighted mortality predictions were highly correlated with the existing basal area-weighted mortality predictions (Pearson correlation = 0.99).

Based on lidar tree mapping and the post-fire NBR analysis, we estimated the fires directly killed a total of 154,629 large live trees (51.1% of total pre-fire estimate). Tree mortality increased with fire severity and percent change in NBR (Table 1). There were 2.27 times more large live trees in areas that experienced unburned to low-severity fire compared to those areas that burned at moderate and high severity (Table 1). The susceptibility of forests to moderate- and high-severity fire was lower in suitable nesting/roosting habitat and higher in unsuitable forest than would be expected by chance (Fig. 6). The differences between low and moderate/high severity were more pronounced in suitable nesting/roosting habitat than unsuitable forest. The odds that suitable nesting/roosting habitat would burn at lower severity was 2–3 times higher than the odds it would burn at moderate-to-high severity. There were significant differences (based on non-overlapping 95% confidence intervals) between odds of burning at low severity and burning at moderate/high severity among forest types. There was no evidence for a difference between the odds (i.e., B/A index) of burning at moderate or high severity within suitable nesting/roosting habitat or unsuitable forest types, but there were differences between suitable and unsuitable forest types (Fig. 6). The odds that unsuitable forest burned at moderate-to-high severity was about twice that of suitable nesting/roosting habitat.

Discussion

Here, we used newly developed tools and lidar data to examine the interaction between mixed-severity fires and northern spotted owl
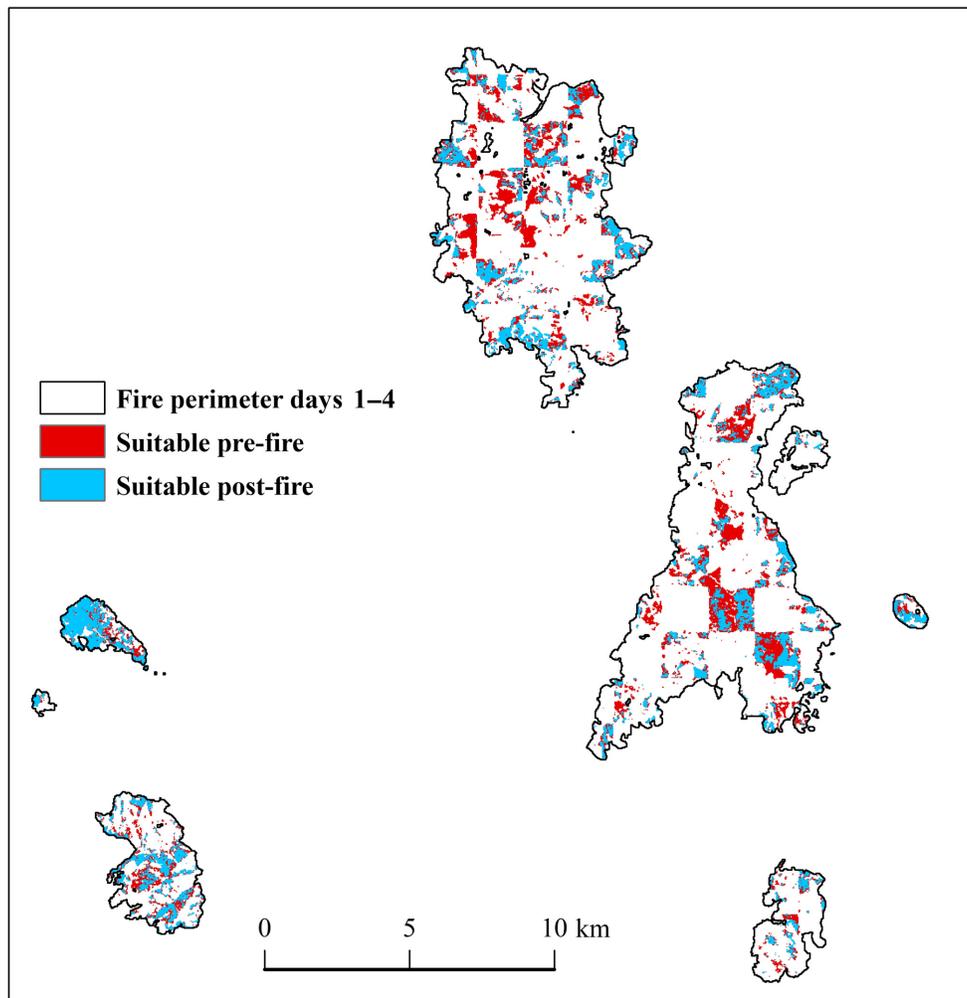
Fig. 5. Patterns of conversion from suitable habitat to unsuitable conditions for northern spotted owl nesting and roosting in the Douglas Complex and Big Windy Fires that burned in southwestern Oregon, USA. Binary classification of nesting/roosting habitat was based on predicted vs. expected ratio threshold of 0.32, and lidar metrics of live vegetation height, canopy cover, stand complexity (rumple index), and large tree density. Area shown is the perimeter of the fires 4 d after the fire ignited on 26 July 2013.

nesting/roosting habitat under high fire weather conditions in a landscape characterized by the interactions between land-use patterns and a mixed-severity fire regime. Because of high site fidelity, northern spotted owls may continue to use areas if suitable nesting/roosting cover remains and prey are available. However, survival decreases through time in areas with a high proportion of high-severity fire likely because post-fire habitat quality decreases to the point that territories are only marginally capable of supporting northern spotted owls (Rockweit et al. 2017). Within a few years post-fire, areas opened up by tree mortality change structurally (i.e., standing dead trees transitioning to fallen logs) and prey may be less accessible with high density of shrubs and herbaceous understory in high-severity burn areas. As expected, in our study the suitability of northern spotted owl nesting/roosting habitat decreased with increasing fire severity, to the degree that much of the pre-fire habitat that burned at high severity was no longer suitable cover for nesting or roosting. The greatest impacts from moderate- and high-severity fire
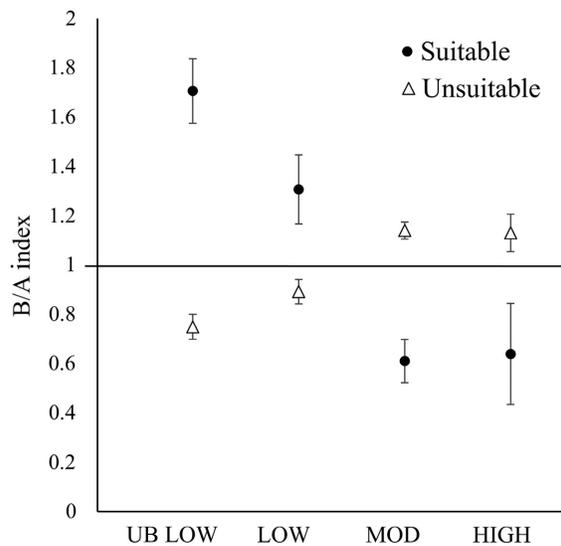
Fig. 6. Ratio of proportion of suitable and unsuitable nesting/roosting habitat that burned (B) at each fire severity to what was available (A) to burn (B/A index) with 95% confidence intervals, Douglas Complex and Big Windy Fires, southwestern Oregon, USA, 2013. We used Monitoring Trends in Burn Severity (MTBS 2017) to determine fire severity types (UB LOW, unburned to low severity; LOW, low severity; MOD, moderate severity; HIGH, high severity) and separated into suitable nesting/roosting habitat for northern spotted owls or unsuitable forest types based on lidar metrics. B/A index < 1 indicates that the forest type (suitable or unsuitable) burned at the severity class less than would have been expected by chance, and B/A index > 1 indicates forest type burned at the class more than by chance alone.

were observed in those forests exhibiting low habitat suitability for northern spotted owl nesting and roosting before the fire.

We found that the old-forest conditions associated with northern spotted owl habitat burned at lower severity despite having higher fuel loading than other forest types on the landscape. The microclimate and forest structure likely played a key role in lower fire severity in nesting/roosting habitat compared to other forest types. As succession progresses and canopy cover of shade-tolerant tree species increases, forests eventually gain old-growth characteristics and become less likely to burn because of higher relative humidity in soil and air, less heating of the forest floor

due to shade, lower temperatures, lower wind speeds, and more compact litter layers (Countryman 1955, Chen et al. 1996, Kitzberger et al. 2012, Frey et al. 2016, Spies et al. 2018). In addition, as the herbaceous and shrub layer is reduced by shading from lower to mid-layer canopy trees, the connection between surface fuels and the canopy declines, despite possible increases in canopy layering (Halofsky et al. 2011, Odion et al. 2014). Alexander et al. (2006) found that in the Klamath-Siskiyou ecoregion, southern aspects tended to burn with greater severity, but exogenous factors also played an important role because areas with large trees burned less and had less fire damage than areas dominated by smaller trees. On the 2002 Biscuit Fire that burned near our study area, Thompson and Spies (2009) concluded that weather and pre-fire vegetation conditions were the primary determinants of crown damage. They found that forests with small-stature vegetation and areas of open tree canopies and dense shrubs experienced the highest levels of tree crown damage, while older, closed-canopy forests with high levels of large conifer cover were associated with the lowest levels of tree crown damage. The moisture content of air and soil in a forest affects the amount of fuel moisture, and thus the probability of ignition and burning temperature (Heyerdahl et al. 2001). In addition to the potential to mitigate negative effects of climate warming at local scales by creating refugia and enhancing biodiversity (Frey et al. 2016), we suggest that northern spotted owl nesting/roosting habitat also has the potential to function as fire refugia (i.e., areas with higher probability of escaping high-severity fire compared to other areas on landscape) in areas with mixed-severity fire regimes under most weather conditions. Thus, in these landscapes, management strategies to conserve old-growth characteristics may also reduce risk of high-severity wildfire (Bradley et al. 2016) and serve as buffer to negative effects of climate change (Betts et al. 2018).

Although it has long been recognized that older forests have lower flammability than other forest types (Countryman 1955), federal agencies are often criticized for not extensively managing old forests to reduce risk of high-severity fire (OFRI 2010). The perception is that forest succession leads to increased flammability with age

(Kitzberger et al. 2012, Duff et al. 2017). Where this view may be correct is in dry forests with historically very frequent fire-return intervals (<10 yr), and contemporary increased fuel continuity has resulted from fire exclusion and led to increased sizes of high-severity patches when fires burn under extreme weather (Reilly et al. 2017). In the driest forest types, fire exclusion converts open forests with grassy understories to dense forests with high fuel loads, and the increased fuel continuity can result in larger patches of high-severity fire than would have occurred historically. In other forest types, succession likely decreases risk of high-severity fire. Compared to older forest, younger forests have lower canopies and thinner barked trees that reduce resistance to fire, and thinned young forests can be susceptible to high mortality from fire unless surface fuels are treated with prescribed fire (Raymond and Peterson 2005). Thinned forests have more open conditions, which are associated with higher temperatures, lower relative humidity, higher wind speeds, and increasing fire intensity. Furthermore, live and dead fuels in young forest or thinned stands with dense saplings or shrub understory will be drier, making ignition and high heat more likely, and the rate of spread higher because of the relative lack of wind breaks provided by closed canopies with large trees.

Primarily as inputs to fire models that estimate likely fire behavior, fuel models involve typing forested stands according to fuel loading and are often used to explore or inform management directions because fuels are under the purview of forest managers (Deeming and Brown 1975, Anderson 1982, Bradshaw et al. 1983, Finney 2004, Scott and Burgan 2005, Andrews 2009). Suitable nesting/roosting habitat often falls in classes rated as highly burnable, with fast rates of fire spread, high flame lengths, and intense fire behavior (Anderson 1982). Thus, fire model results can show nesting/roosting habitat has higher burn probabilities and higher crown fire potential than adjacent areas (Ager et al. 2007, 2012). The results of this study as well as other recent studies show that these older forests in mixed-conifer forest environments are less susceptible to high-severity fire than other successional stages, even under high fire weather conditions and with short return intervals <15 yr (Donato et al. 2009). Running fire models for our

study area based on conditions during the Douglas Complex and Big Windy Fires would be a worthwhile exercise to evaluate model predictions relative to the actual behavior of those fires. However, based on the findings of this study and many others (see review by Duff et al. 2017), we contend that fire models that continue to use fuel models that rate older forests with higher relative fire behavior will likely overestimate fire severity and inflate estimated loss of old forests in the Pacific Northwest. An alternative is to consider forest fuels in a more holistic manner and alternative age–flammability models (Kitzberger et al. 2012, Duff et al. 2017).

Intensive management (especially on timber industry lands) that results in reduced fuel loading does not always equate to less frequent or severe fire. Results by Charnley et al. (2017) in southcentral Oregon showed that private industry lands had more than three times the percentage area of open-canopy forest compared to U.S. Forest Service-managed lands that included thinning trees <53.3 cm diameter, prescribed fire, and no active management. Federal land management practices resulted in forests with more resilience to high-severity wildfire as opposed to management on private lands (Charnley et al. 2017). Furthermore, Zald and Dunn (2018) found that ownership patterns were the best predictor for high-severity fire in the Douglas Complex Fires, where federal lands, with primarily older forests in late-successional reserves, burned at lower severity than non-federal forests that were primarily private timber industry lands.

Gradual changes in temperature or precipitation patterns may have little effect until a disturbance-driven threshold is reached at which a large shift occurs that might be difficult or impossible to reverse (Scheffer and Carpenter 2003). Peterson (2002) described "ecological memory" and how previous patterns of disturbance can predispose an area to follow a certain disturbance pathway. For example, a landscape that experiences severe disturbance (e.g., high-severity fire, clear-cut logging, post-fire salvage logging) can be predisposed to high-severity fire in a mixed-severity fire regime (Thompson et al. 2007, Donato et al. 2009, Thompson and Spies 2009, Zald and Dunn 2018). High-severity wildfire can alter soil and successional pathways and potentially shift the system into an alternative stable state (Peterson 2002). A

key component of overall ecosystem function and sustainability occurs belowground, and with high-severity fire, changes in the soil physical, chemical, and biological functions can be deleterious to the entire ecosystem caused by changes in successional rates and species composition (Neary et al. 1999). Conversely, low-severity fire effects on soil can promote herbaceous flora, increase plant diversity, increase available nutrients, and thin over-crowded forests, all of which can enhance healthy forest ecosystems (Neary et al. 1999). The time for recovery of belowground systems is a key driver of ecosystem processes and depends on burning intensity and on previous land-use practices. Soils are greatly altered and degraded in young intensively managed forest and post-salvage logged sites, which are more susceptible to repeat and short-interval high-severity wildfire, and these forests that experience multiple rapid successions of natural and human-derived disturbances may cross thresholds and be changed catastrophically (Lindenmayer and Noss 2006).

The Klamath-Siskiyou ecoregion is currently dominated by biodiverse temperate coniferous forest and may be near a tipping point toward an alternative stable state (shrub/hardwood chaparral) with extensive loss of conifer forest, dominance by deciduous trees and shrubs, and recurring early-seral and young forest conditions (Tepley et al. 2017, Serra-Diaz et al. 2018). The region has experienced short intervals between recent high-severity fires coupled with intensive timber management in this mixed-severity fire regime area, and the likelihood of further shortening of fire-return intervals with climate change (Davis et al. 2017). Even where climate is suitable to sustain dense mature forests, early-seral and non-forest conditions may perpetuate because of a cycle of short-interval repeat burning and timber harvest and have dramatic impacts on biodiversity and wildlife habitats (Lindenmayer et al. 2011, Tepley et al. 2017). Under this scenario, the persistence of old-forest associated species, including northern spotted owls, within the Klamath-Siskiyou ecoregion would be further threatened.

It was recognized early in the history of northern spotted owl conservation that fire would play a major role in determining the success of management plans (Agee and Edmunds 1992). The 2011 federal northern spotted owl recovery plan calls for increasing fire resiliency in dry forests with focus on active management outside of northern spotted owl core areas to meet project goals (USFWS 2011). For many dry forests in the western United States that historically experienced frequent, low- to moderate-severity fire regimes, prescribed fire and mechanical treatments have been effective at reducing surface fuel loads, forest structure, and potential fire severity (Stephens et al. 2009). In mixed-severity landscapes, the fire severity mosaic is highly variable and the effects of topography and climate are strong predictors for this regime, but forest conditions also are important and much less predictable and stable (Beaty and Taylor 2001), further complicating management decisions aimed at increasing fire resiliency of forests. Management actions employed in dry forest types to reduce wildfire risk may not work equivalently in mixed-severity regimes. Active management actions that include mechanical treatments degrade suitability of forests for nesting and roosting by northern spotted owls (Lesmeister et al. 2018) and may not always decrease risk of high-severity fire. Further, considering trends and forecasts for earlier spring snowmelt and longer fire seasons, climate change may exacerbate the effects of wildfire (Dale et al. 2001, Westerling et al. 2006), and thus the framed conundrum between northern spotted owl habitat and fire management in mixed-severity regimes. Our results indicate that older forest in late-successional reserves (i.e., northern spotted owl nesting/roosting habitat) with no active management can serve as a buffer to the effects of climate change and associated increase in wildfire occurrence. These multi-storied old forests in these environments enhance biodiversity and have the highest probability to persist through fire even in weather conditions associated with high fire activity.

Fuel-reduction treatments such as mechanical thinning can effectively reduce fire severity in the short term, but these treatments, by themselves, may not effectively mitigate long-term dynamics of fire behavior under severe weather conditions and may not restore the natural complexity of historical stand and landscape structure (Schoennagel et al. 2004). On the other hand, prescribed fire that mimics severity and return intervals of natural fire regimes in forests that historically

experienced fire can result in landscapes that are both self-regulating and resilient to fire (Parks et al. 2015). Prescribed fire is generally considered to be the most effective way to reduce the likelihood of high-severity fire in combination with mechanical treatments (Stephens et al. 2009). The 2013 Rim Fire in the Sierra Nevada, California, USA, burned with low severity in areas previously treated with prescribed fires, suggesting that prescribed burning was an effective management tool to reduce fire severity (Harris and Taylor 2017). Many fire-prone forests will require active management to restore ecosystem function, but no single prescription will be appropriate for all areas and, in some portions of the forests, minimal maintenance may be more sustainable in the long term (Noss et al. 2006). Within the Klamath-Siskiyou ecoregion, flexible and multi-scale land management approaches that promote diversity of forest types will likely enhance conservation of a range of species requiring different forest conditions for long-term persistence. An integral component of these approaches could include resistance strategies (i.e., no active management) to protect high-value older forest (Millar et al. 2007) and prescribed fire to promote and maintain a mix of forest conditions in this landscape characterized by mixed-ownership and mixed-severity fire regime. Ultimately, spatial heterogeneity that includes the buffering effects of northern spotted owl nesting/roosting habitat may serve as a stabilizing mechanism to climate change and reduce tendency toward large-scale catastrophic regime shifts.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2696/full