Megafires: an emerging threat to old-forest species

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Increasingly frequent "megafires" in North America's dry forests have prompted proposals to restore historical fire regimes and ecosystem resilience. Restoration efforts that reduce tree densities (eg via logging) could have collateral impacts on declining old-forest species, but whether these risks outweigh the potential effects of large, severe fires remains uncertain. We demonstrate the effects of a 2014 California megafire on an iconic old-forest species, the spotted owl (*Strix occidentalis*). The probability of owl site extirpation was seven times higher after the fire (0.88) than before the fire (0.12) at severely burned sites, contributing to the greatest annual population decline observed during our 23-year study. The fire also rendered large areas of forest unsuitable for owl foraging one year post-fire. Our study suggests that megafires pose a threat to old-forest species, and we conclude that restoring historical fire regimes could benefit both old-forest species and the dry forest ecosystems they inhabit in this era of climate change.

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The frequency and severity of "megafires" (ie large wildfires >10,000 ha in extent [Stephens *et al.* 2014b]) in the dry forests of North America has increased after a century of fire suppression and climate warming (Westerling *et al.* 2006; Miller *et al.* 2009b), incurring considerable societal and economic costs by destroying homes, human infrastructure, and timber resources, in addition to necessitating increased taxpayer-funded support for fire-fighting (Stephens *et al.* 2013, 2014b). In the western US, major reforms in forest fire management have been proposed to restore low- and moderate-severity fire regimes through forest tree thinning (North *et al.* 2015). However, the vision of restoring "pre-European" fire regimes, as well as forest structure and composition, is constrained by concerns over fuels-reduction treatments that simplify the structurally and floristically diverse forests inhabited by old-forest species (ie species that inhabit forests characterized by large, old trees, closed overstory canopy, and complex vertical structure) (Pilliod *et al.* 2006). Potential short-term consequences of fuels-reduction and restoration treatments may be outweighed by long-term benefits of forest restoration if large, high-severity fires negatively affect old-forest species (Sweitzer *et al.* 2015; Tempel *et al.* 2015). However, research suggests that severe fires may have neutral or beneficial effects on biodiversity, including old-forest species (Hutto 2008; Swanson *et al.* 2011; DellaSala and Hanson 2015; Lee and Bond 2015), which seemingly increases the perceived divide between forest restoration and species conservation objectives. Nevertheless, the ecological effects of high-severity fire likely depend in part on the size, distribution, and configuration of burned patches (Fontaine and Kennedy 2012), and the impacts of large, severe fires on old-forest species remain a source of considerable uncertainty.

Here, we demonstrate the negative short-term impacts of a California megafire on a model old-forest species, the spotted owl (*Strix occidentalis*; Figure 1), by taking advantage of a natural before–after control–impact (BACI) experimental design on our long-term (23-year) demographic study area. In September and October 2014, the human-ignited "King Fire" burned 39,545 ha and was one of the largest and most severe forest fires recorded in California history (Figure 2), with high-severity fire (75–100% canopy mortality) occurring on 19,854 ha (50% of the area burned), with one continuous 13,683-ha high-severity burned patch. The King Fire affected 15,594 ha (44%) of our 35,500 ha study area and overlapped 30 of 45 spotted owl sites we have monitored continuously since 1993 (Tempel *et al.* 2014b). Of the 15,594 ha that burned within our study area, 64% burned at high-severity (WebTable 1). The extreme nature of the fire, more than two decades of pre-fire site occupancy data, and location information on owls – outfitted with Global Positioning System (GPS) receivers and tagged with colored leg bands for identification of individual birds – allowed us to draw strong inferences regarding the effect of severe fire on a species considered to be a barometer of old-forest wildlife community health (Simberloff 1998). Our results suggest that (1) reducing the frequency of large, severe fires could benefit spotted owls and, by extension, other old-forest species, and (2) forest restoration and old-forest species conservation objectives may be more compatible than previously believed.

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Figure 1. *A female California spotted owl (*Strix occidentalis occidentalis*) within the Eldorado Density Study Area in the central Sierra Nevada, California.*

Methods

Study area and spotted owl surveys

We conducted our study on the contiguous 35,500-ha Eldorado Density Study Area (EDSA) within the Eldorado National Forest in the central Sierra Nevada, California. The EDSA has been the site of a long-term mark–recapture demographic study of California spotted owls (Tempel and Gutiérrez 2013), and forms the primary part of a larger study area containing a greater number of owl sites (Tempel *et al.* 2014a). We used data from owl sites only within the EDSA because some sites outside of this area experienced a complex history of fire and post-fire management that could have confounded the natural BACI design within the EDSA. Moreover, sites outside of the EDSA were added at various times during the study, potentially complicating our evaluation of the effect of the King Fire on long-term spotted owl population trends.

Approximately 60% of the EDSA was public lands managed by the US Forest Service (USFS) and 40% was private land managed by timber companies. The primary vegetation type within the EDSA was mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), and California black oak (*Quercus kelloggii*). Forests within the EDSA have a complex history of management, logging, and fire suppression dating back at least 100 years. Early timber harvesting generally involved the selective removal of large, commercially valuable trees, with a more recent emphasis on clear-cutting on private lands and "diameter-limited thinning from below" on public lands. Prior to fire suppression, the ingrowth of shade-tolerant trees, and the removal of large trees, historical fire regimes consisted mainly of frequent low- to moderate-severity fire occurring in 5–15-year intervals (Stephens and Collins 2004). Elevation within the EDSA ranged from 360 to 2400 m, and the climate was characterized by cool, wet winters and warm, dry summers.

We surveyed the entire area each year for territorial spotted owls during the breeding season (1 Apr to 31 Aug) without regard to land cover, topography, access, or land ownership, and for this analysis we used survey data from 1993–2015. Spotted owls (usually mated pairs, but sometimes single birds) occupy and defend sites (ie "territories"), the locations of which remain reasonably stable across years. We considered a site to be occupied in a given year when at least one owl was detected. Additional survey details can be found elsewhere (Tempel and Gutiérrez 2013; Tempel *et al.* 2014b).

BACI analysis

We evaluated the potential impact of high-severity fire on spotted owls using a BACI design with multi-season site occupancy data (MacKenzie *et al.* 2003; Popescu *et al.* 2012). We carried out parallel continuous and categorical BACI analyses, where the proportion of a spotted owl site (a circle with radius equal to one-half the mean nearest-neighbor distance across years = ~1100 m; Tempel *et al.* 2014a) affected by high-severity fire was the impact covariate (ie "treatment"). We defined "high-severity" as forests that experienced 75–100% canopy mortality (Lee and Bond 2015), corresponding to a relative differenced Normalized Burn Ratio (RdNBR) threshold of >572 (Miller *et al.* 2009a). The continuous BACI analysis contained two groups: sites that were unburned (n = 15) and sites that overlapped with the King Fire and thus experienced some degree of burn (n = 30). The categorical BACI analysis contained three groups: sites that were unburned (n = 15), sites that experienced <50% high-severity fire (n = 16), and sites that experienced >50% high-severity fire (n = 14). For both continuous and categorical BACI analyses, we followed a hierarchical modeling procedure by first modeling within-season detection probability as a function of covariates (WebTable 2). We then modeled the potential effects of high-severity fire on colonization (γ) and extinction (ε) rates separately using Akaike's information criterion (AIC) to select between competing models (WebTable 3), while allowing the non-focal parameter to vary by year (Tempel *et al.* 2014a).

Previous attempts to test for the effects of wildfire on spotted owls have been hindered by the potential confounding effect of post-fire salvage logging (Lee *et al.* 2012; Clark *et al.* 2013). However, in our study, all surveys used to estimate occupancy metrics were completed before the implementation of proposed post-fire salvage logging on public lands (USFS 2015), which comprised a median of 89% of the area that occurred within burned owl sites (versus ~11% on private lands). We also evaluated the potential effects of post-fire salvage logging on private lands in the continuous site occupancy analysis. Specifically, when fire effects were supported, we introduced a covariate representing the proportion of spotted owl sites that experienced salvage logging. The continuous variables – high-severity fire and salvage logging – were not strongly associated at fire-affected sites (R^2 = 0.10).

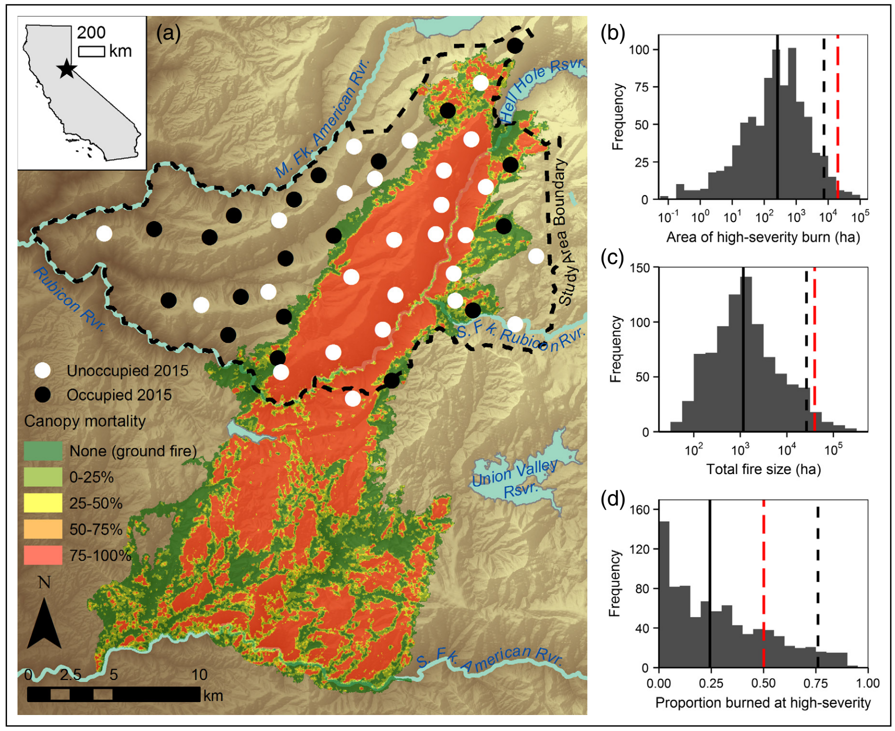

Figure 2. *The geography and historical context of the 2014 King megafire. (a) The distribution of occupied and unoccupied spotted owl sites in 2015 within our 23-year demographic study area, which was located ~20 km west of Lake Tahoe, California. Elevation is represented by brown shading (darker brown = low elevation, lighter brown = high elevation) and ranges from approximately 150 to 3000 m. (b–d) A comparison of the King Fire to all California fires since 1984 in terms of area of high-severity burn (b), total fire size (c), and proportion burned at high-severity (d); the solid black lines represent the 50th percentile, the dashed black lines represent the 95th percentile, and the dashed red lines represent the 2014 King Fire.*

Population trend analysis

We fit a fully time-varying dynamic occupancy model to our 23-year detection/non-detection data to obtain unconstrained annual estimates of occupancy (ψ_t) and rate of change in occupancy (λ_t) for the study area (MacKenzie *et al.* 2003). Our statistical model directly estimated initial occupancy (ψ_1), annual estimates of extinction (ε_t), and annual estimates of colonization (γ_t), so we used the recursive equation

$$\psi_t = \psi_{t-1}(1-\varepsilon_{t-1}) + (1-\psi_{t-1})\gamma_{t-1} \qquad \text{(Eq 1)}$$

to estimate occupancy (ψ_t) for each year of the study period. Then, using the estimates of ψ_t, we calculated λ_t for each year using the equation:

$$\lambda_t = \frac{\psi_{t+1}}{\psi_t} \qquad \text{(Eq 2).}$$

This analysis allowed us to consider occupancy and rate of change in occupancy after the King Fire within the context of a long-term decline in our study population (Tempel and Gutiérrez 2013). We fit several linear models to annual estimates of occupancy ψ_t and used AIC to evaluate relative support for different time trends (linear, log-linear, quadratic) and a segmented (ie "breakpoint") model over the pre-fire years 1993–2014 (WebTable 4). We used the segmented model to evaluate support for an initial decline followed by a period of apparent population stability prior to the King Fire.

Habitat use and selection analysis

We collected post-fire foraging locations from nine spotted owls during the 2015 breeding season using backpacks equipped with a Lotek Pinpoint 100 mini-GPS archival tag and a VHF radio transmitter. GPS tags recorded 1–2 locations at random times between dusk and dawn each night, May–August, to characterize nocturnal habitat use during the breeding season. We collected 1085 locations but discarded ~11 locations per owl with suboptimal measures of precision (dilution of precision [DOP] ≥ 5). Using burn severity maps produced by the USFS, we performed a compositional analysis of habitat use (Aebischer *et al.* 1993) and derived Manly's selection ratios (ω_i; Manly *et al.* 2002)

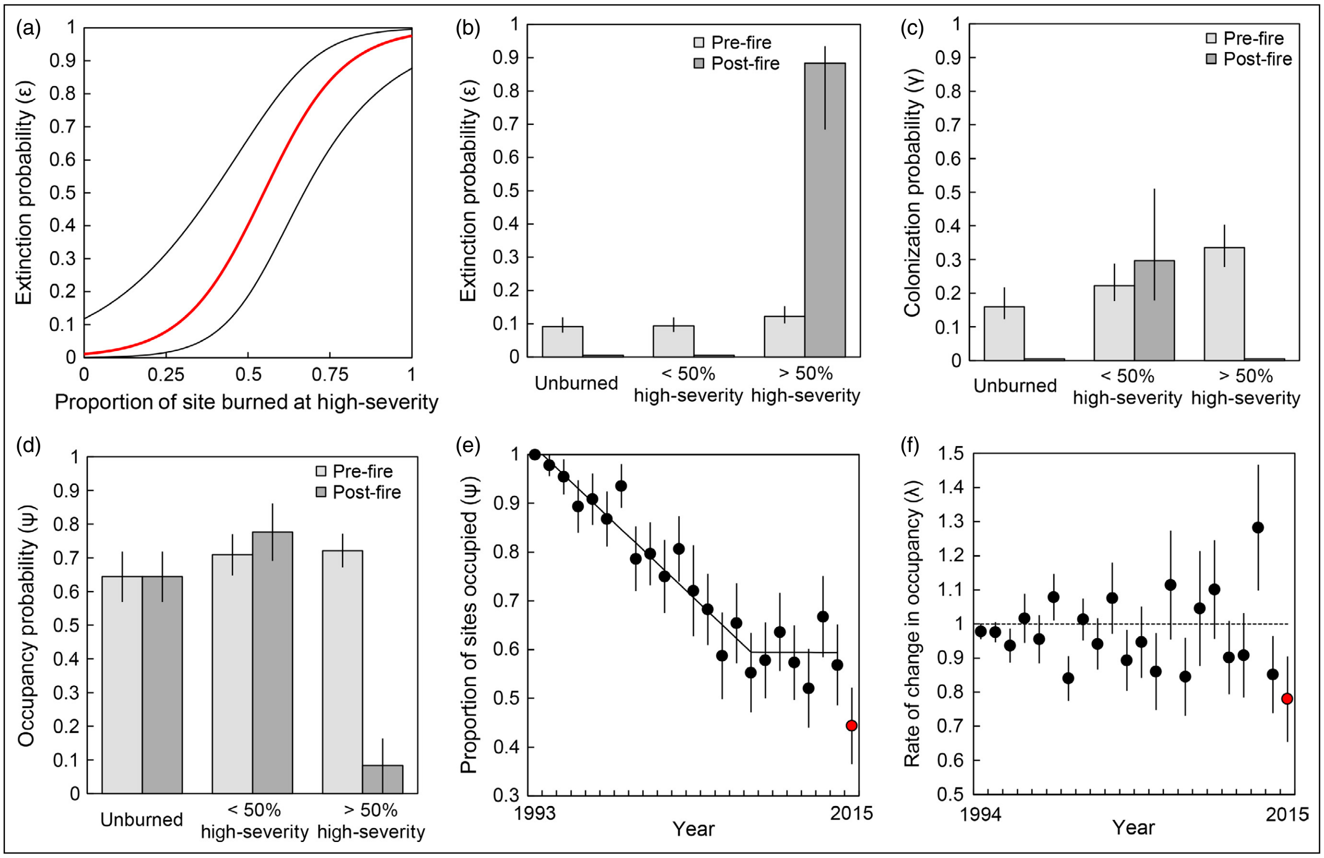

Figure 3. *Before–after control–impact and population analyses. (a) The continuous relationship between the proportion of an owl site that burned at high-severity and the probability of site extinction. (b–d) Colonization (b), extinction (c), and occupancy (d) probabilities for owl sites that experienced different degrees of high-severity burn both pre- and post-fire. (e) Annual estimates of occupancy (ψ) over the study period, where the black line represents a segmented regression function fitted to the mean occupancy for years 1993–2014 (WebTable 4) demonstrating the periods of decline and subsequent stability before the 2014 King Fire (solid red circle). (f) Annual estimates of rate of change in occupancy (λ) over the study period, where the dashed black line at* y = 1 *indicates a stable rate of change, and the solid red circle indicates the rate of change after the 2014 King Fire. The black curved lines in (a) and all error bars in (b–f) represent ± 1 SE of the mean.*

for third-order habitat selection to assess selection or avoidance of forests in different burn classes (unburned, low-severity, high-severity).

We defined available habitat area for each owl using a circle with the center equal to the geometric mean of 2015 nest tree, roosts, and daytime capture locations (ie "activity center") and a radius equal to the 95th percentile of linear foraging distances from the activity center (similar to Bond *et al*. 2009). We used the 95th (not 100th) percentile so that distant areas rarely visited by owls in foraging bouts (Bond *et al*. 2009) were not counted as "available" habitat. As a result, the analysis consisted of GPS locations that occurred within distance ranges used at relatively high frequencies (WebFigure 2). We used a circle instead of a minimum convex polygon (MCP) to define available habitat because MCPs often failed to include the large, high-severity patch as "available" although it was generally within the foraging radius of owls (WebFigure 3). We performed habitat selection analyses using the R package "adehabitatHS" (Calenge 2006).

Results and discussion

The BACI analysis indicated that high-severity fire had a strong negative impact on spotted owls. The probability of site extinction (ε) increased from 0.01 to 0.98 as the proportion of high-severity fire at a spotted owl site increased from 0 to 1 (Figure 3a). Moreover, extinction rates at severely burned sites (>50% of site area burned at high-severity) increased sevenfold following the King Fire ($\hat{\varepsilon}_{1993–2014}$ = 0.12, 95% confidence interval [CI] = 0.08–0.18; $\hat{\varepsilon}_{2015}$ = 0.88, CI = 0.49–0.98), whereas post-fire extinction rates were estimated to be zero at less severely burned and unburned sites (Figure 3b). Sites that burned <50% at high-severity were more likely to be colonized after the fire ($\hat{\gamma}_{<50\%\ \mathrm{High\text{-}severity}}$ = 0.30, 95% CI = 0.07–0.72) than unburned sites and sites that burned >50% at high-severity ($\hat{\gamma}_{\mathrm{Unburned}}$ and $\hat{\gamma}_{>50\%\ \mathrm{High\text{-}severity}}$ = 0; Figure 3c). Colonization of sites after the fire was largely the result of individuals moving to less burned sites after abandoning their original sites that burned at >50% high-severity (WebFigure 4). Predicted occupancy rates ($\hat{\psi}$) at sites that burned >50% at high-severity declined by almost ninefold from their pre-fire value ($\hat{\psi}_{\text{Pre-fire}}$ = 0.72, 95% CI = 0.62–0.82; $\hat{\psi}_{\text{Post-fire}}$ = 0.08, 95% CI = 0.00–0.24), based on a model that combined top colonization and extinction covariate structures in the categorical analysis (Figure 3d).

Using spatially explicit data obtained from privately owned natural resource companies (Sierra Pacific Industries and Mason, Bruce & Girard Inc) that managed timberlands in our study area, we estimated that post-fire salvage logging on private lands constituted a median of only 2% of the area within owl sites. The extent of high-severity fire was large relative to the extent of salvage logging within owl territories (WebFigure 1), strengthening potential inferences because this ratio reduced the confounding effects of high-severity fire and post-fire salvage logging on spotted owls. In addition, the term for salvage logging appeared as an uninformative parameter in the modeling procedure (Arnold 2010), also suggesting that post-fire salvage logging operations did not confound associations between occupancy metrics and high-severity fire (WebTable 3; WebFigures 1 and 5).

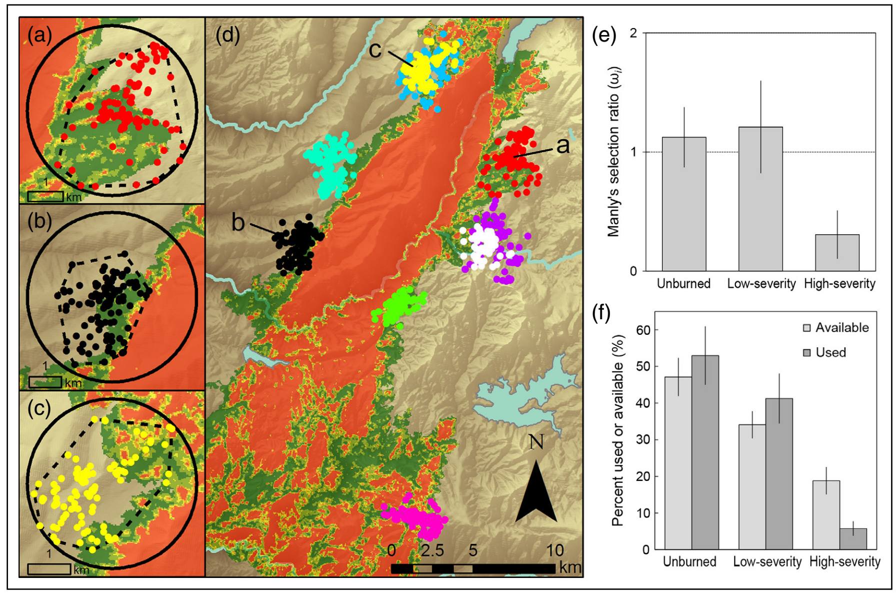

Figure 4. *Distribution of spotted owl foraging locations following a megafire developed from 985 GPS locations from nine owls (individuals represented by different colors) during the 2015 breeding season in relation to the 2014 King Fire (d). Inset examples (a–c) of foraging locations for three owls (small solid-colored circles) and the area defined as available habitat (large open black circles) compared to a minimum convex polygon (black dashed polygon) demonstrate the owls' apparent avoidance of the high-severity burned area. Burn severity for the King Fire is displayed in 25% classes as in Figure 2a. (e) Manly's selection ratios ($\hat{\omega}$) ± 1.96*SE, where a selection ratio $\hat{\omega}$ > 1 indicates habitat preference, $\hat{\omega}$ < 1 indicates habitat avoidance, and $\hat{\omega}$ = 1 indicates neither preference nor avoidance. (f) Mean (± SE) availability and use among nine owls for unburned forests, forests that experienced 0–75% canopy mortality (low-severity), and forests that experienced 75–100% canopy mortality (high-severity).*

The King Fire exacerbated a longer-term decline in spotted owl occupancy within our study area. The proportion of occupied spotted owl sites declined by 43% over a 22-year period leading up to the 2014 King Fire ($\hat{\psi}_{1993}$ = 1.0, standard error of the mean [SE] = 0.0; $\hat{\psi}_{2014}$ = 0.57, 95% CI = 0.41–0.73) (Figure 3e). After the King Fire, occupancy dropped from 0.57 to 0.44 ($\hat{\psi}_{2014}$ = 0.57, 95% CI = 0.41–0.73; $\hat{\psi}_{2015}$ = 0.44, 95% CI = 0.29–0.60) following ~7 years of relatively stable occupancy (Figure 3e). The 22% decline in site occupancy after the fire ($\hat{\lambda}_{2015}$ = 0.78, 95% CI = 0.53–1.03) was the greatest single-year decline recorded over our 23-year study period (Figure 3f).

Analyses of spotted owl foraging locations along the perimeter of the King Fire (no owls were present in the interior of the large patch that burned at high-severity; Figure 3, a–d) indicated that spotted owls foraged non-randomly (Wilks's lambda Λ = 0.40, P = 0.017) by avoiding foraging in areas that burned at high-severity ($\hat{\omega}_{\text{High-severity}}$ = 0.31, 95% CI = 0.10–0.51) (Figure 4, e and f). Forests that burned at low-severity and unburned forests were used in proportion to their availability on the landscape ($\hat{\omega}_{\text{Low-severity}}$ = 1.21, 95% CI = 0.82–1.60; $\hat{\omega}_{\text{Unburned}}$ = 1.12, 95% CI = 0.87–1.38) (Figure 4, e and f).

The observation that lower-severity fire is benign, and perhaps even moderately beneficial, to spotted owls is consistent with previous studies (Roberts *et al.* 2011; Lee *et al.* 2012) and is not surprising given that, within dry mixed-conifer forests, the spotted owl and other old-forest species evolved in association with such fire regimes (Noss *et al.* 2006; North *et al.* 2009). However, we provide the first definitive evidence that a large, high-severity fire (ie a megafire) had strong negative population impacts on an old-forest species and that areas burned at high-severity were avoided by individuals of that species. These findings contrast with a recent spotted owl population study that reported high site occupancy after another megafire (the "Rim Fire"; Lee and Bond 2015). The Rim and King fires could have affected owls differently because of differences in the patterns of patches that burned at high-severity and the resulting distribution of remnant habitat. The largest high-severity patch in the Rim Fire (21,426 ha) was 1.5 times larger than the largest high-severity patch in the King Fire (13,683 ha), but made up a smaller percentage of the total area burned (21% versus 36% for the Rim and King fires, respectively) and, despite its larger area, had an edge-to-area ratio 1.5 times greater than that of the King Fire. The relatively high spatial complexity and heterogeneity in high-severity burn patterns in the Rim Fire may have resulted in a wider range of vegetation conditions and more remnant live trees suitable for owls (Lee and Bond 2015) as compared with the King Fire, where the largest patch of high-severity fire was more homogeneously severe and overlapped a greater density of owl sites (Figure 2; see WebFigure 6). Alternatively, because owls were not individually marked in the Rim Fire study, some detections at "occupied" sites may have involved individuals from neighboring territories or non-territorial "floaters" (Lee and Bond 2015), both of which may have contributed to inflated estimates of territory occupancy. Regardless, our study demonstrates that megafires can have strong negative effects on spotted owls, particularly when severely burned areas occur as large homogenous patches that leave little or no interspersed remnant habitat.

While we used only one year of post-fire data, the substantial decline in occupancy at severely burned sites is unlikely to reflect a temporary loss of individuals that will soon be replaced by colonization, but rather represents a direct loss of suitable nesting and roosting habitat that will likely not be replaced for many decades. Moreover, we found the scorched remains of one adult spotted owl from a severely burned site (WebFigure 7), indicating that, in some instances, this highly vagile species was unable to avoid the rapidly moving fire. It is not unreasonable to suspect that less mobile old-forest specialists will be equally – and perhaps more – affected by megafires like the King Fire. Collectively, these findings suggest that megafires constitute an additional mechanism by which climate change will threaten old-forest species, along with previously recognized climate-associated stressors such as habitat shifts, physiological impacts, and changes in community interactions (Dawson *et al.* 2011).

Conclusions

Our study demonstrates that increasingly frequent megafires pose a threat to spotted owls and likely other old-forest species and, as a result, suggests that forest ecosystem restoration and old-forest species conservation may be more compatible than previously believed. Restoration practices that can demonstrably reduce the frequency of large, high-severity fires and reintroduce low- to moderate-severity fire as the dominant disturbance regime will likely benefit both dry-forest ecosystems and old-forest species such as spotted owls. Yet forest restoration efforts that remove key habitat elements and areas of currently suitable habitat could exacerbate the risk of extirpation in the short term before the long-term benefits of restored fire regimes are realized, particularly in light of the present deficit in large and old trees in natural landscapes (Tempel *et al.* 2015). Rather, implementing fuels and restoration treatments outside of key habitats (eg nesting and denning areas) is more likely to minimize short-term impacts and ensure that old-forest species persist until forest resiliency objectives are achieved (Stephens *et al.* 2014a). However, the calculus behind these trade-offs is complex and depends on several considerations that merit additional research, such as the magnitude of short-term impacts that treatments impose on old-forest species, the relative increase in the frequency of severe fire as a function of climate change, and the efficacy of forest restoration for reducing both severe fires and tree mortality from drought and insects (Asner *et al.* 2015). Managers and policy makers will be faced with challenging decisions regarding the pace and scale of forest restoration efforts in light of scientific uncertainty and conflict among stakeholders (Redpath *et al.* 2013). We suggest, however, that old-forest species should not be viewed as an impediment to forest restoration objectives; rather, ensuring the persistence of old-forest species including the spotted owl, northern goshawk (*Accipiter gentilis*), pileated woodpecker (*Dryocopus pileatus*), Pacific fisher (*Pekania pennanti*), and American marten (*Martes americana*) can serve as a barometer for the successful restoration of the ecosystems they inhabit.

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.1298/suppinfo

