Mexican spotted owl breeding population, site occupancy, and habitat selection 13-15 years after the Rodeo-Chediski fire in east-central Arizona

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ABSTRACT

MEXICAN SPOTTED OWL BREEDING POPULATION, SITE OCCUPANCY, AND HABITAT SELECTION 13-15 YEARS AFTER THE RODEO-CHEDISKI FIRE IN EAST-CENTRAL ARIZONA

MICHAEL A. LOMMLER

This is the first study to demonstrate the interaction between Mexican spotted owls (*Strix occidentalis lucida*) and a large, high-severity wildfire (a “mega-fire”) after more than a decade post-fire. The Rodeo-Chediski fire burned 187,000-ha in east-central Arizona in 2002. During the 2014-2016 breeding seasons we surveyed a 18,800-ha area within the fire perimeter that contained 20 pre-fire Protected Activity Centers (PACs) designated to protect Mexican spotted owl nesting and roosting habitat. We used data from surveys conducted by the U.S. Forest Service both inside (20 pre-fire PACs, from 1990-2013) and outside (61 pre-fire PACs, from 1990-2016) the fire perimeter to compare observed (unmodeled) site occupancy over time and space, as well as fecundity. Within the fire perimeter observed pair occupancy declined by >50% post-fire and remained low or 15 years afterward. Prior to the fire observed occupancy did not differ between PACs inside and outside the fire perimeter. Observed post-fire site occupancy was lower inside the fire perimeter than outside the fire perimeter for both single owls and pairs. Fecundity was similar both inside and outside the fire perimeter over all time periods. We also modeled site occupancy from 2014-2016 across the entire 18,800-ha study area using a grid of 198 1-km^2 (100-ha) cells and across known (historic and new) spotted owl territories using 22 800-m radius (201-ha) core areas as sampling frames and detection data from systematic nocturnal point sampling. We observed no clear trend over this time period in either model. Spotted owl occupancy of 100-ha cells was positively associated with cover of dry mixed-conifer forest and negatively associated with salvage logging. Fire severity was an important predictor of occupancy of 201-ha core areas, but the Bayesian Credible Intervals (BCIs) for this predictor included zero. We used diurnal locations of Mexican spotted owls to create a scale-optimized, multiple-scale Random Forest model of 3rd-order habitat selection. We found that spotted owls selected for the presence of large trees within a 100-m radius around nest and roost sites, and avoided locations where killed 33% or more of the pre-fire tree canopy within 200-m around nest and roost sites while selecting those burned less severely. Our study shows that mega-fires may have large effects on spotted owl populations and habitat selection even several years after a fire. These effects may be difficult to detect using nocturnal detection data. These results emphasize the need for demographic studies of spotted owls and for the use of multiple-scale modeling approaches that reflect how the species perceives and uses the post-fire landscape. Forests used by spotted owls should be managed to increase resilience to fire and to restore important habitat elements used by owls, particularly large trees.

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Preface

This dissertation is presented in journal format. The following manuscript chapters were written to appear as articles in scientific journals. The first chapter serves as an introduction to the Mexican spotted owl and its relationship with wildland fire. The second chapter describes how one fire in Arizona, the Rodeo-Chediski fire, affected the breeding population of spotted owls within a study area located in east-central Arizona. The third chapter describes two models of site occupancy after the fire, and how site occupancy is related to wildfire. The fourth describes a scale-optimized model of nesting and roosting habitat selection by spotted owls on the study area, and how habitat selection may be influenced by wildfire. Some redundancy will occur from combining these articles in journal format. Because these chapters are intended to be published as multi-author articles in journals I have chosen to use “we” in place of one where normally expect to see “I” referenced.

Mexican spotted owl breeding population, site occupancy, and habitat selection 13-15 years after the Rodeo-Chediski fire in east-central Arizona

Chapter 1

Introduction: the Mexican spotted owl and its relationship with wildfire

Michael A. Lommler

Abstract

The Mexican spotted owl (*Strix occidentalis lucida*) is a threatened species found in the Four Corners region of the United States and in the mountains of west Texas and Mexico. Driven by fire suppression and climate change, the montane forests of Arizona and New Mexico, where much of the U.S. population resides, are increasingly vulnerable to large, stand-replacing fires. Other subspecies of spotted owl have displayed varied responses to wildfire, while the Mexican spotted owl is poorly-studied by comparison, particularly with respect to these fires. Sufficiently large, severe fires may constitute a threat to the species. To help understand how wildfire affects owls, we studied how the Rodeo-Chediski fire, a very large wildfire in Arizona, affected the size and fecundity of the local population of Mexican spotted owls 13 to 15 years after the fire. This introductory chapter provides key context for understanding the Mexican spotted owl's relationship with wildfire.

Natural history of the Mexican Spotted Owl:

The Mexican spotted owl is a medium-sized raptor found in the mountains and canyons of the southwestern United States and northern and central Mexico. Two other subspecies, the California (*S. o. occidentalis*) and northern (*S. o. caurina*) spotted owl, are native to California and the Pacific Northwest, respectively. Many Mexican spotted owls are found in areas of mixed-conifer and ponderosa pine (*Pinus ponderosa*) - Gambel oak (*Quercus gambelii*) forest from the Grand Canyon in northern Arizona to southwestern New Mexico, with other substantial populations found in the canyons of southern Utah, the Sky Islands of southeast Arizona, and the Sacramento Mountains of southern New Mexico (Ward et al. 1995).

Mexican spotted owl nests are generally associated with shady forest habitat or steep cliffs and rocky terrain. They do not build nests but rather use nests built by other species or natural platforms and cavities. In the xeric Colorado Plateau canyons nests are typically in caves or on cliff ledges (Rinkevich and Gutierrez 1996). In the forested mountains of Arizona and New Mexico spotted owls typically use tree cavities, broken treetops, witch's brooms, or abandoned hawk nests (Ganey et al. 2013). Breeding season home ranges around these nest sites are highly variable in size, as little as 150 ha and sometimes greater than 800 ha (Ganey and Balda 1989, Ganey et al. 2005, Willey and Van Riper 2007). Wintering ranges are generally larger than breeding ranges.

Spotted owl diet varies by location but commonly includes rodents such as woodrats (*Neotoma* spp.), deer mice (*Peromyscus* spp.), pocket gophers (*Thomomys spp.*), and voles (*Microtus spp.*), but may also include bats, birds, reptiles, and arthropods (Ward and Block 1995).

Annual survival rates of adult Mexican spotted owls are generally high, ranging from 0.8 to 0.9 (White et al. 1995). As a result, adult Mexican spotted owls are relatively long-lived. Spotted owls are monogamous and territorial. They breed sporadically. Most of the population will nest successfully in good years, but a much smaller proportion of the population will nest in poor years (Gutierrez et al. 2003). The timing of good and poor breeding years is often correlated with annual variability in climate, especially precipitation (Seamans et al. 2002). When they do breed, clutch sizes are small, typically 1-3 eggs. The breeding season starts with courtship in March and continues until fledglings disperse in mid-to-late September or early October (Ganey et al. 1998).

Dispersing juvenile owls have been documented more than 70 km from the natal territory, but on average probably settle considerably closer (Ganey et al. 1998). Natal dispersal does not appear to be sex-biased. Annual survival rates of juvenile (< 1 year old) spotted owls are considerably lower (0.06 to 0.29, White et al. 1995) than survival rates of established adult (> 0.8 annual survival) and subadult (1 and 2 years old, > 0.6 annual survival) owls (Seamans et al. 1999). The largest sources of mortality are probably starvation and predation by larger raptors including great horned owls (*Bubo virginianus*), northern goshawks (*Accipiter gentilis*), red-tailed hawks (*Buteo jamaicensis*), and golden eagles (*Aquila chrysaetos*) (U.S. Fish and Wildlife Service 2012).

<u>Conservation status</u>

The U.S. Fish and Wildlife Service listed the Mexican spotted owl as a threatened species in 1993 (U.S. Fish and Wildlife Service 2012). Threats to Mexican spotted owls include habitat destruction or modification, recreational or scientific exploitation, disease, predation, inadequate regulatory protections, and other factors including noise disturbance and climate change (U.S. Fish and Wildlife Service 2012). Habitat destruction or modification is considered the primary threat to spotted owls. In the past habitat modification was driven primarily by timber harvest and fire suppression. Now stand-replacing fire is the primary concern. The 2012 recovery plan divides the range of the owl into ten Ecological Management Units (EMUs) to organize recovery efforts. In the U.S. there are five such units; Colorado Plateau, Southern Rocky Mountains, Upper Gila Mountains, Basin and Range-West, and Basin and Range-East (U.S. Fish and Wildlife Service 2012). The five Mexican EMUs are Sierra

Madre Occidental-Norte, Sierra Madre Oriental-Norte, Sierra Madre Occidental-Sur, Sierra Madre Oriental-Sur, and Eje Neovolcanico. In the United States individual owl territories are protected by the establishment of Protected Activity Centers (PACs). PACs are irregular polygons of 243 ha or greater centered on owl nest and roost locations and drawn to include areas with large trees and other key elements of spotted owl habitat (U.S. Fish and Wildlife Service 2012)

Range-wide population trends are unclear (U.S. Fish and Wildlife Service 2012). Rates of survival and fecundity on two study areas in Arizona and New Mexico showed both populations declining ≥10% annually from 1991-1997 (Seamans et al. 1999). A more recent (2003-2011) demography study from the Sacramento Mountains in New Mexico showed a positive population trend in that region (Ganey et al. 2014a).

<u>Fire risk in spotted owl habitat</u>

Forest types occupied by the three subspecies of spotted owls include wet mixed-conifer, dry mixed-conifer, and pine-oak variants, on a spectrum from wettest to driest. Fire regimes experienced by these forest types are variable. Swetnam and Baisan (1996), summarizing results from several studies, showed that southwestern dry-mixed conifer forests historically experienced fire every 2.9-12.3 years. Huffman et al. (2015) reconstructed an even shorter fire interval (2-8 years), and only small patches (~25 ha) burned at high severity. The wetter forest types may have experienced moderately-long intervals (10-75+ yrs) between mixed-severity (including crown fire) fires (Kaufmann et al. 2007). Evidence suggests these forests were historically of low density and dominated by large trees (Collins et al. 2015, Hagmann 2017).

Current observed fire intervals in the dry forests of the mountains of central Arizona and New Mexico may now be almost twice what was expected historically, and from 1984-2012 about 1.23 million ha less land area has burned than would be expected (Parks et al. 2015). This "fire deficit" is nearly unprecedented over the last 2000 years (Roos and Swetnam 2011). As a result, modern forests are considerably denser and have many more small trees than historic forests. The largest increases in forest density may have occurred in the wettest forest types (Merschel et al. 2014, Rodman et al. 2017), but dry mixed-conifer and ponderosa pine forest types are likely to experience relatively greater increases in fire severity as a result of fuel build-ups (Steel et al. 2015). As a result, large fires have increased in frequency and size in the southwestern U.S. over the past three decades (Westerling et al. 2006, Dennison et al. 2014, Westerling 2016). The largest and most destructive of these fires are sometimes referred to as "mega-fires" (Williams 2013). Over the last two decades several very large fires have occurred in the southwestern U.S., including areas occupied by Mexican spotted owls. These fires include the Rodeo-Chediski (2002, 186,871 ha, 36.6% high severity), Wallow (2011, 228,111 ha, 9.2% high severity), and Whitewater Baldy (2012, 124,208 ha, 11.6% high severity) fires (MTBS Data Access 2014*b*, MTBS Data Access 2014*c,* MTBS Data Access 2014*d,* U.S. Fish and Wildlife Service 2012).

<u>Spotted owl relationship to wildfire</u>

Fire may affect spotted owls in direct and indirect ways, and these effects may vary based upon wildfire severity, habitat type, and other factors (U.S. Fish and Wildlife Service 2012). Spotted owl response to wildfire is highly variable. After many fires, California spotted owls have exhibited little or no significant effect on survival (Bond et al.

2002), territory occupancy (Lee et al. 2012, Lee et al. 2013, Lee and Bond 2015a, 2015b, Roberts et al. 2011), and home range size (Bond et al. 2013). Spotted owls have also been observed selecting burned areas for foraging (Bond et al. 2009, Bond et al. 2016, Roberts et al. 2011, Comfort et al. 2016, Eyes et al. 2017). These results do not hold true across the board. Clark et al. (2011, 2013) showed that a combination of fire and salvage negatively affected survival and occupancy of northern spotted owls. Jones et al. (2016) observed California spotted owls avoided foraging in a large patch burned at high severity (>70% crown mortality), in addition to a large reduction in territory occupancy. Rockweit et al. (2017) found that fires that burned more at lower severities had little effect upon survival by northern spotted owls, but that fires that burned more at medium and high severities negatively affected survival. Some burned territories persisted due to increased rates of colonization from outside. These may represent population sinks that make negative net contributions to the breeding population but persist because of immigration from source populations in areas that were unburned or burned at lower severity.

Compared to the other subspecies, the relationship between Mexican spotted owls and fire is poorly studied. Bond et al. (2002) observed that fire had little effect on survival one year post-fire, but only had a sample of four Mexican spotted owl territories. Jenness et al. (2004) were able to draw from a sample of 33 burned territories, but only 16% of the area of these sites burned at stand-replacement. Their study also drew from several fires across Arizona and New Mexico, rather than a single “megafire”. They found a negative but statistically insignificant effect of fire upon site occupancy. Ganey et al. (2014b) observed Mexican spotted owls selecting burned areas for winter foraging. The two fires in that study were only 6213 and 6073 ha and only affected four radio-marked spotted owls.

Most of these studies took place within 6 years post-fire, and very few studies included data from fires more than 10 years old. Despite the demonstrated significance of landscape composition and arrangement in space upon fitness (Franklin et al. 2000), very few studies have directly looked at how patch size and arrangement has influenced occupancy or survival. Fire has also not been consistently measured, making it difficult to make direct comparisons. Bond et al (2002) and Lee and Bond (2015b) did not indicate what proportion of their sites burned at high severity, and several observers did not report data about fire size, instead limiting their reporting to statistics from within owl territories without broader landscape context (Jenness et al. 2004, Lee et al. 2013, Lee and Bond 2015b, Roberts et al. 2011). Many studies had a sample of <20 burned territories (Bond et al. 2002, 2009, 2010, 2013, and 2016, Roberts et al. 2011, Ganey et al. 2014b, Comfort et al. 2016).

Much of the disagreement in results may be explained by differences in fire severity and the influences of spatial scale. The large negative effect upon occupancy and foraging shown by Jones et al. (2016) can be attributed to the proportion and contiguity of area burned at high severity, which appears to be higher than observed in other studies. Others have found that proportion of a site burned at high severity (Lee et al. 2013, Rockweit et al. 2017) is important. Comfort et al. (2016) took this concept farther by optimizing for scale and showing how northern spotted owls utilize hard (intact forest directly adjacent to non-forest or early seral) and diffuse (gradual transition from intact forest to non-forest or early seral) edges created by fire and salvage logging. Small areas of higher severity fire may produce preferred foraging habitat, while larger areas may lack sufficient cover to be utilized.

The Rodeo-Chediski fire

We attempted to address these conflicts and unanswered questions by investigating Mexican spotted owl response to a large, severe wildfire in Arizona. The Rodeo-Chediski fire resulted from the merging of two different human-caused ignitions on the Fort Apache Indian Reservation in east-central Arizona. After merging, the fire burned onto the adjacent Apache-Sitgreaves and Tonto National Forests. The fire lasted from June 18 to July 7, 2002 and affected approximately 186871 ha of forest land. The fire burned through several vegetation types, including chaparral, pinyon-juniper woodlands (*Pinus edulis-Juniperus* spp.), ponderosa pine (*Pinus ponderosa*) forest, pine-oak (*Quercus gambelii*) forest, and mixed-conifer forest. The fire burned 36.6% of the area at high severity, and an additional 31.6% at moderate severity (MTBS Data Access 2014*c*). Salvage logging and fuels reductions began on Forest Service lands in the summer of 2005 (Ffolliet et al. 2011).

The fire affected 20 PACs on Forest Service land, providing an opportunity to observe how a local population of Mexican spotted owls responded to large, severe wildfires over a span of several years.

Research Questions

With this dissertation we attempted to answer several major questions. Chapter Two addresses how the size and breeding success of the local population has been influenced by the Rodeo-Chediski fire. It also attempts to account for whether reproduction or outside colonization is sustaining the population. Is this a population source or a population sink? Chapter Three compares two models of post-fire site occupancy that attempt to determine the drivers of occupancy, colonization, and extinction in this population, particularly the role of fire. Is the population still in decline, or has it stabilized? Should fire affect how we design studies of occupancy for spotted owls? Chapter Four uses a multi-scale modeling approach to see if the fire has driven changes in habitat selection, whether changes in features used or in the scale at which those features were selected. Do Mexican spotted owls respond to high severity fire differently depending upon the spatial scale?

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Chapter 2

Mexican spotted owl breeding population reduced by 50% for 15 years after a high-severity fire

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Abstract

Studies of the effect of fire on forest animals, especially in forests of Western North America, are increasingly important as size and intensity of fires increase due to past management practices and climate change. Such studies would be useful if they addressed long-term effects of large, severe fire on at-risk species that are dependent on habitat features susceptible to such fires. We compared observed percent of territories occupied and reproduction per observed occupied site for the threatened Mexican spotted owl (*Strix occidentalis lucida*) up to 15 years after Arizona's Rodeo-Chediski fire (187000-ha, 36.6% burned at high severity) to those rates before the fire and in nearby unburned areas. Although spotted owls sometimes forage in patches of high-severity fire, extensive areas burned at high-severity may leave little nesting and roosting habitat, and 15 years is likely longer than time lags due to short-term prey irruptions or site-fidelity of owls resident before the fire. We compared estimates from our 18800-ha burned area to those derived from US Forest Service surveys of designated Protected Activity Centers (PACs) within our study area and in nearby areas outside the fire perimeter in three time periods (0-13 years pre-fire; 1-12 years post-fire; and 13-15 years post-fire). The percent of observed PACs occupied did not change over time outside the fire perimeter. Within the fire area, observed pair occupancy declined by >50% post-fire and remained low for 15 years thereafter. Before the fire, observed occupancy did not differ between PACs within and outside the fire perimeter, but post-fire observed occupancy was lower for PACs within than outside the fire area for both single owls and pairs. Fecundity was similar both inside and outside the fire

perimeter for all time periods. We conclude that “mega-fires” can have severe and persistent impacts on Mexican spotted owl populations.

Introduction

Studies of the effect of fire on forest animals, especially in forests of Western North America, are increasingly important as size and intensity of fires increased over the last 3 decades due to past management practices and climate change (Westerling et al. 2006, Miller et al. 2009, Miller and Safford 2012, Dennison et al. 2014, Westerling 2016, Singleton et al. 2019). These modern forests often carry crown fire over large areas (Keane et al. 2008), leading to mega-fires, i.e., fires ≥10000-ha characterized by extreme fire behavior (Stephens et al. 2014, Williams et al. 2011). Mega-fires may create large forest patches burned at high severity (Stephens et al. 2014). Conifer forests may regenerate poorly after such fires, and large areas may convert to shrubland (Collins and Roller 2013) or hyper-dense stands susceptible to future repeated crown fire (Savage and Mast 2005). Such forests lack large trees, large snags, and other features needed by forest birds sensitive to loss of forest cover (Trzcinski et al. 1999).

Studies of fire effects would be especially useful if they addressed long-term effects of large, severe fire on forest birds that are dependent on habitat features susceptible to such fires. In a meta-analysis of 21 studies of bird responses to high-severity fire, 11 species responded positively and 20 species responded negatively (Fontaine and Kennedy 2012). Because only five of these studies looked at effects from fires > 10 years old, the analysis could not detect time lags in bird response to fire. In ponderosa pine forests of Northern Arizona high-severity fire had a positive effect on site occupancy of 7 bird species, and a negative effect upon 14 species (Sanderlin et al. 2016). One species, the American kestrel (*Falco sparverius*), appeared to respond positively to high-severity fire alone and the interaction between high-severity fire and time since fire (Sanderlin et al. 2016). Time lags in the population-level responses of organisms to environmental perturbations may be especially important for species with life history characteristics that include long generation times, low fecundity and delayed breeding (Thompson and Ollason 2001, Saether et al 2005). As a result, short-term studies of the effects of perturbations may not accurately reflect long-term consequences for populations. For example, studies of long-lived seabirds have shown that the effects of climatic changes may be delayed 5 or more years after the event (Thompson and Ollason 2001). Behavioral traits such as strong site fidelity also can interact with life history characteristics to create lag effects, as when long-lived, site-faithful birds continue to occupy habitat even when fecundity in those habitats falls below that necessary for persistence.

Fire's impact upon the spotted owl (*Strix occidentalis* spp.), an emblematic species of mature western forests, is a point of contention in the literature (Ganey et al. 2017, Lee 2018). Fires burning at low and moderate severities may have no significant effect upon California (*S. o. occidentalis*), Mexican, and northern (*S. o. caurina*) spotted owls (Bond et al. 2002, Roberts et al. 2011, Lee et al. 2012, Rockweit et al. 2017). The effect of high-severity fire is less clear but may depend on the ecological and spatial context. Spotted owls of all three subspecies will often forage in severely burned areas within a few years after fires (Bond et al. 2009, Bond et al. 2016, Eyes et al. 2017), likely due to short-term increases in prey abundance (Converse et al. 2006, Bond et al. 2009, Roberts et al. 2011, Fontaine and Kennedy 2012, Ganey et al. 2014*a*, Bond et al. 2016). Although fires can increase abundance of prey, mega-fires with large patches burned at high severity may have significant long-term negative effects upon both California and northern spotted owls (Clark et al. 2011, Clark et al. 2013, Jones et al. 2016, Rockweit et al. 2017).

Few studies have addressed the longer-term impacts of mega-fires on spotted owls. Of 20 studies of the relationship between spotted owls and fire cited by Ganey et al. (2017), only four included fires greater than six years old, and only two included fires more than 10 years old. Once they become territorial, spotted owls exhibit high site fidelity (Bond et al. 2002, Blakesly et al. 2006, Ganey et al. 2014*b*), which may maintain short-term occupancy rates after a fire (Ganey et al. 2017). Trees killed by fire may also remain standing for several years before falling (Chambers and Mast 2005), delaying the full impact of fire. Short-term studies likely do not capture the full effects of any given fire upon spotted owls.

The impact of mega-fires upon Mexican spotted owls could be particularly significant because Mexican spotted owl habitat is naturally fragmented (Barrowclough et al. 2006), with patches of closed-canopy montane forest or canyon habitat embedded in a matrix of more open woodlands, deserts, and grasslands. Fire might affect Mexican spotted owls by driving patch sizes below acceptable thresholds, or by otherwise degrading habitat quality. Only three published studies address the Mexican spotted owl's response to fire. Bond et al. (2002) found no negative effect on short-term (1-year post-fire) adult survivorship in four burned territories. Jenness et al. (2004) observed a negative but not significant effect on territory occupancy in 33 burned territories (1-4 years post-fire).

Ganey et al. (2014*b*) found four wintering owls foraging in burned areas 2-6 years post-fire.

The Rodeo-Chediski mega-fire provided a rare opportunity to study the effect of a large, severe wildfire on Mexican spotted owls up to 15 years post-fire, a longer time frame than previous studies. The Rodeo-Chediski fire lasted from June 18 to July 7, 2002 and affected approximately 190,000-ha of forest land in east-central Arizona (Figure 1, MTBS Project 2014). At the time, this fire was the largest and most severe in the recorded history of the southwestern United States (Kuenzi et al. 2008). Large forest areas affected by this fire appear likely to convert from ponderosa pine or mixed-conifer forest to chaparral, shrubland, or other ecological types (Strom 2005, Neary 2009, Haffey et al. 2018). The fire affected 20 owl territories on U.S. Forest Service lands, with a record of surveys beginning in 1990 (12 years before the fire) and continuing up through 2013 (11 years after the fire). We augmented this survey record with our own intensive surveys during 2014-2016 to determine if (1) the fire had reduced the observed number of sites occupied by spotted owls and if (2) the fire had affected per-territory reproductive rates.

Methods

Study species

The Mexican spotted owl (*Strix occidentalis lucida*) is a medium-sized raptor found in the mountains and canyons of the southwestern United States and northern and central Mexico. The owl is typically associated with mature, closed-canopy forests with large trees (Ganey and Balda 1989, Grubb et al. 1997), although they also nest in rocky canyonlands featuring caves and shaded cliff ledges. The owl has been listed as a threatened species under the Endangered Species Act (ESA) since 1993. Mexican spotted owl habitat is managed in the form of Protected Activity Centers (PACs), irregular polygons of 243-ha or more drawn around the core of an owl territory (U.S. Fish and Wildlife Service 2012). Wildland fire is considered one of the major threats to the subspecies due to the potential it has to modify or destroy Mexican spotted owl habitat (U.S. Fish and Wildlife Service 2012).

Study area

We studied an 18800-ha area within the perimeter of the Rodeo-Chediski fire that included all 20 pre-fire PACs. The study area was approximately 8 km southwest of Heber-Overgaard, AZ and bounded on the north by Arizona State Highway 260 and on the south by the Fort Apache Indian Reservation. We were limited to this area because we could not get approval to survey owl sites on reservation lands. The study area includes about 14700-ha on the Black Mesa Ranger District of the Apache-Sitgreaves National Forest, and 4100-ha on the Pleasant Valley Ranger District of the Tonto National Forest. This study area included sites above and below the Mogollon Rim, a prominent scarp delineating the southern edge of the Colorado Plateau in this area. The landscape was characterized by large contiguous stands of ponderosa pine forest. Prior to the fire, Mexican spotted owls settled primarily in patches of mixed-conifer and pine-oak forest located within deep canyons or on steep north-facing slopes. Approximately 23% of the study area burned at high severity (Figure 2). An additional 21% of the study area burned at moderate severity. On average, 32.2% of the area of 20 pre-fire PACs burned at high severity ($SD = \pm$ 24.4%). In addition, 1632-ha (about 8.6%) of the study area was subject to some degree of salvage logging, including a total of 65-ha in five

PACs (about 1.3% of total pre-fire PAC area). Another 613-ha of the study area was re-burned at low severity in May of 2012 by the Bull Flat fire (MTBS Project 2014). In 2007 three of the 20 pre-fire PACs were “de-PACed” with the approval of the U.S. Fish and Wildlife Service, due to a lack of recent spotted owl detections and an apparent lack of suitable habitat post fire.

Spotted owl surveys

We conducted nocturnal calling surveys for spotted owls during the 2014-2016 breeding seasons, using the acoustic survey protocol described by Forsman (1983). Surveyors visited call points, from which they projected spotted owl calls and listened for responses from territorial birds for a period of 10 minutes per visit. We established a network of 602 call points (Figure 3), located roughly 0.5-km apart from each other, with the goal of completely surveying the landscape within the study area, including areas outside pre-fire PACs. Where possible we placed points along ridges, trails, and roads to facilitate safe access by surveyors. This still left many points in canyon bottoms or on slopes. In 2016 we omitted 36 points (primarily along a busy highway) due to safety and noise concerns. During each survey season each call point was surveyed four times during the April to August portion of the breeding season. We never called the same point less than six days apart, which limited the risk of owls becoming de-sensitized to calling.

Spotted owl location estimates from acoustic surveys are often imprecise and only indicate species presence. To determine whether nocturnal detections reflected resident owls as opposed to transient or foraging owls, we followed up these detections with diurnal “walk-in” surveys to locate nest and roost sites. Once we visually located owls, we “moused” owls (allowed them to capture live mice) using standard techniques described in the Recovery Plan (U.S. Fish and Wildlife Service 2012, Appendix D, pp. 308-309). Mousing allows surveyors to find nest sites and juveniles or infer if the owls are not nesting. During each season, we inferred the number of PACs with resident owls as the number in which we detected a nest, a pair of owls, or a single territorial owl on at least two surveys (ignoring detections from outside the boundary of our study area). Similarly we inferred owl pairs and the reproductive status (nest attempts and fledglings produced) of each pair from walk-in survey data supplemented by results of nocturnal surveys. Our effort was thus similar to a demography study except that we did not mark and track individual owls, so we could not calculate adult or juvenile survival rates.

Comparison with U.S. Forest Service (USFS) survey data

We used Forest Service data from monitoring of owl PACs to assess patterns in occupancy and reproduction within PACs outside the perimeter of the Rodeo-Chediski fire, and for PACs within the perimeter prior to our study. The Black Mesa and Pleasant Valley Ranger Districts monitored PACs inside the fire perimeter from 1989-2013 and 61 PACs outside the fire perimeter from 1989-2016, using acoustic and walk-in surveys similar to ours. The 61 PACs outside the fire perimeter lay within 45-km of that perimeter and included all PACs on the Black Mesa and Pleasant Valley Ranger Districts that were not burned in the Rodeo-Chediski fire (Figure 4).

We used two-tailed t-tests to determine if PACs inside and outside the fire perimeter were similar with respect to 5 covariates relevant to owls, namely post-fire basal area, canopy cover, percent dry mixed-conifer, elevation, and slope ($\alpha = 0.05$).

Elevation and slope were calculated from the National Elevation Dataset (U.S. Geological Survey 2014), basal area from Sesnie et al. (2009), canopy cover from Homer et al. (2015), and mixed-conifer from LANDFIRE (U.S. Geological Survey 2018). All were based upon a 30-m pixel size.

USFS surveys differed from our surveys in that they usually did not cover areas outside PACs (and thus were less likely to find new territories), and did not monitor all PACs all years, making direct comparisons between our results and USFS results difficult. Because of this variation in annual survey effort and coverage, we summarized data over periods of years (see below) and did not evaluate annual variation.

For each year we calculated the proportion of PACs that were formally monitored, the observed proportion occupied by either single owls or owl pairs (i.e., a single owl or pair was detected at least once), the number of nests, and the number of fledglings in the 20 pre-fire PACs affected by the Rodeo-Chediski fire and the 61 PACs outside the perimeter of the Rodeo-Chediski fire. We calculated the observed proportion of monitored PACs occupied by either a single owl or an owl pair (i.e., PACs that were monitored according to U.S. Fish and Wildlife Service-approved protocol [U.S. Fish and Wildlife Service 2012, Appendix D]). We focus here on raw observations due to variation in annual survey effort and coverage in USFS surveys; we model occupancy and detectability (sensu MacKenzie et al. 2002) as a function of ecological covariates in a companion paper (Lommler et al., *in prep*). We calculated fledging success rate (fecundity) as the number of fledged young per occupied PAC (i.e., PACs with at least one detection of an adult or subadult spotted owl in a given year).

A preliminary pattern of an increase in variance in annual fecundity within the fire perimeter after the fire seemed likely to have been an artifact of small number of active PACs within that area after the fire. To control for the effect of a small number of PACs on variance, we drew random sub-samples from the larger (outside the fire perimeter) set of PACs to match the sampling effort from inside the fire perimeter during each year from 1990-2016. We repeated the sub-sampling 10000 times and then calculated the overall mean and variance.

We summarized mean annual observed occupancy and fledging success rates from 1990-2001 (pre-fire), 2002-2013 (earlier post-fire), and 2014-2016 (the time period of our own surveys, later post-fire). We considered a nest "successful" if it fledged young. When Forest Service surveys inferred that pairs were roosting or nesting on the adjacent reservation lands we censored these results from comparisons to our surveys, as we did not attempt to infer pair occupancy or reproductive status for owls detected on the reservation side of the boundary fence.

Results

Ecological characteristics of PACs inside and outside the fire perimeter

PACs outside the fire perimeter were on average about 130-m lower in elevation (U.S. Geological Survey 2014) than PACs inside the fire perimeter (Figure 5) but had slope characteristics (U.S. Geological Survey 2014) and cover of dry mixed-conifer forest (LANDFIRE 2018) that were not significantly different (two-tailed t-tests, $\alpha = 0.05$). PACs inside the fire perimeter had lower mean basal area and canopy cover than outside the fire perimeter (Figure 5), likely due to fire effects.

2014-2016 survey results

The number of spotted owl detections differed among years, with the fewest detections in 2014, an increase in detections in 2015, and lower detections in 2016 (Table 1). The PACs with detections and number of nest attempts similarly peaked in 2015. The number of inferred owl pairs stayed relatively stable at 4 to 6 pairs per year, and the number of PACs with resident owls was constant at 6 per year (Table 1).

Comparison with USFS survey data

On average a greater proportion of sites was monitored each year inside the fire perimeter compared to outside the fire perimeter, but prior to our surveys the total number of sites monitored was generally greater outside the fire perimeter (Table 2). Single owl observed occupancy rates (Figure 6) did not significantly change over time for PACs either inside or outside the perimeter of the fire. But while observed single-owl occupancy rates did not differ significantly between PACs inside and outside the fire area before the fire, they did differ significantly between these groups of PACs from 2002-2013 and 2014-2016 (Figure 6). Observed pair occupancy rates did not differ significantly between PACs inside and outside the fire area before the fire but differed significantly between these groups of PACs after the fire (Figure 7). Observed pair occupancy within the fire perimeter for the 2014-2016 period declined by >50% from pre-fire levels.

Fecundity (Figure 8) did not differ between time periods for PACs within or outside the fire area. Fecundity also did not differ between those groups of PACs within any of the three time periods evaluated. Post-fire variability in fecundity did not differ between burned and unburned sites during the two post-fire time periods after we controlled for the effect of small sample size of active territories (Figure 8).

Discussion

Our results suggest a significant reduction in observed occupancy 13-15 years after the Rodeo-Chediski fire, with observed single-owl site occupancy rates approximately 42% lower inside than outside the perimeter of the Rodeo-Chediski fire (Figure 6), and observed pair occupancy rates approximately 60% lower inside the fire perimeter than outside that perimeter (Figure 7). The true decline in the number of pairs from 1990-1998 to 2014-2016 may be greater than we observed because USFS survey effort was generally lower during the pre-fire era than during our surveys. Therefore some pairs may not have been detected in some pre-fire years, whereas our systematic surveys detected a nesting pair of owls well outside of any existing PAC and detected single owls outside of established PACs on several occasions. Because we found 6 PACs each year with consistent use by at least one resident owl suggests that the scattered nocturnal locations in other areas likely represented wandering or foraging by owls from these 6 territories. This type of wandering among multiple PACs has been documented for GPS-tagged California spotted owls (Berigan et al. 2019, Blakey et al. 2019).

Pair occupancy rates also may have declined with time since fire. Although large confidence intervals limit strength of inference here, observed pair occupancy declined from the pre-fire period to the 2002-2013 period, then declined further by 2014-2016 (Figure 7), perhaps reflecting the gradual loss of site-faithful pre-fire owls. By the later period, observed pair occupancy was >50% lower than during the pre-fire period. This suggests that the short-term studies of occupancy that dominate the literature on fire effects on spotted owls may not be sufficient to detect longer-term effects.

We could not directly discern fire-driven differences in habitat quality from pre- and post-fire spatial data, but there appeared to be fewer territories of sufficient quality available for colonization from 2014-2016 than prior to the fire. This conclusion is supported by the lower average levels of canopy cover and tree basal area in PACs on our main study area compared to nearby PACs that were not affected by the Rodeo-Chediski fire (Figure 5). These habitat elements are important components of Mexican spotted owl nesting and roosting habitat in northern Arizona (Ganey and Balda 1994, Grubb et al. 1997, May and Gutierrez 2002, Ganey et al. 2003, Timm et al. 2016).

Fecundity (measured in terms of fledglings per occupied territory) did not differ significantly between sites inside and outside the fire perimeter (Figure 8), or between time periods within either group of territories. Jenness et al. (2004) and Clark (2007) also found no significant differences in reproduction by Mexican or northern spotted owls, respectively, in burned and unburned sites or over time. Our data do not support any inferences about survival rates, an important component of spotted owl fitness (Lande 1988, Noon and Biles 1990) that may have been affected by fire. Franklin et al. (2000) showed that rates of fecundity and adult survivorship in northern spotted owls may not be strongly linked. Fecundity and survivorship may also not be strongly linked in Mexican spotted owls.

Conclusions

This study supports a growing literature showing that while spotted owls are fire-tolerant in many respects (Bond et al. 2002, Roberts et al. 2011, Lee et al. 2012, Bond

2016) and may seek out areas burned at high-severity for foraging (Bond et al. 2009, Ganey et al. 2014*a*, Bond et al. 2016, Eyes et al. 2017), mega-fires do pose a significant threat to affected populations (Clark et al. 2011, Jones et al. 2016, Rockweit et al. 2017). We have provided evidence of a mega-fire driving a significant decline in a local population of Mexican spotted owls, primarily through direct loss of observed occupied territories. Observed site occupancy has not rebounded to pre-fire levels after 15 years, suggesting that mega-fires may have significant long-term effects on spotted owl populations. Although the results reported here do not show the mechanism by which the fire reduced observed site occupancy, a companion study (Lommler et al. 2018, *in prep.* [Ch 4]) suggests that effects may occur through reductions in preferred habitat traits.

Occupied territories in the post fire landscape supported levels of reproduction similar to those observed at PACs within the fire, before the fire, and at sites outside the perimeter of the fire. Our results also do not show how mega-fires affect adult and juvenile survival rates, and the literature is ambiguous on this issue. Clark et al. (2011) and Rockweit et al. (2017) documented a negative relationship between severe fires and adult survivorship in northern spotted owls (3-5 years and 0-25 years post-fire, respectively). However, Bond et al. (2002, 1 year post-fire) did not observe a relationship between fire and adult survivorship of all three subspecies. We agree with Ganey et al. (2017) that empirical data about rates of survivorship are necessary to understand the effects of high-severity fire on persistence of spotted owls. Researchers should prioritize demographic studies that mark individual birds over their entire life history, collecting data about adult and juvenile survival rates in addition to fecundity.

Demographic study areas (or networks of smaller study areas) should include sites that are burned and unburned across a broad range of fire severities and patch sizes, and ideally include fires of different ages ranging to 20 years or more.

By linking demographic performance to fire characteristics, researchers can give managers the tools to design and prioritize fuels treatments that will minimize the risks that mega-fires present to Mexican spotted owls. Given time and appropriate forest management our study area may eventually recover to pre-fire population sizes. We are also concerned, however, that observed rates of fecundity both inside and outside the fire perimeter may be lower than necessary to sustain the population. Mexican spotted owl could be affected not only by mega-fires but also past forest management practices, including a lack of large trees on the landscape caused by selective tree harvest during the 20th century (Jones et al. 2018) or from a lack of foraging habitat. Forests in Mexican spotted owl habitat should not only be managed for resiliency to fire, but for the restoration of critical habitat elements, including a balance of nesting, roosting, and foraging habitat by promoting forest heterogeneity.

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Tables

Table 1. Results from surveys of Mexican spotted owls conducted from 2014-2016 within the perimeter of the Rodeo-Chediski fire, Arizona.

	2014	**2015**	**2016**	**Mean**
Spotted owl detections	29	130	66	75
Number of points surveyed	2531	2584	2239	2451.3
PACs with detections	10	15	10	11.6
Number of PACs with resident owls	6	6	6	6
Number of pairs inferred	4	5	6	5
Number of nest attempts	1	5	3	3
Number of successful nests	1	3	1	1.67
Number of young fledged	1	5	1	2.33
Number of fledglings per nest attempt	0.25	1	0.33	0.78
Number of fledglings per successful nest	1	1.67	1	1.4
Number of fledglings per pair	0.25	1	0.17	0.47

Table 2. Comparison of survey effort between U.S. Forest Service (USFS) surveys both inside and outside the fire perimeter and this study's survey effort inside the fire perimeter. The average number and percentage of protected activity centers (PACs) monitored per year in each focal time period is shown. Prior to our study, PACs inside the fire perimeter were surveyed more intensely, but more total sites were surveyed outside the fire perimeter.

PACs surveyed	Pre-fire 1990-1998 # PACs (%)	Post-fire 2002-2013 # PACs (%)	Post-fire 2014-2016 # PACs (%)
Inside fire perimeter	15.0 (75.0%)	6.6 (33.0%)	20.0 (100%)
Outside fire perimeter	23.4 (37.8%)	11.2 (18.1%)	18.6 (30.1%)

Figures

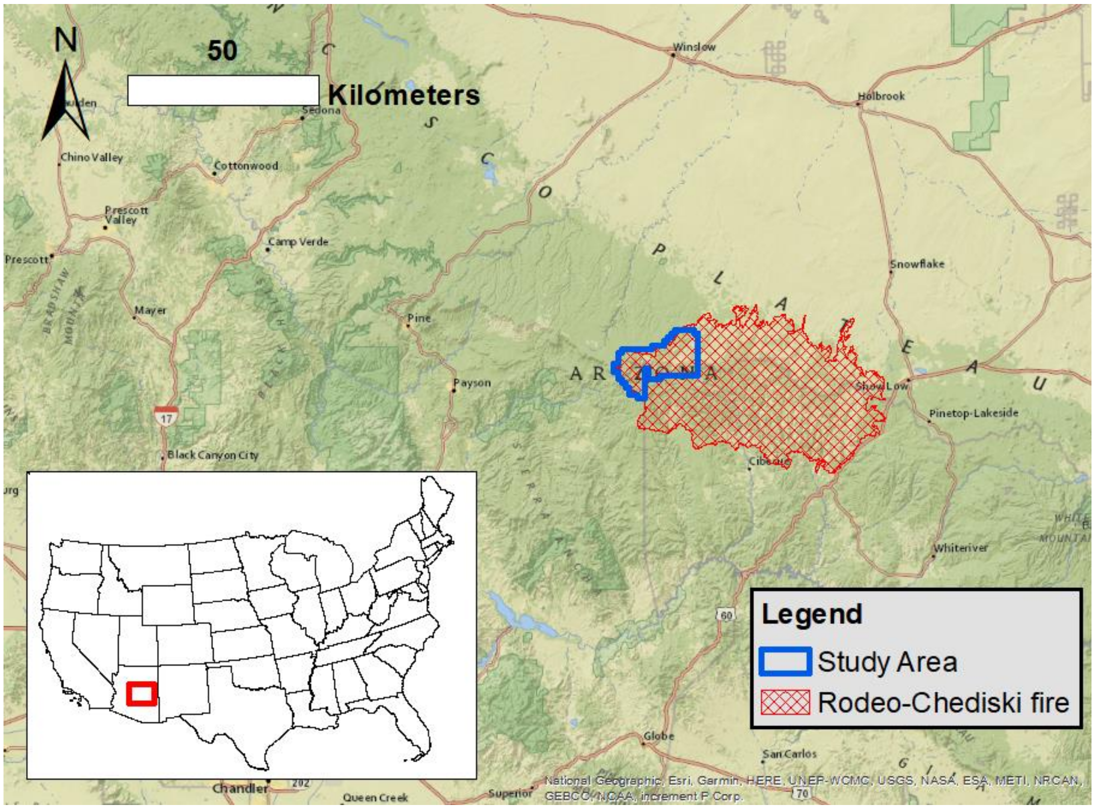

Figure 1. The Rodeo-Chediski fire of 2002 burned approximately 190,000 ha in east-central Arizona at the southern edge of the Colorado Plateau. Our study area was located at the northwestern corner of the fire area.

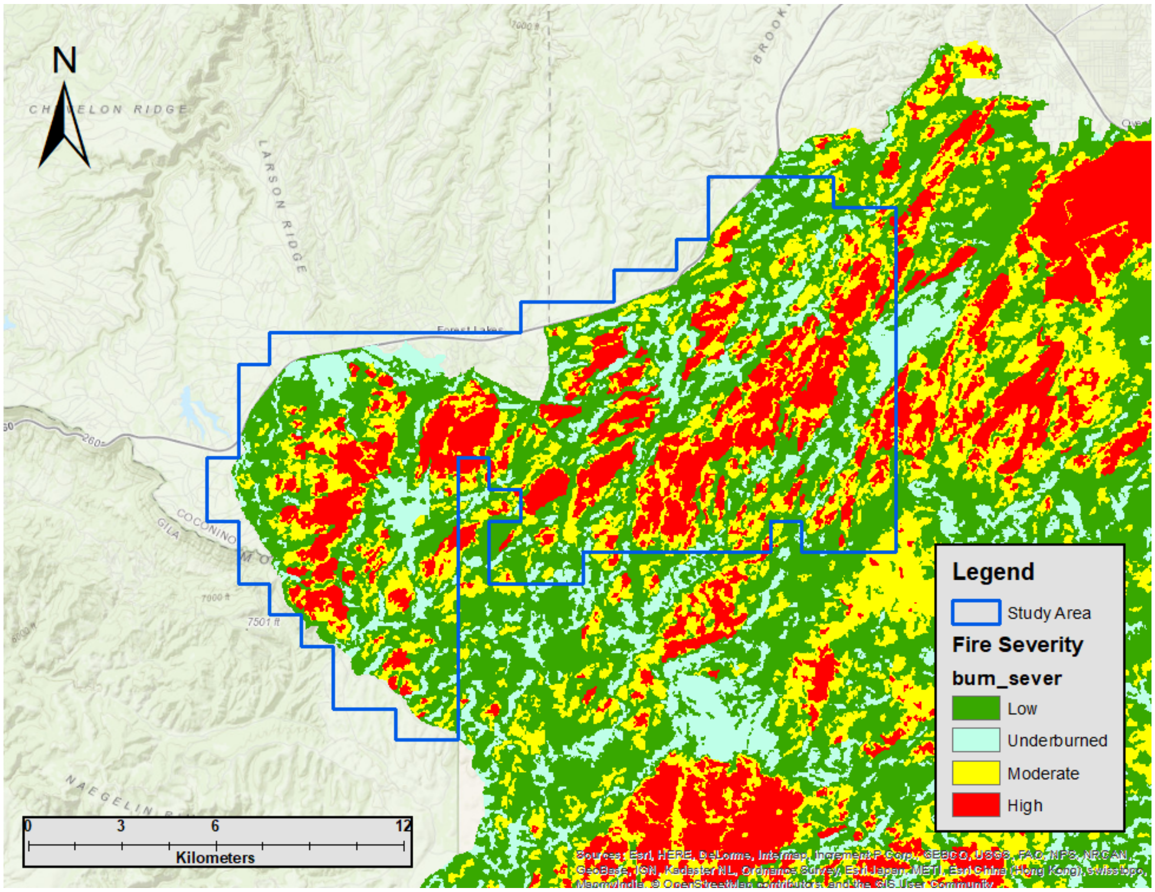

Figure 2. Map showing fire severity within the 2002 Rodeo-Chediski fire in and adjacent to our 18800 ha main study area in east-central Arizona (MTBS Data Access 2014*a*).

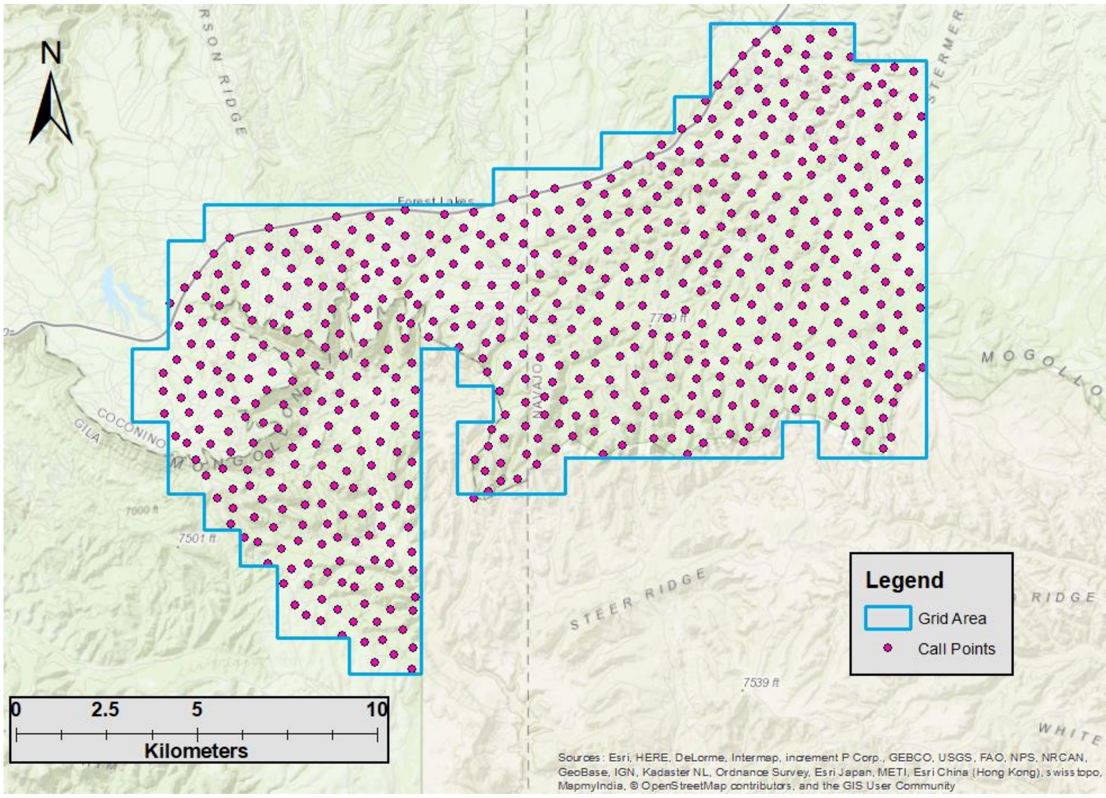

Figure 3. Distribution of call points used in nocturnal calling surveys for Mexican spotted owls conducted from 2014-2016 in our study area within the perimeter of the Rodeo-Chediski fire, Arizona.

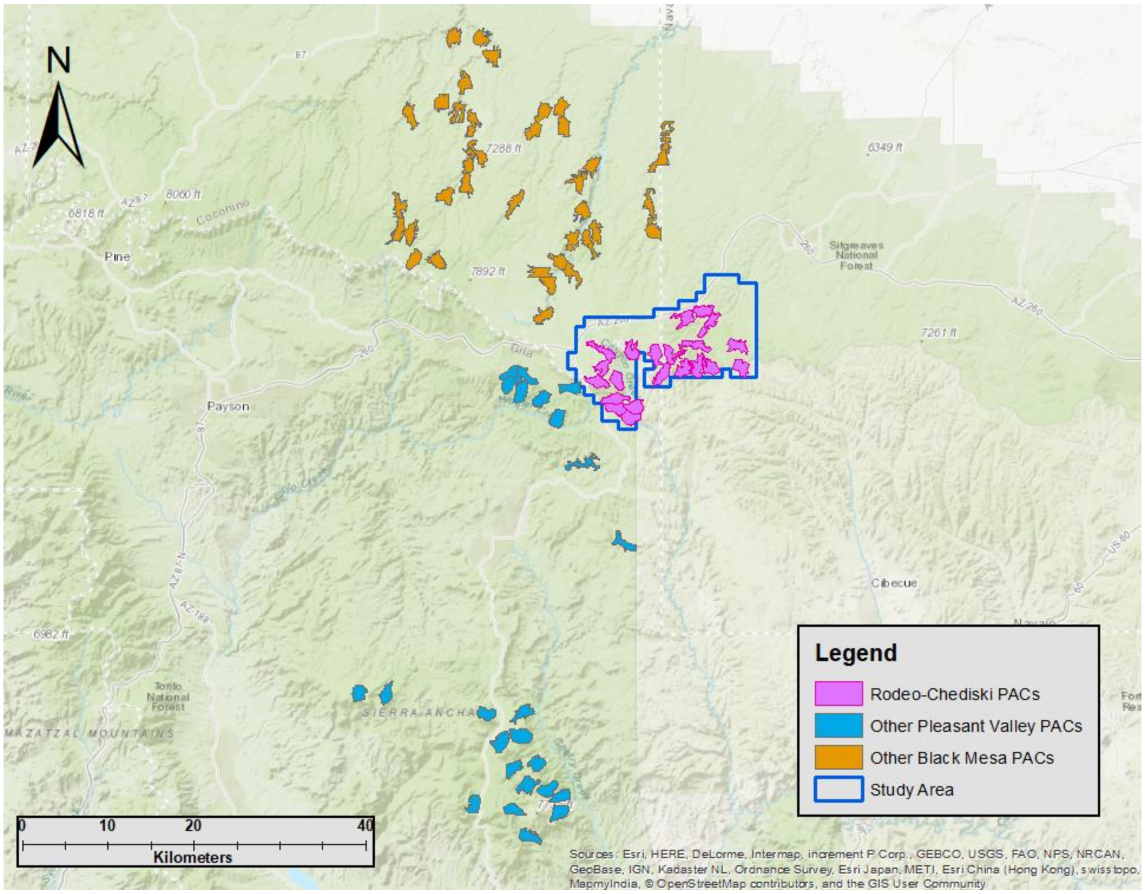

Figure 4. Location of Mexican spotted owl Protected Activity Centers (PACs) within the Black Mesa and Pleasant Valley Ranger Districts, USFS, Arizona. Also shown is the boundary of the main study area within the perimeter of the Rodeo-Chediski fire. PACs within that study area were surveyed as part of this study, while USFS crews surveyed the PACs outside the main study area.

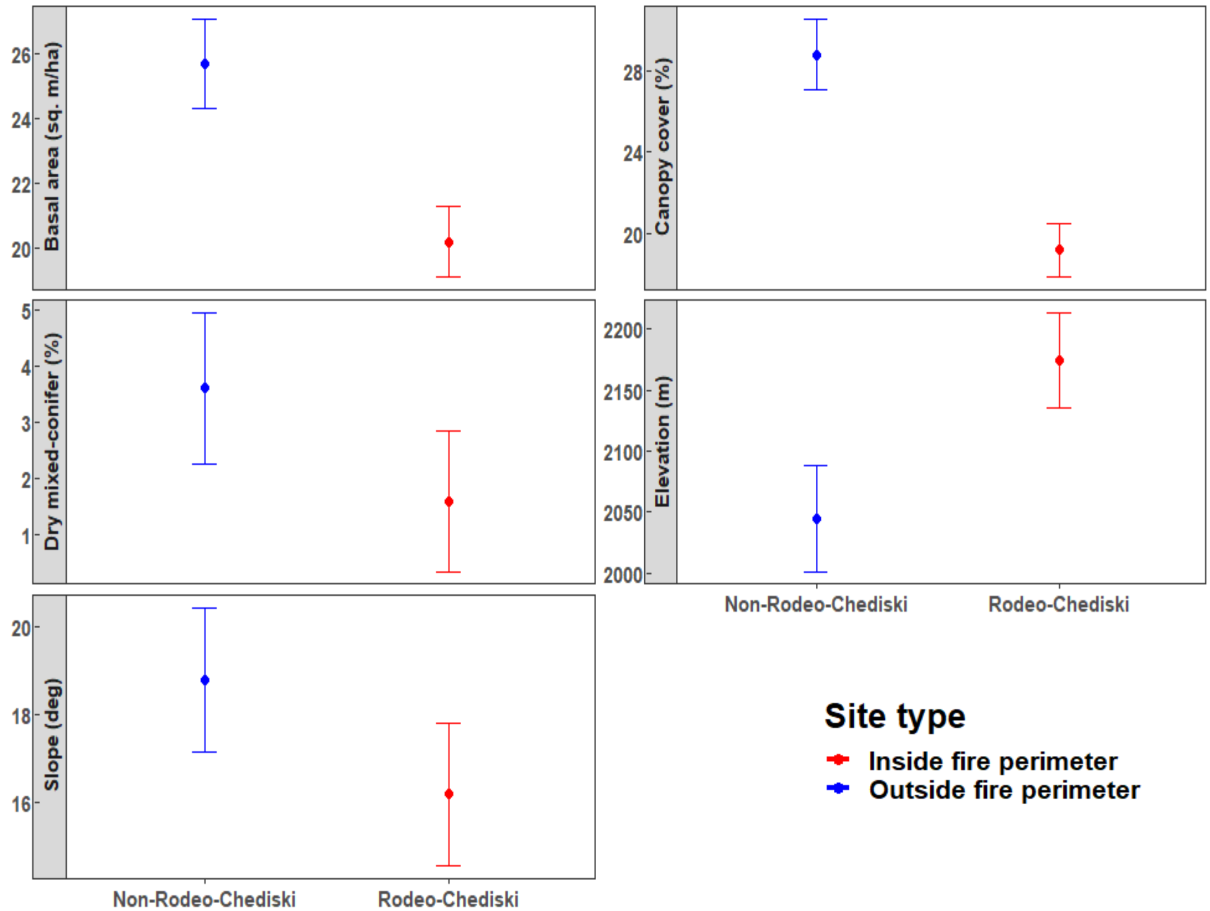

Figure 5. Selected ecological characteristics of Mexican spotted owl Protected Activity Centers inside the perimeter of the Rodeo-Chediski fire (20 pre-fire PACs) and 61 nearby PACs outside the perimeter of the fire (blue). Shown are means and 95% confidence intervals. PACs within the fire perimeter were slightly higher in average elevation, but the two sets of PACs were of similar steepness and had similar cover of dry mixed-conifer forest. PACs outside the perimeter of the fire had larger average basal area and canopy cover.

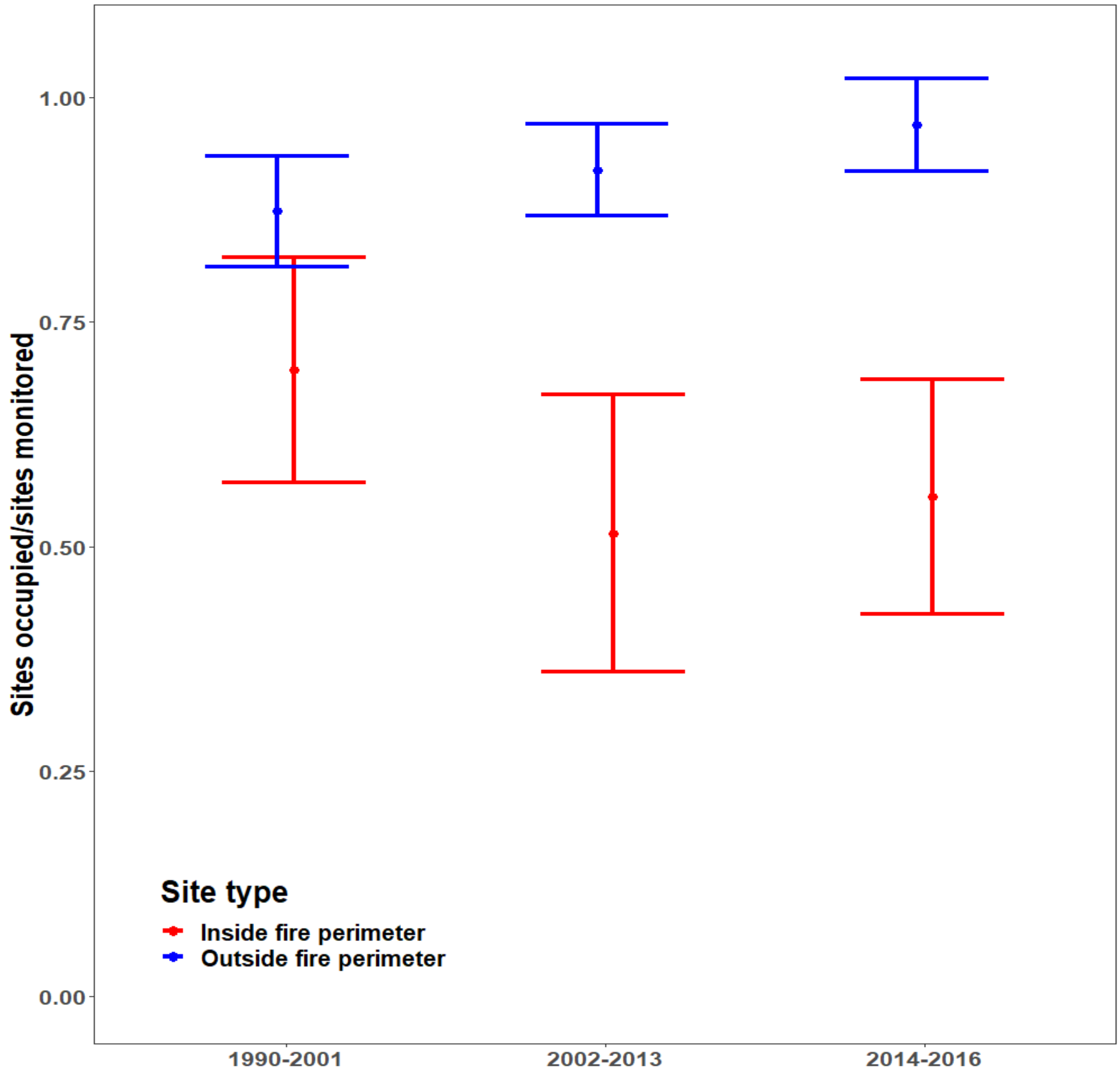

Figure 6. Mean annual observed site occupancy by single owls before the Rodeo-Chediski fire (1990-2001), after the fire (2002-2013) and over the time period of our surveys (2014-2016), for PACs within (red) and outside (blue) the fire perimeter. Shown are means and 95% confidence intervals. Occupancy was not significantly different prior to the fire. After the fire there was a significant difference in occupancy between PACs outside and inside the perimeter of the fire.

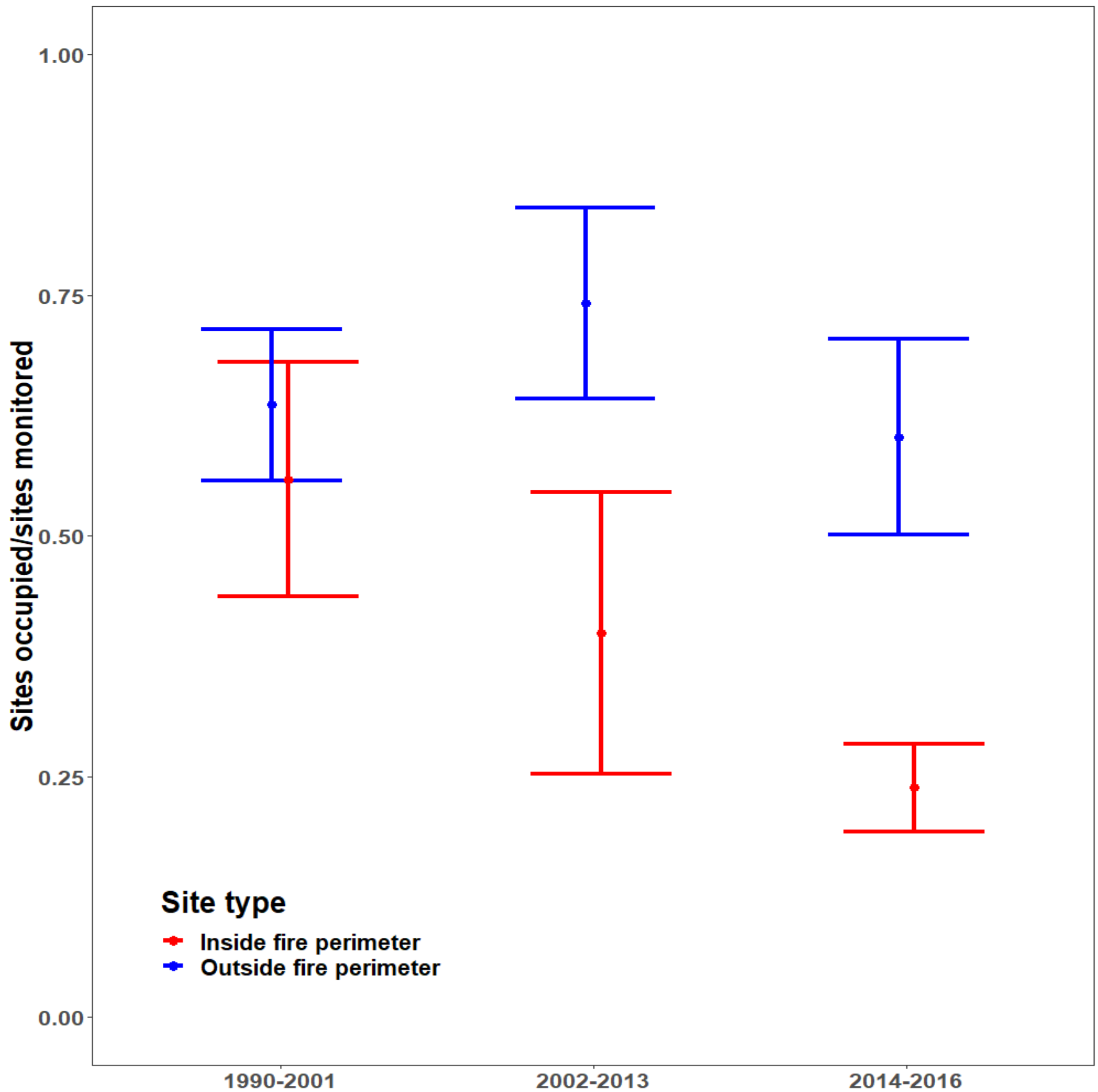

Figure 7. Mean observed annual site occupancy by owl pairs before the Rodeo-Chediski fire (1990-2001), after the fire (2002-2013) and over the time period of our surveys (2014-2016), for PACs within (red) and outside (blue) the fire perimeter. Shown are means and 95% confidence intervals. Occupancy was not significantly different prior to the fire. After the fire there was a significant difference in observed occupancy between PACs outside and inside the perimeter of the fire. Within the fire perimeter pair occupancy was significantly lower from 2014-2016 than it was from 1990-2001.

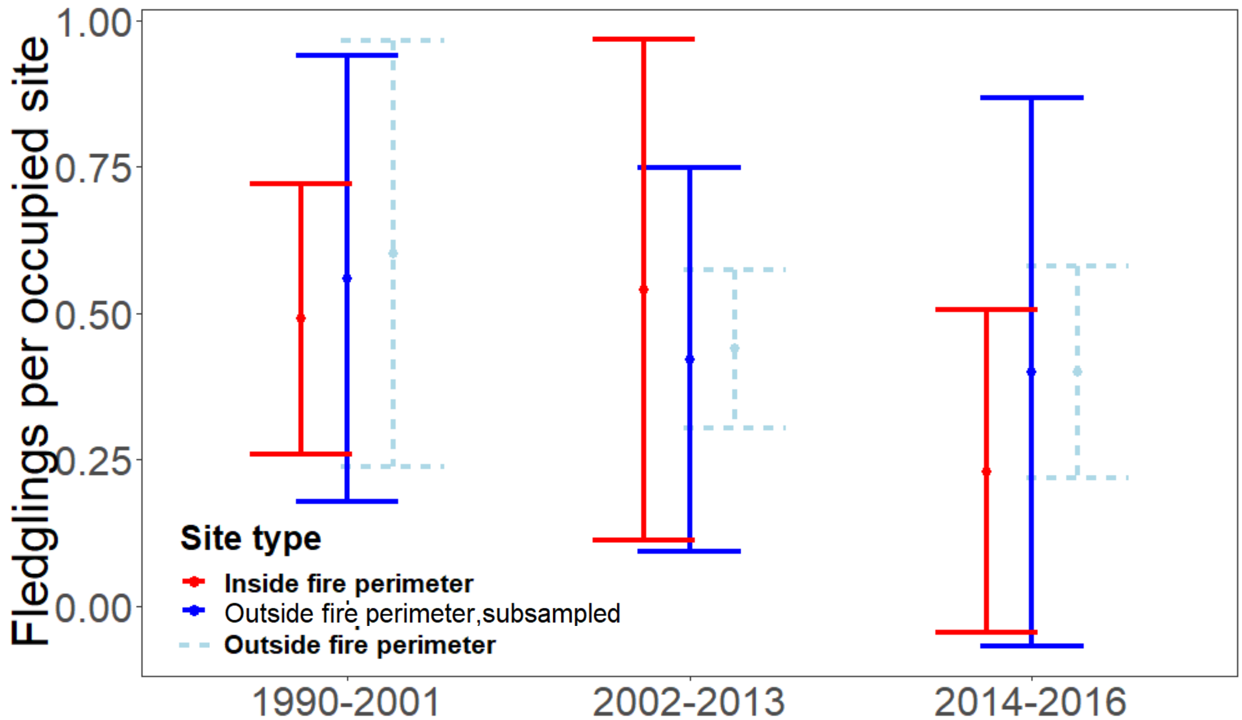

Figure 8. Fecundity per PAC (means and 95% confidence intervals) before the Rodeo-Chediski fire (1990-2001), after the fire (2002-2013) and during the time period of our surveys (2014-2016). Red and dashed light blue bars denote sites inside and outside the fire perimeter, respectively. Solid blue bar shows results for 1,000 subsamples of sites outside the fire perimeter, with each subsample containing a number of sites equal to the mean number of sites occupied within the fire perimeter during the indicated time period. Controlling for number of occupied sites made comparisons more comparable for sites within the fire perimeter relative to sites outside the perimeter.

Chapter 3

Site occupancy by Mexican spotted owls 13-15 years after a large, severe wildfire in Arizona

Michael A. Lommler

Abstract

The influence of wildfire on populations of Mexican spotted owls (*Strix occidentalis lucida*) is controversial. Low- and moderate-severity fires appear to have little effect upon population dynamics of spotted owls. The effect of large, severe fires on spotted owl populations is complex and varies with time since fire and at different spatial scales. In other work, we demonstrated that the 2002 Rodeo-Chediski fire (187000-ha, 37% burned at high severity) in central Arizona had half as many occupied owl territories by 2013-2016 compared to the decade before the fire. Here we investigate whether spotted owl site occupancy was still declining during 2014-2016 (13-15 years post-fire), as would occur if the population was still decreasing toward its long-term post-fire equilibrium (unpaid extinction debt). We used two sampling frames to model site occupancy during 2014-2016 as a function of 17 landscape variables including four fire-related covariates. In the grid-based sampling frame we modeled occupancy across 198 contiguous grid cells and in the territory-based sampling frame we modeled occupancy of 22 known owl activity areas. We observed no clear occupancy trend across 2014-2016 in either the grid- or territory-based model, a finding that does not support existence of a lingering extinction debt. Spotted owl occupancy of 100-ha cells was positively associated with extent of dry mixed conifer and negatively associated with salvage logging; no forest covariates had a strong influence on territory occupancy. The effects of fire may influence site occupancy even 13-15 years post-fire, but are difficult to quantify because habitat features preferred by owls are highly susceptible to fire.

Introduction

Over the last 150 years, Mexican spotted owls (*Strix occidentalis lucida*) in many dry forests of the western U.S. have experienced profound changes in forest structure and fire dynamics that might have long-term impact on owl populations. Prior to European settlement dry forests had lower tree density, more large trees, fewer small trees, and lower basal area than modern dry forests of ponderosa pine (*Pinus ponderosa*) and mixed-conifers (Covington and Moore 1994, Fulé et al. 1997, Hagmann et al. 2013, Hagmann et al. 2014, Merschel et al. 2014, Stephens et al. 2015). The pre-settlement forests experienced frequent surface fire, sometimes over large (>1000-ha) areas but extensive stand-replacing fires were relatively rare (Collins et al. 2015, Huffman et al. 2015, but see Williams and Baker 2012). Modern western dry forests often carry crown fire over large areas (Keane et al. 2008), leading to mega-fires. Mega-fires are fires ≥10000-ha (Stephens et al. 2014) characterized by extreme fire behavior (Williams et al. 2011) that can change vegetation composition and structure (Savage and Mast 2005, Kane et al. 2013, Neeley 2012, Collins and Roller 2013); these changes may persist for decades after a fire (Strom and Fulé 2007). The frequency and severity of large fires in dry forests of the western U.S. has increased significantly over the last three decades (Westerling et al. 2006, Miller et al. 2009, Miller and Safford 2012, Dennison et al. 2014, Westerling 2016, Singleton et al. 2019). The response of Mexican spotted owls to such mega-fires is controversial (Ganey et al. 2017, Hanson et al. 2018, Lee 2018, Jones et al. 2019).

One difficulty with quantifying the response of owls (or other animals with large, well-spaced home ranges) to changes in forest structure is the coarse spatial and thematic resolution of forest structure data. Landscape-scale models of species occurrence have typically relied upon remotely-sensed estimates of forest structure as predictor variables because it is impractical to collect field measurements over large spatial extents. Aerial photography and optical satellites don't directly measure vertical habitat structure (Vierling et al. 2008, Seavy et al. 2009), and grain sizes are typically too coarse (≥30-m) to identify some important fine-scale habitat elements (Garcia-Feced et al. 2011), such as individual large trees or snags (Zielinski and Gellman 1999, Chambers and Mast 2005, North et al. 2017). Airborne light detection and ranging (LiDAR) overcomes these limitations (Vierling et al. 2008, Seavy et al. 2009, Garcia-Feced et al. 2011). Airborne LiDAR instruments emit laser pulses that strike the underlying land, plant, and constructed surface, which reflects a portion of the laser energy back to a sensor on the aircraft. The return times indicate the distances to surface objects, and the resulting three-dimensional "point cloud" yields both a digital elevation model (DEM) and canopy height model. Stand-level attributes (including vertical structure) and individual trees can then be estimated and identified (Lefsky et al. 2002, Garcia-Feced et al. 2011). Thus LiDAR is competitive with traditional stand exams (Hummel et al. 2011) while covering a much larger spatial extent.

We used LiDAR-derived estimates of forest structure and topography, as well as remotely-sensed estimates of forest composition and fire severity, to model site occupancy of Mexican spotted owls (*Strix occidentalis lucida*), a threatened species native to old forests of the southwestern United States and Mexico, 13-15 years after the 2002 Rodeo-Chediski megafire in central Arizona. As mentioned above, fire's impact upon the spotted owl is highly-contested in the literature (Ganey et al. 2017, Hanson et al. 2018, Lee 2018, Jones et al. 2019). Several studies have found spotted owls of all three species preferentially foraging in high-severity patches (Bond et al. 2009, Ganey et al. 2014, Bond et al. 2016), but others have found that high-severity fire negatively affects survival (Clark et al. 2011, Rockweit et al. 2017), site occupancy (Clark et al. 2013, Jones et al. 2016), and number of occupied territories (Lommler et al., in prep. [Ch 2]). Several studies have indicated that fire has little or unclear effects upon spotted owl survival or occupancy (Bond et al. 2002, Jenness et al. 2004, Roberts et al. 2011, Lee et al. 2012, Lee and Bond 2015*a*) or that the effect of fire depends upon prior occupancy state (Lee and Bond 2015*b*) or how much of a site was burned or salvage logged (Lee et al. 2013). Only one of these studies focused exclusively on Mexican spotted owls (Jenness et al. 2004), and only two studies considered fires more than ten years old (Roberts et al. 2011, Rockweit et al. 2017).

Long-term monitoring of spotted owl populations after fire is important because spotted owls have strong site fidelity (Forsman et al. 2002, Zimmerman et al. 2007), even after disturbance events (Bond et al. 2002), and because prey populations may increase for 2-4 years after a fire before reaching longer-term equilibria. “Extinction debt” (Tilman et al. 1994, Kuusaari et al. 2009) is the difference between the species richness or population size immediately after a negative event (habitat loss, habitat fragmentation, loss of genetic diversity) and the lower long-term equilibrium species richness or population size. Loss of large trees from historic logging may still be driving population declines of California spotted owls (*Strix occidentalis occidentalis*) despite logging restrictions imposed in 1992 (Jones et al. 2018).

The 2002 Rodeo-Chediski fire provided an opportunity to study the long-term effect of a large, severe fire on Mexican spotted owls, including any long-term extinction debt and short-term extinction and colonization rates. Lasting from June 18 to July 7, 2002, the fire affected approximately 190000-ha of forest land in east-central Arizona, 36.6% burned at high severity. The fire affected 20 protected spotted owl territories on lands managed by the U.S. Forest Service. In previous work (Lommler et al., in prep [Ch. 2]), we documented half as many occupied owl territories in 2013-2016 compared to the decade before the fire.

If there is a lingering extinction debt from the Rodeo-Chediski fire 13-15 years after the fire, this could manifest as continued declines in site occupancy during those years. Legacy effects of fire would also manifest as statistically significant associations of fire covariates with occupancy, local extinction rates (also known as site abandonment rates), and local colonization rates of sites in the post-fire landscape. For example, if local extinction rates a decade after fire are negatively associated with percent of site burned, this could indicate that burned areas are the first to be abandoned during years of lower population or reproduction. Interpretation of such rates is not always straightforward. For example, a positive association between occupancy and fire severity might reflect the tendency of good owl habitat (large trees on steep slopes) to experience severe fire rather than owl attraction to severely burned areas. Nonetheless, a careful consideration of occupancy trends, extinction and colonization rates, and the influence of fire-related covariates on those rates a decade after the fire might shed light on the legacy effects of large fires.

Occupancy modeling is a common technique for using presence/absence datasets to estimate the probability that a species may utilize a given site. It can be used to identify landscape variables affecting site occupancy of populations of rare species, including spotted owls (Roberts et al. 2011, Lee et al. 2012, Lee et al. 2013, Clark et al. 2013, Lee and Bond 2015a, Lee and Bond 2015b, Jones et al. 2016) because it statistically corrects for imperfect detection during surveys (MacKenzie et al. 2002). Occupancy modeling can be used to detect changes to habitat (i.e., disturbance events) or for monitoring trends in site occupancy (MacKenzie et al. 2005). Site occupancy can be estimated during a single season or over multiple seasons. Occupancy models assume that 1) all detections recorded are true (i.e., no false-positives), and 2) all sites and detections are independent from one another. Single-season occupancy models assume the occupancy state does not change between surveys (i.e., the population is closed); Multi-season models assume the population is closed within-season but not between seasons (MacKenzie et al. 2003).

We built occupancy models using two sampling frames commonly used for Mexican spotted owls. The larger sampling frame is a 200-250-ha area around historic nest and roost sites (Lee et al. 2012, Lee et al. 2013, Lee and Bond 2015*b*) which roughly approximates the Protected Activity Centers (PACs) established by management agencies (U.S. Fish and Wildlife Service 2012). Occupancy surveys based upon this design typically do not survey outside of historic sites. The smaller sampling frame is a random sample of square cells, typically 100-375 ha, within potential spotted owl habitat (Roberts et al. 2011, Lanier and Blakesley 2017). These surveys are not limited to historic sites. In territorial species like spotted owls these models provide reliable inference about species abundance (Tempel and Gutierrez 2012).

We used both territory-based and grid-based occupancy models to quantify site occupancy more than ten years after the Rodeo-Chediski fire. We had three goals. First, we wanted to determine whether the three-year occupancy trend was increasing, decreasing, or stable by comparing local extinction and local colonization probabilities. A decreasing occupancy trend more than ten years post-fire might indicate that disturbance from fire might create an extinction debt. Second, we wanted to see how spotted owl site occupancy was related to fire severity and salvage logging. Finally, we wanted to determine which remnant habitat elements were most strongly-related to spotted owl site occupancy.

Methods

Study area

Our study took place on an 18800-ha subset of the Rodeo-Chediski fire located approximately 8-km southwest of Heber-Overgaard, AZ and bounded on the north by Arizona State Highway 260, on the west by Forest Service Road 512, and on the south by the Fort Apache Indian Reservation (FAIR) (Figure 1). Approximately 14700-ha lie on the Black Mesa Ranger District of the Apache-Sitgreaves National Forest, with the remaining 4100-ha lying on the Pleasant Valley Ranger District of the Tonto National Forest. This area lies entirely within the perimeter of the fire. Elevation gradually rises from north to south, reaching 2350-m at the Mogollon Rim. This steep escarpment is the dominant topographic feature, corresponding with the southern terminus of the Colorado Plateau. South from the Mogollon Rim the land drops away to an elevation of 1890-m in the upper branches of Canyon Creek, which is the only permanent running water on the study area. A series of deep canyons are cut into the southern face of the

Mogollon Rim, generally aligned north to south. This area lies within the Upper Gila Mountains Ecological Management Unit, one of six Ecological Management Units (EMUs) established by the U.S. Fish and Wildlife Service in the United States (U.S. Fish and Wildlife Service 2012). This study area included all 20 PACs affected by the fire on U.S. Forest Service lands.

The vegetation is characterized by large contiguous stands of ponderosa pine (*Pinus ponderosa*) forest with pockets of mixed-conifer and pine-oak forest, located primarily in canyons and on steep north-facing slopes. The mixed-conifer forests are characterized by ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), and/or white fir (*Abies concolor*). The pine-oak forests are characterized by ponderosa pine and Gambel oak (*Quercus gambelii*). Alligator juniper (*Juniperus deppeana*) and Southwestern white pine (*Pinus strobiformis*) are occasional components of these systems on the study area. Twelve years after the Rodeo-Chediski fire, approximately 20% of the study area was nearly treeless (Figure 2). Many burned areas regenerated into shrubby thickets of young Gambel oak, New Mexico locust (*Robinia neomexicana*), and/or Fendler's buckbrush (*Ceanothus fendleri*).

Approximately 23% of the study area burned at high severity (MTBS 2014*b*) (Figure 3). An additional 21% of the study area burned at moderate severity. In addition, 1632 ha, about 8.6% of the study area, were subject to salvage logging, including a total of 65 ha in five PACs. Another 613-ha were re-burned at low severity in May of 2012 by the Bull Flat fire (MTBS 2014*a*), which we ignored in our measures of fire severity for this analysis.

Spotted owl survey design

We divided the study area into 198 contiguous 1-km^2 (100-ha) grid cells (Figure 4). Twenty-four cells included some land outside the fire perimeter. In most cells we established 3 call points for nocturnal acoustic surveys that followed U.S. Fish and Wildlife Service protocols (Forsman 1983, U.S. Fish and Wildlife Service 2012), with 1-2 points in some peripheral cells containing <70-ha of Forest Service land. Call points were never more than 600-m from the nearest adjacent call point, ensuring that if an owl were located between points they could hear us and we could hear them if they called. Over three years (2014-2016) each grid was surveyed four times during the breeding season (April – August) but never more than once during a single 9-day survey period. Owls were recorded as detected or not detected at each visit to create a detection history for the cell.

We defined sample sites for territory-based models by drawing 800-m radius circles (201-ha) around the "best" owl location from each of the 20 pre-fire PACs on the study area. These owl locations were prioritized in order of best to worst, starting with: (1) nest site, (2) roost site, (3) visual location, and (4) audio location based upon past surveys by the U.S. Forest Service or our own surveys. When a PAC had multiple possible "best" owl locations we retained the most recent location. One new PAC, distinct from any pre-fire PAC, was established in 2014 using our survey data. In one instance we found a single spotted owl roosting in an area between two PACs but not within either. We included this location as the center for a unique territory. Ultimately, we had a sample size of n = 22 owl territories (Figure 5). Our call points were assigned to each territory *post hoc,* based upon whether they lay within the 201-ha circular area. The number of call points in each territory varied from 3-7 (Figure 6), which we accounted for in the model. We used these subsets of points to create a detection history for each territory.

Habitat covariates

We used 17 covariates to represent the influence of forest composition, forest structure, fire, and topography upon presence of Mexican spotted owls on our study area (Table 1). The LiDAR-derived covariates of forest structure measured basal area of large trees (from trees ≥ 30, 46, or 60-cm), canopy cover (from 2 to 16-m, and above 16-m), and the number of large trees above several thresholds of diameter (≥ 30, 46, or 60-cm) and height (20-m). Of the fire-related metrics, Relative delta Normalized Burn Ratio (RdNBR, Miller and Thode 2007) provides consistent measurements of severity across fires and greater accuracy in measuring the high severity fire class. An RdNBR value >572 is roughly equivalent to standard measures of high fire severity (75-100% canopy mortality, Miller et al. 2009). The high severity fire covariate measured the proportion (0.0-1.00) of the area burned at high severity around each point, which is the most common method of representing fire effects in studies of spotted owls. Because Jones et al. (2016) suggested that owls could respond differently to high-severity fire depending on patch sizes, we also included largest patch index (LPI), which measured the proportion (0.0-1.00) of the area burned at high severity around each location that was aggregated within the largest single patch. A fourth fire-related covariate, the proportion salvage logged (0.0-1.00), was acquired from GIS databases for the Apache-Sitgreaves National Forests (Apache-Sitgreaves National Forests GIS data 2018) and Tonto National Forest (Tonto National Forest GIS data 2018). We derived slope (in degrees) from our LiDAR-based DEM using the DEM Surface Tools (Jenness 2013) toolset in ArcMap 10.6 (ESRI 2017), using Horn's method (Horn 1981). All the LiDAR-based rasters used a 10-m pixel size. We re-sampled all LANDSAT-based rasters, which are based on a 30-m pixel, to a 10-m pixel in order to match the LiDAR data. We calculated the average value of each covariate within each grid cell and within each core area. Largest patch index was calculated using the Patch Analyst extension in ArcGIS (Elkie et al. 1999). Other covariates were calculated using the Focal Statistics and Extraction tools in ArcMap. Prior to modeling all covariate values were standardized.

On average, high severity fire occurred in 22.4% (range: 0.0-89.8%) of the 100-ha grid cell area and 28.4% (range: 1.0-75.7%) of each 201-ha core area. On average, 13.4% of each grid cell (range: 0.0-99.9%) and 2.9% of each core area (range: 0.0-27.8%) was salvage logged. Mean canopy cover from 2 to 16-m height was 25.2% (range: 5.0-58.9%) in grid cells and 26.6%% (range: 16.7-33.5%) in core areas. Mean slope was 11.0 degrees (range: 1.9-24.7 degrees) in grid cells and 15.5 degrees (range: 8.3-20.5 degrees) in core areas.

Occupancy modeling

We created multi-year models (MacKenzie et al. 2003) of both grid (100-ha) and territory-based (201-ha) occupancy using Bayesian hierarchical formulation (Royle and Dorazio 2008). Mexican spotted owl calling behavior (and thus detectability) generally peaks in May and varies with weather and moon phase (Ganey 1990). Our attempts to use date, weather, and moon phase as detection covariates were not informative, likely because we had only 225 detections during 7354 survey occasions, which can make it difficult to fit models with covariates for both occupancy and detection (Bailey et al.

2004). For the same reason, we modeled occupancy by the species, rather than building multi-state models for single owls, pairs, and nesting pairs (MacKenzie et al. 2009).

Before modeling we calculated pairwise Pearson's correlations among all the covariates at their optimized spatial scales to assess multicollinearity. Where two or more covariates were highly correlated (i.e., $|r| \geq 0.7$) we retained those that explained the most deviance in univariate models. For the grid (100-ha) model this left 8 site covariates (Table 2). For the territory (201-ha) models this left 12 site covariates (Table 3).

Because our grid cells were adjacent to one another, the probability of an owl occupying a given cell *i* was correlated with the occupancy probability in an adjacent cell. Thus, we could not assume that sites were independent. In our model the occupancy probability Ψ in cell *i* depended partially upon the number of adjacent cells which were occupied by spotted owls. For our grid-based model (Appendix I) we assumed that occupancy of Mexican spotted owls at each cell *i* had a spatial autocovariate x_i, which was the number of occupied neighboring sites to site *i*, defined as:

(Equation 1.)

$$x_i = \frac{1}{n_i}\left(\sum_{j \in N_i} z_j\right)$$

where n_i is the cardinality (total number of directions with a neighboring cell) of N_i. We will start with a first-order auto-logistic covariate (e.g., only consider neighboring cells *j* that are north, south, east, or west of grid cell *i*. The auto-logistic model is specified by the conditional distribution $[z_i|\mathbf{z}_{-i}]$, where $\mathbf{z}_{-i}$ is a vector of all latent state variables of occupancy except *i*. Therefore, this conditional distribution is defined with probability of occupancy ψ at grid cell *i* as:

(Equation 2.)

$$[z_i \mid \mathbf{z}_{-i}] \equiv Bernoulli(\psi_i)$$

where

(Equation 3.)

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 x_i + \boldsymbol{\beta}\mathbf{X}$$

Parameter β_0 is the intercept, β_1 is the slope parameter of the spatial auto-covariate, and the vector $\boldsymbol{\beta}$ includes all slope parameters for additional landscape or habitat covariates and vector $\mathbf{X}$ are the covariate values at this grid cell.

For the territory-based model (Appendix II), we assumed that the occupancy probability at each site was independent from the occupancy state of the other sites. That resulted in the true process model

(Equation 4.)

$$z_i \sim Bernoulli(\Psi_i)$$

with

(Equation 5.)

$$\text{logit}\,(\Psi_i) = \alpha + \boldsymbol{\beta}\mathbf{X}$$

We used the same definitions as above in equation numbers 1-2.

We specified vague priors for each β coefficient

(Equation 6.)

$$\beta \sim Normal(0,10)$$

where β is normally distributed with a mean of 0 and precision ($\tau = 1/\sigma^2$) of 10. With large values of σ, normally distributed vague priors can become informative when subjected to the logit transformation (Northrup and Gerber 2018). We chose a value small enough to reduce this potential bias.

For our observation model (for both grid- and territorial modeling approaches), we used a two-dimension data matrix y, where element y_{it} was a binary indicator for spotted owl detection (0 = not detected, 1 = detected) in grid cell i (i = 1, …, 198) during primary sampling year t (t = 1, …, 3). When the binary indicator of detection y_{it} = 1, a spotted owl was detected at site i during year t. For both modeling frameworks this generates the observational model

(Equation 7.)

$$y_{it} \sim Bern(p_{it} * z_{it})$$

with

(Equation 8.)

$$\text{logit}(p_{it}) = d + d1_{t} + d2_{it}$$

where p_{it} is the probability of detecting an owl at site *i* in year *t* (conditional on owl presence) and z_{it} is the latent (unobserved) true occupancy state of site *i* at time *t*, and y_{it} is the observed occupancy state at site *i* during year *t*. In the logit function *d* is the intercept, $d1_t$ is a random effect of survey year t, and $d2_{it}$ is the effect of the number of points at each site *i* on detection probability. We specified vague priors (see Equation 6) for *d* and *d2*.

We calculated local extinction (*ε,* equation 9, the probability an occupied site became unoccupied in a subsequent year) and local colonization (*γ,* equation 10, the probability an unoccupied site became occupied in a subsequent year) rates for each site *i* as derived parameters of *z*.

Equation 9.

$$\varepsilon_{i(t+1)} = z_{it} * \left(1 - z_{i(t+1)}\right)$$

Equation 10.

$$\gamma_{i(t+1)} = z_{i(t+1)} * (1 - z_{it})$$

Typically, occupancy parameters apply to a theoretically infinite population of sites from which the sample is drawn (Royle and Kéry 2007), but we were also interested in occupancy in our sample of sites. Therefore we estimated average occupancy for a finite sample, Ψ_{fs}, by summing the latent occupancy state at each site (z_{it}) and dividing by the number of sites (n) (Royle and Kéry 2007). The grid (Appendix I) and territory-based (Appendix II) models were coded in R and run in OpenBUGS using the package R2OpenBUGS (Sturtz et al. 2005) using a Markov chain Monte Carlo (MCMC) with 3 chains, and 30000 model iterations on each chain, with the first 15000 discarded. We thinned every other model iteration. We used the potential scale reduction factor, $\hat{R}$, to assess model convergence (i.e., model converges at $\hat{R} < 1.1$, Gelman and Rubin 1992).

This analysis generated estimates of 4 parameters: Ψ, the probability that a site was occupied in any given year of the study (occupancy probability); ε, the probability an occupied site became unoccupied in the subsequent year (extinction rate); γ, the probability an unoccupied site becomes occupied in the subsequent year (colonization rate); and ρ, the probability of detecting an owl (detection probability).

Model selection

We used indicator variable selection (Kuo and Mallick 1998, Hooten and Hobbs 2015) to select a subset of important covariates for our models. Indicator variable selection modifies the parameter vector β from the basic linear regression model such that

Equation 11.

$$\beta_j = C_j * \theta_j$$

for j = 1, …, v, where v is the total number of variables and each regression coefficient parameter is written as a product of a binary indicator variable C_j and the original regression coefficient parameter θ_j. In this procedure, the spatial autocorrelation term and year covariates are included in the model without associated indicator variables. Indicator variable selection is computationally intensive (O'Hara and Sillanpää 2009) but saves significant modeling effort where there are many possible model combinations. We specified vague priors for each indicator ($C_j \sim Bernoulli(0.5)$) and the regression coefficient ($\theta_j \sim N(0,10)$). Where C_j was close to 1, it indicated that the jth covariate was important in the model, i.e. the covariate was retained in most MCMC iterations. When C_j was close to 0, it indicates that the jth covariate was not important in the model, i.e. the covariate was not retained in many MCMC iterations. We chose to consider variables with $C \geq 0.75$ important, and variables with $C \leq 0.25$ not as important (i.e., Mutshinda et al. 2013). Variables with $C \geq 0.25$ but ≤ 0.75 were considered potentially important.

We assessed the model fit using the Bayesian posterior predictive p-value (Meng 1994). We used our occupancy models to generate simulated detection data, y_{sim}, and then calculated posterior predictive p-values as

Equation 12.

$$\Pr(\bar{y}_{sim} > \bar{y})$$

where $\bar{y}_{sim}$ is the mean of simulated data and $\bar{y}$ is the mean of observed detection data. The posterior predictive p-value can be interpreted as the probability that the mean of the simulated data will be greater than the mean of the observed data (Gelman 2013). As model fit improves, we expect the value of the posterior predictive p-value to approach 0.5 (Meng 1994). We used this method not with the goal of accepting or rejecting models, but rather as a check to assess if the model is reasonably consistent with our observed data (Gelman 2013).

Results

In both models (Figure 7) detection probability was lowest in 2014 and highest in 2015. In the territory-based (201-ha) model the 95% credible intervals of all detection probabilities overlapped, but in the grid-based (100-ha) model the 2014 detection probability (posterior mean estimate = 0.071, 95% Bayesian Credible Interval [BCI] = 0.045 – 0.105) appeared to be credibly lower than detection probabilities in 2015 (posterior mean 0.283, BCI 0.225 – 0.346) and 2016 (posterior mean 0.210, BCI 0.157 – 0.272).

Spotted owl site occupancy did not show any significant differences from 2014-2016 in our grid-based (100-ha) or territory-based (201-ha) models (Figure 8). Rates of site colonization and extinction indicated significant turnover at individual grid cells and territories (Figure 9) but spotted owl occupancy was generally highest in and around a few historic owl sites within the study area year-after year (Figures 10 and 11). Rates of colonization and extinction over space were similar in both models (Figures 12 and 13) but did not show trends year-over-year.

In the grid-based (100-ha) model covariates for dry mixed-conifer forest, largest patch index, mesic mixed-conifer forest, salvage logging, and slope were of high importance (*C* = 1.0) (Table 2). All other covariates were less important (*C* < 0.25). Only dry mixed-conifer (posterior mean 0.527, BCI 0.135 – 0.956) and salvage logging (posterior mean -0.497, BCI -0.833 – [-0.153]) had 95% credible intervals that didn't overlap zero. All other site covariates had 95% credible intervals that overlapped zero. Spotted owl site occupancy appeared to be positively and significantly correlated with increasing values of dry mixed-conifer forest cover and decreasing values of salvage logging. In the territory-based (201-ha) model covariates for mesic mixed-conifer, RdNBR, and slope were of high importance (*C* > 0.99) (Table 3). 95% credible intervals for all covariates overlapped with zero.

Predictions from both models were reasonably consistent with the observed data. The Bayesian p-value for the grid-based (100-ha) model was 0.634; for the territory-based (201-ha) model the Bayesian p-value was 0.472.

Discussion

Is there a lingering extinction debt 13-15 years after the Rodeo-Chediski fire?

There was no clear trend in occupancy of grid cells or territories during 2014-2016. Territory occupancy was higher than grid cell occupancy because territories are larger than grid cells (201-ha versus 100-ha) and territories included only areas known to be used by Mexican spotted owls since 1989, whereas the grid-based approach sampled the entire study area, including sites where spotted owls were never previously recorded. Consistent with this lack of trend in occupancy, the annual extinction rate was not significantly different from the annual colonization rate for both territories and cells. Our results suggest that the population of Mexican spotted owls on our study area was not clearly decreasing or increasing during the three year study period, which was 13-15 years after the Rodeo-Chediski fire. Thus, although the fire did reduce the number of owl territories by roughly half (Lommler et al. 2019, *in prep*. [Ch 2]) these rates do not support the existence of any remaining extinction debt.

This lack of trend is consistent with the absence of any remaining extinction debt from the fire but is not conclusive proof. A 3-year time series might not accurately reflect long-term trends because of short-term fluctuations in prey numbers, weather, or other factors, or because dying or emigrating owls are being replaced by immigrants from outside the study area. We believe a 10-year study of occupancy (U.S. Fish and Wildlife Service 2012), or multi-year monitoring of tagged birds in both burned and unburned areas, would be needed to fully assess long-term extinction debt.

How does wildfire and salvage logging affect occupancy probabilities?

In our grid-based analyses both largest patch index (LPI) and salvage logging were important predictors of spotted owl site occupancy (Table 2). LPI's relationship with occupancy was positive but not significant. Salvage logging's relationship with occupancy was negative and significant. In our territory-based analyses, which included only sites where spotted owls historically occurred, RdNBR (Table 3) was an important predictor but did not have a significant relationship with site occupancy. In this model salvage logging was not an important predictor. LPI's positive association with occupancy is surprising but may reflect spotted owl habitat's susceptibility to severe fire. Steep canyons and mature mixed-conifer forest used by owls are more likely to burn at mixed- and high-severity (Kaufmann et al. 2007) than the more open ponderosa pine forests that make up much of the study area. Several authors have found that spotted owls avoid areas that have been salvage logged (Clark et al. 2013, Lee et al. 2013, Lee and Bond 2015*b*, Hanson et al. 2018) but we suspect that the grid-based model may exaggerate the influence of salvage logging in this study. Salvage logging on our study area was concentrated in areas outside of PACs (<4% of all salvage logging on our study area occurred in PACs), where owls were detected far less often. The territory-based model, which focuses on historic spotted owl habitat, should better reflect effects of disturbance. Unfortunately, the 95% credible intervals on our territory-based model are large, probably because of our small sample of territories (N = 22).

High variance within each year probably limited insights from these response variables. But perhaps a bigger problem is that acoustic surveys might reflect foraging behavior at the periphery of a territory such that changes reflect shifts in foraging areas rather than true colonization and extinction of 100 ha cells. Estimation of site turnover may be impractical using acoustic surveys on contiguous grids. Researchers interested in estimating such rates for spotted owls should rely upon diurnal surveys (*sensu* Berigan et al. 2018) and avoid using contiguous grid survey designs.

What remnant habitat elements were selected by Mexican spotted owls?

Surprisingly, our remotely-sensed measures of forest structure were not important contributors to either the grid- or territory-based models of site occupancy. Spotted owls did select for mixed-conifer forest in both models (albeit different types of mixed-conifer forest). We believe that two factors may be driving this phenomenon. First, because we used nocturnal detections, our results may best reflect foraging habitat rather than nest and roost habitat. Second, the 100-ha and 201-ha spatial scales of our models may not reflect the scales at which forest structure is selected by Mexican spotted owls in this area. In a companion study (Lommler et al. 2019, in prep. [Ch. 4]) we found that spotted owls selected forest structure at much finer spatial scales than in this study.

Conclusions

We did not detect a negative occupancy trend 13-15 years after fire, but Lommler et al. (2018, *in prep*. [Ch. 2]) demonstrates that the Rodeo-Chediski fire greatly reduces observed site occupancy during 2013-2015 compared to pre-fire observed occupancy. Grid-based site occupancy on our study area (2014-2016 mean = 0.412, range = 0.398 – 0.425) was, on average, slightly lower than estimated occupancy (2014-2016 mean = 0.546, range = 0.421 – 0.611) across 200 burned and unburned 100-ha square cells on Forest Service land in Arizona and New Mexico (Lanier and Blakesley 2017). Unburned sites in east-central Arizona would provide a more meaningful comparison but we do not have comparable occupancy data for those sites. We suspect that, absent disturbance, site occupancies should generally be higher in east-central Arizona (i.e., surrounding our study area) than in most of the Mexican spotted owl's range, because species' abundance is generally greater near the center of the geographic range than in the periphery (Brown et al. 1995). Berigan et al. (2018) found that occupancy estimates based upon nocturnal detections of spotted owls may be inflated by detections of owls roaming outside their typical home range. Thus our occupancy estimates – and the range-wide occupancy estimates of Lanier and Blakesley (2017) – may be inflated compared to diurnal (i.e., nest and roost) locations.

It is difficult to detect fire effects in a landscape where higher fire severities are associated with Mexican spotted owl habitat that occurs in a naturally patchy distribution (Barrowclough et al. 2005). We agree with MacKenzie and Royle (2005) that historic sites should represent the population of interest when studying the influence of disturbance events. When we limited our sampling frame to known territories, RdNBR was an important model component, albeit one with an unclear relationship with site occupancy. Note, however, that surveying outside of historic sites may be important for documenting post-disturbance dispersal events. Because we sampled the entire landscape rather than just historic sites we detected spotted owls in areas not observed in Forest Service surveys, including a previously unknown nest site.

Mexican spotted owls appear to have a complex relationship with fire. Mexican spotted owls commonly forage in burned areas (Ganey et al. 2014). On our study area we observed spotted owls nesting and roosting in caves and ledges in a severely burned canyon (Figure 14). Fire – including high-severity fire within the range of historic natural variability– may help maintain Mexican spotted owl habitat over large temporal and spatial scales. However, while we found no evidence of continued extinction debt, we also found no evidence of post-fire increases in site occupancy. We recommend land managers to continue efforts to increase the fire-resiliency of southwestern forests, both between and within Mexican spotted owl home ranges. We also recommend researchers to continue exploring fire’s relationship with the spotted owl, focused on informing the use and arrangement of fuels treatments in and around spotted owl sites.

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Tables

Table 1. Full suite of 17 predictor variables calculated for a grid of 1-km^2 cells (100-ha) and 800m radius circles (201-ha) around 22 spotted owl territory centers. LiDAR data was collected in 2013 and 2014. LANDFIRE and MTBS data are from 2014. Salvage logging data from the USFS Region 3 GIS database are from 2017. LiDAR covariates based upon a 10-m pixel size. Other covariates resampled to a 10-m pixel from an original 30-m pixel.

Predictor	Source
Basal area (of trees ≥30-cm DBH)	LiDAR
Basal area (of trees ≥46-cm DBH)	LiDAR
Basal area (of trees ≥60-cm DBH)	LiDAR
% Canopy cover between 2-m and 16-m height	LiDAR
% Canopy cover above 16-m height	LiDAR
Number of trees (≥30-cm DBH)	LiDAR
Number of trees (≥46-cm DBH)	LiDAR
Number of trees (≥60-cm DBH)	LiDAR
Number of live trees (≥20-m height)	LiDAR
Number of snags (≥20-m height)	LiDAR
Dry mixed-conifer (% area composed of dry-mixed conifer forest)	LANDFIRE
High-severity fire (% area burned at high severity)	MTBS
Largest patch index (LPI, % high-severity fire aggregated into the largest patch)	MTBS
Mesic mixed-conifer (% area composed of mesic mixed-conifer forest)	LANDFIRE
Relative delta Normalized Burn Ratio (RdNBR, continuous fire severity)	MTBS
Salvage logging (% area salvage logged)	USFS GIS database
Slope (in degrees)	LiDAR

Table 2. Posterior mean estimates of occupancy (*Ψ*), detection probability (*ρ*), colonization (*γ*), and extinction (*ε*) rates across all sites with 95% Bayesian Credible Intervals from both grid (100-ha) and territory (201-ha) -based models of spotted owl occupancy 13-15 years after the Rodeo-Chediski fire.

	Model	
Parameter	**Grid (100-ha)**	**Territory (201-ha)**
2014 Ψ (CI)	0.426 (0.365-0.492)	0.512 (0.409-0.619)
2015 Ψ (CI)	0.419 (0.319-0.543)	0.484 (0.230-0.830)
2016 Ψ (CI)	0.398 (0.312-0.484)	0.359 (0.224-0.489)
2014 ρ (CI)	0.071 (0.045-0.105)	0.251 (0.102-0.458)
2015 ρ (CI)	0.283 (0.225-0.346)	0.505 (0.368-0.643)
2016 ρ (CI)	0.210 (0.157-0.272)	0.362 (0.211-0.524)
2015 γ (CI)	0.420 (0.269-0.613)	0.698 (0.213-1.333)
2016 γ (CI)	0.400 (0.276-0.542)	0.262 (0.133-0.459)
2015 ε (CI)	0.414 (0.315-0.510)	0.267 (0.103-0.454)
2016 ε (CI)	0.392 (0.291-0.487)	0.453 (0.265-0.571)
Bayesian p-value	0.634	0.472

Table 2. Model-averaged importance and model coefficients of covariates in a grid-based (100-ha scale) multi-season model of site occupancy. Important covariates are in italics. Covariates with model coefficients with 95% credible intervals that don't overlap zero are indicated with an asterisk (*).

Covariate	Importance	Model coefficient (CI)
Intercept	N/A	-0.450 (-0.830 – [-0.043])*
Canopy cover (2 to 16-m height)	<0.001	0.017 (-0.561 – 0.562)
Trees (≥60-cm DBH)	<0.001	-0.070 (-0.547 – 0.5346)
Dry mixed-conifer	*1.0*	0.527 (0.135 – 0.956)*
Largest patch index	*1.0*	0.407 (-0.030 – 0.752)
Mesic mixed-conifer	*1.0*	0.255 (-0.388 – 0.703)
Salvage logging	*1.0*	-0.497 (-0.833 – [-0.153])*
Slope	*1.0*	0.206 (-0.418 – 0.604)
Snags (≥20-m height)	<0.001	0.055 (-0.546 – 0.556)
Autocovariate	N/A	0.362 (-0.261 – 0.984)

Table 3. Model-averaged importance and model coefficients of covariates from a territory-based (201-ha) multi-season model of site occupancy. More important covariates are in italics. Every site covariate had a 95% credible interval that included zero.

Covariate	Importance	Model coefficient (CI)
Intercept	N/A	0.067 (-0.391 – 0.548)
Basal area (≥30-cm DBH)	0.004	-0.063 (-0.613 – 0.543)
Canopy cover (2 to 16-m height)	<0.001	-0.058 (-0.599 – 0.540)
Canopy cover (≥16-m height)	<0.001	-0.033 (-0.588 – 0.557)
Trees (≥60-cm DBH)	<0.001	-0.011 (-0.574 – 0.564)
Dry mixed-conifer	<0.001	-0.015 (-0.574 – 0.564)
High-severity fire	<0.001	-0.052 (-0.612 – 0.542)
LPI	<0.001	0.022 (-0.557 – 0.578)
Mesic mixed-conifer	*1.0*	0.305 (-0.411 – 0.825)
RdNBR	*0.994*	-0.101 (-0.641 – 0.526)
Salvage logging	0.002	-0.014 (-0.575 – 0.561)
Slope	*1.0*	0.285 (-0.430 – 0.804)
Snags (≥20-m height)	<0.001	0.061 (-0.534 – 0.607)

Figures

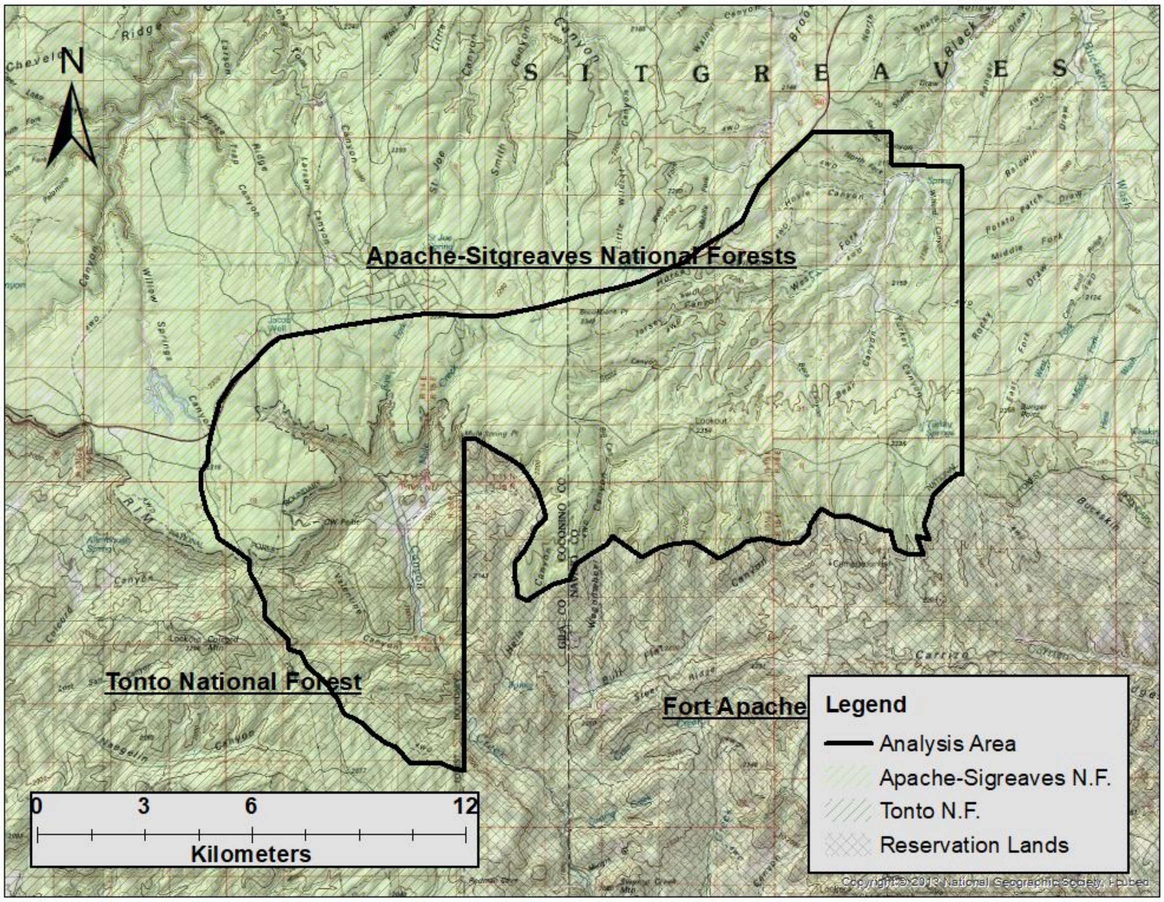


Figure 1. The study area lies on the Apache-Sitgreaves and Tonto National Forests, adjacent to the Fort Apache Indian Reservation.

Figure 2. A large patch burned at high-severity within our study area, on the Apache-Sitgreaves National Forest. Many patches of former forest on the study area were nearly devoid of standing trees and snags, the result of fire, limited salvage logging, and time. Photo taken in 2016 by author.

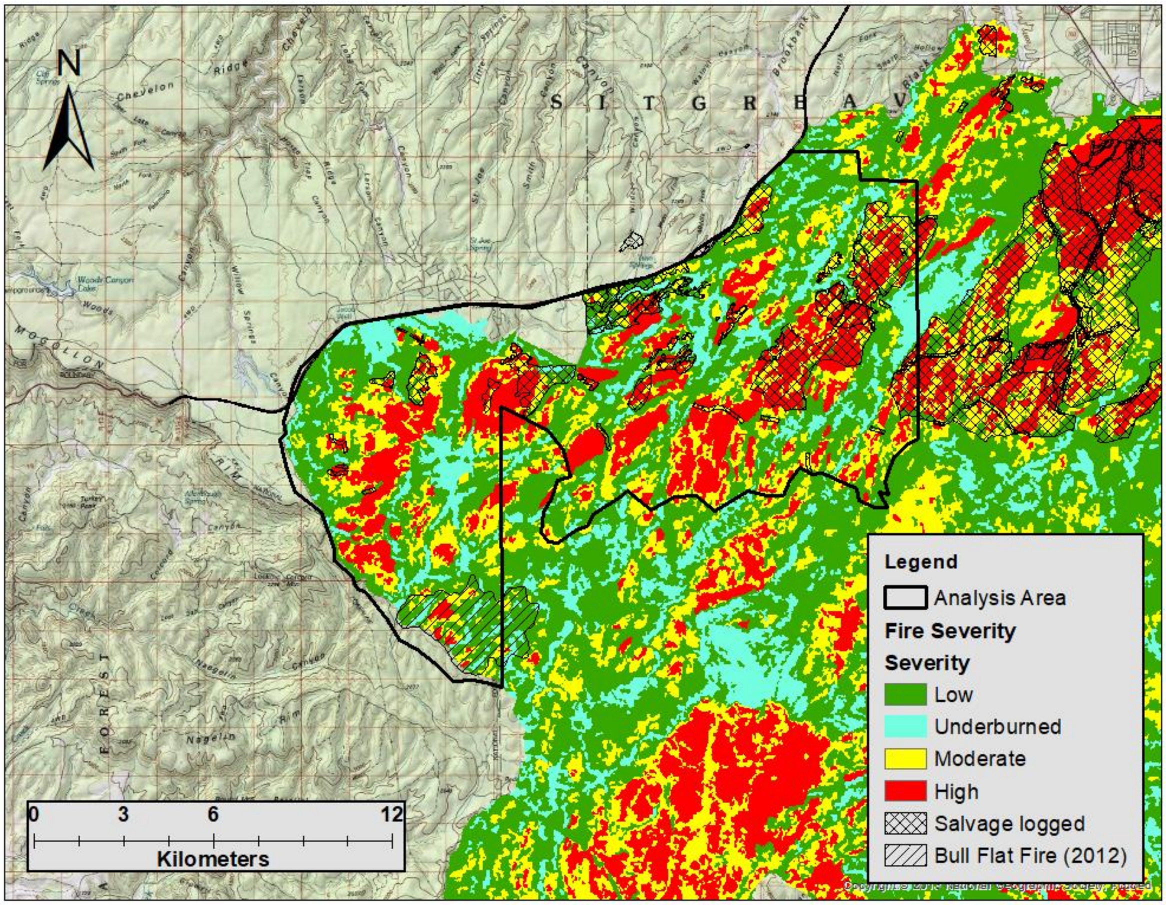


Figure 3. Severity of the Rodeo-Chediski fire on the study area. Approximately 23% of the study area burned at high severity (in red).

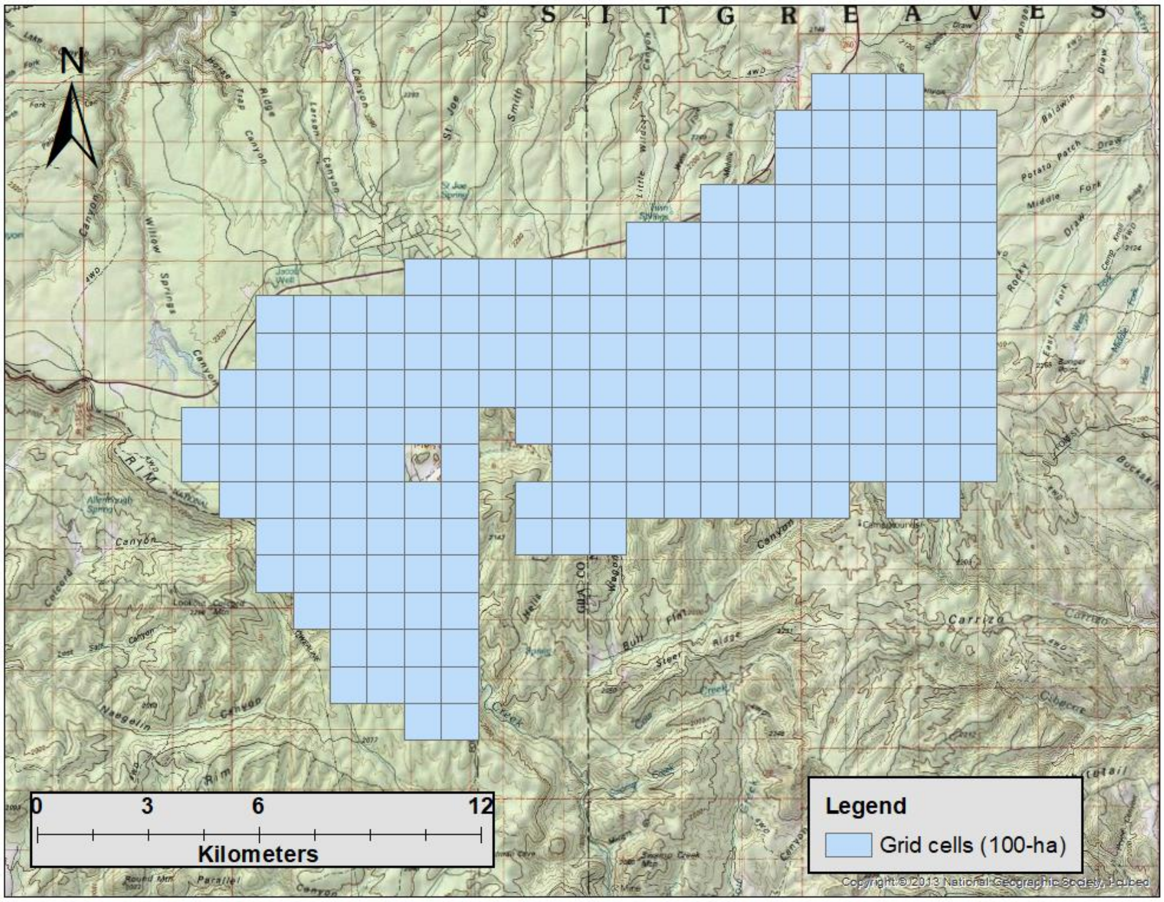


Figure 4. The grid-based model of site occupancy was based upon a continuous grid of N = 198 1-km^2 cells (100-ha) across the study area. Each grid was surveyed four times during each of 3 breeding seasons (April-August, 2014-2016).

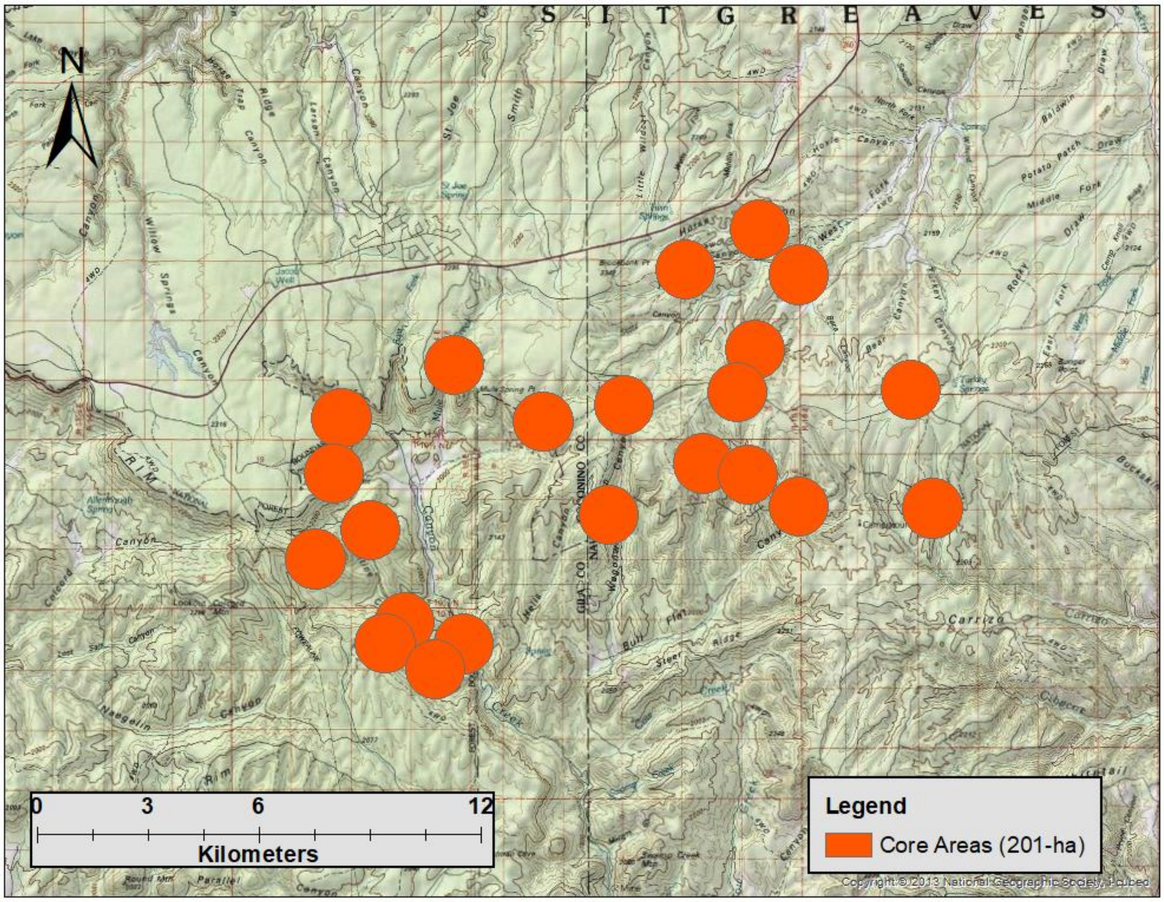


Figure 5. The territory-based model of site occupancy was based upon N = 22 core areas around (800-m radius, 201-ha) established around known Mexican spotted owl locations associated with Protected Activity Centers (PACs). Each core area was surveyed four times during each of the 2014-2016 breeding seasons (April-August).

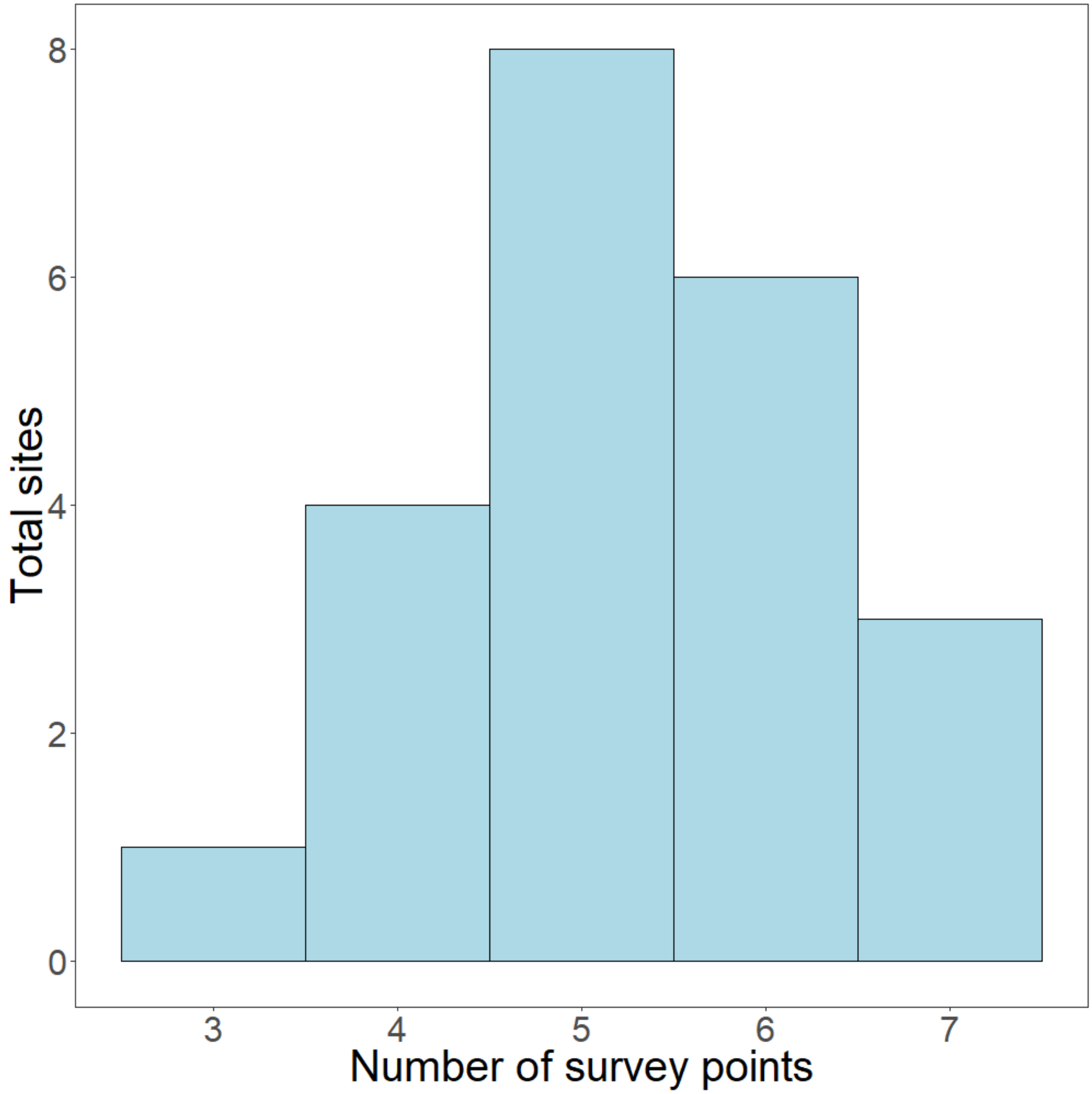


Figure 6. Distribution of *post-hoc* survey points within each 201-ha circular core area around historic spotted owl sites.

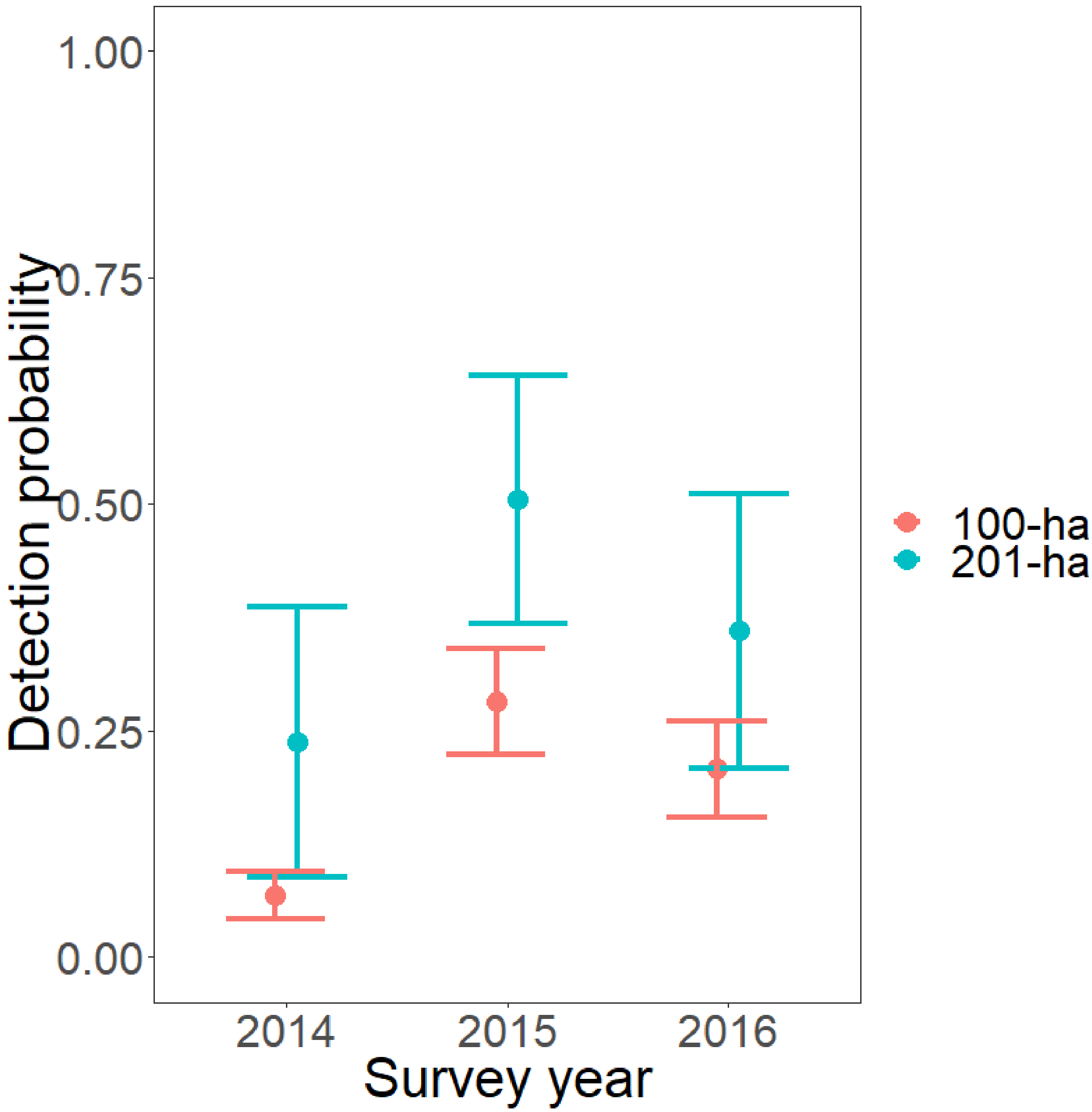


Figure 7. Posterior mean detection probabilities and 95% credible intervals from 2014-2016 based upon 100-ha grid cells (red) and 201-ha core areas around historic spotted owl territory centers (blue).

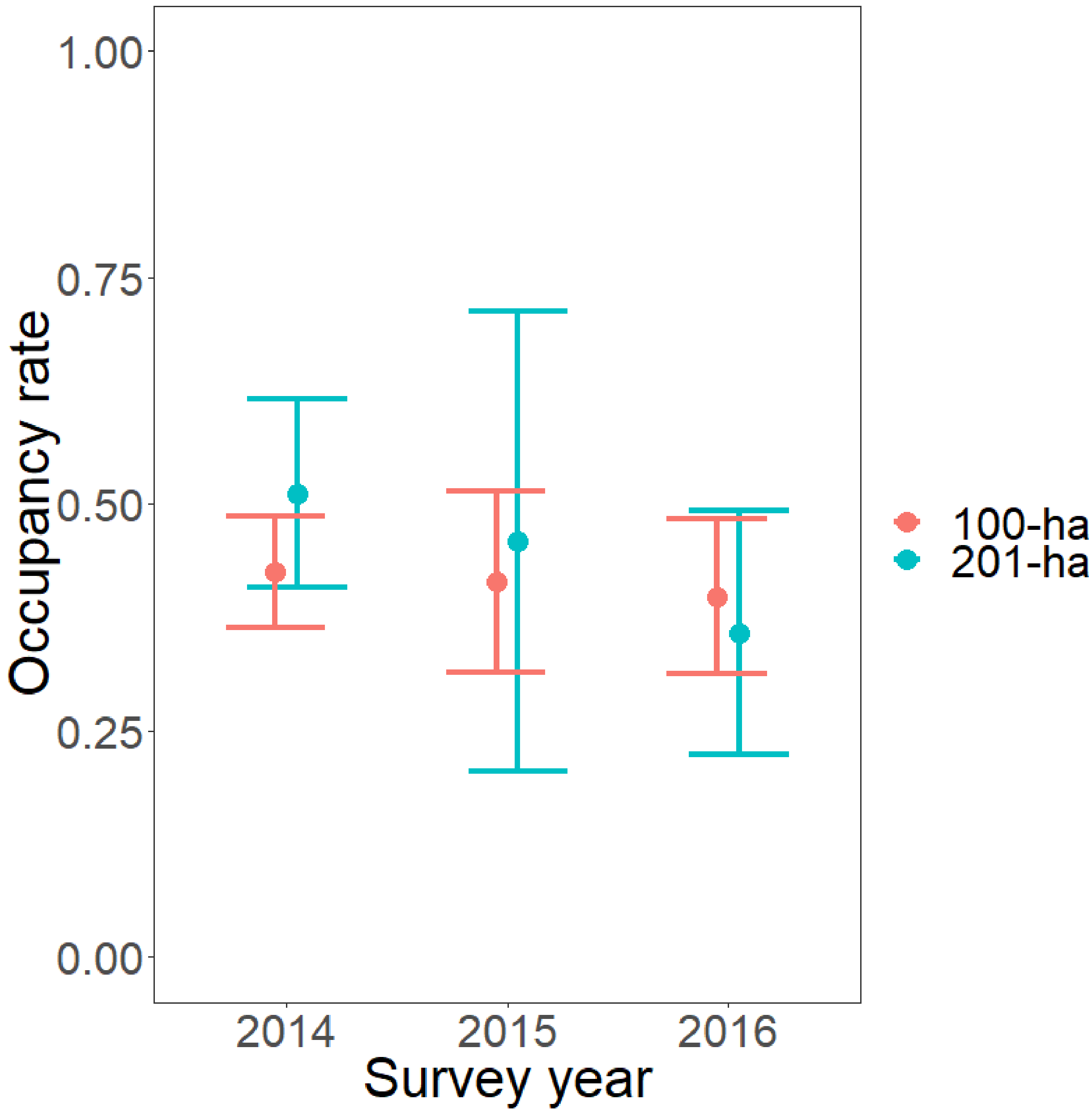


Figure 8. Posterior mean site occupancy rates and 95% credible intervals from 2014-2016 based upon 100-ha grid cells (red) and 201-ha core areas around historic spotted owl territory centers (blue).

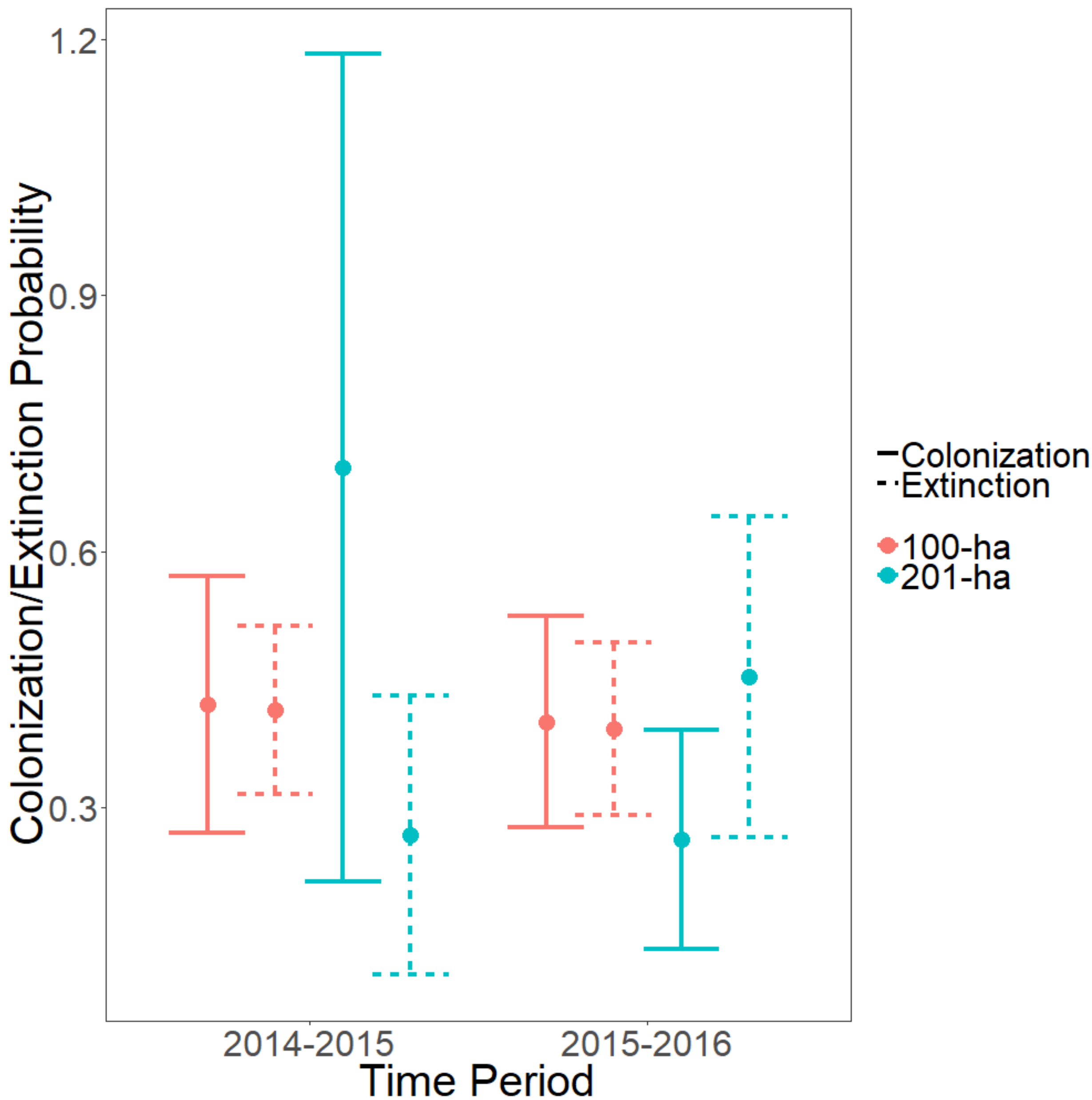


Figure 9. Posterior mean estimates and 95% Bayesian Credible Intervals of colonization (solid lines) and extinction (dashed lines) from the first-to-second and second-to-third years of surveys, based upon 100-ha grid cells (red) and 201-ha core areas around historic spotted owl territory centers (blue).

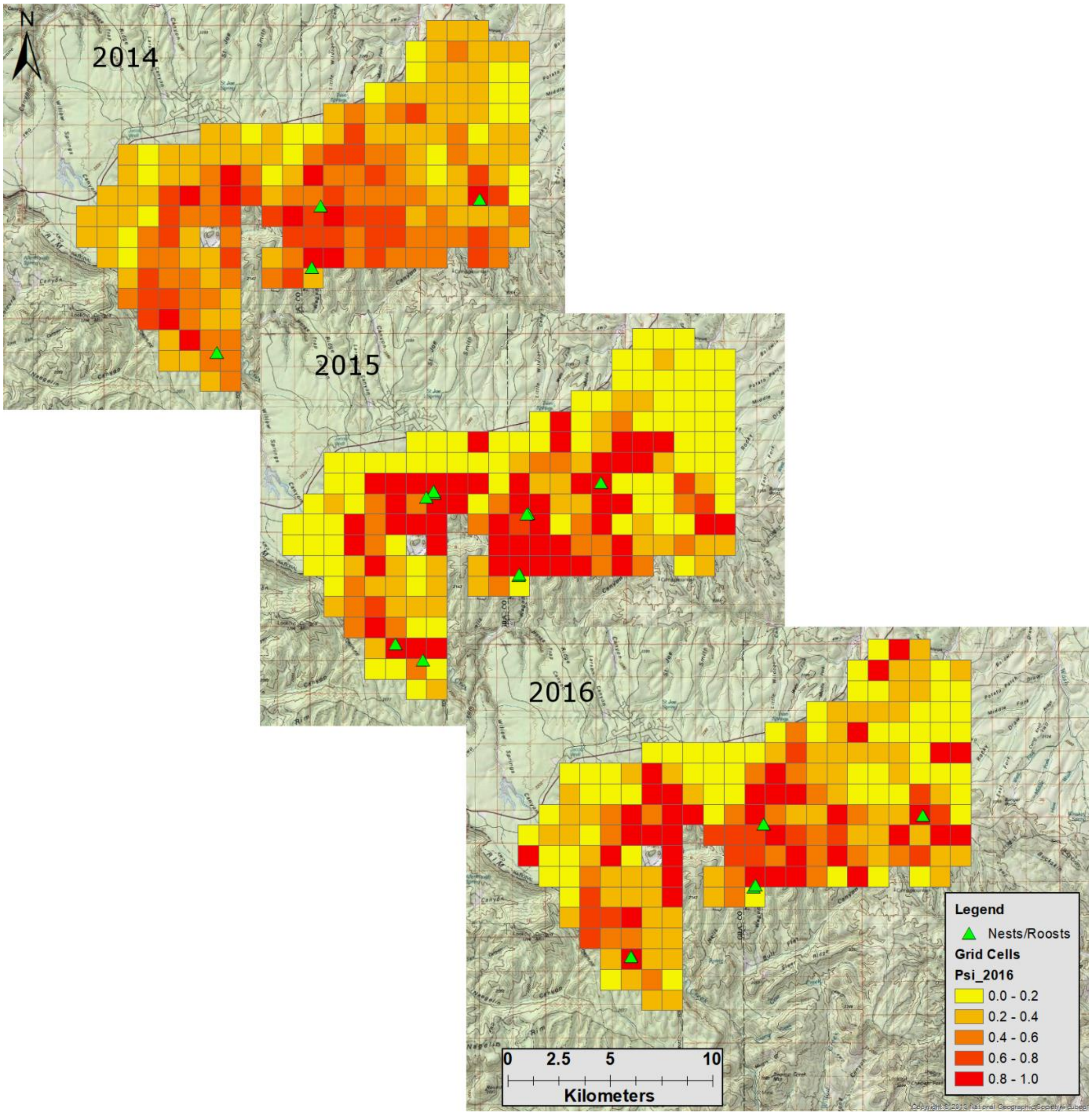


Figure 10. Variation in posterior mean site occupancy over space (100-ha grid cells) and time (2014-2016).

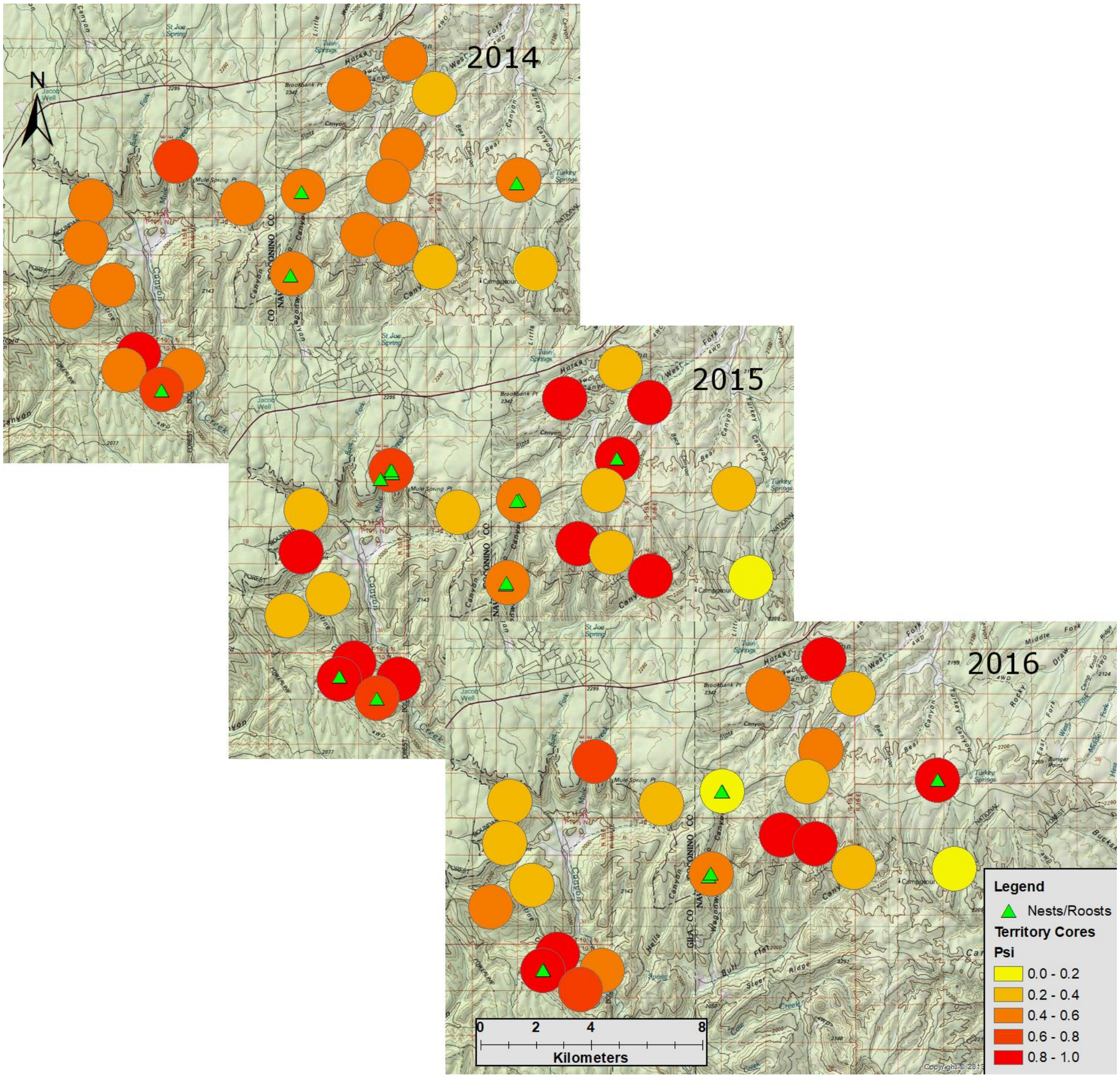
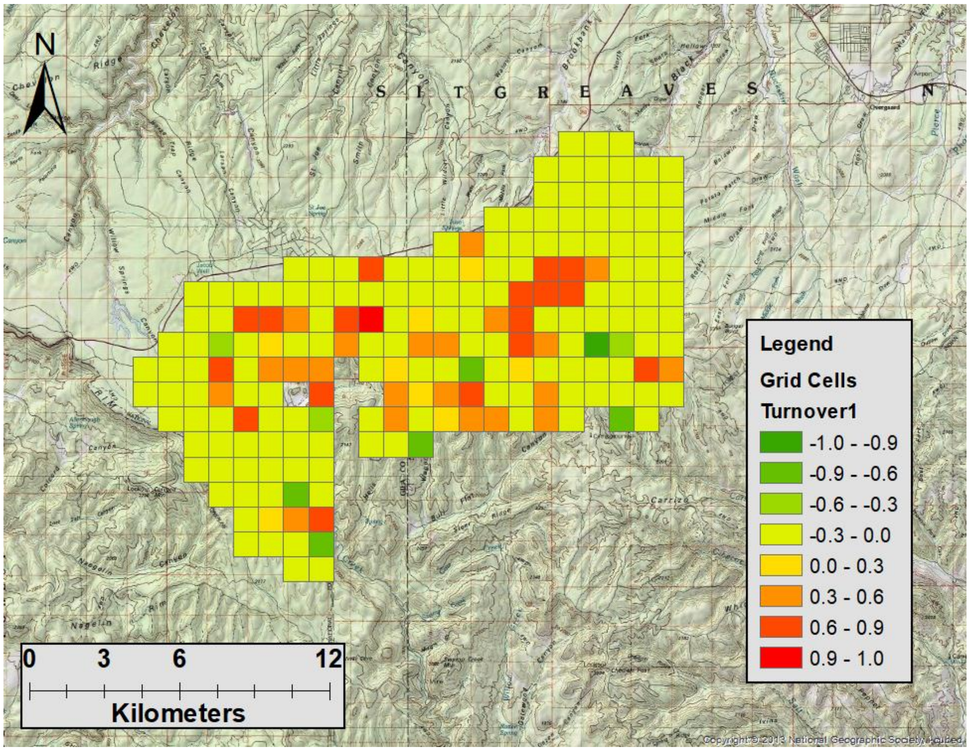


Figure 11. Variation in posterior mean site occupancy over space (in historic 203-ha core areas) and time (2014-2016). Also shown is distribution of nests and roosts sites found each year.

(a)



(b)

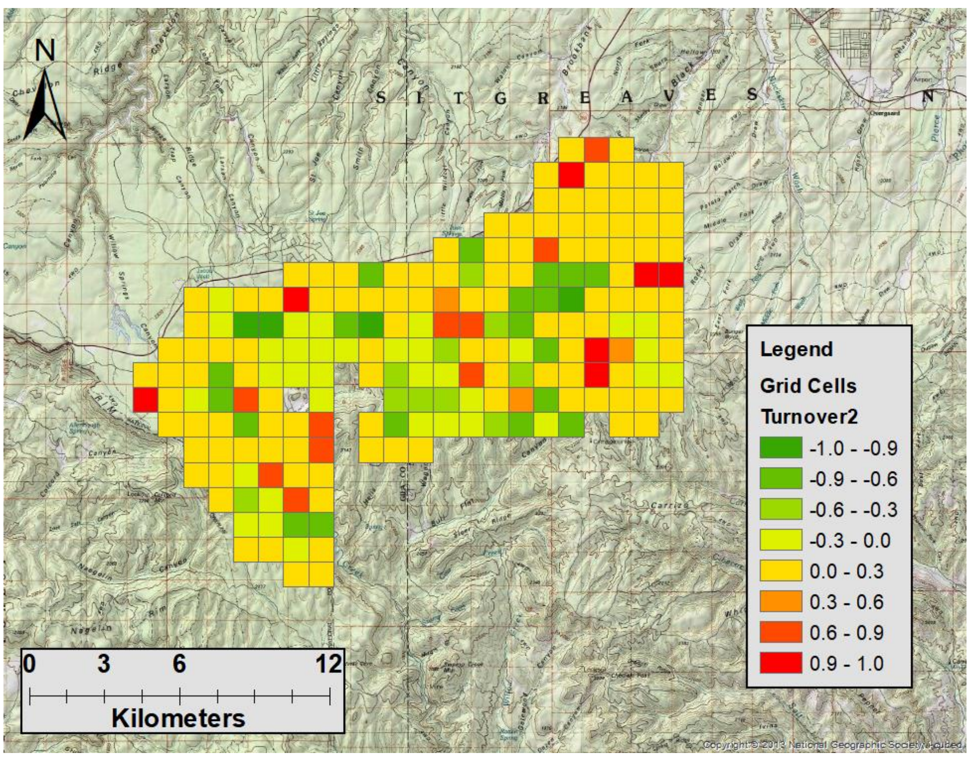


Figure 12. Variation in posterior mean rates of site turnover (colonization – extinction) over space from 2014 to 2015 (a) and 2015 to 2016 (b) from a grid-based model of site occupancy.

(a)

(b)

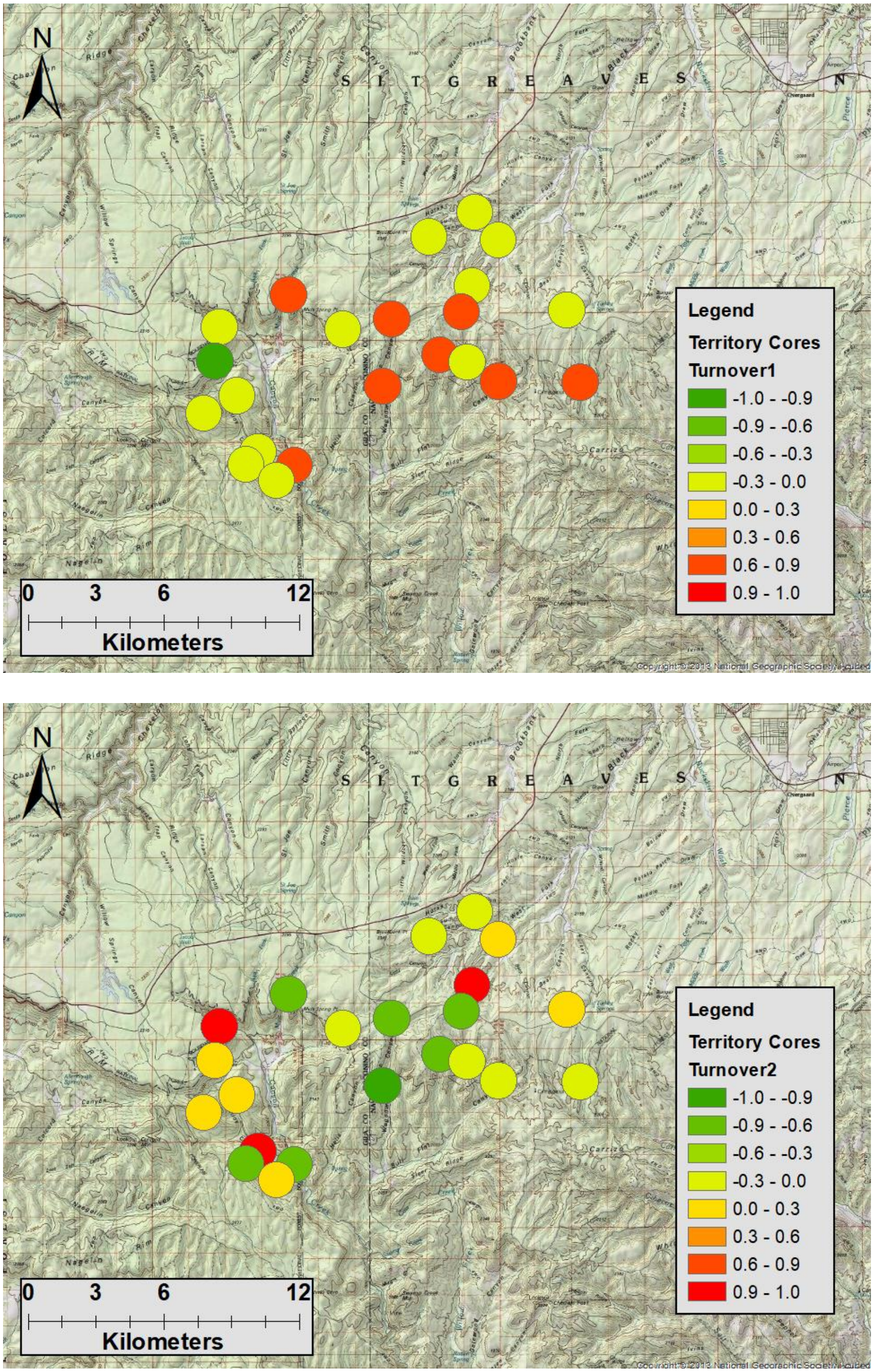


Figure 13. Variation in posterior mean rates of site turnover (colonization – extinction) over space from 2014 to 2015 (a) and 2015 to 2016 (b) from a territory-based model of site occupancy.

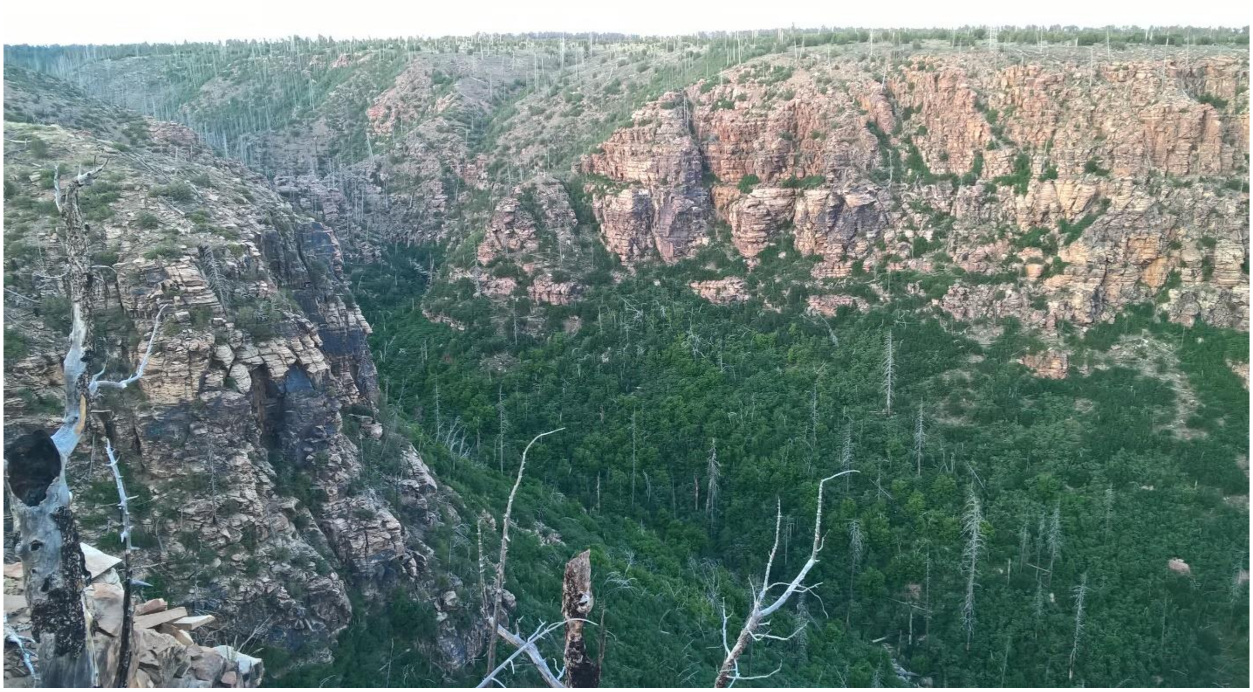


Figure 14. A severely burned canyon occupied by a pair of Mexican spotted owls. This is an example of a site where spotted owls use topographic and geologic features such as cliffs, caves, and crevices to provide thermal cover and nest sites typically provided by mature conifer forests. Photo taken in 2017 by author.

Appendices

Appendix I. Model specification for 3 season, 1 species spatial auto-logistic model of Mexican spotted owl site occupancy for sites based upon a continuous grid of 1-km^2 cells.

```
#Author: original base code by J.S. Sanderlin, adapted and added onto by M.Lommler
#This script is for 3 season, 1 species spatial auto-logistic model of
#occupancy for Mexican spotted owl for 2014-2016
mso = function(ni=30000,nb=15000,nt=2,nc=3){
library("R2OpenBUGS")

Ymat = as.matrix(read.csv('Y_mult.csv',header=FALSE)) # 198 sites by 3 years
numnn = as.matrix(read.csv('numnn.csv',header=FALSE)) # 198 sites, number nearest
neighbors
NN = as.matrix(read.csv('NN.csv',header=FALSE)) # 198 sites X 4, identity of nearest
neighbors
Jrep = as.matrix(read.csv('J.csv',header=FALSE)) # 198 X 3, survey occasions per year
nG = 198 #number of grid cells
CC_2_16 = as.matrix(read.csv('CC_2_16.csv',header=FALSE)) # Canopy cover
between 2-16-m
DIAM_60 = as.matrix(read.csv('DIAM_60.csv',header=FALSE)) # number trees >60-cm
dbh
DMC = as.matrix(read.csv('DMC.csv',header=FALSE)) # % cover of dry mixed-conifer
LPI = as.matrix(read.csv('LPI.csv',header=FALSE)) # patch consolidation of high-
severity fire
MMC = as.matrix(read.csv('MMC.csv',header=FALSE)) # MMC
Salv = as.matrix(read.csv('Salv.csv',header=FALSE)) # % salvage-logged
Slope = as.matrix(read.csv('Slope.csv',header=FALSE)) # mean slope
Tall_Dead = as.matrix(read.csv('Tall_Dead.csv',header=FALSE)) # number snags >20-
m height

############################################################
#arguments for bugs()

data = list(Y=Ymat, numnn=numnn,
        CC_2_16=CC_2_16,
        DIAM_60=DIAM_60,
        DMC=DMC,
        LPI=LPI,MMC=MMC,
```

```
            Salv=Salv,Slope=Slope,
            Tall_Dead=Tall_Dead,
            NN=NN, nG=nG, J=Jrep)

params <-
list("alpha","beta","psi","p","zb1","zb2","zb3","zb4","zb5","zb6","zb7","zb8","b1","b2","b3",
"b4","b5","b6","b7","b8","d","d1","e","e.all",

"g","g.all","beta1","beta2","beta3","beta4","beta5","beta6","beta7","beta8","psi.fs","pvalue
.mean",
              "psi.all")
# d is alpha for detection, "g" = colonization, "e" = extinction

inits <- function(){
  alpha.init=rnorm(1,0,1)
  beta.init=rnorm(1,0,1)
  zb1.init=rnorm(1,0,1)
  zb2.init=rnorm(1,0,1)
  zb3.init=rnorm(1,0,1)
  zb4.init=rnorm(1,0,1)
  zb5.init=rnorm(1,0,1)
  zb6.init=rnorm(1,0,1)
  zb7.init=rnorm(1,0,1)
  zb8.init=rnorm(1,0,1)
  b1.init=rnorm(1,0,1)
  b2.init=rnorm(1,0,1)
  b3.init=rnorm(1,0,1)
  b4.init=rnorm(1,0,1)
  b5.init=rnorm(1,0,1)
  b6.init=rnorm(1,0,1)
  b7.init=rnorm(1,0,1)
  b8.init=rnorm(1,0,1)
  sigma.d1.init=runif(0,3) #random effect for p
  list
(alpha=alpha.init,beta=beta.init,zb1=zb1.init,zb2=zb2.init,zb3=zb3.init,zb4=zb4.init,zb5=
zb5.init,
        zb6=zb6.init,zb7=zb7.init,zb8=zb8.init,
        b1=b1.init,b2=b2.init,
        b3=b3.init,b4=b4.init,b5=b5.init,b6=b6.init,b7=b7.init,b8=b8.init,d1=sigma.d1.init)
}
```

```
modelFilename = "MSO_full_indicator_grid_Lidar.txt"

cat("
   model{
   alpha ~ dnorm(0,10)
   beta  ~ dnorm(0,10)
   d ~ dnorm(0,10)
   sigma.d1 ~ dunif(0,3)
   tau.d1 <- pow(sigma.d1,-2)
   #random effect of p
   for (m in 1:3){
   d1[m] ~ dnorm(0,tau.d1)
   }

   #indicator variable selection
   zb1 ~ dbern(0.5)
   zb2 ~ dbern(0.5)
   zb3 ~ dbern(0.5)
   zb4 ~ dbern(0.5)
   zb5 ~ dbern(0.5)
   zb6 ~ dbern(0.5)
   zb7 ~ dbern(0.5)
   zb8 ~ dbern(0.5)
   # model coefficients
   b1 ~ dnorm(0,10)
   b2 ~ dnorm(0,10)
   b3 ~ dnorm(0,10)
   b4 ~ dnorm(0,10)
   b5 ~ dnorm(0,10)
   b6 ~ dnorm(0,10)
   b7 ~ dnorm(0,10)
   b8 ~ dnorm(0,10)

   beta1 <-zb1*b1
   beta2 <-zb2*b2
   beta3 <-zb3*b3
   beta4 <-zb4*b4
   beta5 <-zb5*b5
   beta6 <-zb6*b6
```

```
    beta7 <-zb7*b7
    beta8 <-zb8*b8


    # for season 1
    logit(p[1])<- d + d1[1]
    for(i in 1:nG){
    x[i,1,1]<-0

    # for all nearest neighbors k (up to 4)
    for(k in 1:numnn[i,1]){
    x[i,1,k+1]<-x[i,1,k]+z[NN[i,k],1]
    }
    # occupancy for time 1
    logit(psi[i,1])<- alpha + beta*(x[i,1,numnn[i,1]+1]/numnn[i,1]) +
    beta1*CC_2_16[i,1] +
    beta2*DIAM_60[i,1] + beta3*DMC[i,1] +
    beta4*LPI[i,1] + beta5*MMC[i,1] +  beta6*Salv[i,1] + beta7*Slope[i,1] +
    beta8*Tall_Dead[i,1]
    z[i,1]~dbern(psi[i,1])
    mu[i,1] <- z[i,1]*p[1]
    Y[i,1] ~ dbin(mu[i,1],J[i,1])

    # simulated data
    mu.sim[i,1] <-psi[i,1]*p[1]
    Y.sim[i,1] ~ dbin(mu.sim[i,1],J[i,1])
}
    # for seasons 2-3
    for(s in 2:3){
    # detection
    logit(p[s]) <- d + d1[s]
    for(i in 1:nG){
    x[i,s,1]<-0

    # for all nearest neighbors k (up to 4)
    for(k in 1:numnn[i,1]){
    x[i,s,k+1]<-x[i,s,k]+z[NN[i,k],s]
    }
    # occupancy for times 2-3
       logit(psi[i,s])<- alpha + beta*(x[i,1,numnn[i,1]+1]/numnn[i,1]) +
```

```
    beta1*CC_2_16[i,1] +
    beta2*DIAM_60[i,1] + beta3*DMC[i,1] +
    beta4*LPI[i,1] + beta5*MMC[i,1] +  beta6*Salv[i,1] + beta7*Slope[i,1] +
    beta8*Tall_Dead[i,1]
    z[i,s]~dbern(psi[i,s])
    mu[i,s] <- z[i,s]*p[s]
    Y[i,s] ~ dbin(mu[i,s],J[i,s])
 #simulated data
    mu.sim[i,s] <-psi[i,s]*p[s]
    Y.sim[i,s] ~ dbin(mu.sim[i,s],J[i,s])
    # extinction and colonization
    e[i,s-1] <- z[i,s-1]*(1-z[i,s])
    g[i,s-1] <- z[i,s]*(1-z[i,s-1])
    Total[i,s-1] <- z[i,s-1]
    }

    }
    # summary of extinction/colonization, where t = time
    for (t in 1:2){
    g.all[t] <- (sum(g[,t]))/(sum(Total[,t]))
    e.all[t] <- (sum(e[,t]))/(sum(Total[,t]))
    }
  # occupancy calculation
    psi.all[1]<-(sum(psi[,1]))/nG
psi.all[2]<-((psi.all[1]*e.all[1])+(1-psi.all[1])*g.all[1])
psi.all[3]<-((psi.all[2]*e.all[2])+(1-psi.all[2])*g.all[2])
    # finite sample occupancy where c = time
for (c in 1:3){
    psi.fs[c] <- (sum(z[,c])/nG) #occupancy
}
 # bayesian p-value
cv.Y <-sd(Y[,])/mean(Y[,])
cv.Y.sim <-sd(Y.sim[,])/mean(Y.sim[,])
mean.Y<-mean(Y[,])
mean.Y.sim <-mean(Y.sim[,])
pvalue.cv<-step(cv.Y.sim-cv.Y)
pvalue.mean<-step(mean.Y.sim-mean.Y) # goodness of fit for apparent occupancy
# Sums of squares
for(h in 1:nG){
for(f in 1:3){
```

```
sq[h,f]<-(Y[h,f]-logit(psi[h,f]))*(Y[h,f]-logit(psi[h,f]))
sq.new[h,f]<-(Y.sim[h,f]-logit(psi[h,f]))*(Y.sim[h,f]-logit(psi[h,f]))
}
}
fit<-sum(sq[,])
fit.new<-sum(sq.new[,])
pvalue.fit<-step(fit.new-fit)
}
",fill=TRUE, file=modelFilename)

out<- bugs(data, inits, params, modelFilename, n.thin=nt,n.chains=nc,
n.burnin=nb,n.iter=ni,debug=TRUE,codaPkg=FALSE, DIC=TRUE)

out

}
mso()
```

Appendix II. Model specification for 3 season, 1 species model of Mexican spotted owl site occupancy for sites based upon an 800m radius around territory centers.

```
#Author: original base code by J.S. Sanderlin, adapted and added onto by M.Lommler
#This script is for 3 season, 1 species spatial auto-logistic model of
#occupancy for Mexican spotted owl for 2014-2016
setwd("C:/Users/MLOM/Dropbox/Dissertation_and_Miscellaneous_Academia/Data/BU
GS_Lidar_PAC")
mso = function(ni=30000,nb=15000,nt=2,nc=3){
library("R2OpenBUGS")

Ymat = as.matrix(read.csv('Y_pac.csv',header=FALSE)) # 22 sites by 3 years
Jrep = as.matrix(read.csv('J_1.csv',header=FALSE)) # number of surveys
nG = 22 #number of sites
BA_30 = as.matrix(read.csv('BA_30.csv',header=FALSE)) # BA of trees >30-cm DBH
CC_2_16 = as.matrix(read.csv('CC_2_16.csv',header=FALSE)) # Canopy cover
between 2-16-m
CC_16_up = as.matrix(read.csv('CC_16_up.csv',header=FALSE)) # Canopy cover
above 16-m
DIAM_60 = as.matrix(read.csv('DIAM_60.csv',header=FALSE)) # Number trees > 60-
cm DBH
DMC = as.matrix(read.csv('DMC.csv',header=FALSE)) # % cover of dry mixed-conifer
```

```
HSF = as.matrix(read.csv('HSF.csv',header=FALSE)) # % high-severity fire
LPI = as.matrix(read.csv('LPI.csv',header=FALSE)) # patch consolidation of high-
severity fire
MMC = as.matrix(read.csv('MMC.csv',header=FALSE)) # % cover of mesic mixed-
conifer
RdNBR = as.matrix(read.csv('RdNBR.csv',header=FALSE)) # relative delta normalized
burn ratio
Salv = as.matrix(read.csv('Salv.csv',header=FALSE)) # % salvage-logged
Slope = as.matrix(read.csv('Slope.csv',header=FALSE)) # mean slope
Tall_Dead = as.matrix(read.csv('Tall_Dead.csv',header=FALSE)) # number snags >20-
m height
Surv_Effort = as.matrix(read.csv('PAC_eff.csv',header=FALSE)) # number of call points
in each core area


##########################################################
#arguments for bugs()

data = list(Y=Ymat, BA_30=BA_30,CC_2_16=CC_2_16,
      CC_16_up=CC_16_up, DIAM_60=DIAM_60,

DMC=DMC,HSF=HSF,LPI=LPI,MMC=MMC,RdNBR=RdNBR,Salv=Salv,Slope=Slope,
      Tall_Dead=Tall_Dead, nG=nG, J=Jrep)

params <-
list("alpha","psi","p","zb1","zb2","zb3","zb4","zb5","zb6","zb7","zb8","zb9","zb10",
       "zb11","zb12","b1","b2","b3","b4","b5","b6","b7","b8","b9",
       "b10","b11","b12","d","d1","e","e.all",

"g","g.all","beta1","beta2","beta3","beta4","beta5","beta6","beta7","beta8","beta9","beta1
0",
       "beta11","beta12","psi.fs","pvalue.fit","p.value.mean","psi.all")
# d is alpha for detection, "g" = colonization, "e" = extinction

inits <- function(){
  alpha.init=rnorm(1,0,1)
  zb1.init=rnorm(1,0,1)
  zb2.init=rnorm(1,0,1)
  zb3.init=rnorm(1,0,1)
  zb4.init=rnorm(1,0,1)
```

```
  zb5.init=rnorm(1,0,1)
  zb6.init=rnorm(1,0,1)
  zb7.init=rnorm(1,0,1)
  zb8.init=rnorm(1,0,1)
  zb9.init=rnorm(1,0,1)
  zb10.init=rnorm(1,0,1)
  zb11.init=rnorm(1,0,1)
  zb12.init=rnorm(1,0,1)
  b1.init=rnorm(1,0,1)
  b2.init=rnorm(1,0,1)
  b3.init=rnorm(1,0,1)
  b4.init=rnorm(1,0,1)
  b5.init=rnorm(1,0,1)
  b6.init=rnorm(1,0,1)
  b7.init=rnorm(1,0,1)
  b8.init=rnorm(1,0,1)
  b9.init=rnorm(1,0,1)
  b10.init=rnorm(1,0,1)
  b11.init=rnorm(1,0,1)
  b12.init=rnorm(1,0,1)
  sigma.d1.init=runif(0,3) #random effect for p
  list (alpha=alpha.init,zb1=zb1.init,zb2=zb2.init,zb3=zb3.init,zb4=zb4.init,zb5=zb5.init,
        zb6=zb6.init,zb7=zb7.init,zb8=zb8.init,zb9=zb9.init,zb10=zb10.init,zb11=zb11.init,
        zb12=zb12.init,
        b1=b1.init,b2=b2.init,

b3=b3.init,b4=b4.init,b5=b5.init,b6=b6.init,b7=b7.init,b8=b8.init,b9=b9.init,b10=b10.init,
        b11=b11.init,b12=b12.init,d1=sigma.d1.init)
}

modelFilename = "MSO_full_indicator_PAC_Lidar.txt"

cat("
   model{

   alpha ~ dnorm(0,10)
   d ~ dnorm(0,10)
   sigma.d1 ~ dunif(0,3)
   tau.d1 <- pow(sigma.d1,-2)
   #random effect of p
```

```
for (m in 1:3){
d1[m] ~ dnorm(0,tau.d1)
}

#indicator variable selection
zb1 ~ dbern(0.5)
zb2 ~ dbern(0.5)
zb3 ~ dbern(0.5)
zb4 ~ dbern(0.5)
zb5 ~ dbern(0.5)
zb6 ~ dbern(0.5)
zb7 ~ dbern(0.5)
zb8 ~ dbern(0.5)
zb9 ~ dbern(0.5)
zb10 ~ dbern(0.5)
zb11 ~ dbern(0.5)
zb12 ~ dbern(0.5)
# model coefficients
b1 ~ dnorm(0,10)
b2 ~ dnorm(0,10)
b3 ~ dnorm(0,10)
b4 ~ dnorm(0,10)
b5 ~ dnorm(0,10)
b6 ~ dnorm(0,10)
b7 ~ dnorm(0,10)
b8 ~ dnorm(0,10)
b9 ~ dnorm(0,10)
b10 ~ dnorm(0,10)
b11 ~ dnorm(0,10)
b12 ~ dnorm(0,10)
beta1 <-zb1*b1
beta2 <-zb2*b2
beta3 <-zb3*b3
beta4 <-zb4*b4
beta5 <-zb5*b5
beta6 <-zb6*b6
beta7 <-zb7*b7
beta8 <-zb8*b8
beta9 <-zb9*b9
beta10 <-zb10*b10
```

```
    beta11 <-zb11*b11
    beta12 <-zb12*b12


    # for season 1
    logit(p[1])<- d + d1[1]
    for(i in 1:nG){
    x[i,1,1]<-0


    # occupancy for time 1
    logit(psi[i,1])<- alpha + beta1*BA_30[i,1] +
    beta2*CC_2_16[i,1] + beta3*CC_16_up[i,1] +
     beta4*DIAM_60[i,1] + beta5*DMC[i,1] + beta6*HSF[i,1] +
    beta7*LPI[i,1] + beta8*MMC[i,1] + beta9*RdNBR[i,1] + beta10*Salv[i,1] +
beta11*Slope[i,1] +
    beta12*Tall_Dead[i,1]
    z[i,1]~dbern(psi[i,1])
    mu[i,1] <- z[i,1]*p[1]
    Y[i,1] ~ dbin(mu[i,1],J[i,1])
# simulated data
    mu.sim[i,1] <-psi[i,1]*p[1]
    Y.sim[i,1] ~ dbin(mu.sim[i,1],J[i,1])
    }

    # for seasons 2-3
    for(s in 2:3){
    # detection
    logit(p[s]) <- d + d1[s]
    for(i in 1:nG){
    x[i,s,1]<-0

    # occupancy for times 2-3
    logit(psi[i,s])<- alpha + beta1*BA_30[i,1] +
    beta2*CC_2_16[i,1] + beta3*CC_16_up[i,1] +
    beta4*DIAM_60[i,1] + beta5*DMC[i,1] + beta6*HSF[i,1] +
    beta7*LPI[i,1] + beta8*MMC[i,1] + beta9*RdNBR[i,1] + beta10*Salv[i,1] +
beta11*Slope[i,1] +
    beta12*Tall_Dead[i,1]
    z[i,s]~dbern(psi[i,s])
```

```
    mu[i,s] <- z[i,s]*p[s]
    Y[i,s] ~ dbin(mu[i,s],J[i,1])
# simulated data
    mu.sim[i,s] <-psi[i,s]*p[s]
    Y.sim[i,s] ~ dbin(mu.sim[i,s],J[i,1])

    # extinction and colonization
    e[i,s-1] <- z[i,s-1]*(1-z[i,s])
    g[i,s-1] <- z[i,s]*(1-z[i,s-1])
    Total[i,s-1] <- z[i,s-1]
    }

    }
    # summary of extinction/colonization, where t = time
    for (t in 1:2){
    g.all[t] <- (sum(g[,t]))/(sum(Total[,t]))
    e.all[t] <- (sum(e[,t]))/(sum(Total[,t]))
    }
  # occupancy calculation
    psi.all[1]<-(sum(psi[,1]))/nG
    psi.all[2]<-((psi.all[1]*e.all[1])+(1-psi.all[1])*g.all[1])
    psi.all[3]<-((psi.all[2]*e.all[2])+(1-psi.all[2])*g.all[2])
    # finite sample occupancy where c = time
for (c in 1:3){
    psi.fs[c] <- (sum(z[,c])/nG) #occupancy
}
# bayesian p-value
cv.Y <-sd(Y[,])/mean(Y[,])
cv.Y.sim <-sd(Y.sim[,])/mean(Y.sim[,])
mean.Y<-mean(Y[,])
mean.Y.sim <-mean(Y.sim[,])
pvalue.cv<-step(cv.Y.sim-cv.Y)
p.value.mean<-step(mean.Y.sim-mean.Y)
# Sums of squares
for(h in 1:nG){
for(f in 1:3){
sq[h,f]<-(Y[h,f]-logit(psi[h,f]))*(Y[h,f]-logit(psi[h,f]))
sq.new[h,f]<-(Y.sim[h,f]-logit(psi[h,f]))*(Y.sim[h,f]-logit(psi[h,f]))
}
}
```

```
fit<-sum(sq[,])
fit.new<-sum(sq.new[,])
pvalue.fit<-step(fit.new-fit)
    }
}
",fill=TRUE, file=modelFilename)

out<- bugs(data, inits, params, modelFilename, n.thin=nt,n.chains=nc,
n.burnin=nb,n.iter=ni,debug=TRUE,codaPkg=FALSE, DIC=TRUE)

out

}
mso()
```

Chapter 4

Mexican spotted owls avoid nesting and roosting in severely burned forest 13-15 years after the Rodeo-Chediski fire, Arizona

Mike Lommler

Abstract

Mexican spotted owls (*Strix occidentalis lucida*) have a complex relationship with wildfire. Previous studies suggest that low- and moderate-severity fire appears to have little effect. The influence of high-severity fire may depend upon threshold effects, patch sizes, or proximity to nest and roost sites. Spotted owls also may avoid high-severity fire for nesting and roosting and select them for foraging or other behaviors. The precise relationship is poorly understood. We modeled spotted owl habitat selection 13-15 years after the 2002 Rodeo-Chediski fire (187000-ha, 36.6% burned at high severity) using a scale-optimized Random Forest model. Mexican spotted owls in this post-fire landscape generally used the same habitat features, especially large trees and mixed-conifer forest with high canopy cover, that they used in unburned settings but may select these features at different spatial scales reflecting how fire changed their availability. Owls responded most strongly to fire within a 200-300-m radius, and avoided locations where fire killed 33% or more of the pre-fire tree canopy. Owls responded positively to less severe fire. Our results suggest that large, high-severity fires can pose a significant threat to Mexican spotted owls. We recommend management to re-establish historic fire regimes and to create fuel breaks within and between Mexican spotted owl habitat areas.

Introduction

Wildfires are becoming larger and more severe in the dry forests of the western U.S. due to a combination of warming climate and overstocked, fire-suppressed forests (Westerling et al. 2006, Dennison et al. 2014, Westerling et al. 2016). These new “mega-fires” are ≥10000-ha in size (Stephens et al. 2014*b*), burn at high severities over large areas and have significant regional impacts (Williams et al. 2011). Large fires have historically been an important part of western U.S. dry forest systems (Keane et al. 2008), but modern mega-fires may not replicate historic disturbance regimes. Instead, patches burned at high severity in mega-fires are larger and occur in more regular shapes than in other fires (Dillon et al. 2011, Stephens et al. 2014*b*, Stevens et al. 2017, Singleton et al. 2019).

The overall impact of mega-fires upon wildlife is unclear, but of significant research concern. Forest heterogeneity provided by disturbance, including high-severity fire, promotes species diversity (Tingley et al. 2016). High-severity fire may not affect or even promote foraging, density, abundance, and/or species richness of some forest birds (Smucker et al. 2005, Kotliar et al. 2007, Hanson and North 2008, Fontaine et al. 2009, Sanderlin et al. 2016), small mammals (Kyle and Block 2000, Fontaine and Kennedy 2012), or bats (Buchalski et al. 2013). Some species may depend on high-severity fire for part of their life history (Hanson and North 2008), but many bird (Latif et al. 2016) and small mammal (Borchert et al. 2014) species adapted to low-severity fire regimes appear to respond negatively to high-severity fire.

Fire-adapted species may only benefit from particular conditions related to fire severity and the passage of time after a fire (Hutto and Patterson 2016). The three subspecies of spotted owl (*Strix occidentalis*) appear to be well-adapted to low- and moderate-severity fire regimes (Bond 2016), but there is considerable disagreement about the owl’s relationship to high-severity fire (Ganey et al. 2017). California (*S.o. occidentalis*) spotted owls may forage in patches burned at high-severity preferentially (Bond et al. 2009) or in proportion to availability (Bond et al. 2016, Eyes et al. 2017), and two studies show California spotted owl site occupancy is not significantly impacted by high-severity fire (Lee et al. 2015, Hanson et al. 2018, but see Jones et al. 2019), but rather by post-fire salvage logging. But several other studies have shown that high-severity fire may negatively impact survivorship (Clark et al. 2011, Rockweit et al. 2017) and site occupancy (Clark et al. 2013, Jones et al. 2016) of northern (*S.o. caurina*) and California spotted owls. Foraging California spotted owls may also avoid large patches burned at high severity (Jones et al. 2016). Historically, dry mixed-conifer or pine-oak forests used by Mexican spotted owls (*S.o. lucida*) have burned frequently at low severities, with occasional patches burned at moderate or high severities (Swetnam and Baisan 1996, Kaufmann et al. 2007, Huffman et al. 2015). This pattern of fire may maintain spotted owl nest and roost habitat while opening up small early seral forest patches used for foraging (Roberts et al. 2011, Eyes et al. 2017). Mega-fires result in a different landscape pattern, producing more or larger patches of early seral forest or non-forest. Several mega-fires have burned in Mexican spotted owl habitat in recent years.

Multi-scale habitat models are a relatively new and potentially powerful way to identify how wildlife respond to habitat features in spatially complex landscapes (Wiens 1989, Levin 1992). In these models, each covariate is modeled independently across several spatial scales (i.e. scale-optimized) to determine the ("optimal") scale at which the covariate is most strongly related with the response variable. Each variable then was included in a multi-scale, multi-variate model at its optimal scale (McGarigal 2016). Scale-optimized modeling approaches significantly out-perform those not optimized for scale (McGarigal 2016, Timm et al. 2016). Notably, spotted owl response to disturbance (like fire) may differ depending upon the scale of analysis. Comfort et al. (2016) found that northern spotted owls in Oregon, up to a threshold, foraged in areas with increasing amounts of hard edge (where high-severity fire or salvage logging abutted directly against intact forest) within small (3.2-ha) extents but avoided hard edges at larger spatial extents (up to 829-ha).

To complicate matters, Mexican spotted owl habitat is naturally fragmented (Barrowclough et al. 2006) and patchy at multiple scales. Across the range of the owl populations are often separated by large expanses of unsuitable habitat like open deserts and grasslands. Within populations, territories are often clustered within areas of suitable habitat, like canyon systems, embedded in a matrix of unsuitable or less suitable habitat. Even within territories patches of nest and roosting habitat may lie adjacent to patches of habitat unsuitable for nesting and roosting, but useful for foraging. We should expect the environmental factors selected for or driving habitat selection to vary in importance depending upon the spatial scale of interest (Graf et al. 2005).

Because spotted owls exhibit strong site fidelity (Gutierrez et al. 1995, Bond et al. 2002, Forsman et al. 2002, Blakesley et al. 2006) and have long life spans (Gutierrez et al. 1995), a study of habitat selection immediately after fire may not reflect long-term owl response to fire. Yet of 20 studies of the relationship between all three subspecies of spotted owls and fire cited by Ganey et al. (2017), only four included fires greater than six years old, and only two included fires more than 10 years old. Of those 20 studies, eight had a sample of fewer than 10 owls or 10 burned territories, and one had an unknown sample size. Among studies that report fire severities, only three report ≥ 30%

high-severity fire. The largest fire was 112480-ha. The Rodeo-Chediski fire in central Arizona in 2002 burned 187000-ha, with 36.6% of that area burned at high severity, and affected 20 known territories. This fire thus provides an opportunity to expand on previous studies and investigate longer-term response of a population of owls to a large, severe wildfire.

We used Random Forests (RF) to develop scale-optimized univariate and multivariate models of nest and roost habitat selection by Mexican spotted owls 13-15 years after the Rodeo Chediski fire and used partial dependence plots to characterize owl response to forest structure, forest composition, topography, and fire. RF is an ensemble learning method that uses many bagged (bootstrap-aggregated) decision trees for classification and regression (Breiman 2001). Bagging reduces the over-fitting associated with using a single decision tree for classification. Major advantages of RF in ecological modeling are high classification accuracies and the ability to represent complex interactions between predictor variables and the response variable (Cutler et al. 2007). RF is also robust even when there are many predictors (*p*) and few observations (*n*) (Breiman 2001); in contrast parametric models generally require $n > 10p$ for reasonable statistical power (Peduzzi et al. 1996). RF is increasingly used in a range of applications, including species distribution modeling (Evans and Cushman 2009, Cushman and Wasserman 2018).

Our goal was to determine how the Rodeo-Chediski mega-fire affected nest and roost habitat selection by Mexican spotted owls. Particularly, we were interested in (1) the spatial scale at which fire, forest structure, forest composition, and topography were selected; (2) which habitat elements were most important in site selection; and (3) whether spotted owls selected or avoided areas burned at high severity.

Methods

Study area

Our study took place on an 18800-ha subset of the Rodeo-Chediski fire located approximately 8 km southwest of Heber-Overgaard, AZ and bounded on the north by Arizona State Highway 260, on the west by Forest Service Road 512, and on the south by the Fort Apache Indian Reservation (Figure 1). This area contained all known occupied Mexican spotted owl habitat on National Forest System lands within the fire perimeter (see below). Approximately 14700-ha of the study area were on the Black Mesa Ranger District of the Apache-Sitgreaves National Forest, with the remaining 4100-ha lying on the Pleasant Valley Ranger District of the Tonto National Forest. This area lies entirely within the perimeter of the fire. The dominant topographic feature is the Mogollon Rim. Elevation gradually rises from north to south, reaching 2350-m on the Rim before dramatically plunging down to 1890-m in the upper reaches of Canyon Creek, the only permanent running water. A series of deep canyons are cut into the southern face of the Rim. Occupied spotted owl habitat is protected in the form of Protected Activity Centers (PACs, designated protected areas as defined in U.S. Fish and Wildlife Service 2012). Our study area contained 20 designated PACs before the fire, although it is unknown how many PACs were occupied immediately before the fire. One additional PAC was established in 2014, based on owl locations developed during this study.

The vegetation is characterized by large contiguous stands of ponderosa pine (*Pinus ponderosa*) forest, with pockets of mixed-conifer and pine-oak forest located primarily in canyons and on steep north-facing slopes. The mixed-conifer forests are characterized by ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), and/or white fir (*Abies concolor*). The pine-oak forests are characterized by ponderosa pine and Gambel oak (*Quercus gambelli*). Alligator juniper (*Juniperus deppeana*) and Southwestern white pine (*Pinus strobiformis*) are occasional components of both forest types on the study area. Many burned areas have regenerated into shrubby thickets of young Gambel oak, New Mexico locust (*Robinia neomexicana*), and/or Fendler's buckbrush (*Ceanothus fendleri*), or currently remain as grasslands.

Approximately 23% of the study area burned at high severity (MTBS 2014*a*) (Figure 2). An additional 21% of the study area burned at moderate severity. In addition, 1632-ha, about 8.6% of the study area, were subject to salvage logging, including a total of 65-ha in five PACs. Another 613-ha (3.3%) were re-burned at low severity in May of 2012 by the Bull Flat fire (MTBS 2014*b*), which we ignored for this analysis.

Spotted owl surveys

We surveyed for spotted owls during the 2014-2016 breeding seasons. Spotted owls were primarily detected by nocturnal acoustic surveys (Forsman 1983) in which surveyors visit networks of call points, from which they project spotted owl calls and listen for responses from territorial birds. On our study area, we established a network of 602 call points within 212 grid cells (100-ha each) with the goal of completely surveying the landscape. We surveyed each call point $\geq$4 times each year (spending 10 min at each point) during the April to August portion of the breeding season.

Because acoustic surveys usually yield imprecise locations, we followed up these detections with diurnal nest and roost surveys, commonly known as “walk-in” surveys. Once visually located, we “moused” owls using a standard protocol approved by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2012). The protocol allows surveyors to find nest sites and juveniles or infer if the owls are not nesting. During each season we inferred the number of owl pairs and reproductive status from a combination of acoustic survey and walk-in survey data.

Presence/pseudoabsence data

We obtained 134 precise (recorded using Garmin 62S GPS units) locations (Figure 3) based upon direct visual observations. Most (104) locations were obtained during walk-in surveys and reflect nesting and roosting areas but 30 were nocturnal detections where spotted owls flew into the sight of surveyors at call points. We chose to omit fly-in locations to better represent nesting and roosting habitat. When locations were within 5-m of each other we used only the first location. This left 87 presence locations.

We generated a set of 87 random points (Figure 4) from within the 21 PACs (20 pre-fire PACs and one post-fire PAC) on our study area to use as pseudoabsence points. We limited our pseudoabsence points to PACs because we were interested in capturing fire effects within spotted owl habitat, rather than in the flatter, relatively open forest that characterized much of the area outside PACs (VanDerWal et al. 2008, Stokland et al. 2011).

Habitat covariates

We selected 16 *a priori* covariates to represent the influence of forest composition, forest structure, fire, and topography upon presence of Mexican spotted owls on our study area (Table 1). We derived two forest composition predictors (proportion of dry and mesic mixed-conifer forest cover) from the LANDFIRE Existing Vegetation Type (EVT) layer (LANDFIRE 2018). We used Airborne light detection and ranging (LiDAR) data from 2013 and 2014 to remotely sense vegetation structure and the underlying land surface. Airborne LiDAR data is competitive with traditional stand exams while covering a much larger spatial extent (Hummel et al. 2011) and is available at finer grain sizes (≤10-m) than most satellite imagery. LiDAR also allowed us to directly characterize vertical habitat structure (Vierling et al. 2008, Seavy et al. 2009, North et al 2017) and identify individual large trees and snags (Garcia-Feced et al. 2011). The LiDAR-derived covariates of forest structure measured basal area of large trees (i.e., basal area from trees ≥ 30, 46, or 60-cm diameter at breast height [DBH]), canopy cover (from 2 to 16-m, and above 16-m), and the number of large trees above several thresholds of DBH (≥ 30, 46, or 60-cm) and height (20-m). We chose thresholds of basal area to reflect desired habitat conditions listed in the recovery plan (U.S. Fish and Wildlife Service 2012) and the upper limits of tree diameter observed on our study area (Lommler, unpublished data). We assessed canopy cover at two strata to reflect that spotted owls may avoid high canopy cover in the lower strata while selecting for it in taller strata (North et al 2017). We chose 20-m as a height threshold for large trees because every nest tree we measured on the study area was >20-m height (Lommler, unpublished data). We calculated slope (in degrees) from our LiDAR-based DEM using the DEM Surface Tools (Jenness ENT 2013) toolset in ArcMap 10.6 (ESRI 2017), using Horn's method (Horn 1981). All LiDAR-based rasters used a 10-m pixel size.

We used three predictors to measure the influence of fire and post-fire logging. Relative delta Normalized Burn Ratio (RdNBR, Miller and Thode 2007) provides consistent measurements of severity across fires and greater accuracy in measuring the high severity fire class. RdNBR values from 643-698 have been estimated to represent the lower threshold of the high-severity fire class in the southwestern U.S. (Holden et al. 2009, Pabst 2010, Dillon et al. 2011, Singleton et al. 2019). The high severity fire covariate measured the proportion (0.0-1.00) of the area burned at high severity around each point, which is the most common method of representing fire effects in studies of spotted owls. The proportion salvage logged (0.0-1.00), was acquired from GIS databases for the Apache-Sitgreaves National Forests (Apache-Sitgreaves National Forests GIS data 2018) and Tonto National Forest (Tonto National Forest GIS data 2018). We re-sampled all LANDSAT-based rasters (i.e., LANDFIRE and MTBS), which are based on a 30-m pixel, to a 10-m pixel in order to match the LiDAR data. Mean values at each spatial scale were calculated using the Focal Statistics and Extraction tools in ArcMap.

Univariate scaling

We ran univariate models across multiple scales for each covariate to identify the ("optimal") scale at which each covariate had the strongest predictive relationship with the presence of spotted owls (*sensu* McGarigal et al. 2016). We used the R package randomForest (Breiman and Cutler 2011), with each covariate modeled separately at scales from radius 100-m to 5000-m in increments of 100-m. We compared model performance using the Model Improvement Ratio (MIR, Murphy et al. 2010), which measures the relative predictive strength (represented by mean decrease in out-of-bag error rate) of each variable at each scale, standardized from 0.0 – 1.0.

Because previous studies of habitat selection by Mexican spotted owls at multiple scales (Timm et al. 2016, Wan et al. 2017) used single-covariate logistic regression to perform scale optimization, we also conducted a separate modeling effort using logistic regression to allow for more direct comparison with those studies For logistic regression analysis we generated a spatial autocovariate using the spdep package in R (Bivand 2009), because our presence points were highly clustered on the landscape. This was not necessary for the RF model because it is a non-parametric method that does not assume independent data (Evans et al. 2011). The autocovariate estimated the effect of owl presence at other sample sites upon the probability of presence at each individual site within a 5000-m radius. We inverse-weighted the spatial autocovariate so that the presence of owls at nearby sites had a greater effect than presence at outlying sites.

Habitat selection modeling

Before running multivariate models we calculated pairwise Pearson's correlations among all the covariates at their optimized spatial scales to assess multicollinearity. When two or more covariates were highly correlated (i.e., $|r| \geq 0.7$) we retained those that were more important in our preliminary models. Our final Random Forests model included 9 of the original 16 predictor variables, modeled over 1000 decision trees with 3 (i.e, $\sqrt{p}$) predictors evaluated at each split in each tree (Breiman and Cutler 2011). We evaluated variable importance using the mean percent decrease in classification accuracy when the value of each variable is randomly permuted. We estimated classification accuracy using the out-of-bag error-rate for observations that were not used in construction of a given tree, averaged across all 1000 trees. We reported these results in the form of a confusion matrix that shows overall classification accuracy, false-positive error rate, and false-negative error rate.

Results

Univariate scaling

Owls responded most strongly to slope, all three measures of basal area, both measures of canopy cover, all measures of large trees, live trees ≥20-m tall, high-severity fire, and RdNBR at fine (100 to 300-m) scales (Figure 5). Owls responded to dry mixed-conifer and mesic mixed-conifer most strongly at intermediate (900 – 1000-m) scales, and to snags ≥20-m tall (2600-m) and salvage logging (3400-m) at coarse scales. The strength of spotted owl response to high-severity fire appeared to be complex (Figure 5) but generally decreased with increasing spatial scale. The strength of owl response to RdNBR also decreased with scale. Optimized scales in logistic regression (Appendix A) were similar (within < 300-m of RF scale) for all covariates except for salvage logging (200-m) and snags (100-m).

Habitat selection modeling

In our Random Forest model the most important habitat covariate was basal area of trees ≥30-cm DBH at the 100-m scale, followed by canopy cover from 2 – 16-m height at the 1800-m scale, then dry-mixed conifer forest at the 1000-m scale (Figure 6). Spotted owls selected for higher values of all these covariates (Figure 7, Figure 8).

RdNBR was the most important fire covariate. Within a 200-m radius, owls selected burned forest up to an RdNBR value of about 400 (Figure 7), after which owls selected against increasing RdNBR. An RdNBR value of 400 corresponds to the loss of about 33% of forest canopy compared to the pre-fire state (i.e. moderate-severity fire, Miller et al. 2009). Spotted owls also selected against forest subject to increasing values of salvage logging (at 3400-m scale) and high-severity fire (at 300-m scale).

The RF model was accurate and not strongly biased towards predicting presence or pseudoabsence (Table 2). The out-of-bag estimate of error for the full model was 5.7% (i.e., 14 out of 174 responses were misclassified).

Discussion

At what spatial scales were forest structure, forest type, burned forest, and topography selected by Mexican spotted owls?

Covariates of forest structure were generally most strongly associated with spotted owl nest and roost habitat at fine scales (100-m), with the exception of canopy cover from 2 to 16-m height (1800-m). RdNBR, high-severity fire, and slope were also most important at fine (100-300-m) scales. Timm et al. (2016) suggested that canopy cover's importance at relatively coarse (2700-m) scale in their study might relate to the suitability of foraging habitat. Our results add some additional nuance. Canopy cover from 2 to 16-m height was selected at a coarse scale that indeed suggests use for foraging habitat, while canopy cover above 16-m was selected at fine scales typically associated with nest and roost habitat. Previous studies of Mexican spotted owl nesting habitat consistently identified large trees as an important component of such habitat at relatively fine spatial scales (Seamans and Gutiérrez 1995, May et al. 2004, Ganey et al. 2013, 2016). This may also reflect that such trees were scarcer and more patchily-distributed within the fire perimeter, compared to outside the fire perimeter (Figure 9). Even at the scale of only 100-m the greatest mean canopy cover above 16-m calculated at any presence or pseudoabsence point was only 40.3%. In unburned or less-severely burned landscapes, Mexican spotted owls appear to select areas with much greater canopy cover for roosting or nesting. For example, in the Coconino National Forest, 70.6% of the area within a 100 m radius around 47 nest sites was in the >70% canopy cover class, and another 21.7% of the area was in the 41-70% canopy class (Grubb et al. 1997; see also Seamans and Gutiérrez 1995, May et al. 2004, Ganey et al. 2013, 2016). This level of canopy cover was not widely available on our study area.

Spotted owls selected mixed-conifer forest types at slightly coarser spatial scales (900-1000-m) than they selected basal area, canopy cover, or large trees in general. This spatial scale, which is similar in size to that of the "core area" most heavily used by territorial Mexican spotted owls (Ganey and Dick 1995), may suggest that mixed-conifer forest types may be more important in selection of the home range (2nd--order habitat selection, *sensu* Johnson 1980) than in nest and roost site selection (3rd-order habitat selection). That is, Mexican spotted owls selected nest and roost sites from stands of large trees within the mixed-conifer forest types. Previous studies have noted the importance of mixed-conifer forest in 2nd-order habitat selection (Seamans and Gutierrez 1995, Peery et al. 1999, May and Gutierrez 2002, Ganey et al. 2013) and in the selection of nest and roost sites, including nest trees themselves (Seamans and Gutierrez 1995, Ganey et al. 2000, Ganey et al. 2013). It is also notable that even as spotted owls selected mixed-conifer forests at intermediate scales, very little dry (mean

= 7.75 ha within a 1000-m radius around presence locations) or mesic (mean = 2.17 ha within a 900-m radius around presence locations) mixed-conifer was available to be selected. Owls in this post-fire landscape selected areas containing small remnant patches of mixed-conifer forest with high canopy cover and basal area embedded in a more open landscape.

What were the most important predictors of spotted owl nest and roost habitat?

Basal area of trees ≥30-cm DBH at the 100-m scale was by far the most important predictor of spotted owl nest and roost habitat (Figure 6, Appendix C). It should be noted, however, that this predictor was also highly (>90%) correlated with basal area of trees ≥46 and ≥60-cm DBH, canopy cover ≥16-m height, total trees ≥30, ≥46, and ≥60-cm DBH, and number of live trees ≥20-m tall (all at 100-m scale). This suggests that the most important predictor(s) of spotted owl nest and roost habitat in this area is the presence of large trees. This is consistent with observations from studies of spotted owl nest and roost site selection in Arizona and New Mexico (Seamans and Gutiérrez 1995, Ganey et al. 2000, 2003, 2013, May et al. 2004), and recommendations from the Recovery Plan (U.S. Fish and Wildlife Service 2012).

Canopy cover from 2 to 16-m height and dry mixed-conifer forest were the next most important predictors. Mexican spotted owls selected for canopy cover at the 2 – 16-m stratum, whereas in North et al. (2017) California spotted owls avoided canopy cover at that stratum. It is possible that the 2 – 16-m height stratum in Arizona is not a good ecological analogue for that same stratum in the taller forests of the Sierra Nevada. Mexican spotted owl habitat varies across its geographic range (Ganey et al. 2000, Ganey et al. 2003), owls inhabiting forested landscapes typically selected nest and roost sites in mature mixed-conifer forest (Peery et al. 1999, May and Gutierrez 2002) characterized by high canopy cover (Seamans and Gutiérrez 1995, Grubb et al. 1997, May et al. 2004, Ganey et al. 2013, 2016).

RdNBR, while the most important predictor related to fire, was less important than forest structure or composition. Predictors directly related to forest structure and/or composition will likely be more robust than simply measuring fire severity. This is likely due to a number of factors. While RdNBR is a robust measure of vegetation mortality, areas burned at similar severity may result in different forest structure based upon the starting condition (Comfort et al. 2016). The same measured fire severity may also result in different forest structure depending on forest type (Kane et al. 2013). Owls are likely directly selecting for forest structure when they select nest and roost sites, and fire severity is only partially correlated with the resultant forest structure.

Did Mexican spotted owls select or avoid areas burned at high severity or salvage logged?

Mexican spotted owls had a complex relationship with fire. Owls responded positively to increasing RdNBR values up to a threshold of about 400 within a 200 m radius around points. At values >400 owls responded negatively. Owls also responded negatively in linear fashion to even relatively low amounts (<20%) of high-severity fire at fine scales around points. These contradictions are curious, but we are not the first authors to find that spotted owls (or other animals) respond differently to fire depending upon spatial and/or temporal scale (Comfort et al. 2016, Hutto and Patterson 2016) or threshold effects (Lee et al. 2013). It is possible that high-severity fire only has a significant negative effect on MSO when concentrated around nest and roost sites (at fine scales) or in very large, contiguous patches (at coarse scales). This is consistent with suggestions made by Jones et al. (2016) and Rockweit et al. (2017). Otherwise, high-severity fire may produce a landscape mosaic that includes a balance of nesting, roosting, and foraging habitat. For example, northern spotted owls may maximize their fitness when their territories included a mixture of mature forest stands used for nesting and early-seral forest types created by disturbance and used for foraging (Franklin et al. 2000).

An alternative explanation for the complex association between fire and owl presence is that forest types selected by spotted owls on our study area are more likely to burn at high severity than other forest types. Spotted owl habitat in northern Arizona typically includes steep canyons and relatively dense mixed-conifer forest stands. These forest types are more susceptible to severe fire than surrounding ponderosa pine forests (Kaufmann et al. 2007). Thus, the remnant patches of mixed-conifer forest in canyons used by owls in this study may be more likely to occur adjacent to severely burned patches than random patches on the landscape. This may create the appearance of a positive association between fire severity and the presence of spotted owls even if the actual relationship is negative, or possibly understate negative fire effects. If this is the case, our results may be confounded. Restricting our pseudoabsence points to PACs should minimize this confounding, however. By definition PACs are designated to include concentrated areas of spotted owl habitat (USDI FWS 2012). This suggests that the observed fire effects are real.

Previous studies of northern and California spotted owls (*Strix occidentalis occidentalis*) have consistently found that those subspecies are negatively affected by salvage logging (Clark et al. 2013, Lee et al. 2013, Lee and Bond 2015, Hanson et al. 2018, Lee 2018). In our study salvage logging was a less important predictor of spotted owl presence than RdNBR, and, similar to fire, we found a complex relationship between salvage logging and owl presence (Figure 8), though higher levels of salvage logging (> 10% area at 3400-m scale) were associated with lower rates of owl presence. Salvage logging occurred on only 8% of our study area, however, including only 65 ha on 5 of the 20 pre-fire PACs. Because both our presence and pseudoabsence points occurred primarily within PACs, where salvage logging was very limited, our ability to detect an owl response to salvage logging was low. Consequently, our results should not be interpreted as minimizing the potential effects of salvage logging.

Conclusions

The relationship between spotted owls and wildfire is complex. There is now considerable evidence that low- and moderate-severity fire has little effect on spotted owls (Bond 2016, Ganey et al. 2017). Our results indicate that high-severity fire and Mexican spotted owls are not necessarily incompatible, depending upon the scale of inference and the spatial location and configuration of the fire. But sufficiently severe fire within 200-300 m of a point appears to have significant negative effects upon Mexican spotted owls. Some previous studies may not have captured these effects because they used a different sampling frame or because the fire effects were not as severe as the Rodeo-Chediski fire.

Because large, contiguous patches of high-severity fire may have significant negative effects upon Mexican spotted owls, we recommend that land managers continue to utilize prescribed fire, managed natural fire, and fuels treatments to return southwestern forests to their historic fire regimes and establish fuel breaks to prevent large, contiguous patches of spotted owl habitat from burning at high severity. Fuel treatments within spotted owl habitat may negatively affect owls in the absence of fire (Stephens et al. 2014*a*, Tempel et al. 2014) but may have long-term benefits when fires occur in extreme weather conditions (Tempel et al. 2015). Important elements of forest structure like high basal area, large trees, and canopy cover should be maintained at fine scales around spotted owl nest and roost sites while still managing for resilience to fire.

Spotted owls in our post-fire landscape generally selected for the same types of habitat elements used by owls for roosting and nesting in unburned landscapes (e.g., large trees and high canopy cover; Seamans and Gutiérrez 1995, Grubb et al. 2017, May et al. 2004, Ganey et al. 2013, Timm et al. 2016, Wan et al. 2017), but the availability of those habitat elements may be reduced in post-fire landscapes. We found spotted owls selecting areas of higher canopy cover at finer scales than previously observed in northern Arizona (Timm et al. 2016). These forest patches also had lower canopy cover than typically observed in spotted owl habitat (Seamans and Gutiérrez 1995, Grubb et al. 2017, May et al. 2004, Ganey et al. 2013), although direct comparisons among studies are hampered by differences in estimation methodology. Spotted owls selected dry and mesic-mixed conifer forests at intermediate scales, but there was relatively little area of these forest types to select. After fire, Mexican spotted owls may be able to persist on or colonize relatively small patches of mature mixed-conifer forest, or use networks of small patches in the absence of larger patches. Managers should take care to protect even small patches of these habitat elements after fire events. Still unknown, however, is whether or not these post-fire landscapes provide habitat in sufficient quantity and quality to support viable populations of Mexican spotted owls. indicating the need for long-term studies of owl demography and habitat relationships in these post-fire landscapes (Ganey et al. 2017, Wan et al. 2018).

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Tables

Table 1. Predictor variables used for multi-scale analysis. Predictors are presented in order of the optimal scale, from lowest to highest. Optimal scale is the radius of a circle at which the variable has its strongest relationship with presence of Mexican spotted owls, as determined by model improvement ratio (MIR). Mean values based upon a 10-m pixel size. Covariates marked with an asterisk (*) were included in the final Random Forest model. Year reflects when data was collected, rather than when published.

Predictor	**Units and definition**	**Source (year)**	**Optimized scale (m)**	**MIR**
BA (≥30-cm)*	Mean basal area in m^2/ha of trees ≥30-cm DBH	LiDAR (2013/14)	100	0.046
BA (≥46-cm)	Mean basal area in m^2/ha of trees ≥46-cm DBH	LiDAR (2013/14)	100	0.043
BA (≥60-cm)	Mean basal area in m^2/ha of trees ≥60-cm DBH	LiDAR (2013/14)	100	0.048
CC (≥16-m)	Percent canopy cover at ≥16-m height	LiDAR (2013/14)	100	0.046
CC (2-16-m)*	Percent canopy cover from 2-16-m height	LiDAR (2013/14)	1800	0.036
Trees (≥30-cm)	Number of trees ≥30-cm DBH	LiDAR (2013/14)	100	0.046
Trees (>46-cm)	LiDAR (2013/14)	LiDAR (2013/14)	100	0.045
Trees (>60-cm)	Number of trees ≥60-cm DBH	LiDAR (2013/14)	100	0.047
DMC*	Proportion dry mixed-conifer forest cover	LANDFIRE (2014)	1000	0.035
HSF*	Percent area burned at high severity	MTBS (2014)	300	0.032
MMC*	Proportion mesic mixed-conifer forest	LANDFIRE (2014)	900	0.030
RdNBR*	Mean value of Relative delta Normalized Burn Ratio	MTBS (2014)	200	0.037
Salvage*	Proportion of area salvage logged	USFS GIS database (2017)	3400	0.029
Slope*	Slope of area in degrees	LiDAR (2013/14)	300	0.035
Snags (≥20-m)*	Number of dead trees ≥20-m in height	LiDAR (2013/14)	2600	0.027
Live trees (≥20-m)	Number of live trees >20-m in height	LiDAR (2013/14)	100	0.043

Table 2. Confusion matrix showing classification error rates from a Random Forest model of Mexican spotted owl habitat selection. The false-positive error rate was 4.5% and the false-negative error rate was 6.8%. Overall classification accuracy was 94.2%.

	Predicted		**Classification error**
	Absent	**Present**	
Absent	83	4	0.045
Present	6	81	0.068

Figures

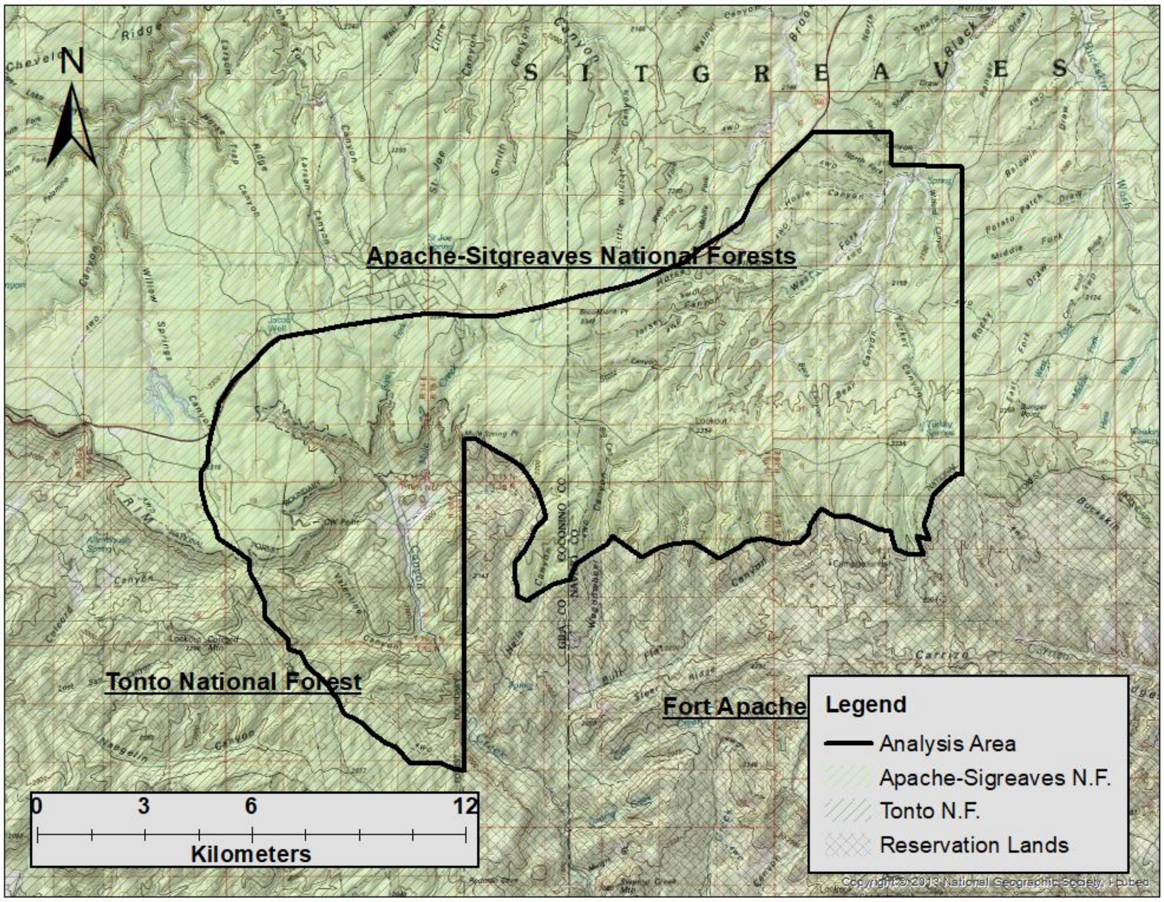

Figure 1. The study area lies on the Apache-Sitgreaves and Tonto National Forests, adjacent to the Fort Apache Indian Reservation.

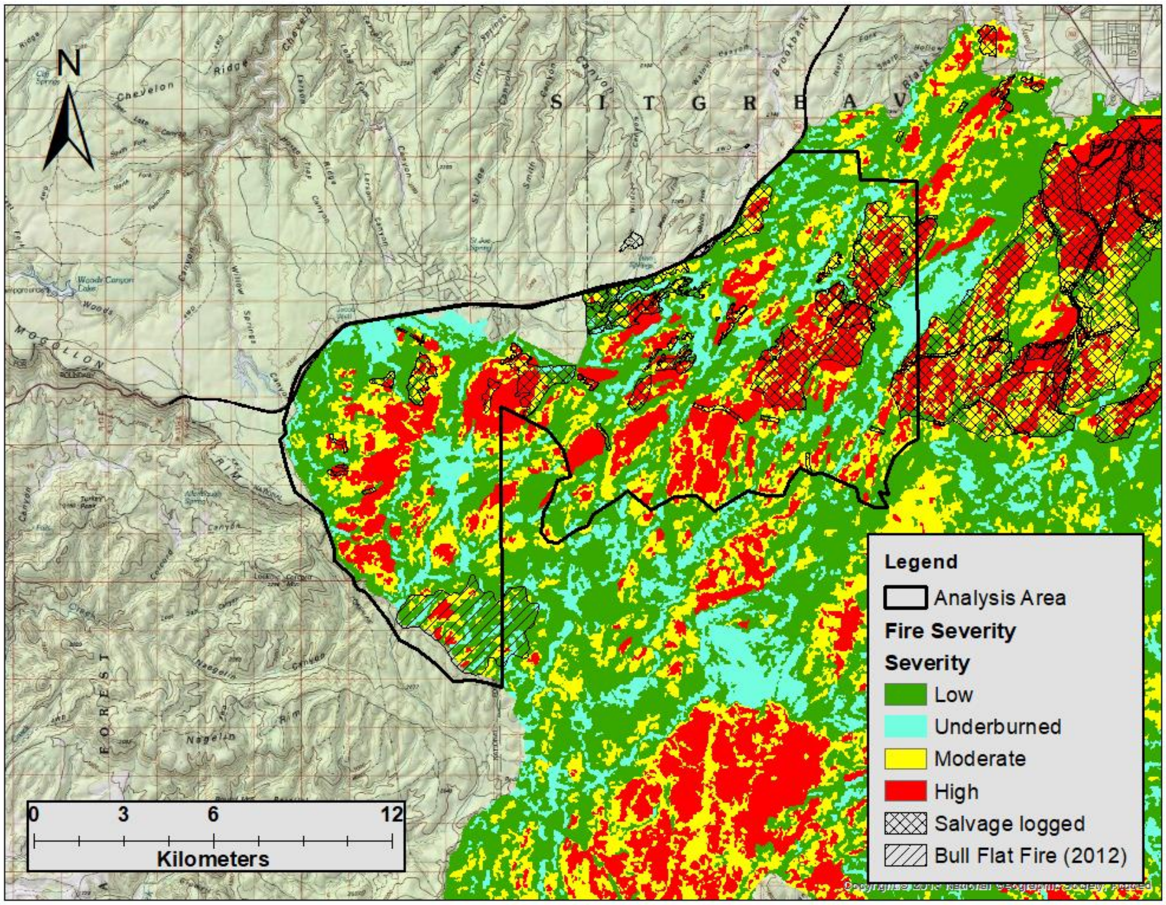

Figure 2. Fire severity within the Rodeo-Chediski fire in and around the study area. Approximately 23% of the study area burned at high severity.

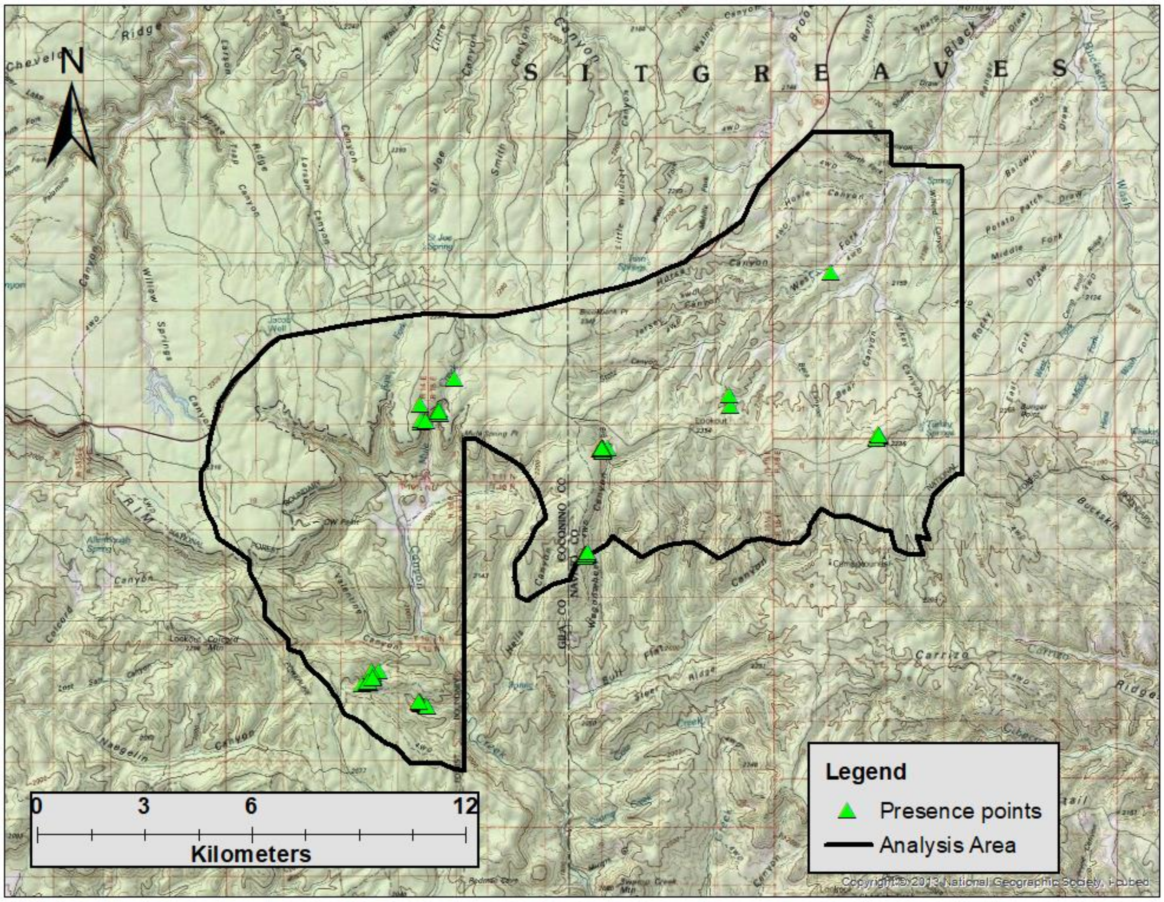

Figure 3. Distribution of 87 presence points used to model MSO habitat selection. Presence points were based upon visual detections of owls from diurnal surveys only. We used a spatial autocovariate in our linear model to account for the clustered nature these points.

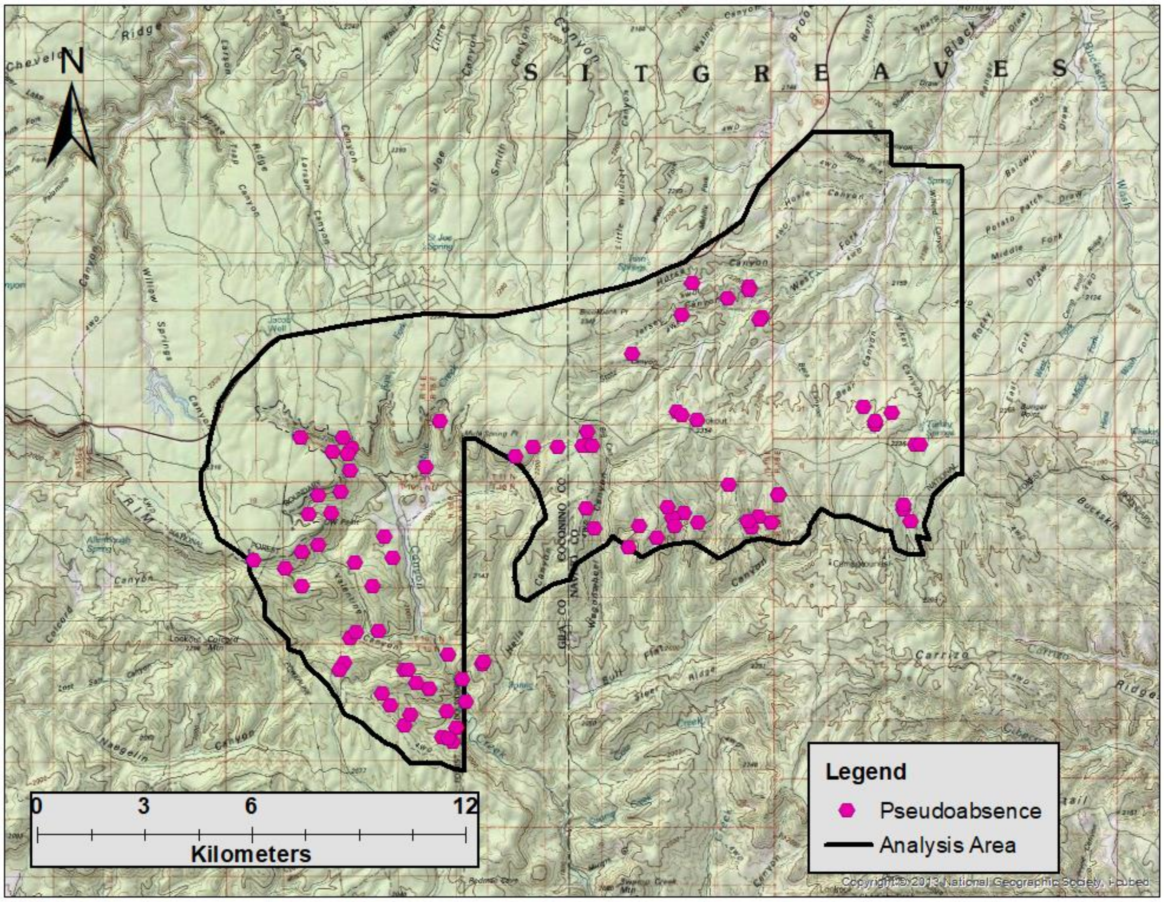

Figure 4. Distribution of 87 pseudoabsence points used to model MSO habitat selection. These points were randomly generated within the 21 PACs on our study area.

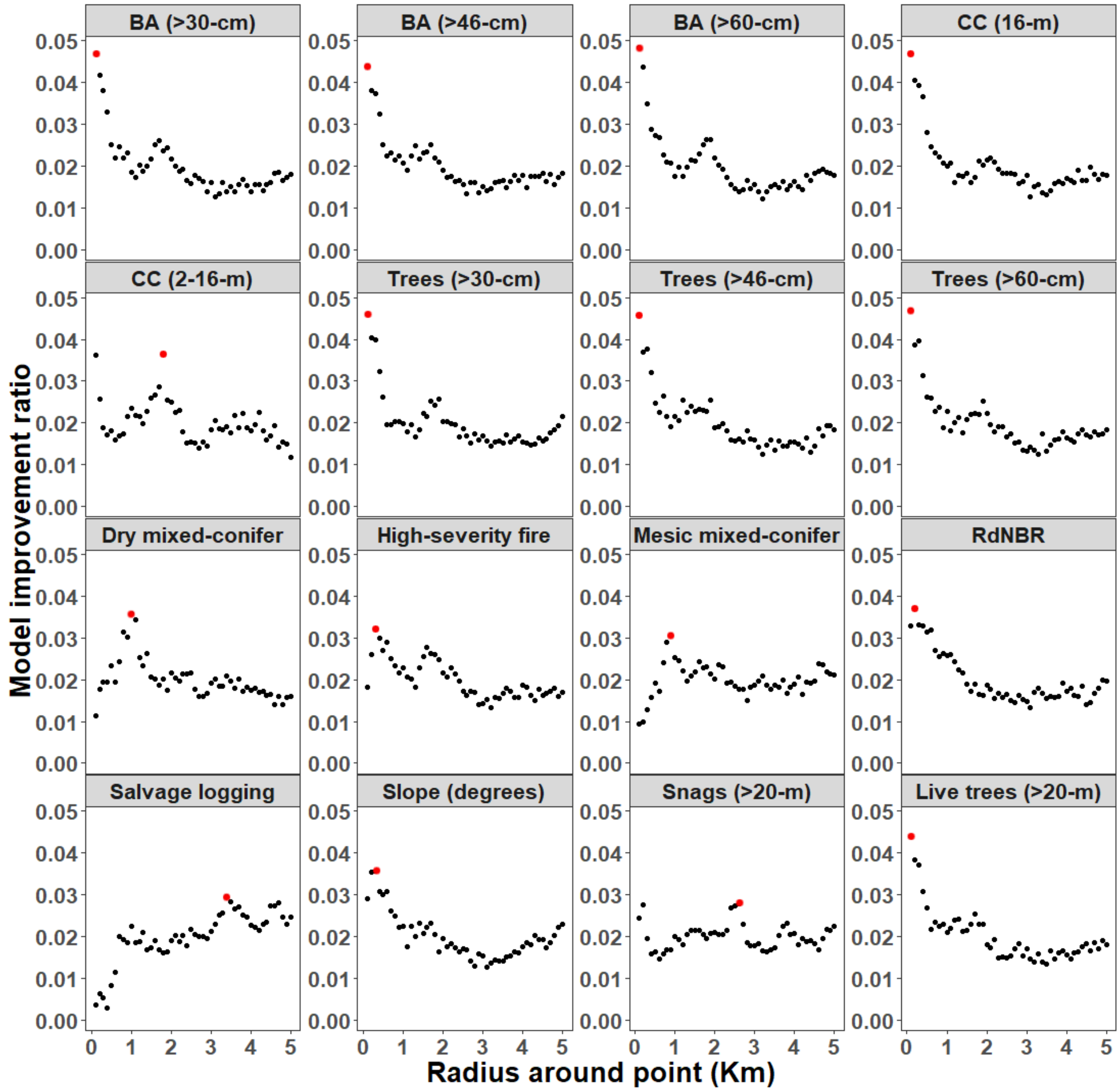

Figure 5. Univariate scaling analysis using Random Forests. Y-axis is model improvement ratio, which is the decrease in permuted model accuracy for each scale divided by the total for all scales. Greater values are better. The optimum spatial scale for each covariate is highlighted in red.

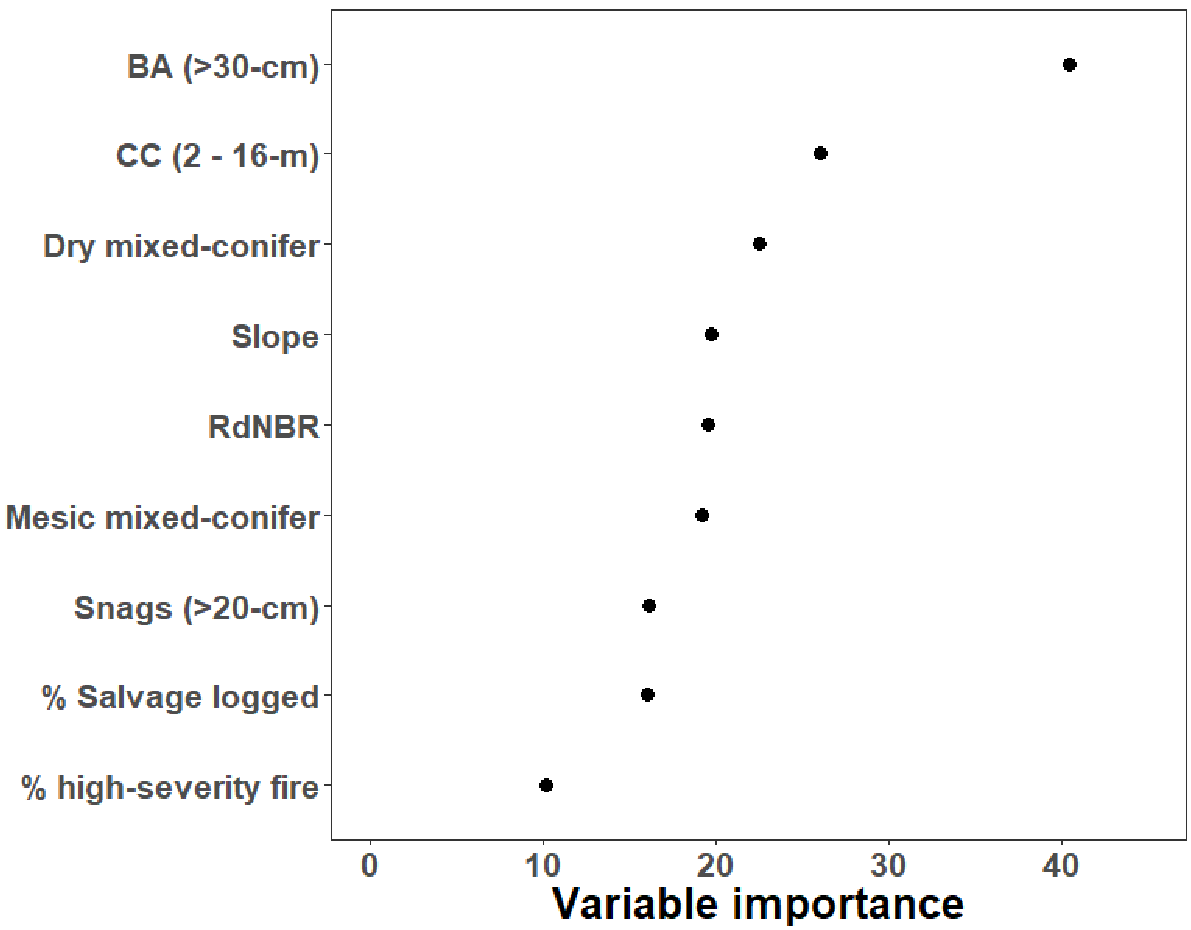

Figure 6. Estimates of variable importance from a Random Forests model of Mexican spotted owl habitat selection. Variable importance is the mean decrease in model accuracy when values of a predictor variable are randomly permuted (effectively removing the predictor from the model). Higher values indicate that the covariate is a more important component of the model.

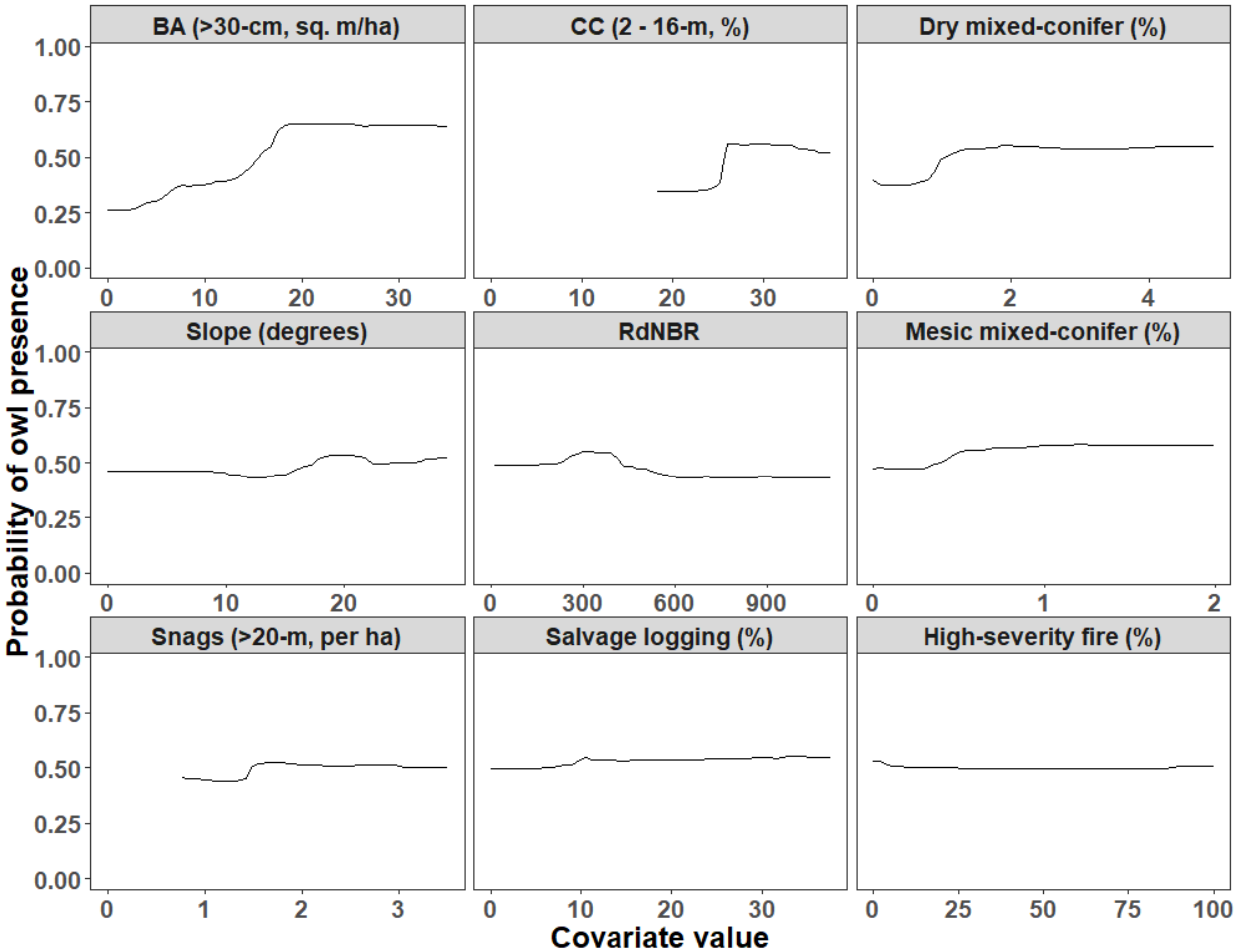

Figure 7. Partial dependence plots showing the relationship between 9 covariates and the probability of presence of Mexican spotted owls. Covariates (x axis) are shown at the optimized scale. Plots are shown in order of variable importance. Spotted owl presence was positively correlated with greater basal area of trees ≥30-cm, higher amounts canopy cover (from 2-16-m), and both dry and mesic mixed-conifer forest. Within 200-m about a location, owls responded positively to increasing RdNBR values up to about 400, after which they responded negatively.

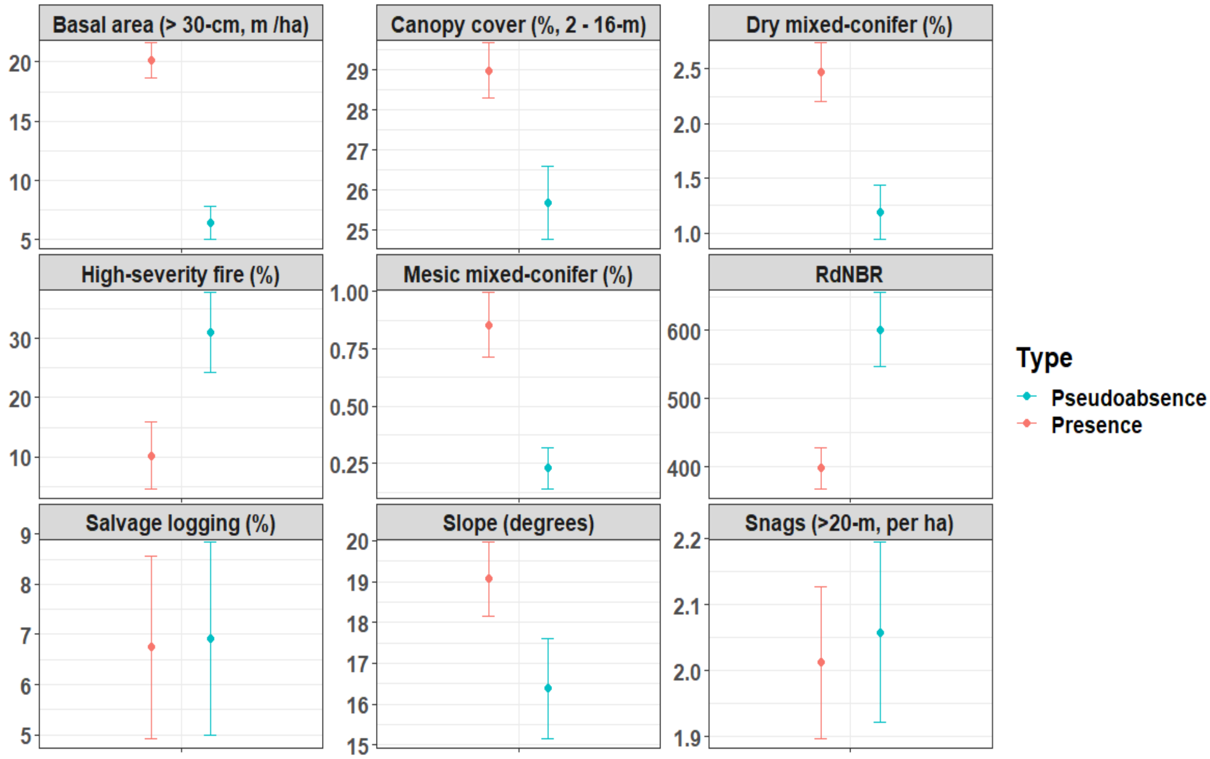

Figure 8. Means and 95% confidence intervals of 9 covariates in the final RF model at their optimized scale, with presence points in red and pseudoabsence points in blue. Variables are presented in order of model importance.

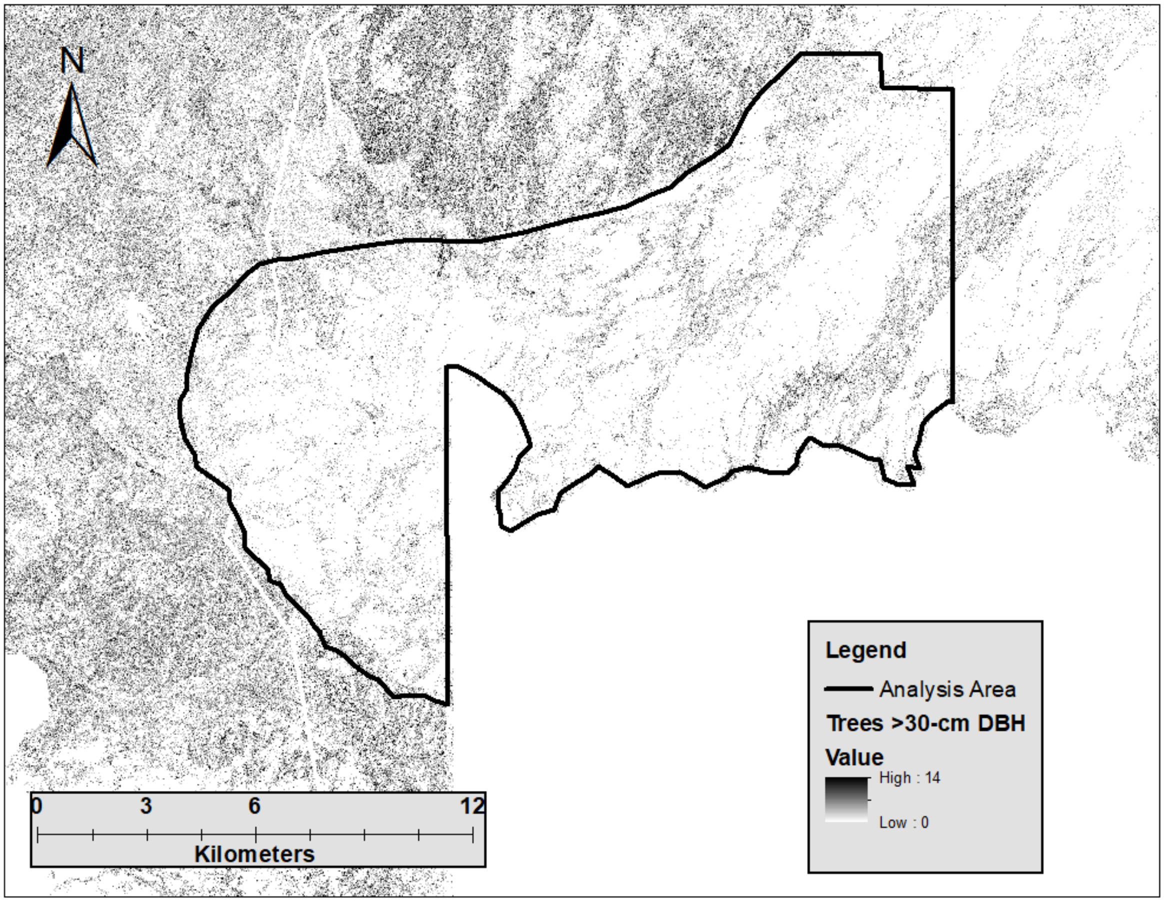

Figure 9. Per-pixel (10 x 10-m) density of trees ≥30-cm DBH inside and outside the study area (and fire perimeter). LiDAR data was not available on reservation lands.

Appendices

Appendix A. Univariate scale analysis of nine covariates using a generalized linear model (GLM). Regression was performed using the R package glmulti, which performs automatic model selection for generalized linear models (Calcagno and de Mazancourt 2010). The package evaluated all possible model combinations using Akaike's Information Criterion corrected for small sample size (AIC*c*, Burnham and Anderson 2002). Functional form describes whether the relationship between the covariate and owl presence was best-modeled as linear or quadratic. Variables are presented in order of AIC*c*. Covariates of basal area, canopy cover (≥16-m tall), large trees (≥30, ≥46, ≥60-cm DBH), and tall live trees (≥20-m tall) were highly correlated (>0.7). We retained basal area (≥30-cm DBH) in the multivariate model because it explained the most deviance. Retained covariates are marked with an asterisk (*).

Covariate	**Scale (m)**	**Functional form**	**AIC*c***
Basal area (≥30-cm DBH)*	100	Linear	134.5
Canopy cover (≥16-m tall)	100	Linear	139
Basal area (≥46-cm DBH)	100	Linear	145.4
Trees (≥46-cm DBH)	100	Linear	149.5
Trees (≥30-cm DBH)	100	Linear	150.4
Live trees (≥20-m tall)	100	Linear	150.7
Basal area (≥60-cm DBH)	100	Linear	163.9
Trees (≥60-cm DBH)	100	Linear	166.1
Mesic mixed-conifer*	900	Linear	210.6
Dry mixed-conifer*	1100	Linear	214.1
RdNBR*	100	Quadratic	214.1
Canopy cover (2-16-m tall)*	1800	Linear	228.3
High-severity fire*	300	Linear	238.1
Slope*	100	Linear	242.1
Snags (≥20-m tall)*	100	Linear	250.2
Salvage logging*	200	Linear	255.2

Appendix B. Results from a generalized linear model (GLM) of Mexican spotted owl habitat selection. Models with ΔAICc < 2.0 were considered jointly supported; collectively these models comprised 69% of the model weight. BA = basal area of trees ≥30-cm DBH, CC_low = canopy cover from 2-16-m, DMC = dry mixed-conifer, HSF = high-severity fire, MMC = mesic mixed-conifer, RdNBR = Relative delta Normalized Burn Ratio (quadratic), Salvage = salvage logging, Slope = slope (in degrees), SAC = spatial autocovariate.

Rank	**Model components**	**AIC*c***	**ΔAIC*c***	**AIC weight**
1	Intercept + BA + DMC + MMC + RdNBR + Slope + SAC	81.292	0.000	0.074
2	Intercept + BA + DMC + MMC + Salvage + Slope + Snags + SAC	81.370	0.078	0.072
3	Intercept + BA + DMC + MMC + RdNBR + Salvage + Slope + Snags + SAC	81.524	0.233	0.066
4	Intercept + BA + DMC + MMC + Slope + Snags + SAC	81.542	0.250	0.066
5	Intercept + BA + DMC + MMC + RdNBR + Slope + Snags + SAC	81.560	0.268	0.065
6	Intercept + BA + DMC + MMC + Slope + SAC	81.733	0.441	0.060
7	Intercept + BA + DMC + MMC + RdNBR + Salvage + Slope + SAC	81.753	0.462	0.059
8	Intercept + BA + DMC + MMC + Salvage + Slope + SAC	82.113	0.821	0.049
9	Intercept + BA + DMC + HSF + MMC + Slope + SAC	82.350	1.058	0.044
10	Intercept + BA + DMC + HSF + MMC + Slope + Snags + SAC	82.544	1.252	0.040
11	Intercept + BA + DMC + HSF + MMC + Salvage + Slope + Snags + SAC	82.779	1.487	0.035
12	Intercept + BA + DMC + HSF + MMC + Salvage + Slope + SAC	83.098	1.806	0.030
13	Intercept + BA + DMC + HSF + MMC + RdNBR + Slope + SAC	83.168	1.876	0.029

Appendix C. Means and 95% confidence intervals for model-averaged coefficients from a generalized linear model of Mexican spotted owl habitat selection. Covariates were optimized for scale. Covariates with 95% confidence intervals that do not overlap zero are marked with an asterisk (*).

Covariate	**Optimized scale (m)**	**Estimate**	**95% Lower**	**95% Upper**
Intercept*	N/A	0.51507	0.45285	0.57729
Basal area (≥30-cm)*	100	0.20739	0.14823	0.26655
Spatial autocovariate*	N/A	0.11836	0.05330	0.18342
Mesic mixed-conifer*	900	0.09470	0.04073	0.14868
Slope*	100	0.07485	0.02206	0.12763
Dry mixed-conifer*	1100	0.07263	0.01260	0.13267
Canopy cover (2-16-m)	1800	-0.00130	-0.01745	0.01485
High-severity fire	300	-0.00769	-0.03881	0.02342
Salvage logging	200	-0.01461	-0.05622	0.02701
RdNBR	100	-0.01516	-0.05773	0.02742
Snags (≥20-m)	100	-0.02126	-0.07649	0.03398

Synthesis

We set out to address how the Rodeo-Chediski fire has influenced the breeding population, site occupancy, and habitat selection of Mexican spotted owls (*Strix occidentalis lucida*) 13-15 years after the fire. We established an 18000-ha study area around the 20 pre-fire PACs on the Apache-Sitgreaves and Tonto National Forests and surveyed for spotted owls during the April-August breeding seasons from 2014-2016. We used acoustic surveys to locate owls and diurnal surveys to locate nest and roost locations and to evaluate nesting and fledging success, and compared our survey data with the results of surveys performed by the U.S. Forest Service starting in 1990. We also used acoustic surveys to generate detection histories for a set of 1-km^2 (100-ha) grid cells distributed across our study area, and for an 800-m radius (201-ha) around a set of 22 known owl territories. We used those detection histories to create grid and territory-based models of site occupancy (MacKenzie et al. 2002) from 2014-2016. Finally, we used locations of spotted owls from diurnal surveys to generate a scale-optimized Random Forest (Breiman 2001) model of nesting and roosting habitat on our study area.

Observed (unmodeled) site occupancy rates were significantly lower post-fire on sites inside the fire perimeter compared to sites outside the fire perimeter (Ch. 2, Figures 6-7). Naïve site occupancy by pairs inside the fire perimeter was >50% lower from 2014-2016 than it was prior to the fire. Fecundity was not significantly different before or after the fire, inside or outside the fire perimeter (Ch. 2, Figure 8).

Both the grid and territory-based occupancy models showed no significant trend in site occupancy from 2014-2016 (Ch. 3, Figure 7). Cover of dry mixed-conifer forest and salvage logging were the only predictors in the grid-based model with Bayesian Critical Intervals (BCIs) that did not include zero (Ch. 3, Table 2). Largest patch index was the only direct measure of fire that was an important predictor in the grid-based model. Mesic mixed-conifer and slope were also important predictors. The posterior mean estimate of the relationship between salvage logging and spotted owl site occupancy was negative; the relationship with largest patch index was positive. In the territory-based model mesic mixed-conifer, Relative delta Normalized Burn Severity (RdNBR), slope were the only important predictors (Ch. 3, Table 3), but the BCIs of all three predictors included zero.

We found that spotted owls on our study area selected forest structure associated with large trees, slope, and direct measurements of fire severity at fine (100-300-m) spatial scales (Ch. 4, Table 1 and Figure 5). Owls selected canopy cover from 2 to 16-m high at the 1800-m scale and large snags at the 2600-m scale. Owls responded most strongly to dry and mesic mixed-conifer forest cover at intermediate (900-1000-m) scales. They responded most strongly to salvage logging at the 3400-m scale. Basal area of trees ≥30-cm DBH around nest and roost sites was the most important factor in habitat selection by Mexican spotted owls, followed by canopy cover from 2 to 16-m height, cover of dry mixed-conifer forest, slope, and RdNBR (Ch. 4, Figure 6). The predicted probability of owl presence was nearly 0.75 when basal area of trees ≥30-cm DBH was 20-m^2/ha or more (Ch 4., Figure 7). Spotted owls also selected for greater values of canopy cover and cover of dry-mixed conifer forest. Spotted owls selected forest burned up to an RdNBR value of about 400 but at greater values the predicted probability of owl presence declined by about 10%.

Our results indicate that the Rodeo-Chediski fire drove a reduction in the number of sites occupied by spotted owls on our study area. 13-15 years after the fire, the occupancy trend was not perceptibly decreasing, which suggested that the fire was not causing a lingering extinction debt (Tilman et al. 1994, Jones et al. 2018). But fire still appeared to shape habitat selection by spotted owls. Owls were less likely to be found nesting or roosting at locations that burned at RdNBR values greater than 400 within a 200-m radius.

Ours is the first study to document a clear, albeit complex, negative relationship between fire and Mexican spotted owls. Previous studies have found that Mexican spotted owls were unaffected by fire (Bond et al. 2002), found a negative but statistically insignificant relationship (Jenness et al. 2004), or observed owls foraging in burned areas (Ganey et al. 2014*a*). Our study differs from these previous efforts in several important ways. First, the Rodeo-Chediski fire was an extreme fire event, with large patches burned at high severity. There is growing evidence that fires with large, contiguous patches burned at high severity may have a negative effect upon spotted owls (Jones et al. 2016, Rockweit et al. 2017). Second, we performed our surveys 13-15 years after the fire, and were able to make used of data going back to 1990. Most studies of spotted owls and fire take place within the first six years after a fire (Ganey et al. 2017). The full impact of a given fire upon spotted owls may not be immediately clear because spotted owls exhibit high site fidelity (Bond et al. 2002, Blakesly et al. 2006, Ganey et al. 2014*b*), even after fires. By studying owls 13-15 years post-fire, our results should not be confounded by site fidelity effects. Finally, in Chapter 4 we optimized for scale. It is notable that the optimum scales we found for high-severity fire and RdNBR were 300-m and 200-m, respectively. Most studies of site occupancy model at larger spatial scales (~800-m, Lee et al. 2012, Lee et al. 2013, Lee et al. 2015). Our scale-optimized models also found clearer fire effects than our occupancy models, neither of which was optimized for scale.

Because Mexican spotted owl habitat is naturally patchy (Barrowclough et al. 2005) it can be difficult to reliably detect fire effects. Future research should emphasize surveying both burned and unburned sites and attempt to optimize for spatial scale when modeling site occupancy or habitat selection. We also believe that demography data should be a priority in future research into the Mexican spotted owl's relationship with fire (Wan et al. 2018). While site occupancy appeared to be stable from 2014-2016, observed fecundity may not have been sufficient to sustain the owl population on our study area. The population may be sustained by immigration from outside the study area. Without demographic data, we cannot be sure. Information on adult and juvenile survivorship rates is also critical to understanding just how fire affects spotted owls.

Some level of high-severity fire may help maintain Mexican spotted owl habitat over large temporal and spatial scales. However, large patches of high-severity fire may present a threat to the recovery of the owl (Jones et al. 2016, Rockweit et al. 2017). We urge land managers to continue efforts to increase the fire-resiliency of southwestern forests, both between and within Mexican spotted owl home ranges. Forests in Mexican spotted owl habitat should also be managed for the restoration of critical habitat elements, including a balance of nesting, roosting, and foraging habitat. Fuel treatments within spotted owl habitat appear to negatively affect owls in the absence of fire

(Stephens et al. 2014, Tempel et al. 2014) but may have long-term benefits when fires occur in extreme weather conditions (Tempel et al. 2015).

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