THESIS

OCCUPANCY DYNAMICS OF BARRED OWLS ON A SPOTTED OWL LANDSCAPE

Submitted by

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ABSTRACT

OCCUPANCY DYNAMICS OF BARRED OWLS ON A SPOTTED OWL LANDSCAPE

Invasive barred owls (*Strix varia*) pose a significant threat to native northern spotted owls (*Strix occidentalis caurina*) in western North America. Barred owls compete with northern spotted owls for resources and habitat, leading to displacement and subsequent declines in northern spotted owl populations. This impact highlights the need for conservation efforts to mitigate the negative consequences of barred owl presence in spotted owl habitats. In my thesis, I explored barred owl habitat use in northern California using data on both lethal removals of barred owls and barred owl occupancy of non-removal areas from long-term studies. These studies provided a unique opportunity to study associations of barred owl land use both during initial colonization and over time. Barred owl land use was influenced by landscape factors such as topographic water accumulation, forest age, tree composition, and canopy cover as well as interspecific effects of northern spotted owls. I used these results to predict variation in barred owl use of landscapes, which can then focus barred owl management efforts in California.

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THESIS INTRODUCTION

Northern Spotted Owl and the Northwest Forest Plan

The spotted owl (S*trix occidentalis*) is native to western North America and is considered one of the most studied owl species (Gutierrez et al. 1995). A spotted owl subspecies, the northern spotted owl (*Strix occidentalis caurinai*; NSO) is a nonmigratory, territorial, medium-sized owl native to western North America from British Columbia to Marin County, California (Gutierrez et al. 1995). Northern spotted owls are habitat specialists associated with mature and old-growth forest and mainly prey on Humboldt's flying squirrel (*Glaucomys oregonensis*) and woodrats (*Neotoma sp.*) (Courtney et al. 2004).

Due to the high value of old growth timber, forests used by NSOs were heavily logged and, by 1990, these forests had been reduced by 60% (Thomas et al. 1990). Over concerns of habitat loss, Federal Endangered Species Act listing of the NSO was petitioned but denied twice (1982, 1987) before finally being federally listed as threatened in 1990 (Thomas et al. 1990, U.S. Fish and Wildlife Service 1990, Gutierrez et al. 1995). At the time of listing, the U.S. Fish and Wildlife Service (USFWS) cited habitat loss and fragmentation as the most important factors threatening NSO populations, although critical habitat was not designated until 1992 (U.S. Fish and Wildlife Service 1990, Franzreb 1993). In 1994, the Northwest Forest Plan (NWFP) was adopted to protect and manage old growth forests on public land in the northwest, including NSO habitat, and to create wildlife monitoring programs (U.S. Department of Agriculture and U.S. Department of the Interior 1994). Each of these determinations were controversial due to the

perceived economic impact on the logging industry by the federal protection of NSO populations (Bonnett and Zimmerman 1991, Ferris and Frank 2021).

The NWFP Effectiveness Monitoring Program selected eight established NSO demographic studies to monitor trends in NSO populations (Lint et al. 1999). Demographic studies of NSOs throughout the NSO range started in 1985 (Anthony et al. 2006) and many were sufficiently standardized to be used in a meta-analysis to track range-wide population trends (Franklin et al. 2021b). Meta-analyses started in 1991 and occur approximately every 5 years, with 7 completed to date (Franklin et al. 2021b). The most recent meta-analysis found NSO populations declining in all study areas after 2010; in most of the study areas, NSO populations in 2017 were only 20-30% of their populations in 1995 (Franklin et al. 2021b). The small population size and continued decline caused urgent concern for the future of the subspecies. In 2020, the USFWS concluded that listing the NSO as endangered was "warranted but precluded by higher priority actions" (U.S. Fish and Wildlife Service 2020). The USFWS identified competition with barred owls and high-severity wildfires as additional important stressors to NSO populations and habitat that warranted NSO up-listing from threatened to endangered.

Northern Spotted Owls and the Barred Owl Invasion

The barred owl (*Strix varia*; BO) is a nonmigratory, territorial, medium-sized owl closely related to the spotted owl (Mazur and James 2021). Originally native to the eastern and midwestern United States, western range expansion of BOs began in the early 1900s through southern Canada, into the Pacific Northwest, and south along the west coast of the United States (Livezey 2009a). The first confirmed detections of BOs occurred in Washington in 1965, Oregon

in 1972, and California in 1981 (Dark et al. 1998, Livezey 2009a). The BO range now completely overlaps the range of the NSO and part of the range of the California spotted owl (*S. o. occidentalis*) (Dark et al. 1998, Seamans et al. 2004, Livezey 2009a, Hofstadter et al. 2022). BO range expansion across the Great Plains was facilitated by an increase in riparian forest in the Great Plains through fire suppression, fire exclusion, and tree planting by European settlers, as well as extirpation and reduction of native wildlife (Livezey 2009b). BO's effect on NSOs in their expanded range causes a "conservation conundrum" (Gutierrez et al. 2007) because of the negative effect one expanding, native species is having on another native species.

BOs occupy smaller home ranges (Hamer et al. 2007), are more aggressive (Van Lanen et al. 2011), use more diverse habitat (Buchanan et al. 2004, Hamer et al. 2007), eat more diverse prey (Hamer et al. 2001, Baumbusch 2023), and produce more offspring than NSOs (Wiens et al. 2014). Therefore, researchers speculated that BOs negatively affect NSOs through resource competition, displacement, predation, and hybridization (Taylor and Foresman 1976, U.S. Fish and Wildlife Service 1990, Dark et al. 1998, Gutierrez et al. 2007, Van Lanen et al. 2011). BOs negatively affect NSO occupancy of their territories (Kelly et al. 2003, Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011), detection probability (Crozier et al. 2006, Bailey et al. 2009), apparent survival (Anthony et al. 2006, Dugger et al. 2016, Franklin et al. 2021b), recruitment, and fecundity (Franklin et al. 2021b).

Barred Owl Management

The USFWS prescribed BO removal as a recovery action to experimentally determine the effects of BOs on NSOs, evaluate the feasibility of the cost and effort of BO removal, and inform

future BO management strategies to protect the NSO (U.S. Fish and Wildlife Service 2008;2013). The large number of established NSO demographic studies made it possible to conduct BO removal experiments using a Before-After-Control-Impact (BACI) design. A pilot BO removal study occurred in 2009 (Diller et al. 2014), and a large-scale BO removal experiment in California, Oregon, and Washington occurred from 2010-2019 (Wiens et al. 2021). Both studies found positive effects of BO removal on NSO survival and recruitment as well as increased rates of population growth in some removal areas (Wiens et al. 2021).

The continued range-wide decline of NSOs requires rapid intervention to prevent further decline and eventual extinction. Yackulic et al. (2019) suggests that without management intervention, NSOs have <5-50% chance of persisting in the next 50 years in most areas. The USFWS created a BO management plan with a draft released November 2023 (U.S. Fish and Wildlife Service 2023) although BO removal continues to be a contentious topic within the stakeholder and scientific community. If BO removal is adopted as a management tool, uncertainty exists regarding where, how, and for how long BO removal will occur within the range of the spotted owl.

Objectives

Overall, my objective was to understand associations of BO land use and occupancy dynamics in northern California from initial invasion to present day. In Chapter 1, I examined spatial associations of BO recolonization of NSO territories after BOs were lethally removed while in Chapter 2, I examined spatial and temporal associations of BO colonization and extinction over time during the BO invasion in a landscape where BO removals did not occur.

Managing BOs is vital to the persistence of the NSOs and understanding BO settlement and occupancy patterns can inform management by prioritizing areas as refugia free of BO and which benefit NSO.

CHAPTER 1: SPATIAL VARIATION IN BARRED OWL RECOLONIZATION OF LANDSCAPES USED BY SPOTTED OWLS

Overview

The northern spotted owl (*Strix occidentalis caurina*) is a threatened owl native to western North America that is adversely affected by the invasive barred owl (*Strix varia*). Observations of negative interactions between barred owls and northern spotted owls led to experimental barred owl removals. As part of a large-scale study to investigate the impacts of barred owls on northern spotted owls, lethal removal of barred owls began on Hoopa Valley Tribal Lands in northern California in 2013. Once barred owls were removed, the numbers of barred owls recolonizing NSO territories exhibited substantial spatial variation. I explored the correlation between the BO recolonization of northern spotted owl territories on Hoopa Valley Tribal Lands from 2013-2021 with biological and methodological variables. I found that barred owl recolonization was higher in northern spotted owl territories that were wetter with a higher proportion of older mixed conifer-hardwood forests that structurally had larger trees and more canopy cover. Barred owl recolonization was lower in areas with spares trees and open canopy. I developed a model using strongly supported variables that predicted the BO recolonization of the nearby Willow Creek Study Area if a removal study was to occur there. This model was then compared to detection data describing barred owl colonization within northern spotted owl territories on the Willow Creek study area. Specifically, I found that the predicted number of barred owls removed was correlated with the order in which barred owl colonized northern

spotted owl territories. Managers of invasive barred owls in California can use these vegetation and landscape factors to predict barred owl recolonization and inform removal efforts.

Introduction

Invasive species are a threat to biodiversity at the individual, population, and ecosystem level (Mack et al. 2000). Invasive species can increase the risk of extinction, change the behavior of native species, and affect their genetic composition, making them a leading cause of extinction for both plants and animals (Pysek et al. 2020). Invasive species threaten 60% of species listed under the U.S Endangered Species Act (Pysek et al. 2020), including the northern spotted owl (*Strix occidentalis caurina*; NSO), a nonmigratory, territorial, medium-sized owl native to western North America (Gutierrez et al. 1995). Although originally listed as threatened due to habitat loss and fragmentation, NSO populations continue to decline due to competition with the dominant, invasive barred owl (*Strix varia*; BO) (Franklin et al. 2021b).

The BO is closely related to the spotted owl (Mazur and James 2021), with similar life-history characteristics. Originally native to the eastern and midwestern United States, western range expansion of barred owls began in the early-1900s into southern Canada, continued into the Pacific Northwest, and reached California in 1981 (Dark et al. 1998, Livezey 2009a). Barred owl range expansion was likely facilitated by anthropogenic changes on the Great Plains, such as fire suppression and exclusion, and tree planting by European settlers (Livezey 2009b). The geographic range of BO now completely overlaps the range of the NSO and part of the range of the California spotted owl (*S. o. occidentalis*) (Dark et al. 1998, Seamans et al. 2004, Livezey

2009a, Hofstadter et al. 2022) causing a “conservation conundrum” (Gutierrez et al. 2007) because of the negative effect that one expanding native species is having on another.

BO occupy smaller home ranges (Hamer et al. 2007), are more aggressive (Van Lanen et al. 2011), and use more diverse habitat (Buchanan et al. 2004, Hamer et al. 2007) than NSO. BO negatively affect NSO territory occupancy (Kelly et al. 2003, Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011), apparent survival (Anthony et al. 2006, Dugger et al. 2016, Franklin et al. 2021b), recruitment, and fecundity (Franklin et al. 2021b) through resource competition, displacement, predation, and hybridization (Taylor and Foresman 1976, U.S. Fish and Wildlife Service 1990, Dark et al. 1998, Gutierrez et al. 2007, Van Lanen et al. 2011). Established NSO demographic studies offered an opportunity to conduct before-after-impact-control studies to examine the effects of removing BO on NSO populations (Wiens et al. 2021). As a part of this large-scale study, two NSO demography studies in northern California were paired with removals occurring on the Hoopa Study Area and the nearby Willow Creek Study Area (WCSA) acting as a control where removals did not occur. When BOs were removed on the Hoopa Study Area, NSO apparent survival, recruitment, and rate of population change increased (Wiens et al. 2021). After resident BOs were removed, certain areas considered “hotspots” of desirable BO habitat were recolonized by BOs that were subsequently removed at a high rate (Higley and Carlson 2020, Wiens et al. 2020)

Peery et al. (2018) suggested that spatial BO removal data could be useful to identify landscape conditions that are attractive to, and positively selected by, BOs. The USFWS is now proposing BO removal as a management action across the range of the NSO (U.S. Fish and Wildlife Service 2023). Thus, understanding and predicting BO recolonization hotspots is important for efficient and effective management of this species. The data provided on the

Hoopa Study Area and the independent data collected on the WCSA provides an opportunity to learn, predict, and compare BO colonization.

Repopulated areas may host dispersing BOs or an underlying floater population (Franklin 1992, Rohner 1997), impacting the effort needed to maintain low BO populations. Understanding the ecological process of BO recolonization can inform effective management strategies, while considering theories of ideal-free and ideal-despotic distributions (Fretwell and Lucas 1969). If BOs followed an ideal-free distribution, individuals selected the highest quality habitat first, while if BOs followed an ideal-despotic distribution, territorial individuals excluded new individuals from high quality habitat (Fretwell and Lucas 1969). I assessed BO recolonization in NSO territories to determine habitat quality, then utilized this information to predict BO recolonization in the Willow Creek Study Area, comparing predictions with empirical data to discern distribution patterns.

In this chapter, I investigated abiotic, biotic, and sampling variables that influence BO recolonization of NSO territories after BOs had been lethally removed to determine why certain areas were more frequently recolonized and the factors attracting BOs to these hotspots. Utilizing supported variables from the Hoopa Study Area, I predicted BO recolonization on the WCSA. Comparisons with actual colonization data over time allowed for insights into distribution patterns, revealing whether BOs exhibited an ideal-free or ideal-despotic distribution during colonization.

Study Areas

The Hoopa Study Area is 360 km^2 on Hoopa Valley Tribal Lands, which are north of Willow Creek in Humboldt County, California (Figure 1.1; Whitaker 2003). Elevation within the study area ranges from 100 m to 1,075 m. Forests are dominated by Douglas-fir (*Pseudotsuga menziesii*), tanoak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*), California black oak (*Quercus kelloggi*), and Oregon white oak (*Quercus garryana*) with a shrub layer of mostly evergreen huckleberry (*Vaccinium ovatum*) or salal (*Gualtheria shallon*). Big-leaf maple (*Acer macrophyllum*), chinquapin (*Chrysolepis chrysophylla*), mountain dogwood (*Cormus nuttallii*), willow (*Salix spp.),* and canyon live oak (*Quercus chrysolepis*) are also present scross the study area (Whitaker 2003). Notably, forests at higher elevations are dominated by conifers, while lower elevation forests have a larger component of hardwood species.

Based on their 1994 Forest Management Plan (FMP), the logging practices of the Hoopa Valley Tribe transitioned from intensive clearcutting to regeneration harvest, which retains significant mature and older forest structure and better mimics natural fire events. The Tribe's FMP also established wildlife habitat reserves on more than 30% of the forest lands.

The Hoopa Valley Tribe initiated a demographic study of NSO in 1992. Due to the increasing population of BOs, BO specific surveys began in 2009 (U.S. Fish and Wildlife Service 2013). Prior to BO removal on the Hoopa Study Area, BOs were detected in >90% of all historic spotted owl territories (Higley and Carlson 2020).

The Willow Creek Study Area (WCSA) is a 292.4 km^2 area about 10 miles south of the Hoopa Study Area (Figure 1.1) and is managed primarily by the Six Rivers and Shasta-Trinity National Forests. The elevation of the study area ranges from 150m to 1,700m and forest

composition is similar to the Hoopa Study Area. The WCSA was established in 1985 as part of a demographic study of NSO with BO-specific surveys starting in 2008 (Franklin et al. 1990).

Methods

Field Methods

BO lethal removals on the Hoopa study area started in 2013 with a total of 431 BOs removed between 2013 and 2019 (Higley and Carlson 2020). BOs were located on the Hoopa study area through surveys and were subsequently lethally removed. To locate BOs for removal, a hexagonal grid consisting of 71 hexagons of 250-500 hectares was overlaid on the study area. Each hexagon was then surveyed during 3 sampling periods throughout the breeding season by calling at 2-8 call stations per hexagon. BO calls were performed using a Wildlife Technologies Mighty Atom or MA-Max caller (Wildlife Technologies 2019). In the first two years, removals only occurred during the non-breeding season (September - February). Beginning in 2015 removals occurred during the breeding and non-breeding seasons, with BOs removed during the breeding season confirmed as non-breeders without dependent young. Field methods for BO removal generally follow Diller et al. (2014). Each removal visit consisted of an observer playing BO calls to lure BOs into shotgun range. Observers removed BOs with a 12-gauge shotgun using size 6─7.5 steel shot at a range of 13-25 m. Locations of each BO removed were recorded as UTM coordinates.

Sampling Units and Variables

To outline areas historically used by NSOs, the sampling units for this analysis were the 57 NSO territories on the Hoopa Study Area, delineated as Thiessen polygons centered around NSO nest, fledgling, and roost locations (Franklin et al. 2021b). Territories range from 239 to 1149 hectares in size and represented the area defended by NSOs during the breeding season. I assumed territories remained constant throughout the study period although territories were not consistently occupied by NSOs through time. After eliminating one NSO territory where >50% was outside the study area boundary, 56 NSO territories were used in my analyses.

The response variable, BO recolonization, was the total number of BOs removed within each NSO territory from 2013 through 2021 (Figure 1.2). I used point locations where BOs were removed on the Hoopa Study Area from 2013-2021 to determine the total number of BO removed in each NSO territory, including points within 200m of a territory boundary (the distance from which a BO can be lured into a territory using BO calls), provided the removed BO was not already counted in a neighboring territory (Appendix Figure 1.1). I assumed all detected BOs were eventually removed from the study area, their removal location represented the area where they settled and defended a territory, and a high number of BOs removed indicated an area of high recolonization.

Based on previous literature on BO habitat use and selection, I hypothesized BO recolonization would be correlated with certain abiotic, biotic, and sampling variables (Wiens et al. 2014, Irwin et al. 2018; Table 1.1). BOs use mature, mixed conifer-hardwood forests with high canopy closure in riparian areas of low slope, low elevation, and mesic conditions (Livezey 2007). Therefore, I used biotic and abiotic variables to represent these conditions (Table 1.1). I

also included NSO presence as a biotic variable because previous literature suggested NSO presence positively influenced both BO extinction and colonization probabilities (Yackulic et al. 2014, Franklin et al. 2021b). This influence could be due to similar habitat preference for both species, BOs possibly using NSOs as a habitat cue, or NSO vocalizations behaviorally attracting BOs (Seamans and Gutierrez 2006, Hamer et al. 2007, Wiens et al. 2014, Jenkins et al. 2019b). Lastly, the size and location of the territory as well as the time spent during survey and removal efforts could impact the number of BOs removed from a territory. I included sampling variables to test whether choice of sampling unit or data collection procedures affected the outcome. I aggregated all predictor variables at the scale of each NSO territory.

Abiotic variables used to represent topographic features included average wetness, aspect, slope, and elevation. Wetness was measured by Topographic Wetness Index (TWI) – an index of static moisture availability (Sørensen et al. 2006). TWI also predicts vegetation species richness, soil pH, groundwater level, and soil moisture (Sørensen et al. 2006). Higher TWI values indicate greater potential for water accumulation and wetter areas. To calculate TWI, I first used 1/3 arc-second digital elevation model (DEM) from the United States Geological Survey National Map (https://apps.nationalmap.gov/downloader/) and ArcGIS Pro 2.9 to calculate slope, aspect, flow direction, and flow accumulation from the DEM. I then estimated the TWI for the area using the equation developed by Beven and Kirkby (1979):

$$TWI = \ln(\alpha/\tan\beta),$$

where α = local upslope area per unit contour length and β = local slope. I calculated the average slope, aspect, and TWI values within each NSO territory using the Zonal Statistics as Table tool in ArcGIS Pro 3.0, with the circular statistics option for slope and aspect variables (GIS workflow found in Appendix Figure 1.2).

Biotic variables used to represent vegetation and interspecies interaction included forest structure variables, forest type variables, and NSO presence. For vegetation variables, I used two approaches to determine which vegetation classifications best explained spatial variation in BO recolonization. Forest structure variables were average tree size defined by average quadratic mean diameter (QMD), tree density, canopy cover, stand age, basal area, percent hardwoods, and stand height. Forest type variables were percent area of open forest, prey habitat, old hardwood forest, young mixed conifer-hardwood forest, old mixed conifer-hardwood forest, young conifer forest, and old conifer forest. Forest types were labeled by forest age and species composition and categorized by percent canopy cover, percent hardwoods (based on basal area), and tree size (Table 1.1, Appendix Table 1.1). Forest structure variables were expressed as an average value for each NSO territory and forest type variables were expressed as a percentage of the total area within each NSO territory.

For biotic variables, I estimated vegetation variables discussed above using the most recent (2017) 30m x 30m rasters of vegetation attributes provided by the Gradient Nearest Neighbor (GNN) Downloader dataset (https://lemmadownload.forestry.oregonstate.edu/). Briefly, these datasets were created using the gradient nearest neighbor (GNN) model, which utilizes 30m Landsat imagery, Forest Inventory and Analysis data, and other geospatial products (Bell et al. 2020) to create a complete cover of the landscape. I used the Zonal Statistics as Table tool in ArcGIS Pro 2.9 to calculate the mean value of the forest structure variables within each NSO territory (Table 1.1). I combined the 11 forest type categories from the vegetation class (VEGCLASS) raster into 6 categories for the forest type variables (Appendix Table 1.1), calculated the area of each forest type, and determined the percent of forest type in each territory by dividing it by the total area of the territory (Table 1.1). I estimated NSO presence as the

percentage of breeding seasons (2013-2021) during which at least one NSO was detected on the territory (100% = NSO detected for all 9 breeding seasons, 0% = no NSO detected during any breeding season) using owl survey data.

Sampling variables used to represent study design and effort were territory distance to boundary of the Hoopa study area, territory area, total survey time, and total removal time. Territory distance was measured from the study area boundary to the NSO territory centroid. Survey effort was the total time spent on nocturnal surveys to detect BOs within each NSO territory (Table 1.1). Removal effort was the total time spent on nocturnal surveys within each NSO territory to locate BO for removal. I calculated both effort variables from nocturnal BO survey data and excluded 256 (1.14%) detections surveys and 24 (0.78%) removal surveys due to data entry errors (e.g., surveys supposedly lasting over 5 hours or those lacking an end time). Both effort variables were calculated and summed across all years for each NSO territory, ending with one total value per territory.

Analysis

I used linear regression and model selection to explore the correlation between BO recolonization and the abiotic, biotic, and sampling variables with the statistical software R (R Core Team 2021). To avoid collinearity among predictor variables that could lead to biased model estimates, I calculated Pearson's correlation among variables using cor() and corrplot() functions in the 'stats' and 'corrplot' (Wei and Simko 2021) packages respectively before creating models. I used a threshold of $|r| > 0.65$ to identify correlated variables, from which I excluded one of the variables.

To explore which variables were associated with BO recolonization, I ran linear models of all possible additive combinations of uncorrelated variables using the dredge() function from the 'MuMIn' package (Barton 2022) in R, limiting the models to five variables per model due to available sample size. This strategy considered all possible models with a balanced model set within the explanatory ability of the sample size (Doherty et al. 2012, Bromaghin 2013, Morin et al. 2020). I determined model importance by ranking the models by AICc, a bias-corrected version of AIC for small sample sizes (Burnham et al. 2011). I determined variable importance and the direction of the association between BO recolonization and the response variable by calculating variable AICc weights using the sw() function and model-averaged estimates of the linear coefficients (β) using the model.av() function in the 'MuMIn' package. I considered variables with AICc weight ≥ 0.5 to be important contributors to the best predicting model (Barbieri and Berger 2002).

To avoid violations that could lead to biased estimates, I checked assumptions of normal linear regression on a model containing all variables with the lm() function in R. I checked the assumption of normality with the Shapiro-Wilks Test (Shapiro and Wilk 1965) using the shapiro.test() function from the 'stats' package and the assumption of homoscedasticity with the Breuch-Pagan Test (Breusch and Pagan 1979) using the bptest() function in the 'lmtest' package (Zeileis and Hothorn 2002). I was lenient in violations of assumptions and continued with the normal linear regression model instead of expected models for count data (e.g., Poisson regression), due to normal linear regression's robustness against violations and Poisson regression's sensitivity to departures from the Poisson distribution (McDonald and White 2010).

I considered variables with a model weight ≥ 0.5 as strongly supported and used those variables to create models in a final model set. I again used the cor() function to check

correlations between variables and eliminated one of the two correlated variables. I then ran all possible combinations of variables in this model set using the dredge() function and calculated variable weights using the sw() function.

Non-linear relationships can suggest that an optimal value of a variable maximizes the outcome. In this case, if there was a value of a variable that maximized the number of BOs removed and therefore, BO recolonization. I used ad-hoc modeling to examine non-linear relationships between BO recolonization and variables representing old forest, prey habitat, and wet areas - specifically, percent old forest, percent prey habitat, wetness, and tree size. Previous literature suggests that NSO fitness is non-linearly related to old forest, mid-to-late seral stage forest, and edge habitat (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005) and as high TWI values can indicate open water, and I hypothesized that BO preferred an optimal amount of wetness on the landscape but not open water. For percent old forest, percent prey habitat, wetness, and tree size I selected the highest-ranking model from initial model sets containing the variable and explored three non-linear relationships for each variable to test for improved model fit. The three non-linear relationships included – mean-centered quadratic, unrestricted quadratic, and pseudo threshold (log-linear). A quadratic relationship indicates an optimal value of a variable that maximizes BO recolonization. I defined a mean-centered quadratic relationship as the square of the difference between a variable value and its overall mean restricting the quadratic relationship to be centered around the variable mean, while not adding an extra parameter to the model.

If BO removals were initiated in new areas, predicting BO recolonization could guide targeted removal efforts by estimating the number of BOs to be removed in each area representing the level of removal required. Therefore, I created a model from the Hoopa Study

Area data and predicted the number of BOs that would be removed from each NSO territory on the Willow Creek Study Area (WCSA) to be tested by future removals. The WCSA also provided an independent data set of BO detections through time, so I compared predictions of BO recolonization to empirical BO colonization to better understand if predictions provided insights on BO recolonization dynamics. I assumed a high level of BO recolonization indicated high BO habitat quality, so comparing predictions with empirical data also connected habitat and colonization dynamics. I created the best predictive model using variables from the final model set with AICc weights ≥ 0.5 and predicted BO recolonization on the nearby WCSA using similar vegetation and topographic data and the predict() function in R. I ranked all NSO territories on WCSA by the order of colonization using BO detection locations from 1991-2022. I used the predicted number of BO removed to rank territories from most to least predicted number of BO removed. I then tested the correlation between the ranks of predicted BO recolonization and empirical colonization order with Spearman's Rank Test for correlation (Hollander and Wolfe 1973). If BOs followed an ideal free distribution (Fretwell and Lucas 1969), then the predicted BO recolonization and the empirical colonization order would be correlated at $|r_s| \geq 0.50$.

Results

I analyzed forest type and forest structure variables in different model sets due to high correlations between variables – leading to a two-step approach with two initial model sets and one final combined model set. Each initial model set included abiotic variables, sampling variables, NSO presence, and either forest type or forest structure variables, respectively. For each model set, I created a global model of all variables considered in the model set and tested

the assumptions of linear regression. Little variation existed in the number of BOs removed for territories with the same removal effort meaning removal effort did not greatly influence the number of BOs removed. Therefore, I did not include removal effort in initial model sets.

In the forest structure model set, many of the initial 15 variables were correlated ($|r| > 0.65$); thus, I selected 10 variables to include in the global model. I eliminated average stand age, stand basal area, stand height, and tree density due to correlation with tree size and elevation, respectively (Appendix Figure 1.3). The global model met the assumption of normally distributed residuals ($W = 0.976$, $p = 0.344$) and homoscedasticity ($BP = 13.52$, $p = 0.196$) (Appendix Figure 1.4). The model set contained a total of 638 models with each variable appearing in the model set 256 times. Wetness and tree size were the most supported variables with summed model weights > 0.90 (Table 1.2). Survey time was also supported with a summed model weight > 0.50 (Table 1.2). The most parsimonious model included canopy cover, tree size, survey time, wetness, and NSO presence (Table 1.3) with an adjusted R^2 value of 0.361. The 95% confidence intervals of model averaged $\hat{\beta}$'s for canopy cover ($\hat{\beta} = 0.534$, 95% CI = -0.008, 1.151) and NSO presence ($\hat{\beta} = -0.047$, 95% CI = -0.116, 0.021) overlapped zero (Appendix Table 1.2), indicating there is not support for an association with these variables. Model averaged $\hat{\beta}$'s for wetness ($\hat{\beta} = 0.013, 95\%\ \text{CI} = 4.565, 21.276$), tree size ($\hat{\beta} = 0.858$, 95% CI = 0.259, 1.457), and survey time ($\hat{\beta} = 0.148$, 95% CI = 0.023, 0.274) were positive, and 95% confidence intervals did not overlap zero (Appendix Table 1.2) suggesting BOs were attracted to wetter areas with larger trees and higher canopy cover. I ran non-linear models for tree size and wetness variables, but they either did not improve model fit, or resulted in very modest improvements in model fit; increases in AICc were < 0.3 AICc.

In the forest type model set, elevation was the only variable eliminated due to high correlation with percent young conifer forest (Appendix Figure 1.5). The global model met the assumption of normally distributed residuals (W = 0.981, p = 0.517) and homoscedasticity (BP = 14.221, p = 0.359) (Appendix Figure 1.6). The model set contained 2380 models with each variable appearing in the model set 794 times. Percent open forest was the most supported variable with a summed model weight of 0.881 (Table 1.2). Percent old mixed conifer-hardwood forest and survey time also had summed model weights > 0.5 (Table 1.2). The most parsimonious model included percent old hardwood forest, percent old mixed conifer-hardwood forest, percent open forest, survey time, and wetness (Table 1.3) with an adjusted R^2 value of 0.416. The 95% confidence intervals of model averaged $\hat{\beta}$'s for percent old hardwood forest ($\hat{\beta}$ = 0.268, 95% CI = -0.082, 0.618) and wetness ($\hat{\beta}$ = 6.755, 95% CI = -1.239, 14.749) overlapped zero (Appendix Table 1.2), indicating there is not support for an association with these variables. Model averaged $\hat{\beta}$ for percent open forest ($\hat{\beta}$ = -2.033, 95% CI = -3.498, -0.569) was negative while the $\hat{\beta}$ for percent old mixed conifer-hardwood forest stands ($\hat{\beta}$ = 0.453, 95% CI = 0.105, 0.800), and survey time ($\hat{\beta}$ = 0.119, 95% CI = 0.001, 0.238) were positive and 95% confidence intervals did not overlap zero (Appendix Table 1.2) suggesting BOs were attracted to areas with less area of open forest, and more area of old mixed conifer-hardwood forest stands. I ran ad-hoc non-linear relationships for percent prey habitat, percent old mixed conifer-hardwood forest, percent old hardwood forest, and percent old conifer forest. Non-linear relationships either did not improve model fit, or only improved model fit by < 0.5 AICc.

In the final model set, I considered percent open forest, percent old mixed conifer-hardwood forest, wetness, tree size, and survey time. I excluded tree size from the model set due to high correlation with percent old mixed conifer-hardwood forest (Appendix Figure 1.7). The

global model did not meet the assumption of normally distributed residuals (W = 0.956, p = 0.039) and met the assumption of homoscedasticity (BP = 5.955, p = 0.203) (Appendix Figure 1.8). The model set contained 16 models with each variable showing up in the model set 8 times. Percent open forest and percent old mixed conifer-hardwood forest were the most supported variables with model weights > 0.9 (Table 1.2). Survey time had a model weight ≥ 0.5 (Table 1.2) while wetness had a model weight very close to 0.5. The most parsimonious model contained percent open forest, percent old mixed conifer-hardwood forest and survey time with an adjusted R^2 value of 0.347 (Table 1.3). Model averaged $\hat{\beta}$'s for percent open forest ($\hat{\beta}$ = -1.964, 95% CI = -3.278, -0.649) was negative while the $\hat{\beta}$ for percent old mixed conifer-hardwood forest stands ($\hat{\beta}$ = 0.444, 95% CI =0.165, 0.722), and survey time ($\hat{\beta}$ = 0.126, 95% CI = 0.014, 0.239) were positive and 95% confidence intervals did not overlap zero (Appendix Table 1.3) suggesting BOs were attracted to areas with less area of open forest, and more area of old mixed conifer-hardwood forest stands.

I created the best predictive model for the WCSA using the estimates for wetness, percent open forest, and percent old mixed conifer-hardwood forest (Appendix Table 1.3), but not survey time due to the likelihood of these data not being available in other regions. The predictive model had an adjusted R^2 value of 0.362. $\hat{\beta}$ for percent open forest ($\hat{\beta}$ = -1.925, 95% CI = -3.240, -0.610) was negative while the $\hat{\beta}$ for percent old mixed conifer-hardwood forest stands ($\hat{\beta}$ = 0.4155, 95% CI =0.135, 0.696) was positive and 95% confidence intervals did not overlap zero suggesting BOs were attracted to areas with less area of open forest, and more area of old mixed conifer-hardwood forest stands. I truncated predicted values to a whole number and negative values to zero for biological feasibility. The areas of highest predicted BO recolonization were in the northwest and northeast of the WCSA (Figure 1.3). The predicted areas of high barred owl

removal visually matched the territories colonized first (Figure 1.3). The rank of BO recolonization and the order of colonization were also correlated (r_s = 0.529; 95% CI = 0.314, 0.743; Figure 1.4).

Discussion

A mixture of abiotic, biotic, and sampling variables best explained the spatial variation in BO recolonizing NSO territories after removal. My results suggested that more BOs were attracted to NSO territories that were wetter with greater area of old mixed conifer-hardwood forest, and less area of sparse trees and open canopy. Structurally, these territories had larger trees and greater canopy cover. Additionally, more BOs were removed in territories with higher survey effort potentially due to increasing BO detection probability or a product of researcher's prior knowledge of high BO activity.

The supported association of wetness with BO recolonization agrees with observations and previous studies. In the eastern United States, BOs are typically found in swamps or other wet areas, with BOs preferentially nesting near water (Livezey 2007). Furthermore, during BO range expansion in California, BOs were first detected in more mesic coastal forest before moving east into drier forests (Livezey 2009a). Many previous studies found a positive relationship between BOs and water in the western United States, using variables such as distance to water (Buchanan et al. 2004) and water as a cover category (Mazur et al. 1997). Most frequently, water is included as a non-forested habitat variable (Herter and Hicks 2000, Pearson and Livezey 2003). Mine is the first study of BO land use that specifically looked at TWI as an index for landscape wetness which was a useful metric for extrapolating my results across a

broader landscape. TWI is more flexible than using water as a cover type or distance to water to explore BO association with wetter areas because it is a complete coverage of the landscape. However, TWI is a static index that does not incorporate environmental changes.

I found mixed support for an association between hardwoods and BO recolonization. BO recolonization was not associated with percent hardwood forest, but I found a strong positive association with percent old mixed conifer-hardwood forest. This result could be driven by differing productivity for prey in a combination of conifer overstory and a hardwood mid-story than pure conifer or hardwood stands that was not captured in my forest type classifications. Multiple habitat studies in Oregon, Washington, and Canada found a positive relationship between BOs and hardwoods (Mazur et al. 1997, Mazur et al. 1998, Buchanan et al. 2004, Hamer et al. 2007, Irwin et al. 2018) where BO preferred and used hardwood forests more often than NSO (Mazur et al. 1998, Buchanan et al. 2004, Hamer et al. 2007). However, BOs in California coastal redwood (*Sequoia sempervirens*) forests were negatively associated with increasing basal area of tan oak (*Notholithocarpus densiflorus*), a dominant hardwood in the region (Irwin et al. 2018). This could be due to the prevalence of hardwoods in drier, steeper areas of the California redwood forest. Tan oak is a common species in the Hoopa Study Area and comprises the mid and understory of the old mixed conifer-hardwood forest. This indicates there could be an interaction between forest structural layers and tree species that influences BO use. My results contradict most studies of BO habitat use in the northern portion of the NSO range. However, my results agree with the one other study in California (Irwin et al. 2018); although that study used resource selection functions of telemetry points of BOs and my study examined broader scale population effects. The contradiction with other studies is possibly due to the difference in landscape, climate, or tree species composition of the physiographic

provinces within the expanded range of the BO, which, ultimately, may reflect differences in prey abundance and availability in different forest stands.

NSO presence was not strongly associated with recolonizing BOs, contrary to previous studies of NSO and BO occupancy dynamics that show BO initial colonization increases in the presence of NSO (Yackulic et al. 2014, Franklin et al. 2021b). Comparing my study to others may reveal how NSO presence is associated with BO dynamics, especially in areas with high or low NSO numbers. It also sheds light on whether BO colonization varies with a growing BO population versus BO recolonization after removal. However, it is difficult to directly compare annual occupancy dynamics to the NSO presence variable I used, which was summed across all years.

The BO's association with wetter areas with greater area of old mixed conifer- hardwood forest, and less area of sparse trees and open canopy highly overlaps with areas typically used by NSO. NSOs are old forest obligates and the high level of BO recolonization of older forest within removal area may disrupt the ability of NSO to recolonize these areas. Furthermore, wetter areas are less prone to high fire intensity and TWI can be used to predict fire intensity in flat areas (Krawchuk et al. 2016), and topography can be used to predict fire refugia in old forests (Meigs et al. 2020). As fire severity and frequency increases, these wetter areas may become important habitat refugia for NSOs. Severe wildfire limiting NSO habitat and high BO recolonization of wetter older forest may increase competition between BO and NSO in these habitat refugia.

The USFWS proposed BO removal as a possible management strategy for NSO conservation in California (U.S. Fish and Wildlife Service 2023), so the selection and prioritization of removal areas is becoming increasingly important. My results provide insights

on the ability to predict BO colonization using landscape features. Models with variables describing forest types were more parsimonious than models with variables describing forest structure. Thus, characterizing vegetation by forest type provides better predictors of BO recolonization. Comparing my model predictions against empirical BO detection data show there is a correlation between my predictions and empirical colonization. Using the predicted number of BO removed as a proxy for habitat quality suggests that colonizing BO are selecting the high-quality habitat first and then moving into lower quality habitat as occupancy on the study area increases following ideal free distribution (Fretwell and Lucas 1969). These areas of low habitat quality and later BO colonization are also the territories with remaining NSO pairs, indicating these could be important areas to focus management to increase NSO persistence.

Some limitations of the study include using removal locations as proxies for land use and the scale of the study. BOs can be lured into a location from a distance using BO calls. However, the timing of my surveys targeted individuals that were more likely to behaviorally respond to defend their territory than non-territorial individuals (i.e. searching for a mate and hoping to establish a territory in the area or territorial individuals in established territories). Therefore, I assumed removed BOs were territorial individuals that were primarily defending the surrounding landscape. NSO territories are the critical areas that will benefit the most from BO removal. By focusing on NSO territories, my inferences remained biologically relevant by determining BO behavior on landscapes used by NSO.

Similar analyses in other BO removal areas within the range of NSO would strengthen the inference of these findings. The pattern of BO recolonization could be different for other removal areas due to habitat and landscape composition. My findings can also be tested in future

removal projects in northern California to help predict efficient locations for BO removal that would best benefit NSO, and ultimately increase their persistence.

Management Implications

Removing BO populations from NSO territories as rapidly and efficiently as possible is a step towards rescuing remaining NSO populations currently experiencing rapid declines. Understanding the effectiveness of removal methods across landscapes strengthens the impact made with limited time and resources. A combination of wetness, percent open forest and percent old mixed conifer-hardwood forest can be used to develop maps to target areas favored by recolonizing BOs (high wetness and percent old mixed forest, low percent open forest) and identify areas of low BO recolonization (low wetness and percent old mixed forest, high percent open forest). Overlaying this map on the range of NSO can determine potential removal areas that can be externally validated by surveys and then removals. Removing BOs in areas with low likelihood of recolonization can increase efficiency of removals by creating BO-free refuges for NSO with less effort. Conversely, targeted removals of areas of high and low likelihood of BO recolonization could create a mosaic of habitat available for NSO recolonization.

Removal strategies depend on NSO conservation goals of either persistence or population growth and vary based on the quality of NSO habitat made free of BO. Efficient removals may target low-quality BO habitat, but these areas could be marginal NSO habitat and potentially compromise NSO population growth. Focusing removals in areas of high NSO habitat quality could improve NSO population growth but could take more effort. Balancing opposing strategies poses a trade-off, and future studies can explore the optimal approach. Given the overlap in NSO

and BO habitat preferences, assessing areas of high BO recolonization in relation to NSO habitat quality could be a valuable direction for future research. Monitoring of NSO must continue in these areas to determine the effectiveness of BO removal towards the goal of NSO persistence or population growth. Adding BO removal to an adaptive management approach including NSO monitoring and habitat restoration is a step forward in protecting the NSO from extinction (Yackulic et al. 2019).

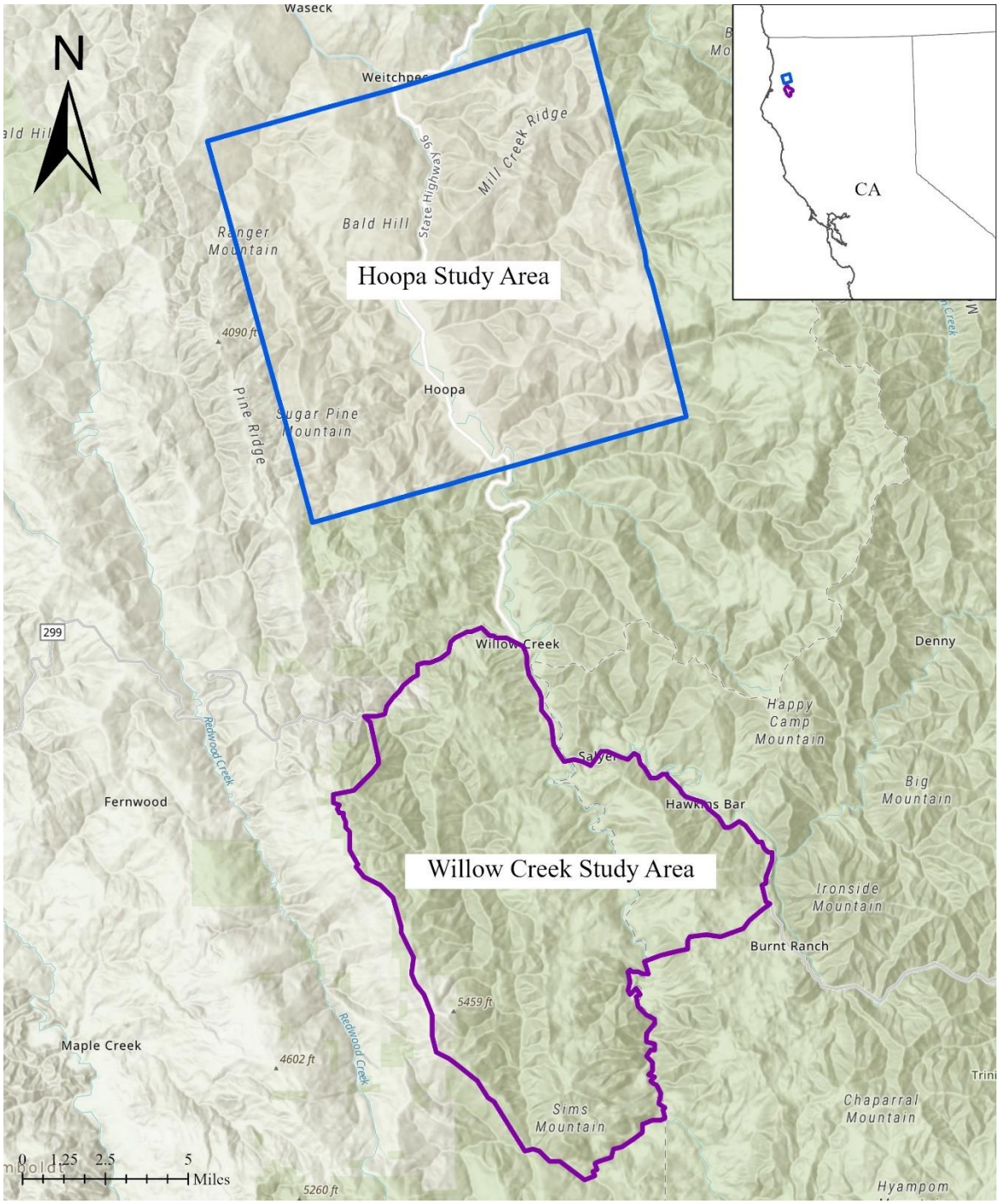

Figure 1.1. Hoopa and Willow Creek Study Areas in Humboldt and Trinity Counties, CA.

Table 1.1. Description of biotic, abiotic, and sampling variables used in the analysis of associations of the level of barred owl (BO) recolonization of northern spotted owl (NSO) territories from 2013-2021.

Variable type	Variable	Description	Range[1]
Biotic			
	Stand age (yrs)	Average forest stand age weighted by basal area based on field recorded or modeled ages of dominant/codominant trees	67.91 - 143.74 yrs
	Basal area (m²/ha)	Average basal area (BA) of live trees ≥ 2.5cm dbh	35.65 - 54.2 m²/ha
	% Hardwoods (%)	Average % of hardwoods based on BA	40.53 - 65.91%
	Canopy cover (%)	Average canopy cover of all live trees	66.97 - 85.12%
	Tree size (cm)	Average quadratic mean diameter (QMD) of all dominant and codominant trees	23.47 - 44.29 cm
	Stand height (m)	Average stand height (calculated as average heights of all dominant and codominant trees)	14.26 - 23.77 m
	Tree density (trees/ha)	Average density of live trees ≥ 2.5cm dbh	1100 - 2632 trees/ha
	Open forest (%)	% area of parse trees with open canopy	0.00 - 7.70%
	Prey habitat (%)	% area of sapling or pole sized hardwood & conifer trees with moderate to closed canopy	6.46 - 54.67%
	Old hardwood (%)	% area of small to large hardwood trees with moderate to closed canopy	6.64 - 49.12%
	Young mixed (%)	% area of small to medium conifer & hardwood trees with moderate to closed canopy	12.87 - 38.75%
	Old mixed (%)	% areas of large to very large conifer & hardwood trees with moderate to closed canopy	4.44 - 46.46%
	Young conifer (%)	% area of sapling to medium conifer trees with moderate to closed canopy	0.02 - 21.63%
	Old conifer (%)	% area of very large conifer trees with moderate to closed canopy	0.44 - 11.91%
	NSO presence (%)	% of breeding seasons during the study the NSO territory was occupied by at least one NSO	0 - 100%

Abiotic			
	Aspect (degrees)	Average aspect	30.53 - 347.95°
	Elevation (m)	Average elevation	235.6 - 1131.4 m
	Slope (degrees)	Average slope	14.21 - 32.41°
	Wetness	Average topographic wetness index (TWI)	5.161 - 6.495
Sampling			
	Territory distance (km)	Distance of centroid of territory to the closest study area boundary	0.004 - 8.443 km
	Territory area (ha)	Area of Thiessen polygon used to define NSO territories	239 - 1149 ha
	Survey time (hrs)	Total amount of time that an NSO territory was surveyed for BO	1.267 - 81.283 hrs
	Removal time (hrs)	Total amount of time spent removing BOs from an NSO territory	10.73 - 91.55 hrs

[1] The minimum and maximum value of each variable in the dataset

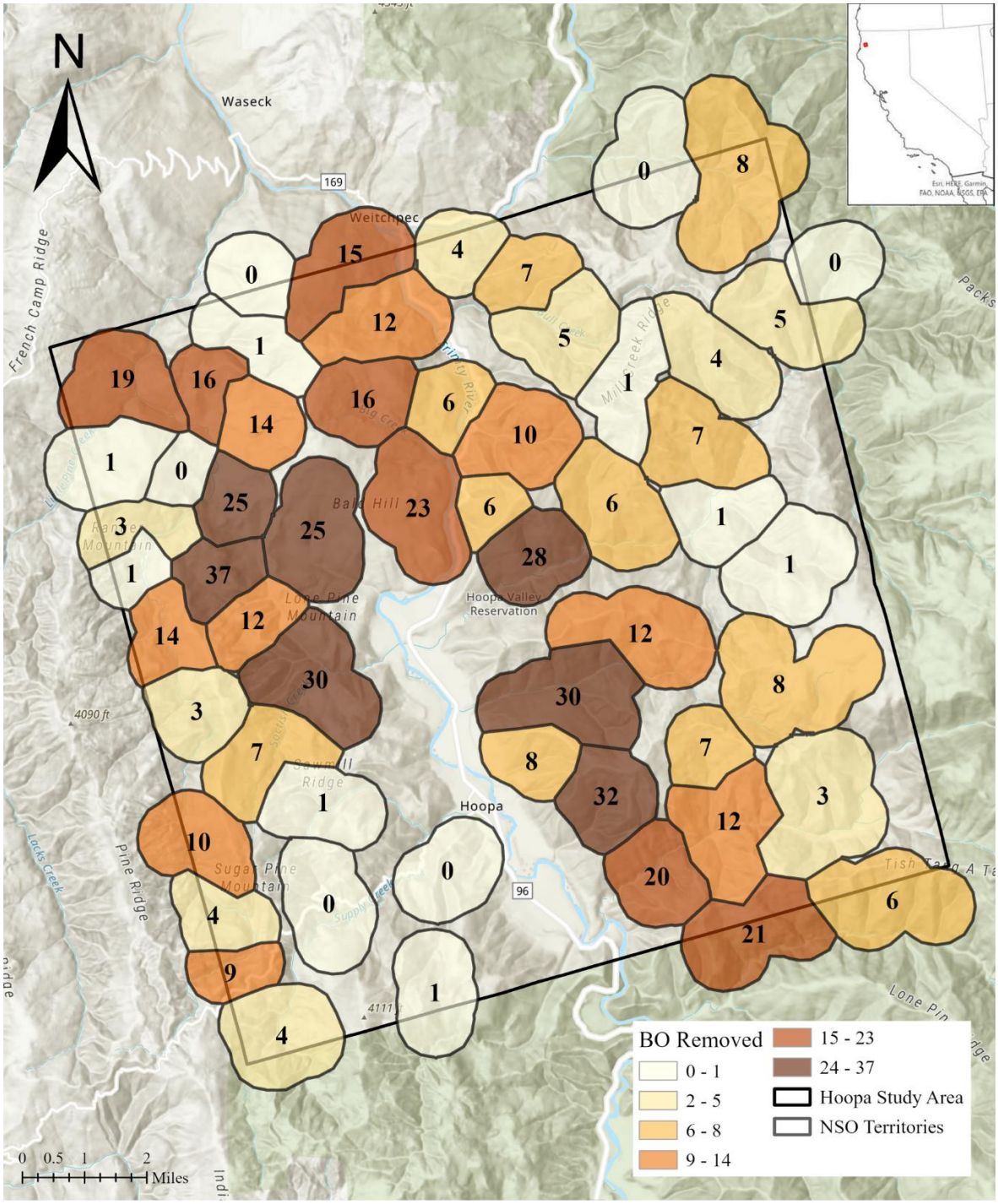

Figure 1.2. Map of the Hoopa Study Area with the total number of barred owls (BO) removed on individual northern spotted owl (NSO) territories from 2013-2021. Colors represent quantiles of removal numbers.

Table 1.2. Summed model weight for variables in the forest type model set, forest structure model set, and final model set. Variables appeared in the forest type model set 794 times each, the forest structure model set 256 times each, and the final model set 8 times each. The response variable is the number of barred owls removed from northern spotted owl territories on Hoopa Study Area. Variables with summed model weight > 0.5 in the final model set were considered important and included in the best predicting model.

Model set	Variable	Summed model weight[1]	Association[2]
Forest structure			
	Wetness	0.973	+
	Tree size	0.952	+
	Survey time	0.713	+
	Territory distance	0.491	+
	Canopy cover	0.422	+
	NSO presence	0.270	-
	Aspect	0.249	-
	Tree density	0.205	+
	% Hardwoods	0.139	+
	Territory area	0.131	+
Forest type			
	Open	0.881	-
	Old mixed	0.736	+
	Survey time	0.516	+
	Old hardwood	0.423	+
	Prey habitat	0.416	-
	Wetness	0.371	+
	Old conifer	0.273	-
	Young mixed	0.206	-
	NSO presence	0.172	-
	Territory distance	0.161	+
	Aspect	0.156	-
	Territory area	0.129	+
	Young conifer	0.121	+
Final			
	Old mixed	0.976	+
	Open	0.959	-
	Survey time	0.793	+
	Wetness	0.496	+

[1] Sum of AICc model weight of all models containing the variable in the model set

[2] Direction of the variable estimated beta value in the model set

Table 1.3. Top models (ΔAICc < 2) in the forest type model set, forest structure model set, and final model set.

Model Set	Model	ΔAICc[1]	Weight[2]	K[3]	Log likelihood	AICc[4]
Forest structure						
	Canopy cover + Tree size + Survey time + Wetness + NSO presence	0.000	0.095	6	-190.041	396.416
	Canopy cover + Tree size + Territory distance + Survey time + Wetness	0.826	0.063	6	-190.454	397.242
	Tree size + Territory distance + Survey time + Wetness	1.197	0.052	5	-191.949	297.613
	Canopy cover + Tree size + Survey time + Wetness	1.315	0.049	5	-192.008	397.731
	Aspect + Canopy cover + Tree size + Survey time + Wetness	1.438	0.046	6	-190.76	397.854
	Tree size + Removal distance + Survey time + Tree density + Wetness	1.689	0.041	6	-190.886	398.105
Forest type						
	Old hardwood + Old mix + Open + Survey time + Wetness	0.000	0.059	6	-187.528	391.389
	Old hardwood + Old mix + Open + Survey time	1.553	0.027	5	-189.613	392.941
Final						
	Old mix + Open + Survey time	0.000	0.383	4	-191.747	394.694
	Old mix + Open + Survey time + Wetness	0.127	0.359	5	-190.553	394.821

[1] AICc units away from the most parsimonius model (lowest AICc) in the model set

[2] AICc model weight

[3] Number of parameters

[4] Akaike Information Criterion (AIC) is a measure that balances the fit of the model with the complexity of the model. AICc is a bias-corrected version of AIC for small sample sizes (Burnham et al. 2011)

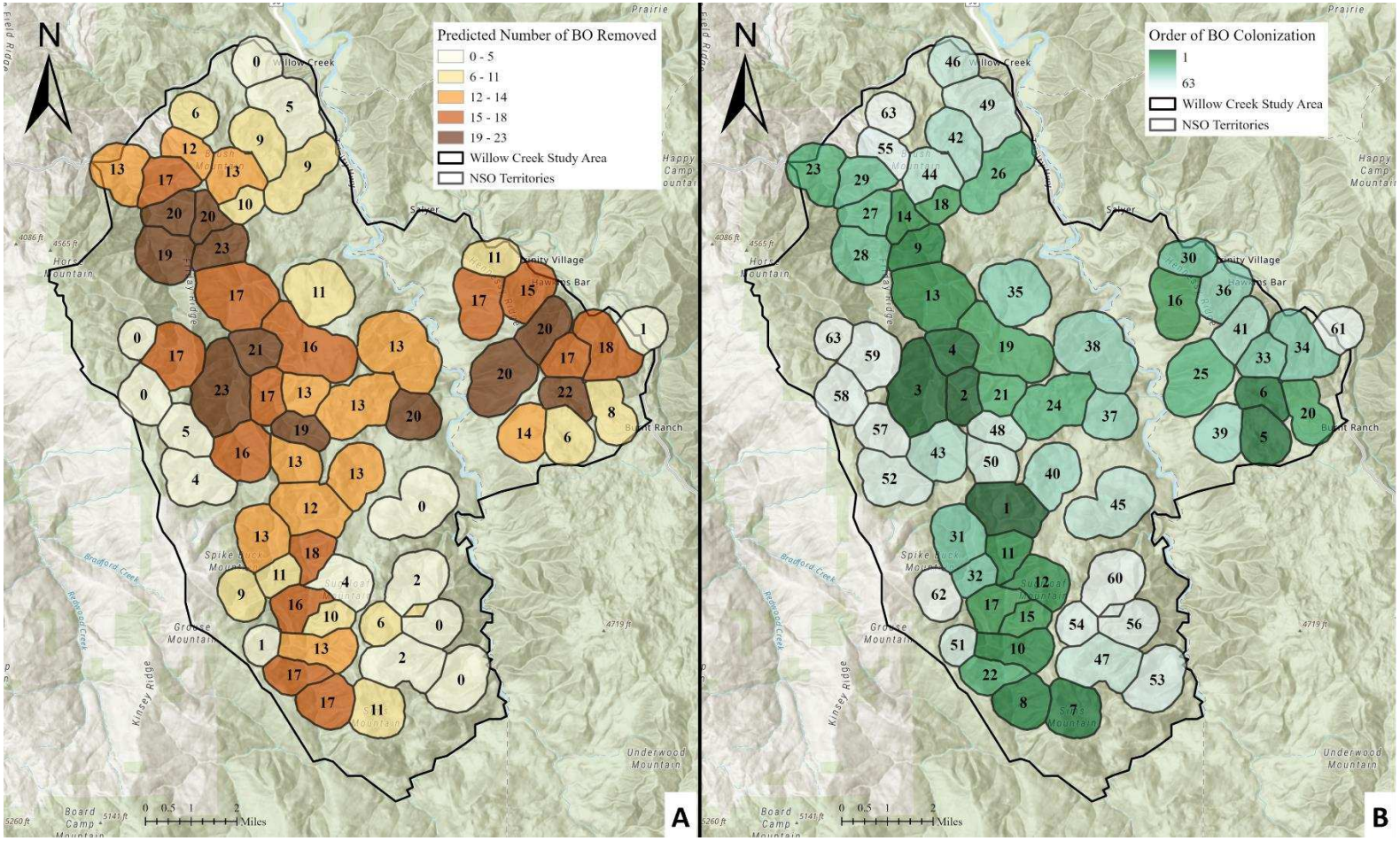

Figure 1.3. A: Map of the Willow Creek Study Area with the predicted number of barred owls (BO) to be removed in northern spotted owl (NSO) territories in a 7-year period using the predictive model developed on the Hoopa Study Area (Number of BO removed = Average wetness + % Open forest + % Old mixed conifer-hardwood forest). B: Map of northern spotted owl territories on the Willow Creek Study Area labeled in order of barred owl colonization based on barred owl detection locations from 1991-2022.

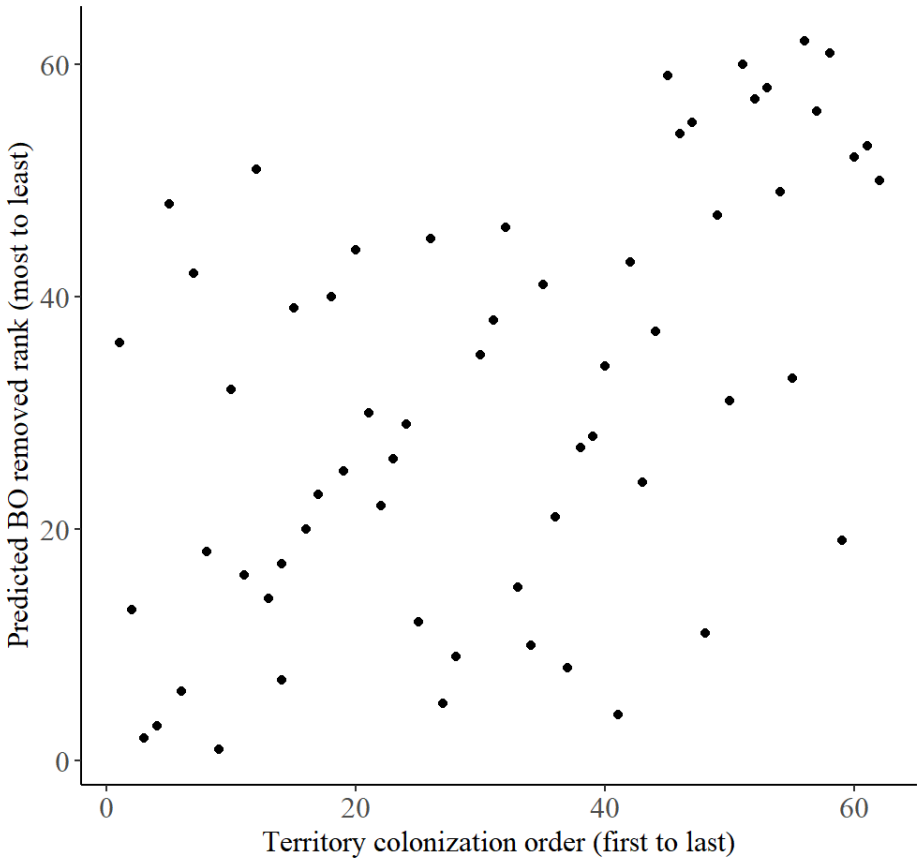

Figure 1.4. Relationship between the order of barred owl (BO) colonization of northern spotted owl territories and the rank of predicted number of barred owls removed per northern spotted owl territory on the Willow Creek Study Area, California.

CHAPTER 2: BARRED OWL LAND USE THROUGH TIME ON LANDSCAPES USED BY NORTHERN SPOTTED OWLS

Overview

In the early 1900s, barred owls (*Strix varia*) expanded westward, leading to an overlap with the native, threatened northern spotted owls (*Strix occidentalis caurina*) in western North America. Initially, northern spotted owl population declines were attributed to habitat loss from logging; however, over time the negative impacts of barred owls on northern spotted owls became evident. To assess these impacts, researchers used occupancy models to understand their interspecies dynamic. While extensive knowledge exists regarding northern spotted owl demography and habitat use, information on barred owl habitat in western North America is limited. I applied autologistic dynamic two-species occupancy models with habitat and interspecific variables to investigate associations with barred owl occupancy dynamics. My results indicate that an increase in barred owl colonization probability was associated with wetter areas, while an increase in barred owl extinction probability was associated with northern spotted owl presence. These results can be used to predict areas of high barred owl use and focus barred owl management efforts in California.

Introduction

Barred owl (*Strix varia;* BO) range expansion from eastern to western North America began in the early 1900s and now completely overlaps the range of the threatened northern

spotted owl (*Strix occidentalis caurina;* NSO) in the Pacific Northwest (Livezey 2009a). The BO range expansion coincided with increased monitoring of NSO following its listing in 1990 (U.S. Fish and Wildlife Service 1990), which recorded the expansion of BOs while providing unique and robust datasets. Researchers utilized long-term dataset to understand mechanisms of NSO presence and absence in relation to BOs using occupancy models (Yackulic et al. 2012, Yackulic et al. 2014, Yackulic et al. 2019).

Occupancy models use presence-absence data to estimate probabilities of colonization and local extinction while considering detection probability (MacKenzie et al. 2018). Previous analyses found that NSO colonization increased, and extinction probabilities decreased on NSO territories with more suitable habitat and older forests (Yackulic et al. 2014, Franklin et al. 2021b). BO presence was linked to increased extinction probability and reduced colonization probability of NSO on their territories (Olson et al. 2005, Kroll et al. 2010, Dugger et al. 2011). Modeling both NSO and BO occupancy revealed interspecies competition, with negative effects of BOs on NSOs more pronounced in areas with better habitat (Bailey et al. 2009, Yackulic et al. 2014, Yackulic et al. 2019).

The habitat associations of BO in western North America remain unclear. BO colonization probability generally increased, and extinction probability decreased, on NSO territories across the NSO range since the 1990s (Yackulic et al. 2014, Franklin et al. 2021b). BO occupancy was positively correlated with forest cover within 120m of streams, structurally diverse mature and old forests, amount of total old forest cover, and negatively correlated with elevation (Wiens et al. 2011, Yackulic et al. 2012, Franklin et al. 2021b). Increasing average BO occupancy on the landscape was correlated with an increase in BO colonization probability, while NSO presence positively related to both BO colonization and extinction probabilities

(Yackulic et al. 2012, Yackulic et al. 2014, Franklin et al. 2021b). However, these results are from a range-wide meta-analysis (Franklin et al. 2021b), which included studies outside of California.

Barred owl populations have been increasing in California since initial BO detection in 1981 (Dark et al. 1998). Peery et al. (2018) identified two of the highest priority BO research needs as 1) understanding barred owl habitat associations and 2) identifying which areas were colonized first by BOs and whether these areas are associated with certain environmental conditions. In this chapter, I retrospectively modeled the invasion dynamics of BOs in NSO territories over time in northern California, aiming to estimate the potential relationships between habitat and BO land use patterns during the invasion of NSO-occupied landscapes by BO.

Study Area

The Willow Creek Study Area (WCSA) is a 292 km^2 area south of Willow Creek, Humboldt County, CA (Figure 2.1; Franklin et al. 1990). The Six Rivers National Forest, Shasta-Trinity National Forest, and private landowners manage land within WCSA. The elevation of the study area ranges from 150m to 1,700m. The forests below 1,200m were dominated by a mixed conifer and hardwood forest consisting of Douglas-fir (*Pseudotsuga menziesii*), madrone (*Arbutus menziesii*), tanoak (*Lithocarpus densiflora*), and canyon live oak (*Quercus chrysolepis*) while above 1,200m forests are conifer forests dominated by white fir (*Abies concolor*), pines (*Pinus* spp), and Douglas-fir (Franklin et al. 1990, Franklin et al. 2000). The WCSA was established in 1985 for a demographic study of NSOs and the first BO in the study area was

detected in 1991 (Franklin et al. 1990, Franklin et al. 2021a). In 2019, the NSO population on the WCSA was 38.8% of the original population from 1987 (Franklin et al. 2021a).

Methods

Field Methods

Field methods followed Franklin et al. (1996), Dugger et al. (2016), and Franklin et al. (2021a). Owl surveys occurred annually from April through August. Surveys consisted of researchers playing or imitating NSO or BO calls to illicit a response from NSO to determine their location. NSO-specific surveys used NSO calls, while BO-specific surveys used BO calls. Surveys for both species were conducted between dusk and 1:00 am. For each detected owl, observers recorded the species, sex, time, and location as UTM coordinates. NSO-specific surveys started on the study area in 1985, while BO-specific surveys began in 2008. Prior to 2008, BOs were frequently detected and recorded during NSO-specific surveys. I used data from 1993-2022, starting the year after the first BO was detected on the study area.

Sampling Units and Variables

To outline areas historically used by NSOs, the sampling units for this analysis were the 63 NSO territories on the WCSA, delineated as Thiessen polygons centered around cumulative NSO nest, fledgling, and roost locations (Franklin et al. 2021b). I assumed the boundaries of

NSO territories remained constant through time and aggregated all variables at this scale. To understand what factors were associated with BO colonization and extinction probabilities, I tested three types of variables in this analysis: neighborhood occupancy, forest types and structure, and interspecific.

Neighborhood occupancy variables represented average BO presence on the landscape through time. Neighborhood occupancy was estimated using autologistic models where the average estimated occupancy of BOs across the study area in the previous time step was used as a variable for territory colonization or extinction probability in the next time step. For example, Yackulic et al. (2012) analyzed 21 years of BO detection data using autologistic models with a variable for average neighborhood BO occupancy calculated in the previous time step in the models for BO colonization and extinction for the next time step. Using the entire study area as the neighborhood due to large dispersal distances of BOs, Yackulic et al. (2012) found that BO colonization and extinction probabilities were positively correlated with average neighborhood BO occupancy. The positive correlation between BO colonization probabilities and average neighborhood BO occupancy was prominent in the beginning of the invasion and decreased as the BO population neared equilibrium. I tested the autologistic variable against annual effects, including linear time trends across years and year-varying variables to determine if increasing BO presence through time or general temporal trends were associated with BO extinction and colonization (Table 2.1).

I selected forest type and structure variables based on the previous literature to describe the biotic and abiotic components of the landscape occupied by BO and NSO. In a review of BO habitat across the United States and Canada, Livezey (2007) found BOs used low elevation, low slope areas with old forest. The effect of distance to water and edge habitat varied between

studies (Livezey 2007). In Oregon, Jenkins et al. (2019a) found BOs prefer forest structure consisting of high canopy closure, tall trees, lower understory cover during the breeding season, and higher understory cover during the non-breeding season. In Washington, Singleton et al. (2010) found BOs occupied sites concentrated in areas with low elevation, low slope, large overstory tree-crown diameter, high Normalized Difference Vegetation Index (NDVI), high overstory canopy closure, and moderate solar isolation.

I used forest type and structure variables that included percent area open forest, percent area prey habitat, percent area old hardwood forest, percent area young mixed conifer-hardwood forest, percent area old mixed conifer-hardwood forest, percent area old conifer forest, average wetness measured by Topographic Wetness Index (TWI), average aspect, and the predicted number of BO removed determined by the predictive model in Chapter 1 (Table 2.1). To estimate forest types and structure variables, I used yearly 30 x 30 m vegetation class (VEGCLASS) raster from 1993-2017 from the GNN Downloader (https://lemmadownload.forestry.oregonstate.edu/), following the same process outlined in Chapter 1. To account for any potential land change on the study area over time, I averaged the annual values across all years. Topographic variables were determined from elevation digital elevation models (DEMs) from the USGS National Map following the procedure in Chapter 1.

Interspecific effects described how NSO presence influenced BO colonization and extinction. Additive effects implied a constant difference in BO behavior due to NSO, while interactive effects suggested that BO behavior varied unpredictably with NSO presence. Franklin et al. (2021b) and Yackulic et al. (2014) found NSO presence was positively correlated with both BO extinction and colonization probabilities on NSO territories. They hypothesized increased probabilities were due to similar habitat preference between the species, BOs possibly

using NSOs as a habitat cue, or NSO vocalizations behaviorally attracting BOs (Yackulic et al. 2014, Franklin et al. 2021b). These hypotheses were based on the high overlap in NSO and BO habitat preference, BOs territorial response to NSO vocalizations, and BO attraction to areas already occupied by NSOs (Seamans and Gutierrez 2006, Hamer et al. 2007, Wiens et al. 2014). Discerning causation of positive correlation between NSO presence and BO colonization probabilities is difficult because of high overlap of preferred habitat but both studies suggest the correlation may be due to unmodeled habitat variables (Yackulic et al. 2014, Franklin et al. 2021b).

Analysis

To determine the association between neighborhood occupancy, forest type and structure, and interspecific interaction with BO colonization and extinction, I used the dynamic two-species occupancy model (MacKenzie et al. 2018) implemented in program PRESENCE (Hines 2006) and MARK (White and Burnham 1999) to test *a priori* hypotheses of associations of the variables with BO colonization and extinction (Franklin et al. 2001). I created a base model to best explain NSO occupancy dynamics while remaining as general as possible (see *NSO Base Model Structure* in Chapter 2 Appendix). My model selection process first consisted of model sets for each variable type with models that included only a single variable for BO colonization and extinction parameters to reduce the potential effects of multicollinearity and overparameterization (Figure 2.2). I then included strongly supported variables from each model set in a final model set, where I tested all possible combinations of the variables. The all-possible combinations approach produces a balanced model set to better consider hypothesized variables

of interest within the explanatory ability of the dataset (Doherty et al. 2012, Bromaghin 2013, Morin et al. 2020).

Interspecific effects were tested by setting equal BO colonization and extinction parameters that represented an effect of NSO presence. I ranked models by AICc, a bias-corrected version of AIC for small sample sizes (Burnham et al. 2011), then ranked variables by model weight in each model set. While no straightforward estimate of effective sample size exists for calculating AICc with occupancy models (MacKenzie et al. 2018), I used the common practice of the number of sites times the number of primary sampling periods to determine effective sample size (effective sample size = 63 territories * 30 primary sampling periods = 1890). I determined variable importance through model AICc values, summed AICc weight for individual variables, and β estimates for variables (White and Burnham 1999, Burnham and Anderson 2002). Variables with the highest model weight in the respective model set, or all variables with model weight > 0.5 in the respective model set were used in the final model set after confirming the 95% confidence intervals for $\hat{\beta}$s did not overlap zero.

Results

Individual model sets for BO colonization indicated that a linear year trend, wetness, and an additive NSO effect were the most supported variables with the highest model weights in the respective model sets (Appendix Table 2.1). However, the 95% confidence intervals for the $\hat{\beta}$ of linear year trend overlapped zero ($\hat{\beta}$ = 0.021, SE = 0.013, 95% CI = -0.005, 0.046), so the next ranked model (the intercept-only model) became the highest ranked. Only the additive NSO effect had a weight > 0.5 (Table 2.2).

Individual model sets for BO extinction indicated that a linear year trend, percent young mixed conifer-hardwood forest, and an additive NSO effect were the most supported variables with the highest model weights in the respective model sets (Appendix Table 2.2 and 2.3). However, the 95% confidence intervals for the $\hat{\beta}$ of the linear time trend ($\hat{\beta}$ = -0.030, SE = 0.016, 95% CI = -0.061, 0.002) and percent young mixed conifer-hardwood forest ($\hat{\beta}$ = -0.030, SE = 0.016, 95% CI = -0.062, 0.002) [sic] overlapped zero, so the intercept-only time effect and percent old mixed forest became the highest rank. Both the percent old mixed conifer-hardwood forest and the additive NSO effect had model weights > 0.5 (Table 2.2).

The final model set tested all combinations of wetness and an additive NSO effect on BO colonization and percent old mixed conifer-hardwood forest and an additive NSO effect on BO extinction (Appendix Table 2.4). The top ranked model was a model with the wetness variable on BO colonization and an additive NSO effect on BO extinction. Summed model weights also show these were the most supported variables with values > 0.5 (Table 2.3). Estimates for wetness ($\hat{\beta}$ = 0.771, SE = 0.375, 95% CI = 0.036, 1.506) and the additive NSO effect ($\hat{\beta}$ = 2.155, SE = 0.765, 95% CI = 0.656, 3.654) were positive in the top model of the final model set, indicating that an increase in colonization and extinction probability was associated with an increase in wetness and NSO presence, respectively (Figure 2.3). The 95% confidence intervals for the $\hat{\beta}$ of the additive NSO effect on BO colonization ($\hat{\beta}$ = -0.149, SE = 0.322, 95% CI = -0.781, 0.482) and old mixed conifer-hardwood forests on BO extinction ($\hat{\beta}$ = 0.010, SE = 0.012, 95% CI = -0.131, 0.033) overlapped zero in models where included. Using estimates from the top model, the estimated BO occupancy probability steadily increased through time (Figure 2.4).

Discussion

BO colonization and extinction probabilities were constant through time; however, BO occupancy steadily increased in the study area because the colonization probabilities exceeded extinction probabilities for BO. BO colonization probability was positively associated with wetness and BO extinction probability was positively associated with NSO presence. The associations suggest there was a higher probability a BO would colonize a wetter area and there was a higher probability a BO would go locally extinct in an area where NSOs were also present (but see below).

The positive association between NSO presence and BO extinction probability seemed contradictory as NSO numbers continue to decline with increasing BO populations. However, this association may have arisen from NSOs that remained on the study area in the latter part of the study. The behavioral plasticity of NSOs could mean that these last remaining NSO were more aggressive than others and were able to fend off BOs in their territories. These NSOs may be in marginal habitat within the study area, increasing the importance of managing BO presence and improving NSO habitat quality. Sustaining a source population of NSOs is important to colonize BO-free refugia in the future. Exploring the relevance of areas with remaining NSOs on the study area compared with BO colonization is needed to further understand this relationship.

In the eastern United States, BOs are often observed in marshes, swamps, and damp forests (Livezey 2007). In the western United States, BO range expansion appeared to start in coastal areas before expanding to drier regions. In California, BOs were first detected in the moist coastal redwoods before being detected in eastern California (Dark et al. 1998). An

increase in BO colonization probability in wetter areas is potentially due to increased amphibian prey availability, which can be a frequent item in BO diets (Kryshak et al. 2022).

Interspecific interactions can decouple habitat associations. Yackulic et al. (2014) found that interspecific competition between NSOs and BOs weakened the relationship between habitat and NSO occupancy. In this study, I found little evidence for an association between old mixed conifer-hardwood forest and BO extinction probability. NSO could possibly weaken the relationship between BO occupancy and old mixed conifer-hardwood forest, but teasing apart the effects of habitat and competition is difficult. However, the effect of NSO presence weakening the relationship between habitat and BO colonization could not be seen here because there was little support for an association with NSO presence.

Unlike studies in Oregon (Yackulic et al. 2012, Yackulic et al. 2014), my analysis did not support an association between BO neighborhood occupancy and BO occupancy dynamics. This difference could be due to a higher number of BOs and longer residency of BO populations in Oregon than in California. The autologistic effect is easier to discern when a large difference between initial and equilibrium occupancies exists (Yackulic et al. 2012). Due to California being in an earlier stage of BO invasion than Oregon, this difference may not be as great, or equilibrium occupancy has not been reached. As BO numbers continue to increase in California, the association with neighborhood occupancy may become evident in the future.

A limitation of this study Is that occupancy analysis relies solely on presence-absence data and lacks the ability to quantify intensity of use or discern use among different individuals (Rockweit et al. 2017). In this case, “used” or “occupied” might indicate multiple individuals in an area, limiting the ability to discern finer-scale occupancy dynamics. Alternative approaches,

such as estimating demographic parameters, can offer more insights into how habitat influences this population.

Management Implications

The association of wetness and NSO presence with BO colonization and extinction probability increases the understanding of BO occupancy dynamics in northern California. Barred owl management could proceed in two ways, either targeting areas of high colonization probability and low extinction probability or targeting areas of low colonization probability and high extinction probability. The difference between these two approaches is either targeting areas with naturally high BO persistence to artificially lower persistence, or to target areas with naturally low BO persistence to artificially lower persistence even further. The latter could make a bigger impact on BO presence with less effort. Focusing management in areas of low BO persistence would target drier areas without NSOs to open the area for dispersing NSO. Then areas with high BO persistence could be used as sinks for remaining BOs. However, the targeting of BO management depends on conservation goals for NSOs, focusing on either persistence or population growth. Removal effectiveness varies based on the quality of NSO habitat in which BO are managed. Balancing these conflicting strategies involves a trade-off, and future research can explore the optimal approach. Regardless, BO management in conjunction with active NSO habitat management will increase the persistence of NSO and forest ecosystem stability (Yackulic et al. 2019).

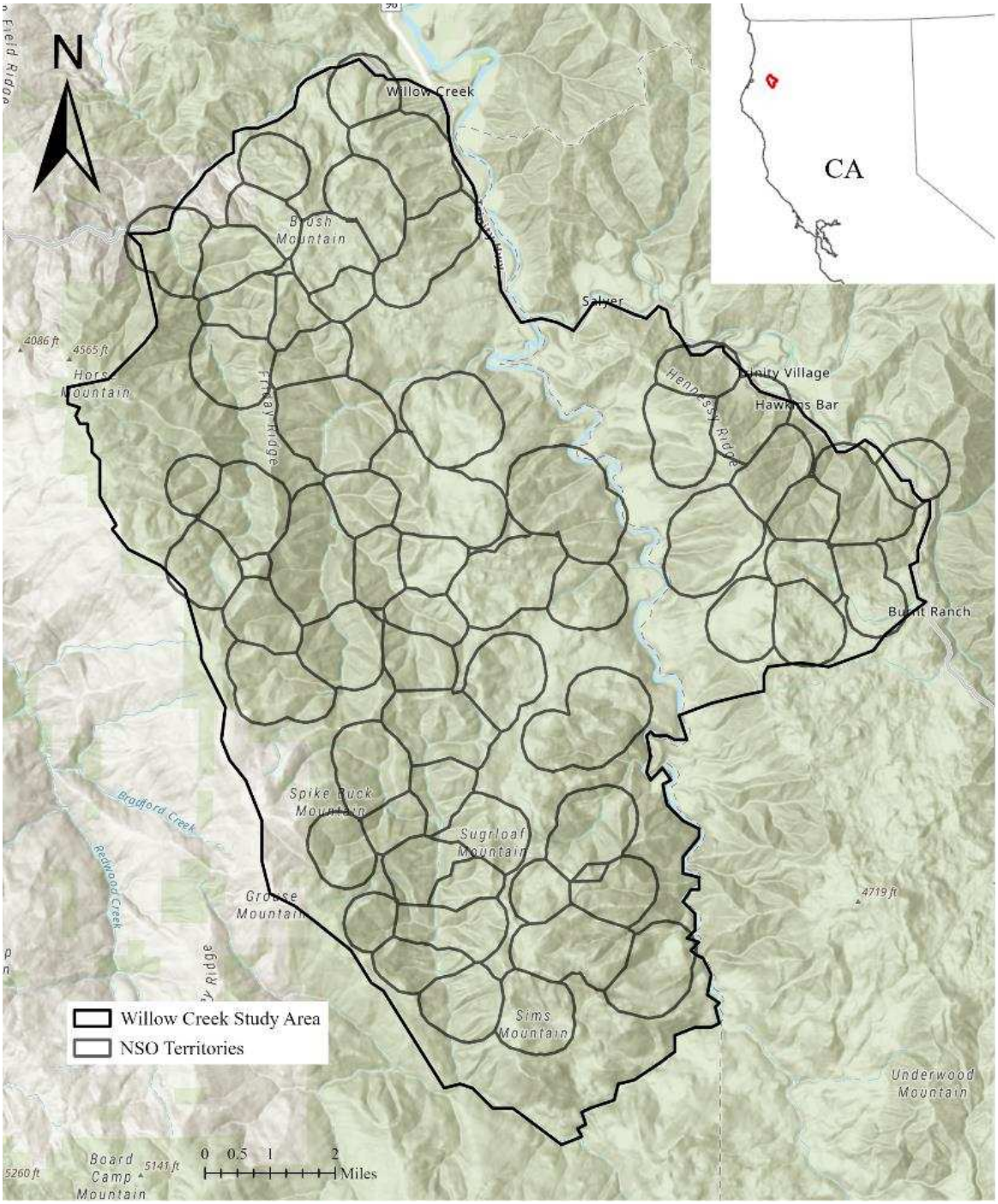

Figure 2.1. Distribution of northern spotted owl (NSO) territories on the Willow Creek Study Area in Humboldt and Trinity Counties, California.

Table 2.1. Description of variables used in the occupancy analysis of barred owls (BO) on northern spotted owl territories (NSO) in the Willow Creek Study Area in northern California.

Variable type	Variable	Description	Range[1]
Forest type and structure			
	Open forest (%)	% area of sparse trees with open canopy	0.1 – 25.4%
	Prey habitat (%)	% area of sapling or pole sized hardwood & conifer trees with moderate to closed canopy	3.0 – 32.0%
	Old hardwood (%)	% area of small to large hardwood trees with moderate to closed canopy	0.7 – 26.3%
	Young mixed (%)	% area of small to medium conifer & hardwood trees with moderate to closed canopy	10.1 – 40.4%
	Old mixed (%)	% areas of large to very large conifer & hardwood trees with moderate to closed canopy	3.6 – 43.5%
	Old conifer (%)	% area of very large conifer trees with moderate to closed canopy	0.5 – 41.9%
	Aspect (degrees)	Average aspect	3.4 – 343.8°
	Predicted BO removed (#)	# of predicted BO removed from prediction model in Chapter 1	0 – 24
	Wetness	Average topographic wetness index (TWI)	4.83 – 6.00
Neighborhood and time			
	Year	Parameter varying by each year of the study	1 – 30
	Year trend	Parameter varying by year in a linear trend	NA
	Neighborhood	Average BO occupancy of the study area in the previous time period	NA

[1] The minimum and maximum value of each variable in the data

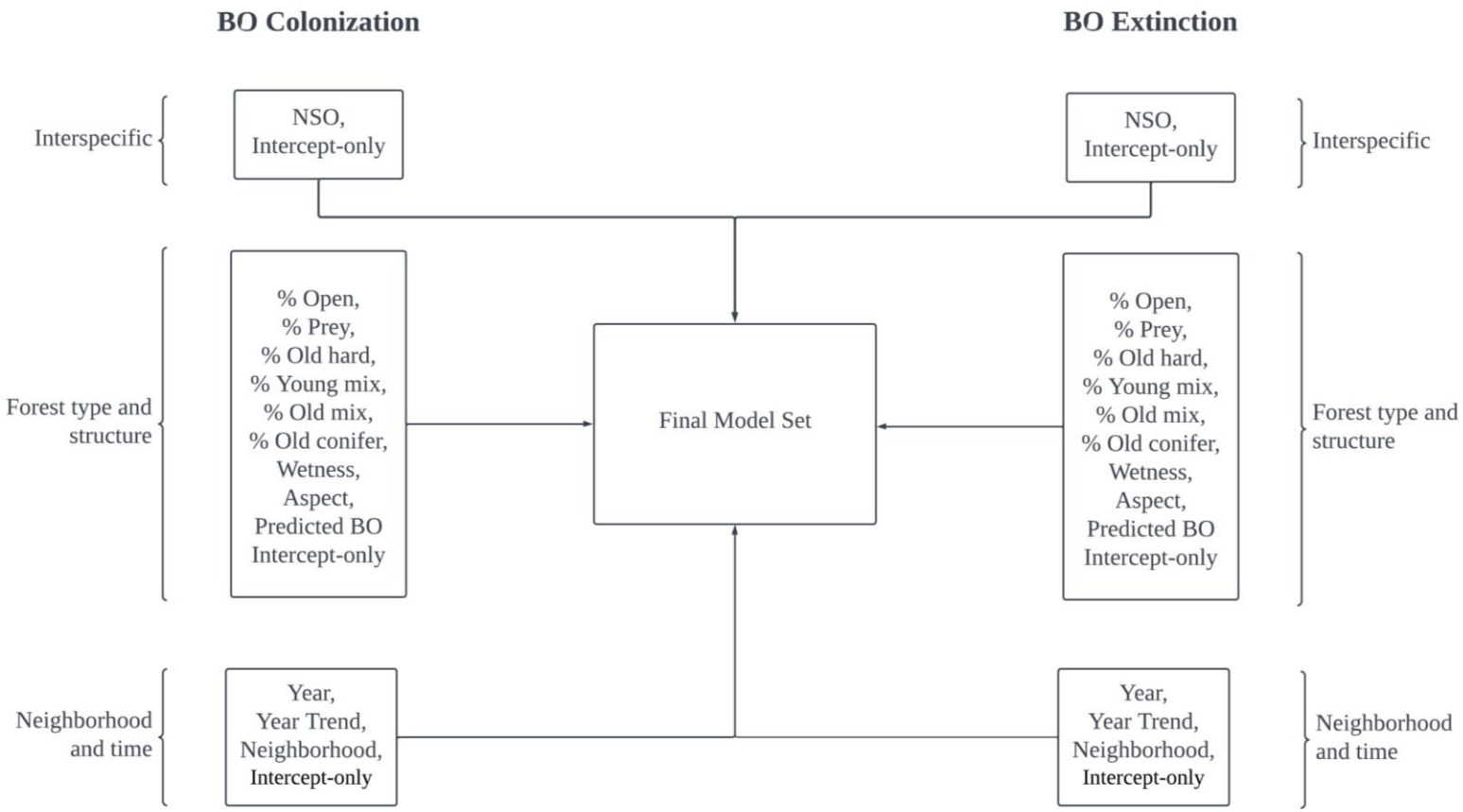

Figure 2.2. Approach used for model building and selection in the two-species occupancy dynamics analysis for barred owls (BO) and northern spotted owls (NSO). Each box represents a different model set. Variables with the highest ranked model weight in their respective set were tested by all-possible combination in the final model set.

Table 2.2. Occupancy modeling results for barred owl (BO) colonization and extinction from different model sets. Model sets tested interspecific, forest type, forest structure, neighborhood, and time variables on BO colonization and extinction.

	BO Colonization		BO Extinction	
Model set	Variable	Weight	Variable	Weight
Interspecific				
	NSO (Additive)	1.000	NSO (Additive)	1.000
	Intercept-only	0.000	Intercept-only	0.000
	NSO (Interaction)	0.000	NSO (Interaction)	0.000
Forest type and structure				
	Wetness	0.337	Old mixed	0.906
	Old mixed	0.254	Open	0.090
	Old conifer	0.091	Old conifer	0.004
	Young mixed	0.070	Wetness	0.000
	Aspect	0.063	Intercept-only	0.000
	Predicted BO removed	0.053	Aspect	0.000
	Open	0.046	Old hardwood	0.000
	Prey habitat	0.044	Prey habitat	0.000
	Old hardwood	0.043	Predicted BO removed	0.000
	Intercept-only	0.000	Young mixed	NA[1]
Neighborhood and time				
	Year trend	0.427	Year trend	0.596
	Intercept-only	0.373	Intercept-only	0.298
	Neighborhood	0.200	Neighborhood	0.106
	Year	0.000	Year	0.000

[1] Model deleted from model set due to estimated beta 95% confidence intervals overlapping zero. (See Appendix Table 2.2).

Table 2.3. Model weights for variables on barred owl (BO) colonization and extinction from the final model set in an occupancy analysis. NSO is northern spotted owl.

Parameter	Variable/Effect	Model weight
BO Colonization		
	Wetness	0.764
	NSO presence	0.252
BO Extinction		
	NSO presence	1.000
	Old mixed	0.218

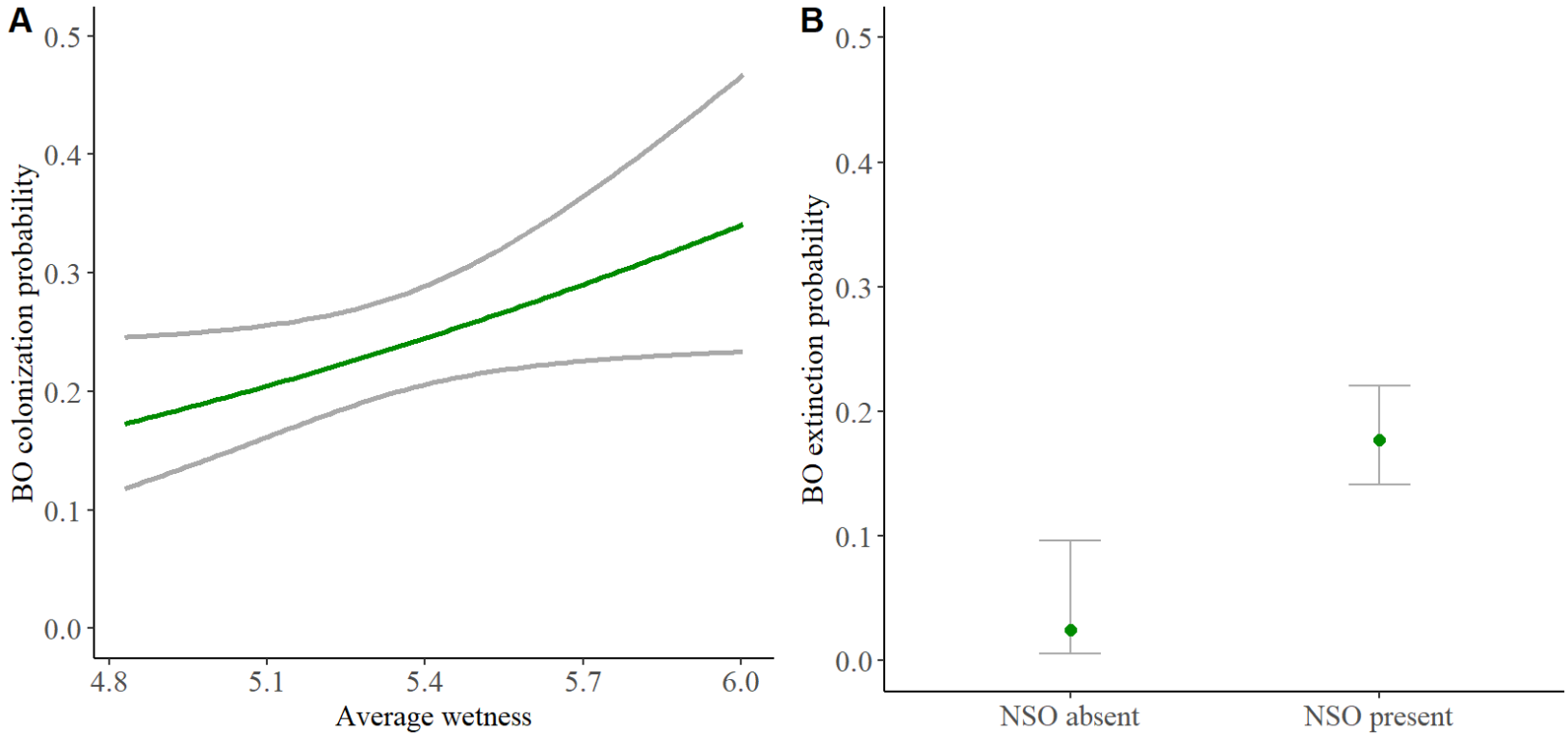

Figure 2.3. Estimates and 95% confidence intervals from the top model in the final model set of the two-species occupancy analysis. (A) is the association between barred owl (BO) colonization probability and average wetness index of northern spotted owl (NSO) territories. (B) is the association between BO extinction probability and NSO presence.

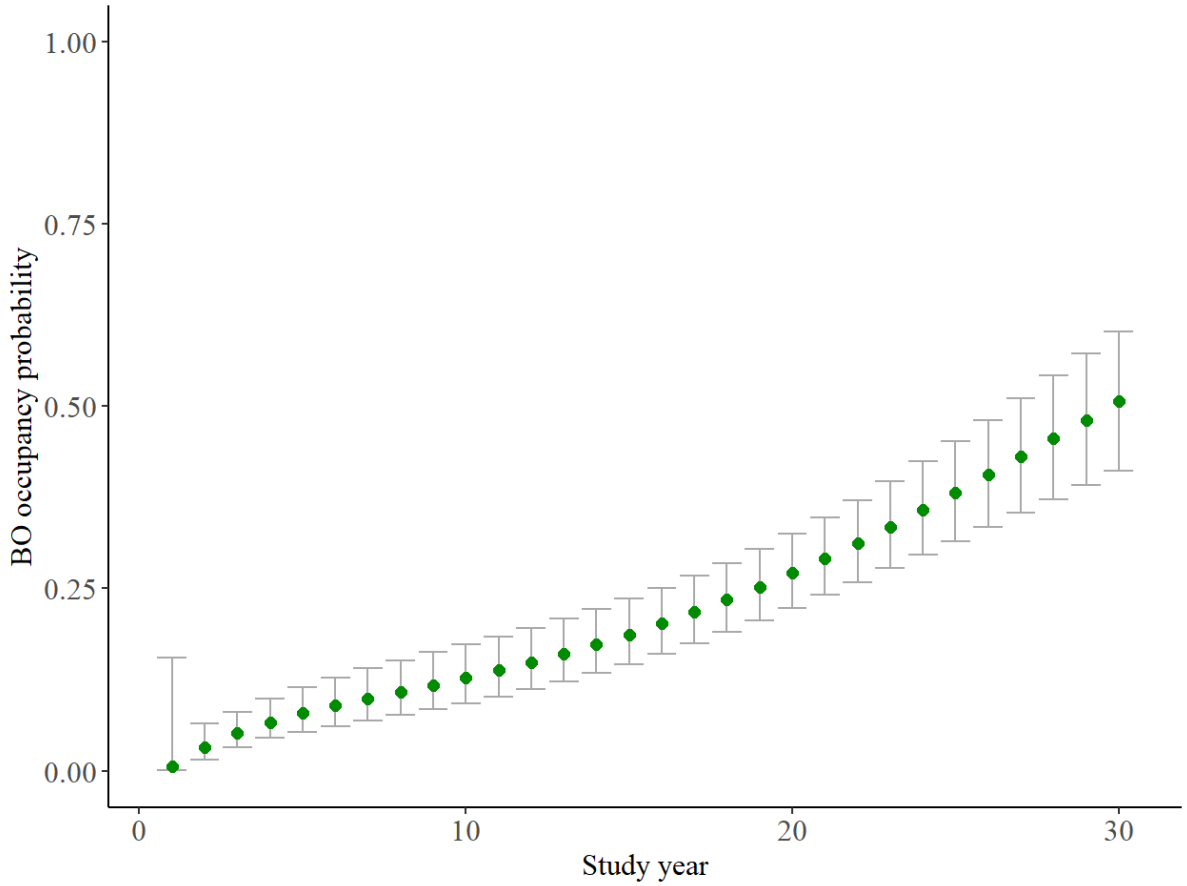

Figure 2.4. Annual estimates and 95% confidence intervals of barred owl (BO) occupancy probability on the Willow Creek Study Area. Estimates are from the top ranked model in the final model set of the two-species occupancy analysis.

THESIS CONCLUSIONS

In these chapters, I explored associations of BO land use on a NSO landscape during initial colonization by BO and over time in areas where BO removal did and did not occur. The data from Willow Creek and Hoopa Study Areas provided independent data sets for prediction and testing, offering a unique perspective on BO land use in a NSO landscape. The predictive ability of the model presented in Chapter 1 has exciting potential as BO management continues to expand using BO removals. This model can be empirically tested with BO removals and can help target management efforts in California.

Wetness plays a consistent role in both BO initial colonization and occupancy of NSO territories, emphasizing its importance in BO habitat. Both chapters indicate that wetter areas are associated with higher BO colonization, potentially due to wetter areas providing more habitat for amphibious prey, which form part of the BO diet in California (Kryshak et al. 2022). Wetter areas are increasingly important to NSO as they are less susceptible to high severity wildfire, another significant threat to NSO populations. Increasing wildfires can further reduce NSO habitat and drive NSOs into more intense competition with BOs. Old mixed conifer-hardwood forest also plays a consistent role in BO initial colonization. Areas with higher areas of old mixed conifer-hardwood forest are associated with increased BO colonization; however, this relationship may be partially decoupled due to competition with more aggressive NSOs that remain towards the end of the BO invasion.

Overall, my thesis research provided insights on the associations of BO land use in northern California. By comparing predictions with empirical order of colonization, I found areas with a high predicted level of BO removal were correlated with areas first colonized by BO.

Predicting required levels of BO removal in a novel area is a step towards planning more efficient and effective BO management in California. These predictions and targeted removal strategies can be tested in ongoing removal experiments of BO in northern California to provide further insights. Overall, BO management strategies will depend on the goal of NSO conservation and further studies to determine an optimal approach.

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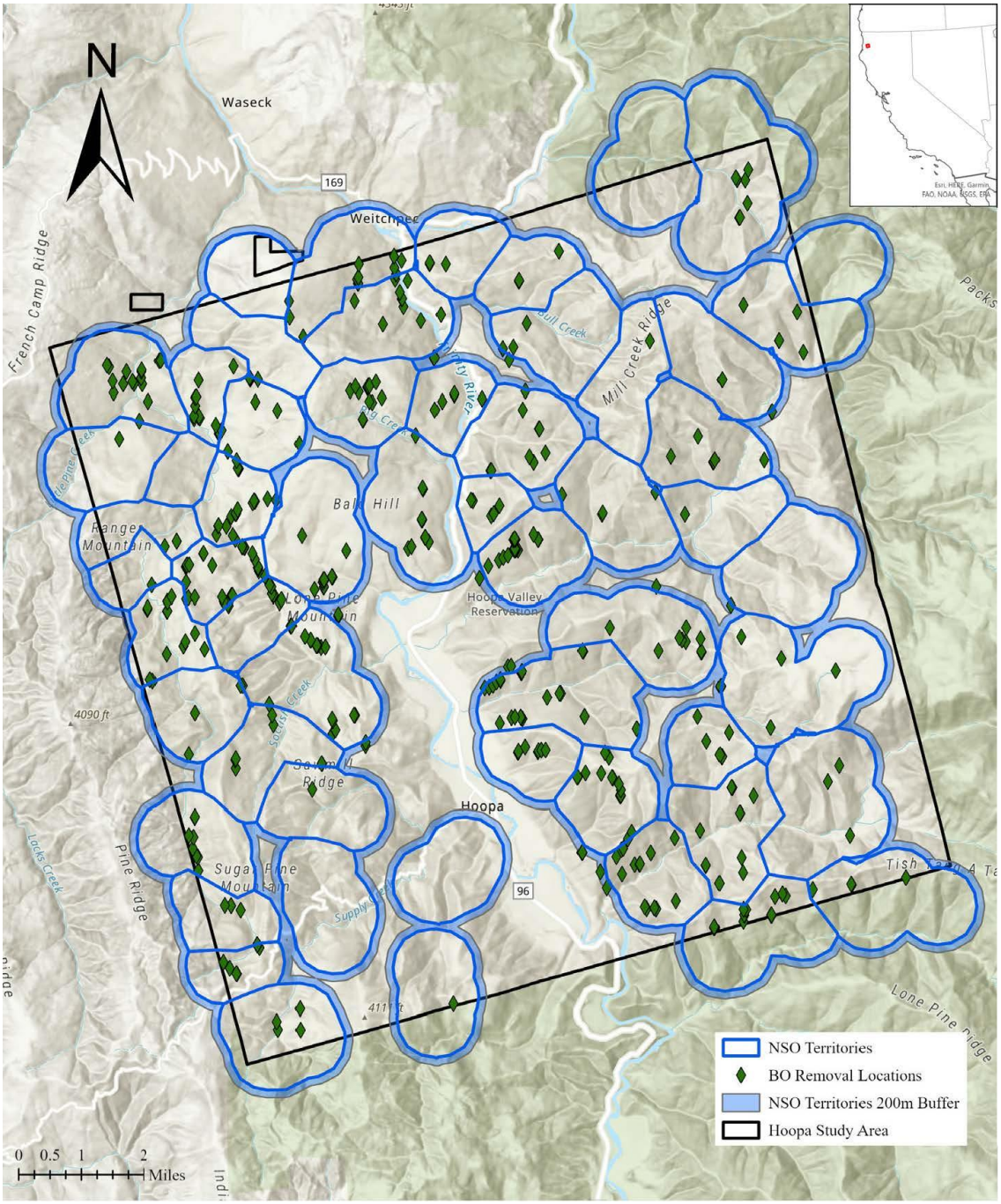
APPENDICES

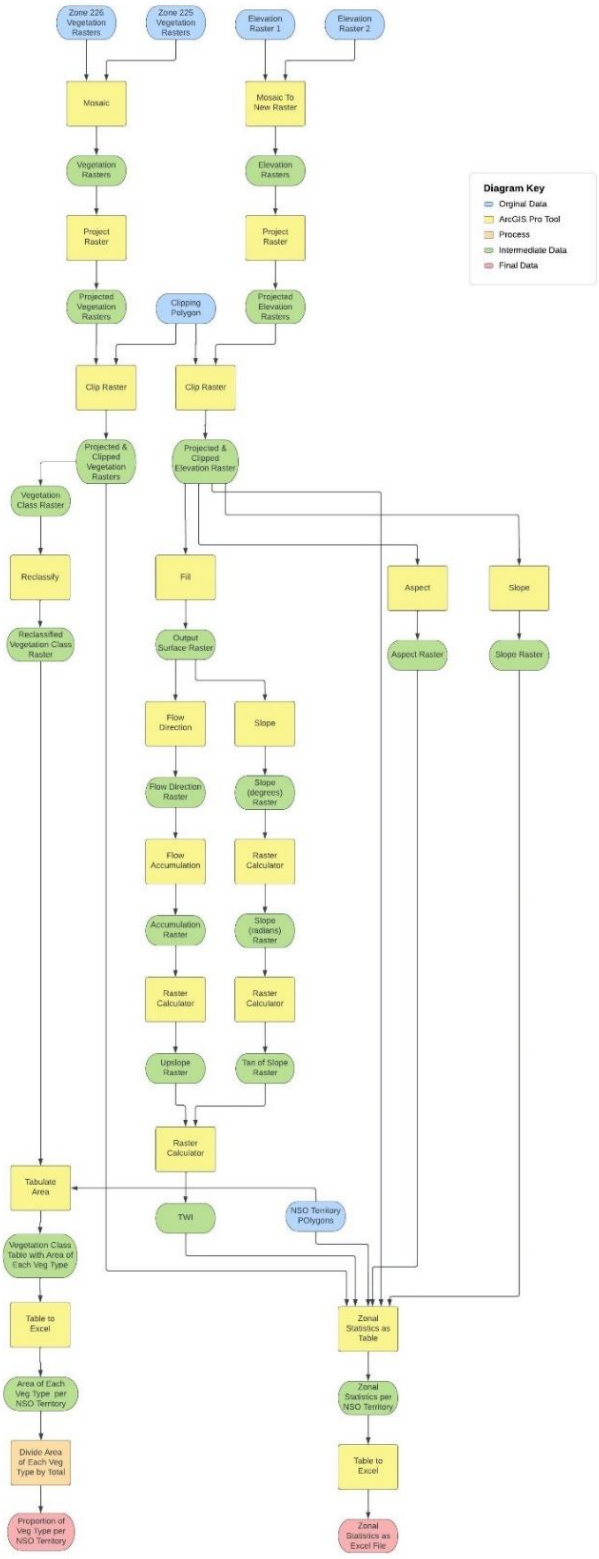
Chapter 1 Appendix



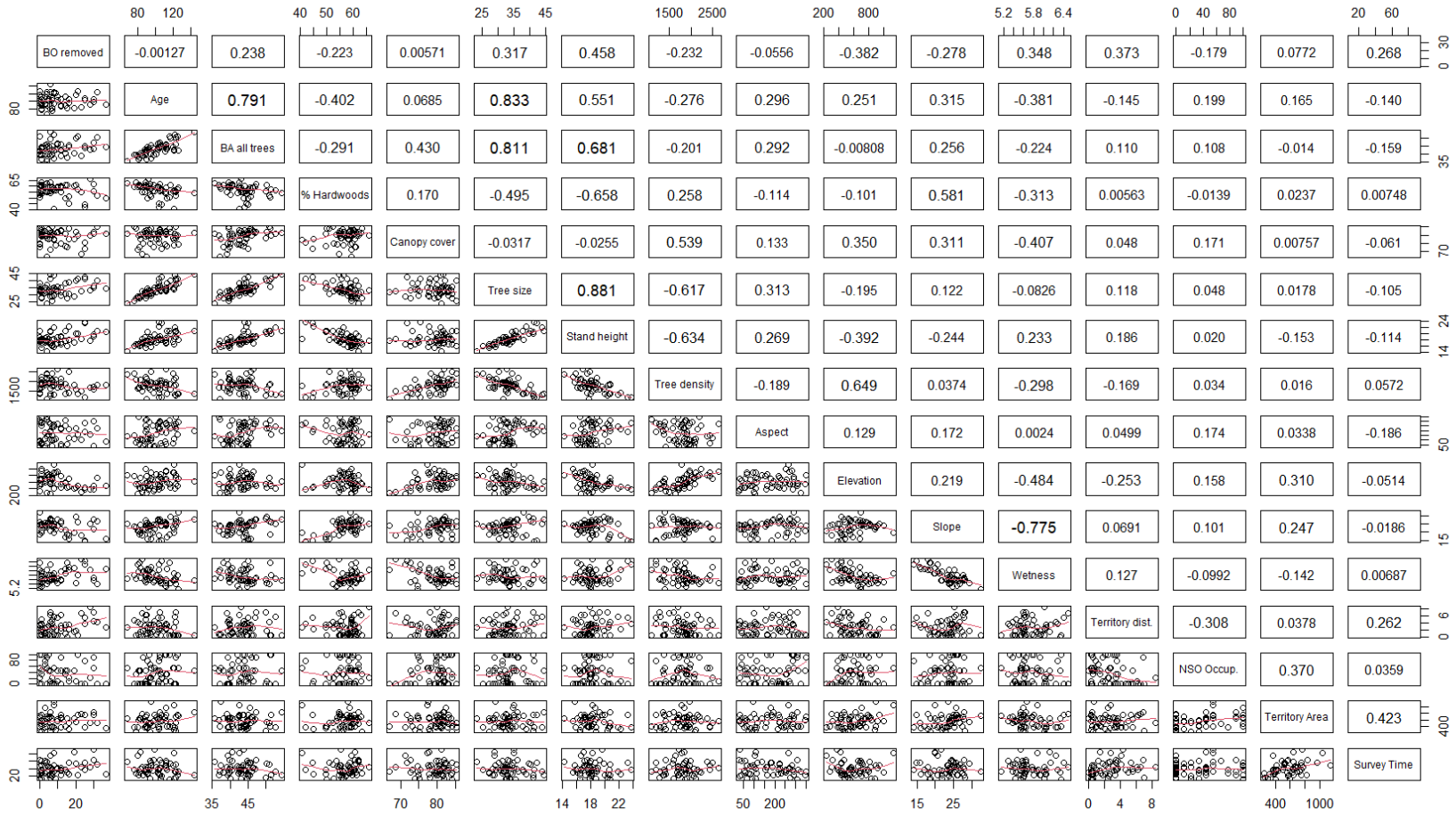
Appendix Figure 1.1. Barred owl (BO) removal locations within northern spotted owl (NSO) territories on the Hoopa Study Area from 2013-2021. Blue areas indicate 200m buffers to account for the distance a BO can be lured into a territory.

Appendix Table 1.1. Description of forest type variables used in analysis of barred owl recolonization after removal. The percentage of hardwoods was determined by basal area. Quadratic mean diameter (QMD) represents the average size of the trees in an area.

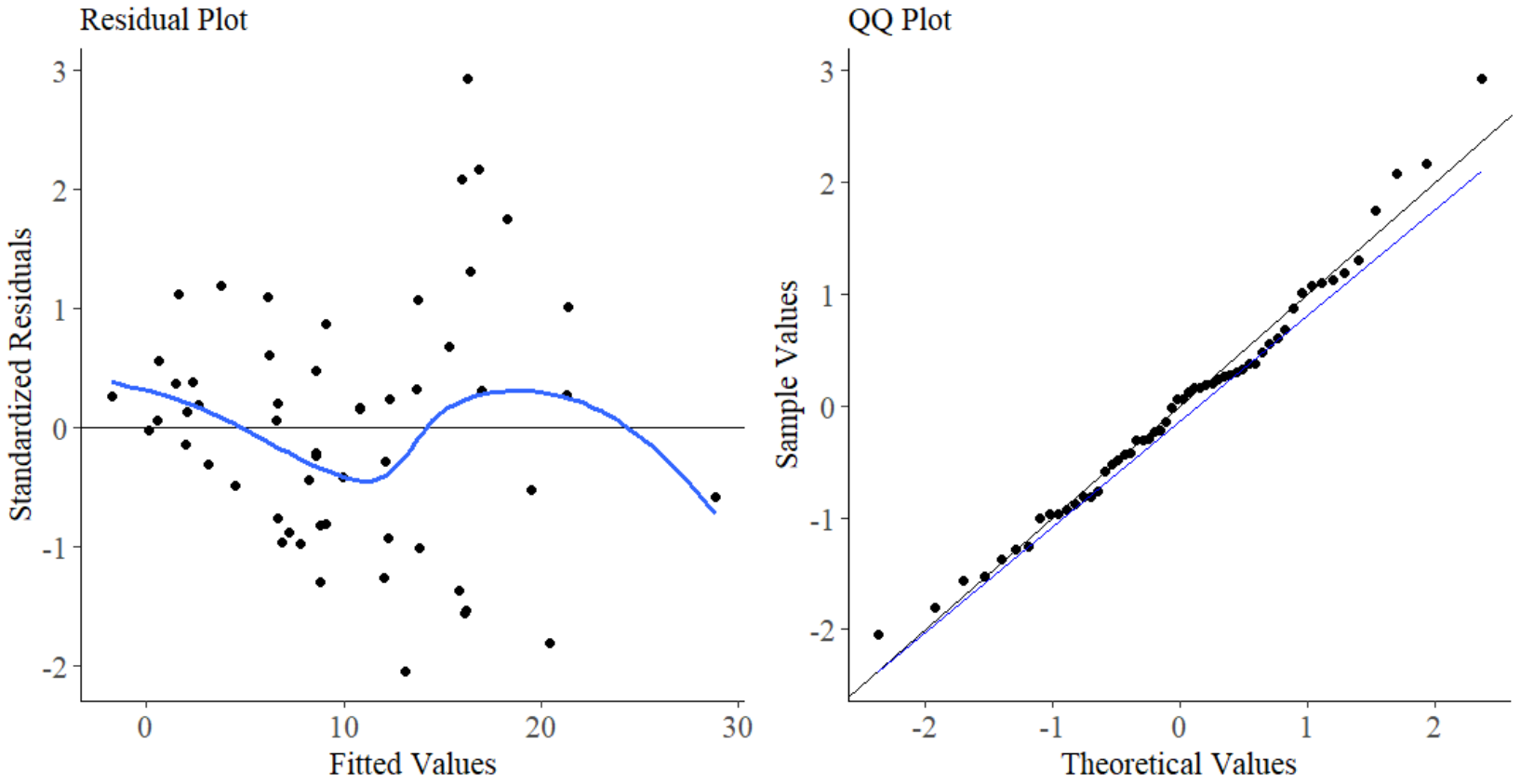
		Composition		
Forest type	Description	Canopy cover	% Hardwoods	QMD
Open	Sparse trees with open canopy	< 39%	NA	NA
Prey habitat	Sapling or pole sized hardwood & conifer trees with moderate to closed canopy	≥ 40%	≥ 20%	< 25cm
Old hardwood	Small to large hardwood trees with moderate to closed canopy	≥ 40%	≥ 65%	> 25cm
Young mixed	Small to medium conifer & hardwood trees with moderate to closed canopy	≥ 40%	20-64%	25-50cm
Old mixed	Large to very large conifer & hardwood trees with moderate to closed canopy	≥ 40%	20-64%	> 50cm
Young conifer	Sapling to medium conifer with moderate to closed canopy	≥ 40%	< 20%	≤ 50cm
Old conifer	Very large conifer trees with moderate to closed canopy	≥ 40%	< 20%	> 50cm



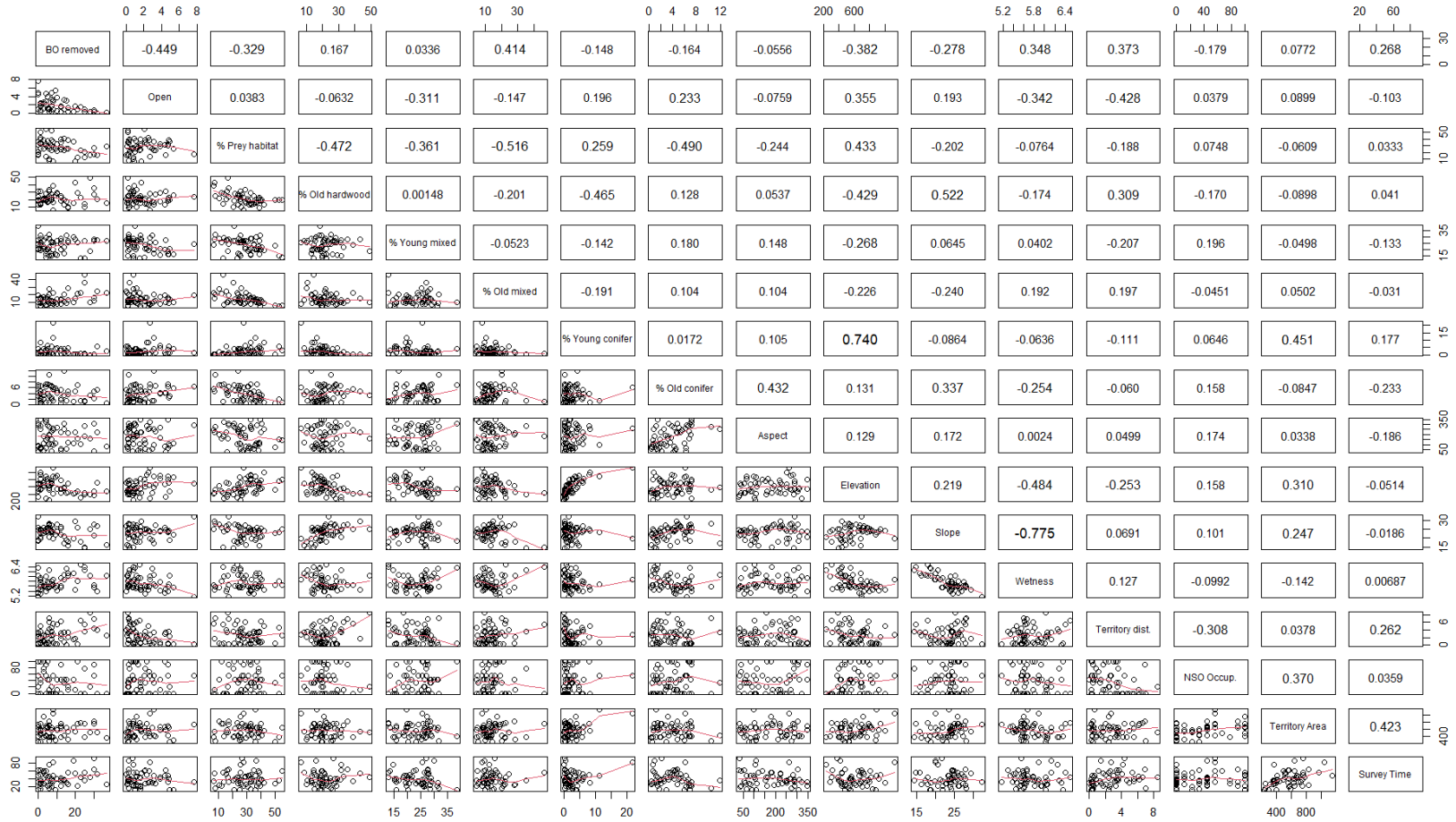
Appendix Figure 1.2. GIS workflow to calculate forest type and structure variable values in northern spotted owl territories using ArcGIS Pro 2.9.



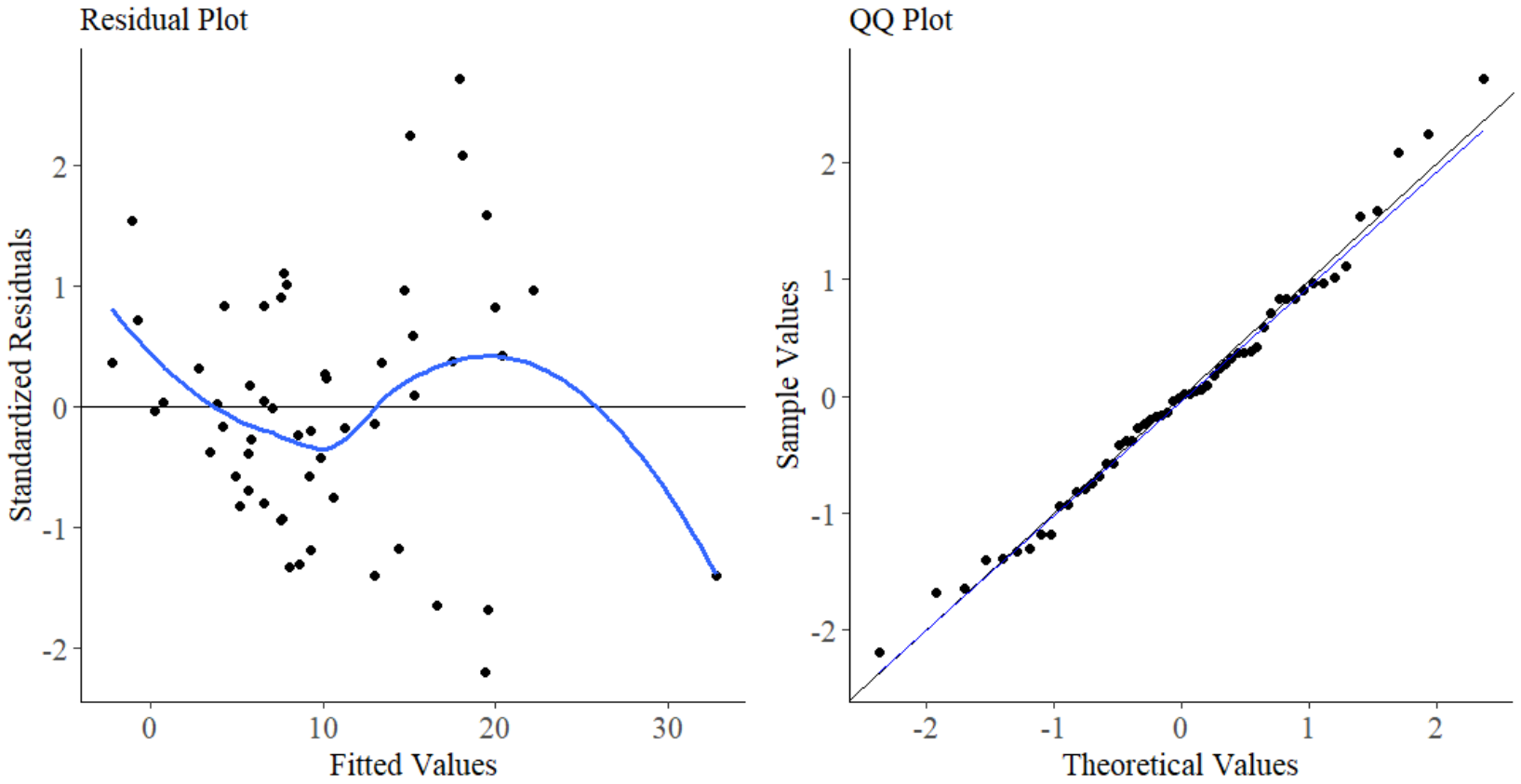
Appendix Figure 1.3. Correlation matrix of the variables considered in analysis of the forest structure model set for barred owl (BO) recolonization of northern spotted owl (NSO) territories.



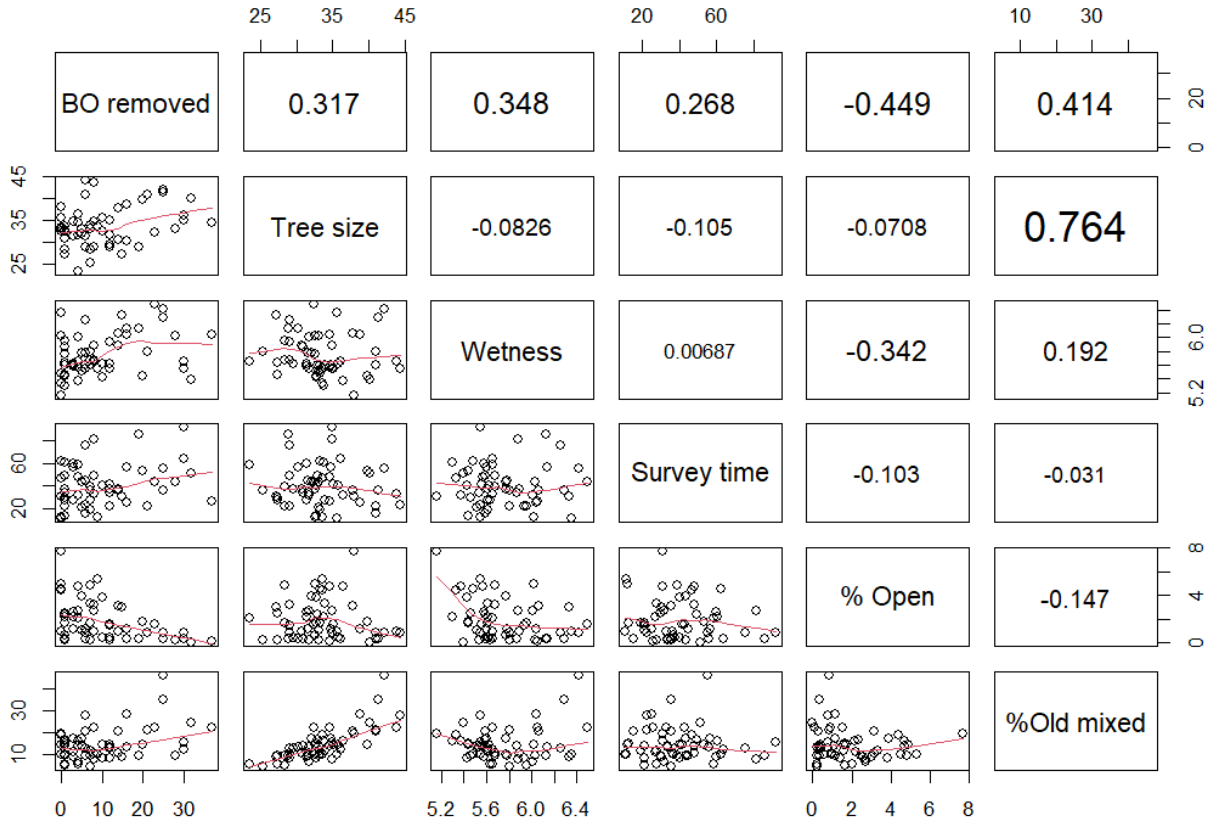
Appendix Figure 1.4. Residual and QQ plots of the global model in the forest structure analysis of the number of barred owls (BO) removed on northern spotted owl (NSO) territories. (Number BO removed per NSO territory = % hardwoods + canopy cover + tree size + aspect + tree density + wetness + territory distance + NSO presence + territory area + survey time).



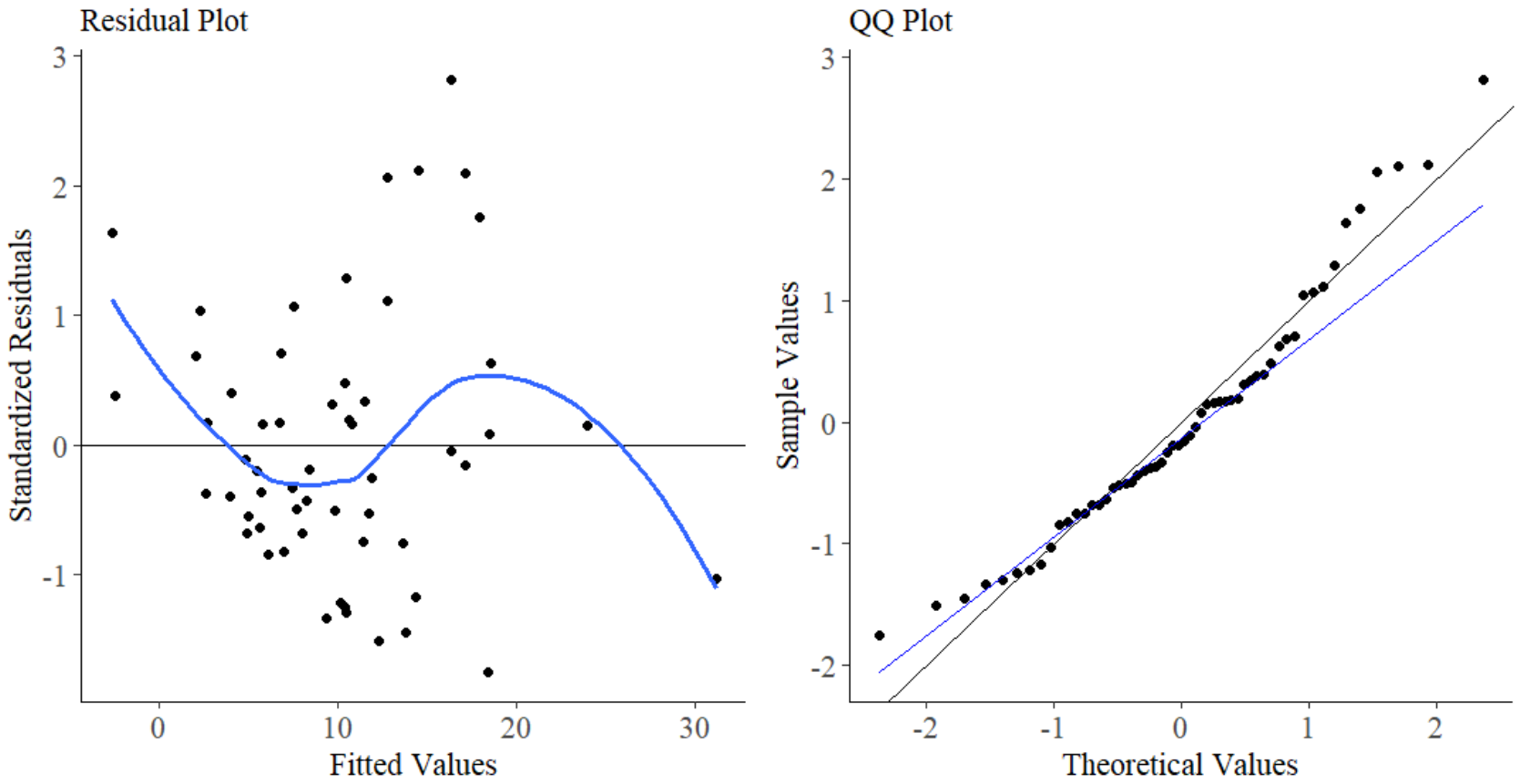
Appendix Figure 1.5. Correlation matrix of the variables considered in analysis of the forest type model set for barred owl (BO) recolonization of northern spotted owl (NSO) territories.



Appendix Figure 1.6. Residual and QQ plots of the global model in the forest type model set for the analysis of the number of barred owls (BO) removed on northern spotted owl (NSO) territories. (Number BO removed per NSO territory = % open forest + % prey habitat + % old hardwood forest + % young mix conifer-hardwood forest + % old mixed conifer-hardwood forest + % young conifer forest + % old conifer forest + aspect + wetness + territory distance + NSO presence + territory area + survey time).



Appendix Figure 1.7. Correlation matrix for variables considered in analysis of the final model set for barred owl (BO) recolonization of northern spotted owl (NSO) territories.



Appendix Figure 1.8. Residual and QQ plots of the global model in the final model set for the analysis of the number of barred owls (BO) removed on northern spotted owl (NSO) territories. (Number BO removed per NSO territory = survey time + % open forest + % old mixed conifer-hardwood forest + wetness).

Appendix Table 1.2. Estimates ($\hat{\beta}$), standard errors (SE), and 95% confidence intervals (95% CI) for variables in the top model and model averaged in the forest structure, forest type, and final model sets in the analysis of barred owl recolonization of northern spotted owl (NSO) territories after barred owls were removed.

		Top model			Model averaged		
Model set	Variable	Estimate	SE	95% CI	Estimate	SE	95% CI
Forest structure	Wetness	14.522	3.698	7.094, 21.951	0.013	4.178	4.565, 21.276
	Tree size	0.860	0.230	0.398, 1.321	0.858	0.300	0.259, 1.457
	Survey time	0.171	0.056	0.058, 0.284	0.148	0.063	0.023, 0.274
	Territory distance	NA	NA	NA	1.129	0.561	0.005, 2.253
	Canopy cover	0.613	0.278	0.055, 1.171	0.534	0.308	-0.008, 1.151
	NSO presence	0.057	0.030	0.117, 0.003	-0.047	0.034	-0.116, 0.021
	Aspect	NA	NA	NA	-0.017	0.013	-0.042, 0.008
	Tree density	NA	NA	NA	0.004	0.006	-0.008, 0.016
	% Hardwoods	NA	NA	NA	0.154	0.318	-0.480, 0.787
	Territory area	NA	NA	NA	0.004	0.007	-0.010, 0.018
Forest type							
	Open	-1.541	0.629	-2.804, -0.279	-2.033	0.733	-3.498, -0.569
	Old mixed	0.489	0.134	0.219, 0.759	0.453	0.174	0.1053, 0.800
	Survey time	0.124	0.054	0.016, 0.232	0.119	0.059	0.001, 0.238
	Old hardwood	0.297	0.124	0.047, 0.547	0.268	0.176	-0.082, 0.618
	Prey habitat	NA	NA	NA	-0.293	0.176	-0.641, 0.056
	Wetness	6.912	3.515	-0.148, 13.972	6.755	3.996	-1.239, 14.749
	Old conifer	NA	NA	NA	-0.804	0.566	-1.933, 0.326
	Young mixed	NA	NA	NA	-0.272	0.289	-0.846, 0.302
	NSO presence	NA	NA	NA	-0.035	0.033	-0.100, 0.031
	Territory distance	NA	NA	NA	0.638	0.667	-0.695, 1.970
	Aspect	NA	NA	NA	-0.012	0.012	-0.036, 0.013
	Territory area	NA	NA	NA	0.004	0.007	-0.009, 0.017
	Young conifer	NA	NA	NA	0.132	0.426	-0.716, 0.980

Appendix Table 1.3. Estimates ($\hat{\beta}$), standard errors (SE), and 95% confidence intervals (95% CI) for variables from the top model and model averaged from the final model set of the analysis of barred owl recolonization of northern spotted owl territories after barred owls were removed.

		Top model			Model averaged		
Model set	Variable	Estimate	SE	95% CI	Estimate	SE	95% CI
Final							
	Open	-2.077	0.622	-3.308, -0.845	-1.964	0.664	-3.278, -0.649
	Old mixed	0.460	0.138	0.187, 0.733	0.444	0.141	0.165, 0.722
	Survey time	0.125	0.057	0.012, 0.237	0.126	0.057	0.014, 0.239
	Wetness	NA	NA	NA	5.624	3.752	-1.805, 13.052

Chapter 2 Appendix

NSO Base Model Structure

I analyzed the relationship between BO colonization/extinction over time using a dynamic two-species occupancy model. Parameters included NSO initial occupancy, extinction, colonization, detection, and BO initial occupancy, extinction, colonization, and detection. To assess interspecific, forest type, structure, and time effects on BO extinction/colonization and estimate NSO occupancy, all models used a baseline structure for NSO parameters. NSO initial occupancy did not include the effect of BO due to estimation issues possibly due to low number of BOs on the landscape in the first year of the study. Due to over parameterization and estimation issues, I tested different time structures for NSO colonization/extinction, leading to a model with a linear time trend and BO effect on both NSO colonization and extinction. Estimation issues for NSO colonization without BO present were addressed with a separate intercept and no time trend. NSO and BO detection models used varying structures with BO and NSO effects, respectively. Estimation issues led to a shared intercept for BO detection in years 1-3 due to the low number of BO on the landscape. I used additive model structures for all interspecific effects. This base model was then used for testing the relationship between BO colonization/extinction and interspecific, forest type and structure, autologistic, and time variables. Parameters for BO colonization and extinction were constant for forest type and structure and interspecific model sets.

Appendix Table 2.1. Models for the initial model sets testing variables on parameters for barred owl (BO) colonization of northern spotted owl (NSO) territories in a two-species dynamic occupancy model.

Parameter	Model Set	Variable	ΔAICc[1]	Weight[2]	K[3]	-2Log likelihood	AICc[4]
BO Colonization							
	Interspecific						
		NSO (Additive)	0.000	1.000	73	11650.959	11802.978
		Intercept-only	362.206	0.000	72	12015.331	12165.184
		NSO (Interaction)	362.926	0.000	73	12013.885	12165.904
	Forest type and structure						
		Wetness	0.000	0.337	73	11651.096	11803.115
		Old mixed	0.567	0.254	73	11651.663	11803.682
		Old conifer	2.618	0.091	73	11653.714	11805.733
		Young mixed	3.154	0.070	73	11654.250	11806.269
		Aspect	3.346	0.063	73	11654.442	11806.461
		Predicted BO removed	3.701	0.053	73	11654.797	11806.816
		Open forest	3.966	0.046	73	11655.062	11807.081
		Prey habitat	4.076	0.044	73	11655.172	11807.191
		Old hardwood	4.125	0.043	73	11655.221	11807.240
		Intercept-only	362.069	0.000	72	12015.331	12165.184
	Neighborhood and time						
		Year trend	0.000	0.427	73	11601.500	11753.450
		Intercept-only	0.270	0.373	72	11603.930	11753.720
		Neighborhood	1.520	0.200	73	11603.020	11754.970
		Year	21.880	0.000	100	11564.040	11775.330

[1] AICc units away from the most parsimonious model (lowest AICc) in the model set

[2] AICc model weight

[3] Number of parameters

[4] Akaike Information Criterion (AIC) is a measure that balances the fit of the model with the complexity of the model. AICc is a bias-corrected version of AIC for small sample sizes (Burnham et al. 2011)

Appendix Table 2.2. Models form the initial model sets of an analysis of testing variables on parameters for barred owl (BO) extinction on northern spotted owl (NSO) territories in a two-species dynamic occupancy model.

Parameter	Model Set	Variable	ΔAICc[1]	Weight[2]	K[3]	-2Log likelihood	AICc[4]
BO Extinction							
	Interspecific						
		NSO (Additive)	0.000	1.000	73	11633.126	11785.145
		Intercept-only	380.039	0.000	72	12015.331	12165.184
		NSO (Interaction)	381.964	0.000	73	12015.090	12167.109
	Forest type and structure						
		Young mixed	0.000	1.000	73	11651.777	11803.796
		Old mixed	342.783	0.000	73	11994.560	12146.579
		Open forest	347.398	0.000	73	11999.175	12151.194
		Old conifer	353.838	0.000	73	12005.615	12157.634
		Wetness	360.922	0.000	73	12012.699	12164.718
		Intercept-only	361.388	0.000	72	12015.331	12165.184
		Aspect	362.324	0.000	73	12014.101	12166.120
		Old hardwood	362.417	0.000	73	12014.194	12166.213
		Prey habitat	363.209	0.000	73	12014.986	12167.005
		Predicted BO removed	376.558	0.000	73	12028.335	12180.354
	Neighborhood and time						
		Year trend	0.000	0.596	73	11600.380	11752.330
		Intercept-only	1.390	0.298	72	11603.930	11753.720
		Neighborhood	3.450	0.106	73	11603.830	11755.780
		Year	24.030	0.000	100	11565.070	11776.360

[1] AICc units away from the most parsimonious model (lowest AICc) in the model set

[2] AICc model weight

[3] Number of parameters

[4] Akaike Information Criterion (AIC) is a measure that balances the fit of the model with the complexity of the model. AICc is a bias-corrected version of AIC for small sample sizes (Burnham et al. 2011)

Appendix Table 2.3. Alternate forest type and structure model set for barred owl (BO) extinction using a two-species dynamic occupancy model after the deletion of young mixed variable due to 95% confident intervals for $\hat{\beta}$ overlapping zero.

Parameter	Model Set	Variable	ΔAICc[1]	Weight[2]	K[3]	-2Log likelihood	AICc[4]
BO extinction							
	Forest type and structure						
		Old mixed	0.000	0.906	73	11994.560	12146.579
		Open forest	4.615	0.090	73	11999.175	12151.194
		Old conifer	11.055	0.004	73	12005.615	12157.634
		Wetness	18.139	0.000	73	12012.699	12164.718
		(.)	18.605	0.000	72	12015.331	12165.184
		Aspect	19.541	0.000	73	12014.101	12166.120
		Old hardwood	19.634	0.000	73	12014.194	12166.213
		Prey habitat	20.426	0.000	73	12014.986	12167.005
		Predicted BO removed	33.775	0.000	73	12028.335	12180.354

[1] AICc units away from the most parsimonious model (lowest AICc) in the model set

[2] AICc model weight

[3] Number of parameters

[4] Akaike Information Criterion (AIC) is a measure that balances the fit of the model with the complexity of the model. AICc is a bias-corrected version of AIC for small sample sizes (Burnham et al. 2011)

Appendix Table 2.4. Models from the final model sets of the analysis of barred owl (BO) colonization and extinction parameters in a two-species dynamic occupancy model. All northern spotted owl (NSO) relationships are additive.

BO colonization	BO extinction	ΔAICc[1]	Weight[2]	K[3]	-2Log likelihood	AICc[4]
Wetness	NSO	0.000	0.420	74	11628.955	11783.142
Wetness	NSO + Old mixed	1.757	0.174	75	11628.541	11784.899
NSO + Wetness	NSO	1.960	0.158	75	11628.744	11785.102
Intercept-only	NSO	2.003	0.154	73	11633.126	11785.145
NSO	NSO	4.236	0.050	74	11633.191	11787.378
NSO	NSO + Old mixed	5.209	0.031	75	11631.993	11788.351
NSO + Wetness	NSO + Old mixed	6.999	0.013	76	11631.610	11790.141
NSO + Wetness	Intercept-only	17.844	0.000	74	11646.799	11800.986
NSO + Wetness	Old mixed	19.648	0.000	75	11646.432	11802.790
NSO	Intercept-only	19.836	0.000	73	11650.959	11802.978
Wetness	Intercept-only	19.973	0.000	73	11651.096	11803.115
NSO	Old mixed	21.210	0.000	74	11650.165	11804.352
Wetness	Old mixed	21.632	0.000	74	11650.587	11804.774
Intercept-only	Old mixed	363.437	0.000	73	11994.560	12146.579
Intercept-only	NSO + Old mixed	365.556	0.000	74	11994.511	12148.698
Intercept-only	Intercept-only	382.042	0.000	72	12015.331	12165.184

[1] AICc units away from the most parsimonious model (lowest AICc) in the model set

[2] AICc model weight

[3] Number of parameters

[4] Akaike Information Criterion (AIC) is a measure that balances the fit of the model with the complexity of the model. AICc is a bias-corrected version of AIC for small sample sizes (Burnham et al. 2011)