

AN ABSTRACT OF THE THESIS OF

Katherine E. Halstead for the degree of Master of Science in Forest Ecosystems and Society, presented on September 19, 2013.

Title: A 'Bird's Eye View': Using a Species-centered Approach to Examine Patterns and Drivers of Avian Species Richness in the Rogue Basin, Oregon.

Abstract approved:

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The combined effects of habitat loss, degradation, and fragmentation pose a serious threat to Earth's biodiversity, imperiling even relatively common species. 'Habitat' is necessarily a species-specific concept, and investigations of bird diversity relationships and subsequent efforts to prioritize conservation areas, are challenged by the difficulty of estimating complex habitat gradients for multiple species across broad spatial scales. Technologies such as fine-resolution remote sensing combined with enhanced species distribution modeling techniques hold promise for more accurate assessments of multi-species habitat distributions.

In this research, I focused on forest bird species which utilize and/or are highly associated with threatened Oregon white oak and California black oak (*Quercus garryana* and *Q. kelloggii*) vegetation types in the Rogue Basin of southwest Oregon. I created individual species distribution models (SDMs) for 48 bird species as a function of fine-resolution (30 x 30 m) remotely sensed land cover and other environmental variables using boosted regression tree (BRT) models. I then 'stacked' SDMs for spatially explicit regional estimates of multi-species avian richness.

In my first chapter, I examined the potential for site-level species richness to be influenced by local vegetation and environmental conditions (e.g. the "local vegetation heterogeneity hypothesis") or by landscape-level dispersal potential (e.g.

the “regional species pool hypothesis”). I summarized ‘stacked’ SDMs for indices of 1) habitat amount at a local scale relevant bird territory use and 2) habitat amount at a broad scale relevant to forest bird dispersal, and ask whether local- or landscape-scale habitat amount is relatively more important to site-level bird species richness. I hypothesized that greater importance of either habitat amount metric would indicate greater influence of local or landscape drivers to local richness. I found evidence that for a large pool of bird species with diverse habitat associations, landscape-scale habitat amount may be relatively more important to local (i.e., territory level) richness of forest birds than is local habitat amount. In contrast, for more specialized (i.e., oak-associated) guilds, local-scale habitat may be considerably more important than amount of habitat within the surrounding landscape. My results suggest the importance of local- and landscape-scale processes in structuring bird communities, supporting both ‘local vegetation heterogeneity’ and ‘regional species pool’ hypotheses.

In my second chapter, I examined the relationships between landownership, oak vegetation distribution, and bird diversity, with the objective of determining which of five primary landownership types contribute most strongly to bird species habitat in the Rogue Basin. I asked whether individual bird species distributions and estimated richness are ‘additive’ or ‘redundant’ among land ownership types, hypothesizing that differences among owners will be apparent and related to the amount of oak-dominant vegetation held by each owner regionally. I found that estimated local mean species richness of oak-associated birds in private non-industrial (PNI) ownerships is approximately double that of other Rogue Basin public and private ownerships examined. This result may be driven by disproportionate PNI ownership of limited oak cover types, and/or by hypothesized variation in management goals and activities among owners which influence local vegetation structure.

Relatively greater importance of territory-scale habitat to local oak-associated species richness suggests management for these species should maximize site-level

habitat amount and quality. The importance of private non-industrial owners to oak-associated avian richness validates current focus on engaging private landowners in bird-focused oak conservation and restoration. Overall, my research links efforts to conserve avian habitat with efforts to understand multi-scale drivers of bird diversity, using a novel methodology that embraces the complexity of species' habitat gradients.

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A 'Bird's Eye View': Using a Species-centered Approach to Examine Patterns and
Drivers of Avian Species Richness in the Rogue Basin, Oregon

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CONTRIBUTION OF AUTHORS

Dr. Matthew Betts and Dr. John Alexander were involved in overall conceptual design of this research. Dr. John Alexander and Jaime Stephens provided data, and Jaime Stephens and Bob Altman contributed to study design and implementation. Dr. Matthew Betts additionally contributed to analysis implementation, interpretation, and writing of all chapters. Dr. John Alexander, Dr. John Bliss, and Dr. Douglas Robinson contributed to development and editing of all chapters. Dr. Bruce McCune contributed to editing of Chapters 2 and 3.

TABLE OF CONTENTS

	<u>Page</u>
Chapter 1: Introduction	1
Literature Cited	5
Chapter 2: Multi-scale habitat amount relationships with oak-associated avian diversity in southwest Oregon: Testing local versus landscape drivers of richness using a species-centered approach	8
Abstract	8
Introduction	9
Methods	14
Study Area	14
Species distribution models	16
Data analysis	20
Results	27
Species distribution models	27
Species richness as a function of habitat amount	27
Discussion	31
Habitat amount relationships	31
Implications for habitat amount research	34
Comparison of SDM stacking methods	36
Effects of spatial autocorrelation	37
Study limitations	38
Conclusions	41

Literature Cited	43
Tables	49
Figures	55
Appendices	60
Chapter 3: The implications of land ownership for modeled avian species richness and habitat distribution within oak vegetation types of southwestern Oregon	70
Abstract	70
Introduction	71
Methods	77
Study area	77
Species distribution models	78
Data analysis	82
Results	88
Land ownership and vegetation type	88
Model evaluation	89
Local and regional species richness among owners	90
Individual species distributions among owners	92
Discussion	93
Distribution of species richness and individual species habitat	93
Mechanisms for landowner relationships to species richness and distribution	95
Implications for management	99
Study limitations	101

Conclusions	102
Literature Cited	104
Tables	110
Figures	118
Appendices	127
Chapter 4: Conclusion.....	138
Literature Cited	145

LIST OF TABLES

<u>Table</u>	<u>Page</u>
2.1. Common names, scientific names, and AOU four letter codes for 48 species used in species distribution models for the Rogue Basin, Oregon.	49
2.2. Summary of BRT model parameters (<i>lr</i> and <i>tc</i>), results for within-model cross validation training (AUC and SE), and results for model prediction to independent evaluation data (AUC) for 48 Rogue Basin forest bird species.	51
2.3. Descriptions of three predictor variable types used in modeling species richness as a function of habitat amount.	53
2.4. Results for linear regression models testing the relationship between species richness, habitat amount (<i>local</i> and <i>landscape</i>), and a spatial autocovariate term representing residual spatial autocorrelation at approx. 10,000 m (<i>space</i>).	54
3.1. Common names, scientific names, and AOU four letter codes for 48 species used in species distribution models for the Rogue Basin, Oregon.	110
3.2. Summary of BRT model parameters (<i>lr</i> and <i>tc</i>), results for within-model cross validation training (AUC and SE), and results for model prediction to independent evaluation data (AUC) for 48 Rogue Basin forest bird species.	113
3.3. Summary of vegetation type holdings by five key Rogue Basin land owner types.	115
3.4. Results for pairwise comparisons (Tukey's HSD) of mean species richness between landowners for each of three species subsets.....	117

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
2.1. Conceptual figure for creation of local and landscape ‘habitat amount’ metrics for forest bird species of the Rogue Basin, Oregon.	55
2.2. Species distribution maps (30m ² resolution) within the Rogue Basin, Oregon for 11 oak-associated species with the most strongly-performing SDMs	56
2.3. Predicted avian species richness maps within the Rogue Basin, Oregon for two species subsets and both SDM stacking methods used.	57
2.4. Standardized regression coefficients for effects of local (150m) and landscape (10,000m) habitat amount on species richness for the ‘probabilities’ (A) and ‘threshold’ (B) stacking methods, in four species subsets	58
2.5 Results of quantile regression analysis, for ‘all species’ and ‘oak species’, and using both stacking methods	59
3.1. Map of ownership and oak vegetation categories (GAP) in the Rogue Basin, Oregon.	118
3.2. Species distribution maps (30 x 30 m resolution) within the Rogue Basin, Oregon for 11 oak-associated species with the most strongly-performing SDMs	119
3.3. Predicted avian species richness maps within the Rogue Basin, Oregon for for the two primary species subsets (‘all species’ and ‘oak species’) using a ‘threshold’ SDM stacking method.	120
3.4. Mean species richness among the five key Rogue Basin landowners, compared among the three species analysis subsets	121
3.5. Species accumulation curves for five Rogue Basin landowners, compared among the three species analysis subsets	122
3.6. Comparison of total area within species richness intervals for five Rogue Basin landowners, compared among two species analysis subsets.	123
3.7. Total area classified as ‘present’ for the analysis subset of oak-associated species, compared among five Rogue Basin landowners.	124

3.8. Total area classified as ‘present’ for the 20 species showing significant declines in the state of Oregon according to Breeding Bird Survey (BBS) trends, compared among five Rogue Basin landowners.	125
3.9. Total area classified as ‘present’ for the analysis subset of species with high AUC models (AUC >0.8) tested with independent evaluation data, compared among five Rogue Basin landowners.....	126

LIST OF APPENDICES

<u>Item</u>	<u>Page</u>
2A. Appendix A Table 1. Names and descriptions of vegetation types targeted by a 2011 study of avian communities within oak vegetation types of the Rogue Basin, Oregon.....	60
2B. Appendix A Table 2. Summary of membership in analysis subsets for 48 Rogue Basin forest bird species.....	64
2C. Appendix A Table 3. ROC cut points calculated independently for each species, to convert probability of occurrence to presence/absence for analysis.	66
2D. Appendix A Table 4. Comparison of correlation (adjusted R ² from linear regression) between estimated habitat amounts at a local scale (150m) and three landscape scales	67
2E. Appendix A Figure 1. Map of model training and evaluation point count locations within the Rogue Basin	69
3A. Appendix B Table 1. Names and descriptions of vegetation types targeted by a 2011 study of avian communities within oak vegetation types of the Rogue Basin, Oregon.....	127
3B. Appendix B Table 2. ROC cut points calculated independently for each species, to convert probability of occurrence to presence/absence for analysis.	131
3C. Appendix B Table 3. Summary of membership in analysis subsets for 48 Rogue Basin forest bird species.....	133
3D. Appendix B Table 4. Examination of means and standard deviations (SD) of elevation and key climatic variables used in species distribution modeling among five Rogue Basin landowners.....	135
3E. Appendix B Figure 1. Map of model training and evaluation point count locations within the Rogue Basin, with sub-basins labeled.	136
3F. Examination of means and standard deviations (SD) of reflectance values for all non-infrared Landsat TM bands within each of five primary land ownership types in the Rogue Basin, Oregon	137

2F. Examination of means and standard deviations (SD) of reflectance values for all non-infrared Landsat TM bands within each of five primary land ownership types in the Rogue Basin, Oregon	137
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CHAPTER 1: INTRODUCTION

Combined effects of habitat loss, degradation, and fragmentation pose a serious threat to Earth's biodiversity (Pimm et al. 1996, Pimm et al. 1995), imperiling even relatively common and vagile species such as many North American forest birds (Robbins et al. 1989). 'Habitat' is necessarily a species-specific concept, involving complex and unique responses by individual species to environmental gradients (Fischer and Lindenmayer 2006, Cushman et al. 2010). Investigations of species distribution and diversity relationships to multi-scale habitat amount, as well as efforts to prioritize conservation areas, are challenged by the difficulty of simultaneously estimating habitat for multiple species across broad spatial scales (Ferrier et al. 2009, Fahrig 2013).

'Continuum' models of habitat employ a 'species-centered' perspective, in which it is explicitly acknowledged that each species responds uniquely to important environmental gradients (Fischer and Lindenmayer 2006, Betts et al. 2007). In this way, continuum models contrast with the 'patch/matrix' paradigm inherited from Island Biogeography Theory (MacArthur 1967) in which 'islands' of habitat (usually based on researcher-defined vegetation cover types) are embedded in a 'sea' of unsuitable habitat. This simplification is likely not realistic for most terrestrial landscapes, in which gradients of vegetation cover abound, and are important to habitat use by birds (Betts et al. 2007, Cushman et al. 2008, 2010). Adopting a continuum approach within the context of multi-species and multi-scale habitat amount investigations may aid understanding of the drivers of avian species richness, but has not been fully explored. In this research, I apply a 'continuum' model of forest bird species' habitat relationships (Fischer and Lindenmayer 2006) to 1) a local-versus landscape-scale habitat amount investigation, and 2) a multi-owner assessment of species richness and individual species habitat distributions, with a view toward

testing a methodology which might be of potential value for such research more generally.

In this research, I focus on forest bird species which utilize and/or are highly associated with Oregon white oak and California black oak (*Quercus garryana* and *Q. kelloggii*) vegetation types in the Rogue Basin of southwest Oregon. Systems dominated by these oak species are an important component of Pacific Northwest (PNW) ecology and biodiversity, but are highly threatened throughout the PNW due to factors including fire suppression, conifer encroachment, and development (Schindel et al. 2013). Many avian species are considered obligate or highly dependent on oak vegetation types (Altman 2011, Altman and Stephens 2012). A number of oak-associated avian species have been extirpated from, or are declining in, the PNW broadly and the Rogue Basin specifically (Altman 2011). Interest in using oak-associated avian species as focal taxa for management assessment (Alexander et al. 2007) has contributed to increasing investment in bird-focused oak conservation and restoration in southwestern Oregon, particularly on private lands which are estimated to contain the majority of intact oak vegetation (Altman and Stephens 2012, NABCI, U.S. Committee 2013).

In Chapter 2, I examine the relative influences of local- and landscape-scale habitat amount on local bird species richness. Habitat amount is important locally to species richness to the extent that it relates to a site's ability to simultaneously accommodate the survival and reproduction requirements of multiple species. Environmental processes which drive the local quality of habitat for multiple species are well-studied and include heterogeneity of local vegetation (MacArthur and MacArthur 1961), site-level productivity related to climatic conditions (White and Hurlbert 2010), and species interactions (Wisz et al. 2013). However, it is increasingly well understood that landscape context may also influence local richness (Harrison and Cornell 2008, Belmaker and Jetz 2012). Habitat amount at broad scales may shape

local community assembly to a large degree by filtering the dispersal of species to a target community (Zobel 1997), or by allowing the ‘spillover’ of species from one cover type to another in areas of high vegetation heterogeneity (Tscharntke et al. 2012). The ‘regional species pool’ hypothesis posits that the pool of species available regionally may be of primary importance to a site’s eventual species occupancy, above and beyond the site’s inherent vegetation, productivity, or environmental characteristics (Ricklefs 1987, 2008). However, efforts to disentangle the relative influences of local- and landscape-level habitat amount on local species richness have not produced consistent results across regions or taxa (Prugh et al. 2008). This may be due in part to the technical challenges associated with quantifying ‘habitat amount’ for multiple species with varying associations to particular vegetation or environmental conditions (Fahrig 2013).

In Chapter 3, I examine individual species distributions and predicted richness in the context of land ownership, with the objective of determining how five primary owners of forested lands in the Rogue Basin contribute to oak-associated species habitat and diversity. Specifically, I ask whether species distributions across owners are redundant (i.e., evidence for similar levels of species richness and individual species suitable habitat among owners) or additive (i.e., evidence that individual owners may support distinct components of the regional avian diversity). Research explicitly examining the relationships between diversity and multiple owners in a forested landscape (such as in McComb et al. 2007, Spies et al. 2007) are rare. However, ownership can be associated with gradients of vegetation cover due to historical settlement patterns (Schindel et al. 2013), and can additionally be influential to forest structure and composition via differences in management goals and activities (Stanfield et al. 2002). Avian species are often highly sensitive and responsive to land cover changes, due to strong associations with vegetation structure and composition (MacArthur and MacArthur 1961), and so ownership patterns have a strong potential to be meaningful to avian habitat distribution and species diversity.

In this research, I use a species distribution modeling approach for the purposes of examining questions related to avian species richness, habitat amount, and land ownership as described above. I create individual species distribution models (SDMs) for bird species as a function of fine-resolution (30 x 30 m) remotely sensed land cover, climate, and elevation using boosted regression tree (BRT) models. Technologies such as fine-resolution remote sensing combined with enhanced species distribution modeling techniques hold promise for more accurate assessments of multi-species avian habitat distribution (Swatantran et al. 2012, Shirley et al. 2013). Species examined include 48 relatively common forest bird species and a nested subset of 25 bird species highly associated with oak vegetation types. Probabilities of occurrence from SDMs are employed as measures of habitat distributions for individual species (as in Betts et al. 2007 and discussed in Fahrig 2013). I additionally use 'stacked' SDM (S-SDM) methods to create spatially explicit and fine-resolution estimates of species richness and multi-scale habitat amount to address research objectives.

Conservation and restoration efforts are often necessarily focused on the stand-level, but truly effective landscape planning must account for landscape effects (Tscharntke et al. 2012) and socio-political context (Ferrier and Wintle 2009). I seek to use the S-SDM approach described above to explore relative influences of multi-scale processes on bird species richness, and to quantify the relationship between landowner type and oak-associated species richness and habitat distributions. The methodology I employ may have the potential to aid conservation efforts specific to oak-associated birds in the Rogue Basin, but should also have broad applicability to spatial conservation prioritization and diversity-ownership investigations elsewhere.

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CHAPTER 2: MULTI-SCALE HABITAT AMOUNT RELATIONSHIPS WITH OAK-ASSOCIATED AVIAN DIVERSITY IN SOUTHWEST OREGON: TESTING LOCAL VERSUS LANDSCAPE DRIVERS OF RICHNESS USING A SPECIES-CENTERED APPROACH

Abstract

It is increasingly well understood that multi-scale processes contribute to local avian species diversity; local habitat amount and quality influences survival, reproduction, and species interactions, while landscape-scale habitat amount may facilitate dispersal, and subsequent emigration of individuals. ‘Habitat’ is necessarily a species-specific concept, and efforts to disentangle the relative influences of local- and landscape-level habitat amount on local species richness are challenged by the difficulty of accurately estimating complex habitat gradients for multiple species across broad spatial scales. Technologies such as fine-resolution remote sensing combined with enhanced species distribution modeling techniques hold promise for assessments of multi-species habitat. I used Landsat TM-based ‘stacked’ species distribution models (S-SDMs) to estimate local-scale (150 m) and landscape-scale (10,000 m) habitat amount for 48 bird species which utilize and/or are highly associated with oak cover types in southwestern Oregon. S-SDM models explained approximately 18 - 31% of the variation in local species richness at fine (30 x 30 m) resolutions. I found evidence for greater importance of estimated landscape-scale habitat to local (i.e., territory level) richness of the 48 forest birds, while local-scale habitat may be considerably more important for a nested subset of 25 highly oak-associated birds. These results reveal potential differences in the degree to which fine- and broad-scale processes influence local community assembly, depending on the species pool considered. The S-SDM approach used might be valuable to future investigations of habitat amount relationships which seek to incorporate the complexity of species’ habitat gradients.

Introduction

Local processes and patterns such as habitat structure and heterogeneity (MacArthur and MacArthur 1961, Tews et al. 2004), competition and predation (Wiens 1992, Shurin and Allen 2001), social information (Danchin et al. 2004), and spatial aggregation (Lichstein et al. 2002, Julie Bourque and André Desrochers 2006) are all thought to be of direct importance to local, or stand-level, bird species richness. However, within the past several decades landscape ecology and metacommunity theory have contributed perspectives that landscape and regional- scale processes are likely to be strong determinants of local species richness (Ricklefs 1987, B. Shurin and G. Allen 2001, Harrison and Cornell 2008). Key mechanisms for these broader scale influences include animal dispersal from regional species pools (Leibold et al. 2004, Özkan et al. 2013), landscape level vegetation heterogeneity (Grand and Cushman 2003, Belmaker and Jetz 2012), and broad-scale abiotic patterns such as in climate and topography (Currie 1991, Rahbek and Graves 2001). Disentangling the control of local and landscape-level processes on local species richness has become a primary focus in ecology research (Whittaker et al. 2001, Ricklefs 2008, Tschamntke et al. 2012).

Local species richness is the result of both local and broad-scale processes which may either limit or increase the number of individual species that can occur at any given locality (Tschamntke et al. 2012, Belmaker and Jetz 2012). Metacommunity theory predicts that local and landscape-level processes may be reciprocal; in other words, regional processes may limit or increase the number of species able to occur locally, while the summed effects of local conditions and species interactions may limit or increase the regional pool (Harrison and Cornell 2008). While the direction of such effects may be difficult to determine in observational studies (Belmaker and Jetz 2012), gaining perspective on their relative importance to local richness patterns is critical to a better understanding of the processes that shape biodiversity (Gaston 2000). A clearer understanding of the importance of local and landscape drivers of

species richness may also be critical to crafting better responses to conservation challenges (Loreau et al. 2001), including to the recent declines of avian species (Flather and Sauer 1996). Although applied conservation and restoration efforts are often necessarily focused on direct protection or improvement of habitat at the local scale, these are not likely to be successful in the long term without an appreciation of the broad-scale processes that may influence species distributions and local populations (Opdam and Wascher 2004, Tschardt et al. 2012).

The influences of local-scale processes on determining community structure are relatively well known. Mechanisms include structural heterogeneity of vegetation (MacArthur and MacArthur 1961), site productivity (White and Hurlbert 2010), and competition (Wisz et al. 2013). Until recently, tests of landscape or regional-scale effects on species richness have been less well explored in terrestrial systems – despite well-established theory indicating that such broad scales *should* exert strong influences on community structure (MacArthur and Wilson 1967, Ricklefs 1987). The “regional species pool” hypothesis posits that the availability of habitat at the regional level is of primary importance to determine which species can disperse to a local site, regardless of local conditions (Tschardt et al. 2012). Higher amounts of ‘habitat’ – across all individual species – at the landscape scale should be indicative of a larger potential species pool, insofar as it suggests that there is more suitable habitat for more species at the given spatial extent (Zobel 1997). The more habitat there is at landscape and regional scales surrounding a particular site, the greater the potential for dispersal by multiple species to that site, therefore increasing local richness (Leibold et al. 2004). Congruent with this hypothesis are many studies indicating that species richness correlates with broad-scale vegetation heterogeneity (Tschardt et al. 2012). However, effectively examining the influences of the species pool vs. local conditions on local richness has proven elusive (Lessard et al. 2012).

There are several important challenges to investigating the relative influence of local- and broad-scale influences on species richness. First, until recently it has been

challenging to find sufficiently fine-resolution land cover data relevant to species richness that can be measured at multiple spatial scales, and whose influence can then be directly compared (Rahbek and Graves 2001, Betts et al. 2006). However, advances in remote sensing (Swatantran et al. 2012) and species distribution modeling (Elith et al. 2006, Shirley et al. 2013) have the potential to address this challenge. Second, the fundamental problem of defining “habitat” for multiple species with dissimilar habitat requirements has necessitated the patch/matrix simplification, where ‘habitat’ and ‘matrix’ (or non-habitat) are researcher-defined, often on the basis of vegetation type. This paradigm has become common in fragmentation research, influenced heavily by the island/ocean model of island biogeography theory (MacArthur 1967, Fahrig 2013). The need for habitat/matrix models may constrain investigation of habitat amount effects to groups of species thought to share a strong affinity with a selected cover type (Fahrig 2013), which may limit the capacity to detect processes important at the level of the entire regional species pool (Belmaker and Jetz 2012). In reality, areas classified as habitat or matrix contain unique gradients of individual species responses to environmental conditions (Cushman et al. 2010), and so binary delineation also has the potential to produce error in the habitat amount metric. Prugh et al. (2008) suggested that many idiosyncrasies in richness versus habitat amount relationships may be due in part to the incorrect assumption that ‘matrix’ areas are not used by any species. Additionally there is the difficulty of discriminating among cover types within terrestrial landscapes in ways that are consistently meaningful measures of ‘habitat’ for particular species. For example, Cushman et al (2008) found that vegetation cover types were an ineffective proxy for habitat of forest bird species, and that the efficacy of this proxy differed considerably among species guilds.

The ‘continuum model’ (Fischer and Lindenmayer 2006) involves fitting a response (e.g. species abundance or occurrence) to important *gradients* such as food, shelter, climate, and space for a prediction of individual species habitat suitability. Importantly, ‘habitat’ is recognized as a species-specific concept in this model.

Continuum or gradient-based approaches, while being significantly more complex than the patch/matrix model, are well-aligned with Gleasonian ecological theory of individualistic distribution of organisms in relationship to their environment, and may be a more realistic way to view the interactions between organisms and their habitat (Gleason 1936, Cushman et al. 2010). Application of continuum, or gradient-based approaches has shown promise in better predictive accuracy of spatial patterns, for example in distribution of conifer species (Evans and Cushman 2009) and forest bird species (Shirley et al. 2013). While one weakness to this approach may be the lack of explicit integration of species interactions important to community assembly (Guisan and Rahbek 2011), species distribution models (SDMs) trained on observed species occurrence data are thought to effectively model a species' realized niche, representing the end result of these interactions in addition to environmental filtering (Elith and Leathwick 2009, Dubuis et al. 2011). Adopting a continuum approach within the context of multi-species and multi-scale habitat amount investigations may aid the mechanistic understanding of the drivers of avian species richness, but appears to remain unexplored – perhaps due to the technical challenges associated with quantifying 'habitat amount' for multiple species with disparate habitat associations (Fahrig 2013).

Research objective

My primary research objective is to test the relative importance of local vs. landscape habitat amount on local (or site-level) bird species richness. The amount or suitability of habitat within a particular area around a local site is of clear relevance to species distributions (Betts et al. 2007), and so may be a good option for examining processes influential to species diversity that operate at various scales. Building on Fahrig's (2013) proposal that landscape context effects on richness can be explored in terms of a simple 'habitat amount' metric, I propose a method for testing the relative importance of local and landscape habitat amount for species richness that reflects

both realities that (1) ‘habitat’ is a species-specific concept and (2) in terrestrial systems, habitat rarely occurs as islands, but is characterized by gradients in suitability. I use a species-centered approach, constructing and summing continuum-based species distribution models (SDMs) for each member of a species pool to estimate multi-species ‘habitat amount’ at local and landscape scales. In this approach, SDMs are continuum-based in the sense that they model species distribution as a function of gradients of land cover (among other environmental predictors), rather than discrete researcher-defined vegetation types. The approach is species-centered in that the final metric for habitat amount will reflect gradients of habitat suitability for each member of the species pool. This is in contrast to the alternative of direct ‘macroecological modeling’ (MEM) of species richness, in which numbers of species, rather than individual species distributions, are expected to vary along environmental gradients.

The process employed in the proposed method is illustrated in Figure 1. In this approach, probabilities of occurrence from fine-resolution SDMs are employed as measures of habitat suitability for individual species (as in Betts et al. 2007 and discussed in Fahrig 2013). I construct and then sum (or ‘stack’) individual species SDMs for a continuous prediction of species pool habitat suitability. The stacked SDM (or S-SDM) approach has been increasingly used to model the distribution of species richness or multi-species habitat suitability across landscapes (Dubuis et al. 2011). Finally, I summarize the values of the S-SDMs at various scales to estimate pool-level indices of local and landscape habitat amount. This final step constitutes a novel application of S-SDMs in habitat amount research. I test the relative importance of local and landscape-scale habitat amount for a selected subset of forest bird species that are relatively common across a vegetation gradient of oak savannah, oak woodland and chaparral, and mixed oak/hardwood-conifer dominated cover types in the Rogue Basin, Oregon. In order to assess potential differences in relationships based on the membership of the species pool considered, I compare these results to

those from a nested subset of bird species that are considered highly associated with oak-dominated vegetation types in the Rogue Basin.

If local forest bird species richness in the Rogue Basin is primarily limited by the availability of dispersers from the regional pool, I expect to see higher relative importance of landscape-scale habitat amount in predicting local richness. If however, the quantity of available local habitat is ultimately responsible for filtering or limiting the local bird community, I expect to see higher relative importance of local habitat amount in predicting local species richness. The Rogue Basin has retained more area of oak-dominated vegetation types than much of the Pacific Northwest region of the U.S., but these face interacting threats from fire suppression, development, disease, and changing climate. Associated with these vegetation types is a suite of bird species that although relatively common in the Basin, are at risk of decline due to their dependence on increasingly rare oak systems regionally. Increased interest by Rogue Basin land managers in using birds as indicators of overall habitat quality to evaluate the effectiveness of oak system restoration and management (Alexander et al. 2007) makes information on importance of local and landscape-level habitat amount particularly relevant and applicable in this region.

Methods

Study Area

I collected data on bird distributions in the Rogue Basin, or the Rogue River Watershed, located in southwest Oregon. The Rogue Basin is composed of five subbasins (or HUC8 watersheds: the Upper, Lower, and Middle Rogue; the Applegate; and the Illinois), and drains into the Pacific Ocean. The Basin is part of the Klamath Mountains ecoregion, at the convergence of the Western Cascades and the Coast Range, and contains the cities of Grants Pass (42.4389° N, 123.3283° W), Ashland (42.1914° N, 122.7008° W), and Cave Junction (42.1667° N, 123.6469° W). This

region is characterized by complex topography, with elevation ranging from sea level to approximately 2,300 m. The Rogue Basin is characterized by spatially heterogeneous vegetation types which includes prairies, riparian systems, shrub fields, and forest types dominated by a number of coniferous and deciduous tree species with varying amounts of canopy cover. The climate is Mediterranean-type with cool, wet winters (precipitation in the form of both rain and snow), and hot, dry summers (Myers et al. 2000). Mean monthly precipitation ranges from 5.85 ml (July) to 849 ml (December), and mean monthly temperatures from -4.41 °C (December) and 33.29 °C (July; PRISM Climate Group, <http://www.prism.oregonstate.edu>). This region is additionally part of the California Floristic Province biodiversity hotspot (Myers et al. 2000).

The oak-dominated vegetation types of the Rogue Basin are considered the most ecologically diverse in the Pacific Northwest (Altman and Stephens 2012). Oregon white oak (*Quercus garryana* Dougl.) and California black oak (*Quercus kelloggii* Newb.) are the primary oak species within the Basin, but canyon live oak (*Quercus chrysolepis* Liebm.) can also be found, particularly in the southwest portion of the Basin. The three primary oak species are dominant or important in a wide range of vegetation types, including oak savannah, oak woodland, oak chaparral, mixed oak-conifer. A number of conifer species (e.g. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), ponderosa pine (*Pinus ponderosa* Dougl.), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and incense cedar (*Calocedrus decurrens* Torr.) and other hardwood tree species (e.g. bigleaf maple (*Acer macrophyllum* Pursh), Oregon ash (*Fraxinus latifolia* Benth.), Pacific madrone (*Arbutus menziesii* Pursh) (USDA, NRCS 2013) are also found in these vegetation types in varying degrees of dominance. Individuals of all three oak species are variable in form, depending on site soil and climate conditions. They may occur in shrub-form in dry conditions, such as in south facing chaparral fields, as tall thin trees where light is limited such as in foothill oak woodlands or mixed-conifer forests, or as large, wide-trunked trees with spreading

limbs on sites with abundant light and moisture such as in lowland savannahs (Altman and Stephens 2012).

Species distribution models

My general approach was comprised of three major steps. First, I generated spatial predictions of distribution for 48 avian species in the Rogue Basin. This step involved using bird detection/non-detection data (henceforth referred to as “occurrence”) from a training dataset along with a suite of spatial predictor variables (i.e., remotely sensed land cover, and modeled climate and elevation data) to develop species distribution models (SDMs) for all species. SDMs were used to map each species’ distribution across the study area, and these maps were summed for a spatial estimate of pool-level habitat suitability (the S-SDM method described above). Second, I used S-SDMs to calculate quantitative estimates of ‘habitat amount’ across all species at multiple scales. At the landscape scale, this variable is intended to represent the total dispersal potential for a site across species (i.e., the regional species pool). At the local scale, the habitat amount variable represents the potential for local vegetation structure and resource availability to simultaneously support a number of species. Finally, I used these variables to compare the relative influence of local versus landscape habitat amount on species richness estimated from an independent evaluation dataset.

SDM response variables

Occurrence data from avian point counts collected across the Rogue Basin from 2000 to 2011 by the Klamath Bird Observatory (KBO) and Redwood Science Lab were used as response variables for SDMs. Point count transects were established along gradients of elevation and vegetation cover, with individual points spaced at 150 - 250 m to limit redetection of individual birds (Shirley et al. 2013). Counts were

conducted between 5:30 and 10:30 am between late May and early July to coincide with hours of peak forest bird activity during the main portion of the breeding season, using 5-minute fixed- and variable-radius point count methodologies (Ralph et al. 1993, Stephens et al. 2010). In fixed radius point counts, there is a set maximum distance radius from the observer (e.g., 50 m) within which detected birds are recorded, while in variable-radius surveys there is no set distance. All birds detected by sight or sound were recorded, along with detection type (e.g., visual or auditory) and estimated distance in meters to each bird. Flyovers, or non-territorial individuals who are detected moving over the point but not using the local vegetation, were noted and excluded from analysis. These point count locations are often visited across multiple years and sometimes several times per year. For the purposes of species distribution modeling, data from a single visit and a single year were randomly selected for each point count location. Data were constrained to all auditory and visual detections (with the exception of flyovers) occurring within 50 m of point count locations, and those which fell within the Oregon portion of Rogue Watershed and the boundaries imposed by land cover variables, hereafter the “study area” (Appendix A, Figure 1). This resulted in a dataset of 2,612 sample points that I used in SDMs.

SDM evaluation and hypothesis testing data

I collected bird species presence/absence data in a 2011 point count study focused on oak vegetation types within the Rogue Basin. I used these data as an independent test of the prediction success of SDMs as well as to test my central hypotheses about the relationship between species richness and local versus landscape habitat amount. I used aerial photography, land owner data, and Gap Analysis Program (US Geological Survey 2011, <http://gapanalysis.usgs.gov/gaplandcover/>) land cover data in a Geographic Information System (GIS) to identify 55 sample areas (each containing 5 to 16 point count locations) containing oak savannah, oak woodland, oak chaparral, or mixed oak/conifer/hardwood vegetation types across the

Rogue Basin (Appendix B, Table 1). The points count locations (n=627) used in this analysis were constrained to the same study area boundaries applied to training data (Appendix A, Figure 1). Each of these point count locations were surveyed once, using a methodology identical to that used to collect data used in model training, described above (Ralph et al. 1993, Stephens et al. 2010), except that only variable-radius surveys were used. Only detections within 50 m of point count locations were used in model evaluation and to calculate species richness for testing habitat amount relationships.

Accessibility to potential sampling areas was limited to public ownerships (e.g., BLM, USFS, City of Ashland) and individual private properties for which permission to survey had been granted and public road access was available. While the sampling design was thus influenced by accessibility, an effort was made to sample as evenly as possible across the vegetation types described in Appendix A, Table 1. However access issues did limit the ability to survey in oak savannah, woodland, and chaparral types, which are regionally scarce and primarily exist on private lands. This resulted in an approximately 4-fold greater number of survey points falling within mixed oak/hardwood-conifer types than in oak savannah, woodland, and chaparral.

SDM predictor variables

Three types of data representing conditions important to forest bird distributions (land cover, elevation, and climate) were used as predictors in SDMs. Landsat Thematic Mapper (TM) imagery with a 30 x 30 m pixel resolution, corresponding to the year of data collection for each point within the model training dataset, were used as a continuous land-cover variables (again, rather than discrete classifications of vegetation type). Images were acquired from the (US Geological Survey USGS (USGS 1982, <http://earthexplorer.usgs.gov/>). A cosine-Theta (COST) correction was applied to each image to minimize noise from atmospheric conditions, according to the process in Kennedy et al. (2007). Landsat images are collected in the

form of 170 km (north-south) by 183 km (east-west) “scenes”, each with a unique Path/Row identification, and each containing seven spectral bands corresponding to different portions of the light spectrum. Two Landsat scenes (Path/Row 46/30 and 46/31) collected on the same day were merged to create single large scenes for each year of point count data collection which covered the majority of the Rogue Basin study area. I chose to exclude adjacent scenes due to potential error resulting from differences in reflectance values associated with data collection on different days, resulting in a slight truncation of the study area boundary in the northeast portion of the Basin.

I selected relatively cloud-free Landsat scenes from the months of July and August, which allowed reflectance data to be relevant to the timing of the study species’ breeding period as well as to the vegetation growing season. As clouds could not be avoided completely, I applied cloud masks developed using Vegetation Change Tracker from (Huang et al. 2010) to exclude cloudy pixels from analysis. For all non-infrared Landsat TM bands (i.e. 1, 2, 3, 4, and 7) the means and standard deviation of reflectance values were averaged at radii of 150 m, 500 m, 1000 m, and 2000 m at each pixel using a moving window analysis in GIS (following Shirley et al. 2013). This process resulted in 48 predictor variables (mean and SD for each of six bands), represented as 48, 30 x 30 m grids of mean and SD values.

I also included elevation as a predictor using a 30 x 30 m digital elevation model (DEM; <http://www.oregon.gov/DAS/CIO/GEO>). I acquired climate variables from the PRISM Climate Group at Oregon State University (<http://www.prism.oregonstate.edu>), in the form of 800m grids of month-by-month means of temperature and precipitation data from years 1981 to 2010. I selected a total of 6 variables describing the minimum and maximum precipitation (July and December, respectively), minimum and maximum temperature (December and July, respectively), and mean precipitation and temperature for June (corresponding to mid-breeding season for Rogue Basin forest bird species).

Data analysis

I constructed SDMs for the 48 oak- and deciduous-vegetation associated bird species that occurred most commonly within the 2011 oak-focused point count dataset (Table 1), representing a regional pool of species that are expected to occur within the full range of Rogue Basin oak vegetation types. Boosted regression tree (BRT) models (Friedman et al. 2000, Friedman 2001) were used to analyze the relationship between bird occurrence (from the training dataset) and environmental variable (land cover, climate, and elevation variables). BRTs have been increasingly used and tested in ecological applications (Elith and Graham 2009, Benito et al. 2013). Shirley et al. (2013) demonstrated that BRTs are well suited to predicting distribution of forest birds as a function of continuous Landsat TM data. Rather than attempt to fit a single parsimonious model, BRTs add a “boosting” method to a traditional regression tree methodology to improve model accuracy; beginning with a single regression tree, new trees are added iteratively in a forward, stagewise fashion that minimizes loss of predictive performance (Elith et al. 2008). BRTs model both non-linear relationships and interactions among predictors, and can be used with a variety of response distribution types.

I fit all BRT models using the package ‘dismo’ in R (R Development Core Team 2008), with additional source code from Elith et al (2008). For first runs, the user-controlled model parameters of ‘learning rate’ (*lr*), ‘tree complexity’ (*tc*), and ‘bag fraction’, were those suggested in Elith et al. (2008) and validated for use in forest bird distribution models in Shirley et al. (2013). However, where necessary, *lr* was adjusted slightly on an individual species basis to optimize the number of trees (*nt*) produced (with a goal of at least 1000 trees), with *tc* being adjusted in tandem with *lr* for optimization of *nt* as suggested in Elith et al. (2008). I evaluated prediction success for each species in two ways. First, area under the receiver operating

characteristic curve (AUC) and its standard error was calculated within the model training data using a ten-fold cross validation procedure in the package ‘dismo’ (Elith et al. 2008). AUC essentially represents the probability of correct classification of true versus false positives, and is a standard way of evaluating the discriminatory power of SDMs (Lobo et al. 2008, Elith and Graham 2009). Second, AUC was used to evaluate the performance of each model in predicting species occurrence from the independent 2011 oak-focused point count survey of the Rogue Basin, using the R package ‘pROC’ (Table 2).

Using the packages ‘raster’ and ‘dismo’ in R, I extrapolated individual BRT models for each of the 48 study species to predicted probability of species occurrence to the entire study area on a 30 x 30 m pixel basis. Predictions were fitted using climate data (temperature and precipitation means for June, July, and December) and elevation grids identical to those used in BRT models. Because the final goal of the analysis was to predict species richness at the locations of the 2011 oak-focused point count study, I selected 2011 Landsat data for land cover variables in the extrapolations, using means and SDs of reflectance values for the six spectral bands as in BRT models.

Estimation of Rogue Basin bird species richness

I used an SDM stacking method (S-SDM) to convert predictions of occurrence for individual species to a prediction of species richness (or multi-species habitat suitability) across the Basin. While continuous probability of occurrence predictions has been informative in individual species distribution studies (Betts et al. 2007, Fahrig 2013), for the purposes of species diversity or community analysis using S-SDM, probabilities are generally converted to binary presence/absence predictions using a threshold methodology that reduces probabilities to presence or absence of each species being considered (Pellissier et al. 2013). Importantly, the summing of probabilities assumes that cells with a value of “1” are equivalent, whether that value

was derived from two species with probabilities of 0.5, or from ten species with probabilities of 0.1. In contrast, after summing species predictions to which a threshold has been applied, a value of “1” simply means that one species is predicted to occur. Wilson et al. (2005), Dubuis et al. (2011), and Pellisier (2013) assessed sensitivity of S-SDM richness predictions using various probabilistic vs. threshold methods. All authors suggested that further work needed to address the benefits and drawbacks of these S-SDM methodologies in various taxa and regions. In this study, I conduct a sensitivity analysis to compare the ‘probabilities’ versus the ‘threshold’ method of SDM stacking as two potential approaches for examining relationships between species richness and local versus landscape habitat amount.

For the ‘probabilities’ method, I summed the value of probability of occurrence of all species at each 30 x 30 m pixel for a prediction of total species richness at each pixel. For the ‘threshold’ method, I selected an objective posteriori probability cutpoint at which to determine presence/absence of each species. I calculated cutpoints using the “youden” method (or Youden’s J statistic) in the R package ‘pROC’. The “youden” method maximizes the sum of the specificity and sensitivity of the ROC curve, and is recommended by (Liu et al. 2005) for SDMs. I then reclassified the 30 x 30 m prediction grids for each species to presence or absence based on the unique cutpoint for that species (Appendix Table 3). Finally, I summed all reclassified grids to generate a prediction of the total species richness at each pixel across the study area.

I examined two primary species subsets for potential differences in the relationship between richness and habitat. These nested subsets were the following: 1) ‘all species’, defined as all of the 48 study species, and 2) ‘oak species’, defined as 25 highly oak-associated species selected from Altman and Stephens (2012). Two additional subsets were examined for use in sensitivity analysis, to determine whether the results for influence of habitat amount might be influenced by individual SDM performance (as measured by AUC): 1) ‘all species - high performance’, defined as 8

species from the ‘all species’ subset with highest AUC values ($AUC > 0.8$) when independently evaluated with the 2011 oak-focused point count dataset, and 2) ‘oak species - high performance’, a nested subset of ‘all species - high performance’ that contained only those oak-associated species with $AUC > 0.8$ (see Appendix Table 2 for summary of all subsets). For each subset, I used the above process of stacking SDMs to create gridded estimates of species richness for a total of eight basin-wide estimates of species richness distribution (i.e., four species subsets, two stacking methods each).

Estimation of habitat amount at local and landscape scales

I used a moving window analysis on grids of predicted species richness (all four species subsets and both stacking methods) to create an estimate of habitat amount at local and landscape scales, following Betts et al. (2007). At each pixel across the ‘all species’ richness grid, the mean species richness was calculated within radii of 150 m (corresponding to general territory size for passerine-sized forest birds in this study (Betts et al. 2007), for an index of habitat amount for all species at the local scale. Moving window analysis was then performed for the ‘all species’ subset at 2000 m, 5000 m, and 10,000 m. These scales, though not selected specifically for each study species, correspond to the potential range of habitat use as well breeding and natal dispersal distances for passerine birds (Paradis et al. 1998, Bowman 2003, Betts et al. 2007). I tested for collinearity among local and all landscape predictor variables using linear regression. I subsequently selected the 10,000 m scale as representing the regional species pool as it showed the lowest correlation with the 150 m scale (R^2 for 150 m ~ 10,000 m = 0.329 and 0.439 for ‘probabilities’ and ‘threshold’ methods respectively; Appendix Table 3). The 10,000 m scale should represent the higher end of passerine dispersal ranges (Matthysen et al. 1995, Paradis et al. 1998, Bowman 2003) and its correlation with 2,000 m and 5,000 m ensure that affect from these smaller scales would be indirectly included in the landscape habitat amount term. I

performed moving window analysis for the remaining species subsets for an index of habitat amount at 150 m (local) and 10,000 m (landscape) for all species subsets.

Testing species richness as a function of habitat amount

To address my primary research objective to test the relative power of local- and landscape-level habitat amount in explaining local forest bird species richness, I used multiple linear regression to model species richness from an independent dataset (i.e. the 2011 evaluation dataset) as a function of the local and landscape habitat amount metrics derived from S-SDMs. To allow direct comparison of effect sizes, I standardized local and landscape habitat amount terms to a mean of 0 and a standard deviation of 1.

In addition to terms describing local and landscape-scale habitat amount, I included an autocovariate term in the model to control for variation in species richness resulting from the influence of spatial autocorrelation, which may result from both biotic and abiotic processes (Legendre 1993). Using the package ‘ncf’ in R, I tested for spatial autocorrelation in the residuals of the following model (performed for all species subsets and both stacking methods; model term definitions in Table 5):

$$local\ species\ richness \sim local + landscape$$

using a lag distance of 0.0025 decimal degrees (approximately the distance between the closest point count locations, or 250m). I found significant spatial autocorrelation in the residuals of the linear models up to a distance of 0.1 decimal degrees (approximately 10,000 m), and developed a autocovariate term (hereafter ‘space’) to account for autocorrelation at this distance using the R package ‘spdep’ for addition to the final linear models (Betts et al. 2009). I examined diagnostic residual plots for all models to assess linearity between predictors and model fitted values.

The resulting global model was the following:

$$(1) \quad local\ species\ richness \sim local + landscape + space$$

This global model effectively allowed the examination of each habitat amount term after controlling for the effects of the other habitat amount term and *space*.

Model selection and comparison

To assess potential differences in importance of *local* and *landscape* terms related to whether species were highly associated with oak cover types, the test above (1) was performed for each of the two primary species subsets for which local and landscape habitat amount had been calculated ('all species' and 'oak species') and for both S-SDM methods ('probabilities' and 'threshold'). I used Akaike's Information Criteria (AIC) to determine whether the global model was appropriate for the 'all species' and 'oak species' subsets for both stacking methods, and if not, to select the best alternative model. The simple relative influence of local and landscape habitat amount (i.e. the effect of local after controlling for landscape and vice versa) was the primary biological question addressed by this study, so only additive models with no interaction terms were considered in AIC analysis. To evaluate the relative effect size of models terms, I directly compared the standardized regression coefficients for *local* versus *landscape* terms within models for both species subsets, and between both methods. Use of standardized coefficients to compare effect size has been recently identified as a least-biased option for comparing the relative importance of predictors in regression analysis when using collinear habitat variables (Smith et al. 2009).

I examined uncertainty in the prediction of species richness within the 'all species' and 'oak species' subset with quantile regression analysis (Cade and Noon 2003, Belmaker and Jetz 2012), using asymmetric likelihood in the package "VGAM". While ecological data may adequately fit the assumptions of linear regression, heterogeneous variation in the response is common and rate of change with respect to the mean of the response in normal linear regression may not describe rates for all parts of the response distribution (Cade and Noon 2003). Quantile regression can complement traditional linear regression by exploring potential curvilinearity in

relationships (Cade and Noon 2003), and helping to identify parts of the response distribution at which unmeasured processes might be limiting or causing unexplained variation (Belmaker and Jetz 2012). My goal in this analysis was to determine whether the effect size of local habitat amount and landscape habitat amount were variable at different intervals of local species richness, with a view toward indicating limiting influence of unmeasured predictors and adding to interpretation of the relative effects of habitat amount on observed local species richness.

Sensitivity analysis

For examination of sensitivity of model results to the AUC estimates of SDM performance, I tested richness and habitat amount relationships for the ‘all species - high performance’ and ‘oak species - high performance’ subsets (both stacking methods). Because these tests were done primarily for purposes of sensitivity analysis, I only considered simple global models and did not use AIC-based model selection for these tests.

High-quality predictions of species richness are necessary for meaningful management recommendations, however studies explicitly comparing efficacy of S-SDMs versus ‘macroecological model’ (MEM) approaches (in which species richness is modeled directly based on environmental predictors) are rare (Dubuis et al. 2011). Dubuis et al. (2011) found that threshold-based S-SDMs overpredicted plant species richness but had a higher correlation with observed richness compared to an MEM. To evaluate my S-SDM richness predictions, I constructed a direct MEM of species richness within the training dataset as a function of the same land cover, climate, and elevation predictors used in individual species models. The MEM was constructed using the same BRT technique as was used for SDMs, using the package ‘dismo’ in R (R Development Core Team 2008), with additional source code from Elith et al (2008, Appendix). The user-controlled parameter of lr and tc were set at 0.01 and 5, respectively.

Results

Species distribution models

Prediction success for species distribution models (SDMs) was generally high for within-model tests on the training dataset (i.e. cross-validation), with a mean AUC of approximately 0.80 (SD = 0.08; Table 2). A total of 45 species had prediction accuracies ranging from >0.7 to 0.935, (>0.7 is considered a threshold for good discriminatory power; (Hosmer and Lemeshow 2005). Three species had AUC values between 0.6 and 0.7. Pellissier et al. (2013) determined in an SDM stacking study of butterfly communities that inclusion of models with cross-validation AUC scores less than 0.6 into predictive species richness stacks did not alter correlations with observed species richness. Based on this, I chose to retain species with AUC between 0.6 and 0.7 for my estimation and analysis of bird species richness. AUC was ≥ 0.8 (the threshold for excellent prediction success) for 26 species. Prediction success within the evaluation dataset was lower and more variable, with a mean AUC of approximately 0.66 (SD = 0.11). Of the 48 species, 18 had AUC ≥ 0.7 , and 8 species had AUC >0.8 (i.e. the ‘all species - high performance’ analysis subset, Appendix Table 2).

Species richness as a function of habitat amount

Model selection

The two approaches for summing species richness estimates (‘probabilities’ and ‘threshold’), while resulting in differing values of predicted species richness across the Basin, produced visually similar patterns of species richness distribution (see Figure 2 and 3 for examples of individual and stacked predictions respectively). Species richness was positively correlated with local habitat amount, landscape habitat amount, and ‘space’ in both stacking methods for ‘all species’ (‘probabilities’:

$R^2=0.18$, $F(3, 6230)=46.16$, $p<0.0001$; ‘threshold’: $R^2=0.18$, $F(3, 623)=47.09$, $p<0.0001$) and for ‘oak species’ (‘probabilities’: $R^2=0.30$, $F(3, 623)=89.96$, $p<0.0001$; ‘threshold’: $R^2=0.31$, $F(3, 623)=94.7$, $p<0.0001$; Table 4), although ‘oak species’ models were stronger in terms of variance explained. For ‘all species’ and ‘oak species’ subsets and both stacking methods, the global model – including *landscape*, *local* and *space* terms – was the best supported according to AIC (Table 4). Diagnostic residual plots for all models showed linearity with all predictors and with model fitted values.

Model comparison: probabilities method

Within the ‘all species’ model using the ‘probabilities’ method, all terms except *local* were strongly and positively correlated with species richness (*local*: 95% CI [-0.048, 0.362], $p=0.1$; *landscape*: 95% CI [0.169, 0.579], $p=0.0001$; *space*: 95% CI [0.639, 0.982], $p<0.0001$; Table 4). For ‘all species’, effect size for landscape habitat amount was slightly more than double that of local habitat amount (Figure 4A). All model terms were strongly and positively correlated with species richness for the ‘oak species’ subset (*local*: 95% CI [0.326, 0.675], $p<0.0001$; *landscape*: 95% CI [0.120, 0.469], $p=0.0004$; *space*: 95% CI [0.723, 1.032], $p<0.0001$; Table 4). Model term effect sizes were reversed for ‘oak species’, with local habitat approximately 1.5 times larger than landscape habitat (Figure 4A). However, effect size of *landscape* was not unimportant in ‘oak species’, falling only slightly below the effect size of *landscape* for ‘all species’ (Figure 4A). In contrast, the effect size of local for ‘oak species’ was more than 3 times that for ‘all species’.

Model comparison: threshold method

Within models using the ‘threshold’ stacking method, all model terms were significantly and positively correlated with species richness for the ‘all species’ subset (*local*: 95% CI [0.045, 0.492], $p=0.01$; *landscape*: 95% CI [0.087, 0.534], $p=0.003$;

space: 95% CI [0.627, 0.971], $p < 0.0001$; Table 4) and the ‘oak species’ subset (*local*: 95% CI [0.449, 0.820], $p < 0.0001$; *landscape*: 95% CI [0.013, 0.384], $p = 0.02$; *space*: 95% CI [0.713, 1.020], $p < 0.0001$; Table 4). Models using the ‘threshold’ stacking method had similar patterns of relative importance of local and landscape in terms of standardized regression coefficients (Figure 4B). Landscape habitat amount was again more important than local habitat amount for ‘all species’. Although the difference in effect size was not as pronounced as in the ‘probabilities’ method; non-overlapping confidence intervals for all model terms (reported above) indicate that they were statistically indistinguishable (Figure 4B). Local habitat amount was again relatively more important than landscape habitat amount for ‘oak species’, and the three-fold difference in *landscape* vs. *local* effect size was considerably greater than the difference using the ‘threshold’ method; however, non-overlapping confidence intervals for all model terms (reported above) indicate that they were statistically indistinguishable (Figure 4B). Consistent with ‘probabilities’ models, the effect size for *landscape* in ‘oak species’ fell somewhat below that of *landscape* for ‘all species’, while the effect size for *local* in ‘oak species’ was more than double that of *landscape* for ‘all species’ (Figure 4A & B).

Model comparison: quantile regression

Quantile regression analysis for ‘all species’ and ‘oak species’, showed some change in the importance of *local* and *landscape* terms with increasing levels of local species richness (Figure 5). In general, the effect size (in terms of standardized regression coefficients) for both model terms was smallest within the 10th percentile of the response, increasing in a slightly curvilinear fashion through the 90th percentile of the response. Greater variance around the estimated effect size was evident for all terms in all models at the lowest levels of local species richness. For ‘all species’ effect size of *local* and *landscape* terms appeared to converge at the highest levels of observed species richness for the ‘threshold’ method. In both stacking methods for

‘oak species’, the estimated effect of *local* and *landscape* terms was approximately equal at the 10th percentile, with considerable divergence of importance as species richness increased.

Sensitivity analysis

The relative importance of local versus landscape-scale habitat amount did not appear to be highly sensitive to the prediction success of individual SDMs. Species richness was positively correlated with local habitat amount, landscape habitat amount, and space for “all species - high performance” (‘probabilities’: $R^2=0.23$, $F(3, 623)=63.17$, $p<0.0001$; ‘threshold’: $R^2=0.21$, $F(3, 623)=58.12$, $p<0.0001$) and ‘oak species - high performance’ (‘probabilities’: $R^2=0.27$, $F(3, 623)=78.32$, $p<0.0001$; ‘threshold’: $R^2=0.27$, $F(3, 623)=79.24$, $p<0.0001$), with total variance explained slightly higher for ‘all species - high performance’ than for ‘all species’ and slightly lower for ‘oak species - high performance’ than for ‘oak species’. Effect sizes for *local* and *landscape* terms for high performance models, while generally consistent in pattern with ‘all species’ and ‘oak species’ models, were somewhat smaller using both stacking methods (Figures 4 and 5).

There was a positive and statistically significant correlation between observed species richness (from 2011 the evaluation dataset) and predicted species richness from S-SDMs using the ‘threshold’ method for both ‘all species’ ($F(1, 625)=29.76$, $p<0.0001$) and ‘oak species’ ($F(1, 625)=109.8$, $p<0.0001$). Consistent results were achieved using the ‘probabilities’ method ($F(1, 625)=19.32$, $p<0.0001$ for ‘all species’; $F(1, 625)=93.22$, $p<0.0001$). Explanatory power of species richness from S-SDMs was low for ‘all species’ ($R^2=0.04$ for ‘thresholds’, $R^2=0.03$ for ‘probabilities’) and slightly higher for ‘oak species’ ($R^2=0.15$ for ‘thresholds’, $R^2=0.13$ for ‘probabilities’). In contrast, the MEM (i.e., species richness modeled directly by BRT) was not correlated with observed ‘all species’ richness ($R^2= -0.001$, $F(1, 625)=0.06$, $p=0.80$),

but was correlated with ‘oak species’ richness’ ($F(1, 625)=66.66$, $p<0.0001$), with low explanatory power ($R^2=0.09$)

Discussion

Overall, my results provide support for both local and landscape scale habitat amount as predictors of forest bird species richness. My primary research objective was to test the relative importance of local versus landscape habitat amount on bird species richness. Unlike previous efforts, I used a species-centered approach which recognizes that ‘habitat’ is defined differently across all species, incorporating individual species distributions into multi-species habitat amount estimates at local and landscape scales. Using similarly derived habitat amount variables at both spatial extents enabled me to quantify the relative influence of these variables to local avian species richness. Interestingly, landscape-scale habitat amount was a stronger predictor of species richness for a large pool with disparate habitat associations, while local habitat amount was more important for richness of a nested subset of oak-associated species. However, both local and landscape terms were generally important to richness within both subsets. These results suggest that broad-scale processes such as dispersal from the regional species pool may be at least as important as local filtering in shaping local species richness. This finding is consistent with previous hypotheses that the influence of regional species pools may overwhelm local habitat effects in determining local which species ultimately occupy a site, particularly for vagile species such as forest birds (Ricklefs 1987, Belmaker and Jetz 2012).

Habitat amount relationships

When considering all species for which SDMs were possible, ‘all species’ landscape habitat amount was more influential than local habitat amount, regardless of the stacking method used. This appears to support the “regional species pool”

hypothesis (Ricklefs 1987, Zobel 1997), which posits that availability of habitat at the regional level is of primary importance to availability and ability of individuals of a species to disperse to a local site, beyond local conditions. This result may also indicate the presence of ‘spillover’ effects (Tscharntke et al. 2012), in which site-level species richness is increased by greater broad-scale heterogeneity of vegetation. In particular for the ‘all species’ pool, comprised of forest bird species with relatively diverse habitat associations, higher levels of landscape ‘habitat amount’ may correspond to higher levels of vegetation heterogeneity. Further examination is necessary to determine the precise biological mechanisms indicated by the relationship between local richness and broad-scale habitat amount in this study.

Alternately, for ‘oak species’, local habitat amount was considerably more important than landscape habitat amount, again with no statistically distinguishable difference between S-SDM methods (Table 4; Figures 4 and 5). Results for this subset suggest that for a local assemblage of oak-associated birds, a site’s local quality for multiple species is more important than the capacity for those species to disperse through the landscape. This result for ‘oak species’ lends support to hypotheses for local mechanisms, for example the “vegetation heterogeneity” hypothesis which posits an overriding importance of local habitat quality and structure (incorporated into SDMs using Landsat TM reflectance as a proxy) over landscape context (MacArthur and MacArthur 1961, Tews et al. 2004). It might also suggest the importance of productivity gradients (incorporated into SDMs indirectly via climate variables) (Mitchell et al. 2001, White and Hurlbert 2010). The reversed importance of local habitat amount between the species subsets may be indicative of a dynamic particular to this highly oak-associated bird species group. For example specialists, such as the ‘oak species’, are perhaps so highly adapted to and dependent on particular territory-level vegetation and environmental conditions that the ability to disperse to a site is secondary to the ability to occupy the required niche-space within the site. While some research has found that specialists are more sensitive than generalists to landscape

fragmentation (Devictor et al. 2008), decreased sensitivity to landscape effects by specialists was suggested in a meta-analysis by Prugh et al. (2008).

The observed switch in the relationship of habitat amount to species richness in the two species subsets may indicate that habitat relationships are relative to the regional habitat context of the species group being examined. ‘Habitat amount’ may be an effective proxy for both patch size and isolation, as hypothesized by Fahrig (2013). Thus, my results may support the suggestion that avian species associated with the PNW’s naturally patchy and isolated oak vegetation should be less sensitive to landscape-level vegetation structure (i.e., both configuration and composition) than species associated with cover types that have been historically more continuous (Altman and Stephens 2012) such as Douglas-fir forest in the PNW (Spies et al. 2007). Effective conservation planning requires consideration of the influences of both local- and landscape-scale processes (Tscharntke et al. 2012). For the highly management-relevant group of oak-associated bird species (Altman 2000, Stockenberg et al. 2008), the results imply that focus on improving habitats via conservation or restoration of oak vegetation types in the Rogue Basin should prioritize maximizing the quality of stand-level conditions over maintaining high levels of landscape-level habitat connectivity. Though many of the remaining species in the ‘all species’ subset utilize non-coniferous vegetation, the majority are more likely to occur in conifer-dominated than broadleaf-dominated sites; indeed nine of the ‘all species’ subset are considered “focal species” for Northwest conifer forests (Altman 1999). The possibility that conifer vs. broadleaf-associated birds in this region might be differentially sensitive to landscape context is an interesting hypothesis that may warrant further investigation. Finally, the consistent increase in effect size for *local* and *landscape* terms with increasing species richness (Figure 5), suggests that high local species richness is particularly dependent on landscape-level dispersal of regional species to a site, as well as on the ability of the local habitat to accommodate multiple niche spaces of forest bird species.

Implications for habitat amount research

The continuum-based S-SDM approach used in this study allowed deviation from traditional patch/matrix models of “habitat” in two important ways. First, it allowed “habitat amount” relationships to be investigated for multiple species without the need to first carefully select the cover type and the species group under consideration, as Fahrig (2013) cautioned was critical when defining habitat on the basis of cover type. All regional species theoretically have the potential to emigrate to any given site that is within their dispersal range (Belmaker and Jetz 2012). Hence, the ability to ask questions about relative importance to local assemblages of scale-dependent processes such as local environmental filtering and landscape level dispersal in the context of entire regional pools could be useful in future “habitat amount” studies. While limitations to computational effort and to accurately modeling very rare species using SDMs (Elith and Leathwick 2009) limited the number of species I could examine, I was able to use S-SDM methods to address the importance of local vs. landscape scale habitat amount for a large group of regional species (the ‘all species’ subset) with divergent habitat associations. As SDM techniques using remote sensing data improve, the opportunities for rigorous testing using this method will only increase.

Second, for species which are expected to use more similar cover types (such as the ‘oak species’ subset), a continuum approach may be a more realistic way to quantify the amount of habitat available to the entire group at a particular scale. Use of S-SDMs in this study avoided the problematic nature of using human-defined cover types to identify ‘habitat’ for multiple species. Unless each species under consideration is highly associated with the given cover type, it is unlikely that there will be evidence for consistent responses to changing amounts of that cover type at local or landscape scales (Cushman et al. 2008, Fahrig 2013). Additionally,

delineating cover types as “habitat” within gradients of forest cover will likely produce error by assuming that 1) all species respond in a similar way to the amount of that “habitat” within a particular scale, and 2) the “matrix” as defined is equally unsuitable for all species (Cushman et al. 2010). The widespread use of cover type-based habitat amount estimation, while a useful simplification given the reality of ecological complexity, may be responsible for producing idiosyncratic results in habitat amount studies (as in Prugh et al. 2008) if cover types are not perfect proxies for habitat (Cushman et al. 2008). This study demonstrates a potentially useful way to address questions relating to species responses to habitat while embracing some of that complexity.

It may be argued that the choice of predictor variable in SDMs limited the explanatory power of my habitat amount models; other studies examining local versus landscape effect on bird occurrence or species richness tend to use a number of carefully selected predictor variables relevant to each scale of examination, thereby increasing their ability to explain more variation in the response (e.g., Saab 1999). My technique, while perhaps not capturing all of the variation in species richness, was beneficial in that local and landscape habitat amount metrics were derived using the same methods and units; it is therefore unlikely that effect size for either *local* or *landscape* terms was biased by the choice of predictor variables. Importantly, effect sizes for standardized local and landscape habitat amount estimates were directly comparable in terms of their relative relationship to species richness. Differences in these relationships between the species subsets are thereby able to more clearly suggest potential differences in the degree to which fine- and broad-scale processes influence local community assembly, depending on the species pool considered. Finally, my methods could theoretically be applied for habitat amount investigations across taxa and regions, with biologically informed adjustments, and in this way could aid in elucidation of general effects of habitat amount on diversity patterns (Prugh et al. 2008, Fahrig 2013).

Comparison of SDM stacking methods

One important objective of my research was to test the ability of summed probabilities from individual species SDMs to generate an effective metric for habitat amount across the entire species pool at multiple spatial scales. S-SDM approaches that use raw summed probabilities are rare in the literature (Wilson et al. 2005), so the relative accuracy compared to threshold methods has not been well explored. In the most relevant example, Dubuis et al. (2011) found that a summed raw probability approach for S-SDMs resulted in a plant species richness estimate that better correlated to observed richness at a 25 m resolution, compared to over-estimation of richness using the same threshold method that was applied in my study (Liu et al. 2005). In my study, the ‘probabilities’ method provided similar, though not identical, estimates of the relative importance of local and landscape habitat amount compared with the ‘threshold’ method, as previously described. Overall, the two methods agreed on the general degree and direction of local versus landscape habitat amount importance with minor differences; the threshold method produced slightly higher R^2 values for both the ‘all’ and ‘oak’ species subsets, while regression coefficients were more similar for ‘all species’ and more divergent for ‘oak species’ using thresholds, although none were statistically distinguishable (Table 4). Importantly, all models were able to produce a statistically significant prediction for species richness at a very fine resolution (i.e., 30 x 30 m) which likely relevant to bird-habitat relationships (Shirley et al. 2013).

From the most conservative perspective, the consistency of results between the two methods indicates that the use of summed probabilities to derive metrics of multi-species habitat amount is worth consideration for this type of investigation. I additionally suggest that the demonstrated ability of the ‘probabilities’ method to produce results similar to threshold methods more commonly used in S-SDMs (e.g.

Pineda and Lobo 2009) presents an exciting and novel way to test hypotheses regarding the importance of species pool-level habitat amount at multiple scales. One potential strength of the ‘probabilities’ method lies in the ability to estimate multi-species habitat amount on a continuum. As individual species habitat exists as gradients of suitability and perception across a landscape (Fischer and Lindenmayer 2006), a multi-species habitat amount metric that takes these gradients into account may be more biologically realistic and more flexible than threshold-based approaches that convert continuous surfaces of individual species habitat suitability into a binary value (i.e., habitat vs. matrix).

Effects of spatial autocorrelation

I tested for the influence of spatial autocorrelation in model residuals to control for underlying aggregation patterns in tests for the effect of local and landscape habitat amount on species richness (Legendre 1993). However, the existence of spatial autocorrelation might also indicate important mechanisms for biotic patterns (Legendre 1993, Mattsson et al. 2013). In this study, spatial autocorrelation alone was highly influential in predicting species richness for both stacking methods in the ‘all species’ and ‘oak species’ subsets. The autocovariate term used in all linear models accounted for spatial autocorrelation from 250 m (roughly the same scale as local habitat amount) through 10,000 m (the same spatial scale as landscape habitat amount). Hence, the *space* term may have represented spatially aggregated aspects of local habitat use and dispersal that were not well modeled by the S-SDM based *local* and *landscape* terms. Spatial autocorrelation effects may also be suggestive of local biotic processes, such as competition and predation, that I did not explicitly account for but are generally recognized as being of high potential importance to local, and perhaps regional, species assembly (Wisz et al. 2013). In community ecology, it is thought that such species interactions may to an extent have a limiting influence on

local species richness (Cornell and Lawton 1992). This interpretation is supported by the results of quantile regression in this chapter (Figure 5), where high variance in estimates of habitat amount effect size at low levels of species richness suggested the influence of unmeasured parameters (Cade and Noon 2003).

Study limitations

Prediction success for SDMs using the evaluation dataset was relatively low; only 8 of the 48 species had AUC >0.8. AUC is thought to be a useful and objective way to evaluate model discrimination for SDMs (Elith and Graham 2009), and so models with relatively low AUC scores may represent model error which limited my ability to predict species richness. However AUC may also vary according to species traits, such as generalism vs. specialism (Lobo et al. 2008), and Pellissier et al. (2013) found that inclusion of low AUC models (AUC <0.6) in S-SDMs had no effect on correlation between predicted and observed species richness. In this study, high performance models did a good job at predicting species richness for high performance species; overall results were similar to habitat amount tests for ‘all species’ and ‘oak species’, though effect sizes were lower (Table 4, Figures 4 and 5). Importantly, exclusive examination of high-AUC models did not improve explanatory power, suggesting that modeled habitat distribution at multiple scales may be insufficient to fully explain richness no matter the models’ strength. This interpretation would strongly implicate other unmeasured processes such as biotic interactions for helping to shape local richness (Blois et al. 2013) and would support effort to incorporate these into SDM approaches (Guisan and Rahbek 2011).

Results for AUC in SDM cross-validation was mostly consistent with results from Shirley et al. (2013), a study which similarly used Landsat TM data to create SDMs for forest birds, and which shared some of the same species occurrence data as the current study. Shirley et al. (2013) had a greater proportion of species with AUC

>0.8 (90%) than was found in this study (approx. 54%), however these values can only be indirectly compared. Shirley et al.'s (2013) study area was larger (all of western Oregon) and more environmentally heterogeneous, and so may have more effectively captured the full environmental gradients along which each species might be expected to occur in this region. The resulting potential for a mean increase in environmental distance across training sites for all species could have resulted in individual species receiving higher AUC scores (Lobo et al. 2007).

Explanatory power for richness as a function of *local*, *landscape*, and *space* terms was relatively low (~18% for 'all species', ~30-31% for 'oak species'), which suggests caution should be taken in application to management. My R^2 values agreed in direction of effect, but were relatively low, compared to other reported multi-scale efforts to predict forest bird richness, though this might be related to mismatches in scale or resolution (e.g., a study by Rahbek and Graves (2001) employing resolutions of at least 100 km²; research by Saab (1999) using principle components analysis to describe richness relationships with more than three dozen multi-scale predictor variables in a small riparian area). Belmaker and Jetz (2012) had somewhat greater explanatory power than I found, in an examination of total North American bird species richness with local assemblages characterized at a median of 411 km². White and Hulbert (2010) achieved at least double my explained variance using 'local' habitat variables at a 40 km radius to model bird richness from BBS data. Compared to the above studies, my analyses were conducted at a relatively broad scale and fine resolution, which likely made prediction more difficult due to the introduction of high heterogeneity among sample sites and potentially high propagated model error within local species richness estimates. Additionally, the use of only three predictor variables (*local*, *landscape*, and *space*) made it likely that some important processes controlling local richness would not be accounted for. It is important to note that the goal of my research was not to explain high amounts of variation in species richness, but rather 1) to explicitly test for relative effects of local- and landscape-level habitat amount on

local species richness, and 2) to do so using a novel method of calculating habitat amount metrics that would be both biologically realistic and directly comparable among scales.

Additionally, I would urge caution in the application of the results to management action due to the relatively low explanatory power of both threshold- and summed probabilities-based S-SDMs in predicting observed species richness at a 30 x 30 m pixel resolution ($R^2=0.03$ to 0.04 and $R^2=0.13$ to 0.15 for ‘all’ and ‘oak’ subsets respectively). However, it is interesting to note that the species-centered S-SDM approach outperformed a direct model of oak-associated species richness at this fine resolution ($R^2= -0.001$ and $R^2=0.09$ for ‘all’ and ‘oak’ subsets respectively). Biological processes may be differently modeled by the MEM and S-SDM techniques, as MEM predicts relationships between a site’s total species and local conditions while S-SDM represents the total suitability of habitat for multiple species modeled individually (Dubuis et al. 2011). While S-SDM better fits a species-centered conceptual framework, the consequences and implications of using MEM vs. S-SDM in terms of ability to predict fine-resolution species richness requires further examination in the context of this study.

Finally, it has become increasingly clear that accounting for imperfect detection via occupancy modeling in the analysis of point count data can have dramatic influences on values for observed richness used as model response variables (Jones et al. 2012). Current occupancy modeling tools allow probability of detection to be incorporated into a species habitat model, but require linear relationships between the response and the predictors (Jones et al. 2011). My decision to use BRT to model species habitat suitability, based on its ability to fit complex and non-linear relationships between species occurrence and variables such as Landsat TM spectral data, precluded the use of occupancy modeling. While I did not expect to explain all of the variance in species richness with *local*, *landscape*, and *space* terms, it is possible that the inability to account for detection may have contributed to relatively low power

to explain the variance in species richness. Potential biases in detection due to local and landscape factors will be addressed in future work and compared to the results reports here.

Conclusions

My results provide evidence for the importance of local and landscape scale habitat amount for local forest bird species richness in oak vegetation types of the Rogue Basin, Oregon. Variation in the magnitude and direction of these relationships between the ‘all species’ subset and the nested ‘oak species’ subset reveal potential differences in the degree to which fine- and broad-scale processes influence local bird diversity. I found that a metric for landscape-level habitat amount derived from S-SDMs had a more important relationship with ‘all species’ richness than did such a metric for local habitat amount, pointing to dispersal from the regional species pool as a key mechanism for local assembly. I found the reverse for ‘oak species’; local habitat amount had a more important relationship with richness than did landscape habitat amount. This observation supports the “vegetation heterogeneity” hypothesis (MacArthur and MacArthur 1961, Tews et al. 2004) and may be evidence for region-specific hypotheses regarding the sensitivity of oak-associated species to landscape-level habitat configuration and fragmentation (Altman and Stephens 2012). My results have particular significance for prioritization of bird-focused oak vegetation restoration and conservation efforts. While landscape habitat amount for oak-associated species is significant and should not be ignored, my results suggest that optimization of stand-level habitat quality may pay greater dividends in terms of supporting greater local species richness.

Finally, I propose that the results of this study are evidence for the utility of an approach that embraces the unique ways in which individual co-existing species perceive and utilize “habitat”. The continuum model put forth by (Fischer and

Lindenmayer 2006) has great conceptual advantages in that it embraces the complex reality of habitat suitability gradients and unique perception of habitat by each species. Yet to my knowledge this model had yet to be applied for investigations of the importance of multi-scale habitat amount for pools of species with divergent habitat associations. I demonstrated that the S-SDM approach was able to explain approximately 18 - 31% of the variation in local species richness at fine resolutions, and was able to directly compare the results between two spatial scales that are theoretically relevant to breeding forest birds, as well as between two nested subsets of the regional species pool. Based on these results, I suggest that further investigation into the generality of this approach among different regions and taxa may prove fruitful.

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Tables

Table 2.1. Common names, scientific names, and AOU four letter codes for 48 species used in species distribution models for the Rogue Basin, Oregon. Species are those oak or deciduous vegetation associated species that were most prevalent in a 2011 Rogue Basin oak-focused point count study.

Common name	Scientific name	Code
Acorn Woodpecker ^{2,6}	<i>Melanerpes formicivorus</i>	ACWO
American Goldfinch	<i>Spinus tristis</i>	AMGO
American Robin	<i>Turdus migratorius</i>	AMRO
Ash-throated Flycatcher ^{2,6}	<i>Myiarchus cinerascens</i>	ATFL
Black-capped Chickadee ^{4,6}	<i>Poecile atricapillus</i>	BCCH
Bewick's Wren ^{2,4,6}	<i>Thryomanes bewickii</i>	BEWR
Blue-gray Gnatcatcher ^{4,6}	<i>Polioptila caerulea</i>	BGGN
Brown-headed Cowbird	<i>Molothrus ater</i>	BHCO
Black-headed Grosbeak ⁶	<i>Pheucticus melanocephalus</i>	BHGR
Brown Creeper ⁵	<i>Certhia americana</i>	BRCR
Black-throated Gray Warbler ^{5,6}	<i>Dendroica nigrescens</i>	BTYW
Bullock's Oriole ³	<i>Icterus bullockii</i>	BUOR
Bushtit ^{2,6}	<i>Psaltiriparus minimus</i>	BUSH
California Towhee ^{4,6}	<i>Pipilo crissalis</i>	CALT
Cassin's Vireo ⁶	<i>Vireo cassinii</i>	CAVI
Chestnut-backed Chickadee	<i>Poecile rufescens</i>	CBCH
Chipping Sparrow ^{2, 6}	<i>Spizella passerina</i>	CHSP
Dark-eyed Junco	<i>Junco hyemalis</i>	DEJU
Downy Woodpecker ^{2, 3, 6}	<i>Picoides pubescens</i>	DOWO
Dusky Flycatcher	<i>Empidonax oberholseri</i>	DUFL
Hermit Warbler ⁵	<i>Dendroica occidentalis</i>	HEWA
House Wren ^{2, 6}	<i>Troglodytes aedon</i>	HOWR
Hutton's Vireo ^{5, 6}	<i>Vireo huttoni</i>	HUVI
Lazuli Bunting ⁶	<i>Passerina amoena</i>	LAZB

Common name	Scientific name	Code
Lesser Goldfinch ^{4, 6}	<i>Spinus psaltria</i>	LEGO
MacGillivray's Warbler	<i>Oporornis tolmiei</i>	MGWA
Mourning Dove	<i>Zenaida macroura</i>	MODO
Nashville Warbler ^{2, 4}	<i>Vermivora ruficapilla</i>	NAWA
Northern Flicker	<i>Colaptes auratus</i>	NOFL
Oak Titmouse ⁴	<i>Baeolophus inornatus</i>	OATI
Orange-crowned Warbler ⁵	<i>Vermivora celata</i>	OCWA
Pacific-slope Flycatcher ⁵	<i>Empidonax difficilis</i>	PSFL
Purple Finch ⁶	<i>Carpodacus purpureus</i>	PUFI
Red-breasted Nuthatch	<i>Sitta canadensis</i>	RBNU
Rufous Hummingbird ⁵	<i>Selasphorus rufus</i>	RUHU
Spotted Towhee	<i>Pipilo maculatus</i>	SPTO
Steller's Jay	<i>Cyanocitta stelleri</i>	STJA
Townsend's Warbler	<i>Dendroica townsendi</i>	TOWA
Tree Swallow ³	<i>Tachycineta bicolor</i>	TRES
Warbling Vireo	<i>Vireo gilvus</i>	WAVI
White-breasted Nuthatch ^{2, 6}	<i>Sitta carolinensis</i>	WBNU
Western Bluebird ^{5, 6}	<i>Sialia mexicana</i>	WEBL
Western Scrub-Jay ⁶	<i>Aphelocoma californica</i>	WESJ
Western Tanager ⁶	<i>Piranga ludoviciana</i>	WETA
Western Wood-Pewee ^{2, 6}	<i>Contopus sordidulus</i>	WEWP
Wilson's Warbler ⁵	<i>Wilsonia pusilla</i>	WIWA
Wrentit ^{3, 4}	<i>Chamaea fasciata</i>	WREN
Yellow-rumped Warbler	<i>Dendroica coronata</i>	YRWA

¹ Grassland/savannah focal species, Altman 2000; ² Oak woodland focal species, Altman 2000;

³ Riparian focal species, Altman 2000; ⁴ Chaparral focal species, Altman 2000; ⁵ Conifer forest focal species, Altman 1999; ⁶ Oak focal species, Altman and Stephens 2012

Table 2.2. Summary of BRT model parameters (*lr* and *tc*), results for within-model cross validation training (AUC and SE), and results for model prediction to independent evaluation data (AUC) for 48 Rogue Basin forest bird species.

Common name	Learning rate	Tree complexity	CV AUC (within-model cross validation)	CV SE (within-model cross validation)	AUC (2011 evaluation data)
Acorn Woodpecker	0.001	5	0.872	0.022	0.72
American Goldfinch	0.0005	5	0.84	0.046	0.70
American Robin	0.001	5	0.736	0.012	0.46
Ash-throated Flycatcher	0.001	5	0.884	0.02	0.82
Black-capped Chickadee	0.001	5	0.859	0.021	0.52
Bewick's Wren	0.001	5	0.896	0.012	0.77
Blue-gray Gnatcatcher	0.001	5	0.935	0.013	0.75
Brown-headed Cowbird	0.001	5	0.816	0.014	0.63
Black-headed Grosbeak	0.005	5	0.788	0.011	0.56
Brown Creeper	0.001	5	0.72	0.014	0.72
Black-throated Gray Warbler	0.005	5	0.852	0.014	0.55
Bullock's Oriole	0.001	5	0.882	0.023	0.78
Bushtit	0.001	5	0.761	0.02	0.78
California Towhee	0.001	5	0.929	0.007	0.87
Cassin's Vireo	0.001	5	0.729	0.016	0.54
Chestnut-backed Chickadee	0.001	5	0.712	0.011	0.82
Chipping Sparrow	0.001	5	0.859	0.021	0.70
Dark-eyed Junco	0.005	5	0.739	0.011	0.52
Downy Woodpecker	0.0003	5	0.669	0.064	0.84
Dusky Flycatcher	0.001	5	0.824	0.02	0.52
Hermit Warbler	0.005	5	0.853	0.008	0.60
House Wren	0.005	5	0.811	0.014	0.63
Hutton's Vireo	0.001	5	0.7	0.044	0.55
Lazuli Bunting	0.005	5	0.814	0.012	0.65
Lesser Goldfinch	0.001	5	0.852	0.017	0.72
MacGillivray's Warbler	0.005	5	0.745	0.021	0.66

Common name	Learning rate	Tree complexity	CV AUC (within-model cross validation)	CV SE (within-model cross validation)	AUC (2011 evaluation data)
Mourning Dove	0.001	5	0.787	0.019	0.51
Nashville Warbler	0.005	5	0.813	0.01	0.55
Northern Flicker	0.001	5	0.649	0.028	0.46
Oak Titmouse	0.0005	5	0.9	0.026	0.82
Orange-crowned Warbler	0.001	5	0.826	0.032	0.61
Pacific-slope Flycatcher	0.001	5	0.77	0.016	0.70
Purple Finch	0.001	5	0.768	0.024	0.60
Red-breasted Nuthatch	0.001	5	0.772	0.015	0.57
Rufous Hummingbird	0.001	5	0.656	0.033	0.61
Spotted Towhee	0.005	5	0.84	0.009	0.67
Steller's Jay	0.001	5	0.689	0.021	0.54
Townsend's Warbler	0.0005	5	0.637	0.089	0.85
Tree Swallow	0.001	5	0.927	0.015	0.69
Warbling Vireo	0.001	5	0.741	0.023	0.64
White-breasted Nuthatch	0.001	5	0.756	0.057	0.65
Western Bluebird	0.0005	8	0.721	0.073	0.86
Western Scrub-Jay	0.001	5	0.896	0.009	0.82
Western Tanager	0.005	5	0.768	0.013	0.53
Western Wood-Pewee	0.005	5	0.821	0.015	0.58
Wilson's Warbler	0.001	5	0.801	0.029	0.65
Wrentit	0.001	5	0.845	0.027	0.76
Yellow-rumped Warbler	0.005	5	0.834	0.011	0.48

Table 2.3. Descriptions of three predictor variable types used in modeling species richness as a function of habitat amount. Variables were calculated uniquely for each of the three species subsets used in analysis.

Variable name	Description
local	Mean local-scale habitat amount, calculated for each pixel in the study area at a radius of 150m
landscape	Mean landscape-scale habitat amount, calculated for each pixel on the landscape at a radius of 10,000m
space	Autocorviate term accounting for the amount of spatial autocorrelation at 0.1 decimal degrees (approx. 10,000m)

Table 2.4. Results for linear regression models testing the relationship between species richness, habitat amount (*local* and *landscape*), and a spatial autocovariate term representing residual spatial autocorrelation at approx. 10,000 m (*space*).

Species subset	Stacking method	Intercept	β (local)	β (landscape)	β (space)	Total adjusted R ²	AIC	p-value
All species	probabilities	4.121***	0.157	0.374***	0.810***	0.18	2640.826	> 0.0001
	threshold	4.121***	0.268*	0.311**	0.799***	0.18	2638.531	> 0.0001
Oak species	probabilities	2.910***	0.501***	0.295***	0.877***	0.30	2401.889	> 0.0001
	threshold	2.910***	0.635***	0.198*	0.867***	0.31	2391.980	> 0.0001
All species high performance	probabilities	0.3181***	0.097***	0.194***	0.577***	0.23	NA	> 0.0001
	threshold	0.3181***	0.084**	0.191***	0.576***	0.21	NA	> 0.0001
Oak species high performance	probabilities	0.3181***	0.17***	0.14***	0.030	0.27	NA	> 0.0001
	threshold	0.3181***	0.175***	0.043***	0.043*	0.27	NA	> 0.0001

* P < 0.05

** P < 0.01

*** P < 0.001

Figures

Figure 2.1. Conceptual figure for creation of local and landscape ‘habitat amount’ metrics for forest bird species of the Rogue Basin, Oregon. Process is as follows: A) Species occurrence data from an observational study is modeled as a function of predictors including B) Landsat TM land cover data and C) elevation. The resulting species distribution model is used to interpolate probability of species occurrence across all pixels in a landscape; within this landscape subset (D), high probabilities of occurrence for lazuli bunting are red, and low probabilities are blue. Multiple SDMs for individual species are ‘stacked’, or summed (E), for a prediction of total richness at each pixel within a landscape (F). Finally, a moving window analysis is applied to calculate an index of habitat amount at a given scale, in this case, the mean of all pixels within a 150 m radius (G) and a 10,000 m radius (H) of each pixel in the landscape. For (G) and (H), highest summed mean values are white, and lowest values are black.

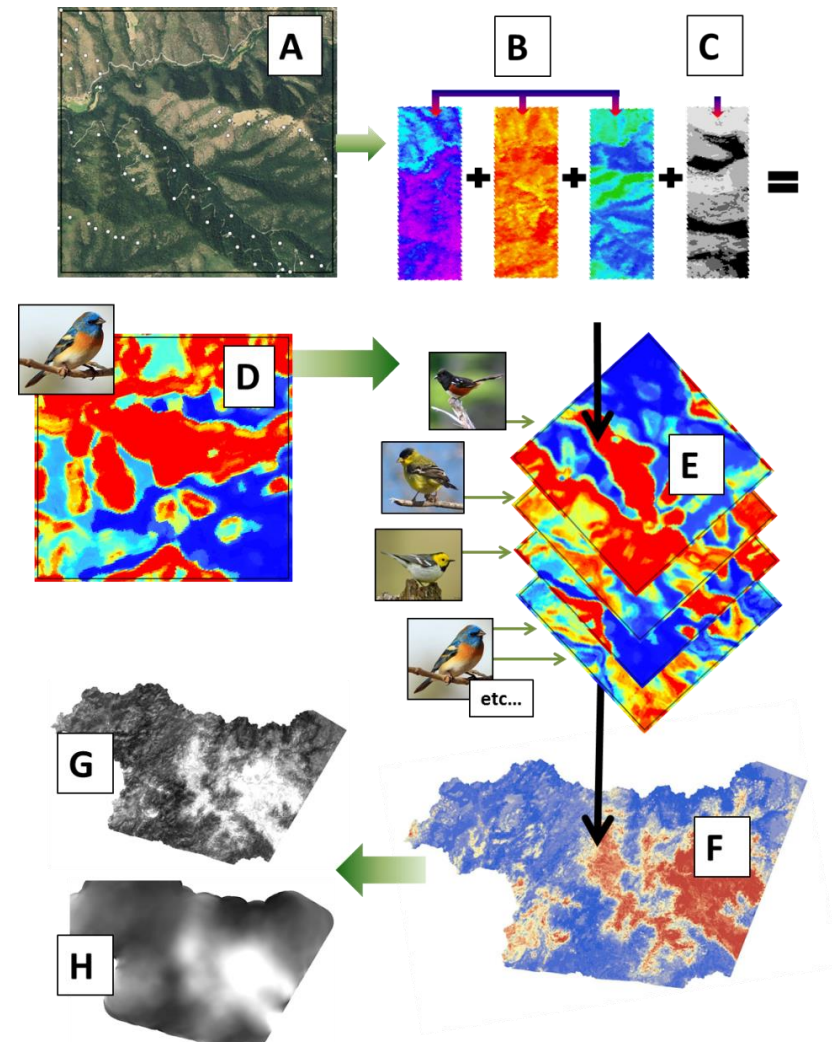


Figure 2.2. Species distribution maps (30m² resolution) within the Rogue Basin, Oregon for 11 oak-associated species with the most strongly-performing SDMs (AUC >0.7 tested against independent evaluation data). Species depicted are a smaller subset of the “oak species” analysis subset. Darkest red areas indicate areas of highest probability of occurrence, and areas of dark blue indicate areas of lowest probability of occurrence. Species code definitions are in Table 1.

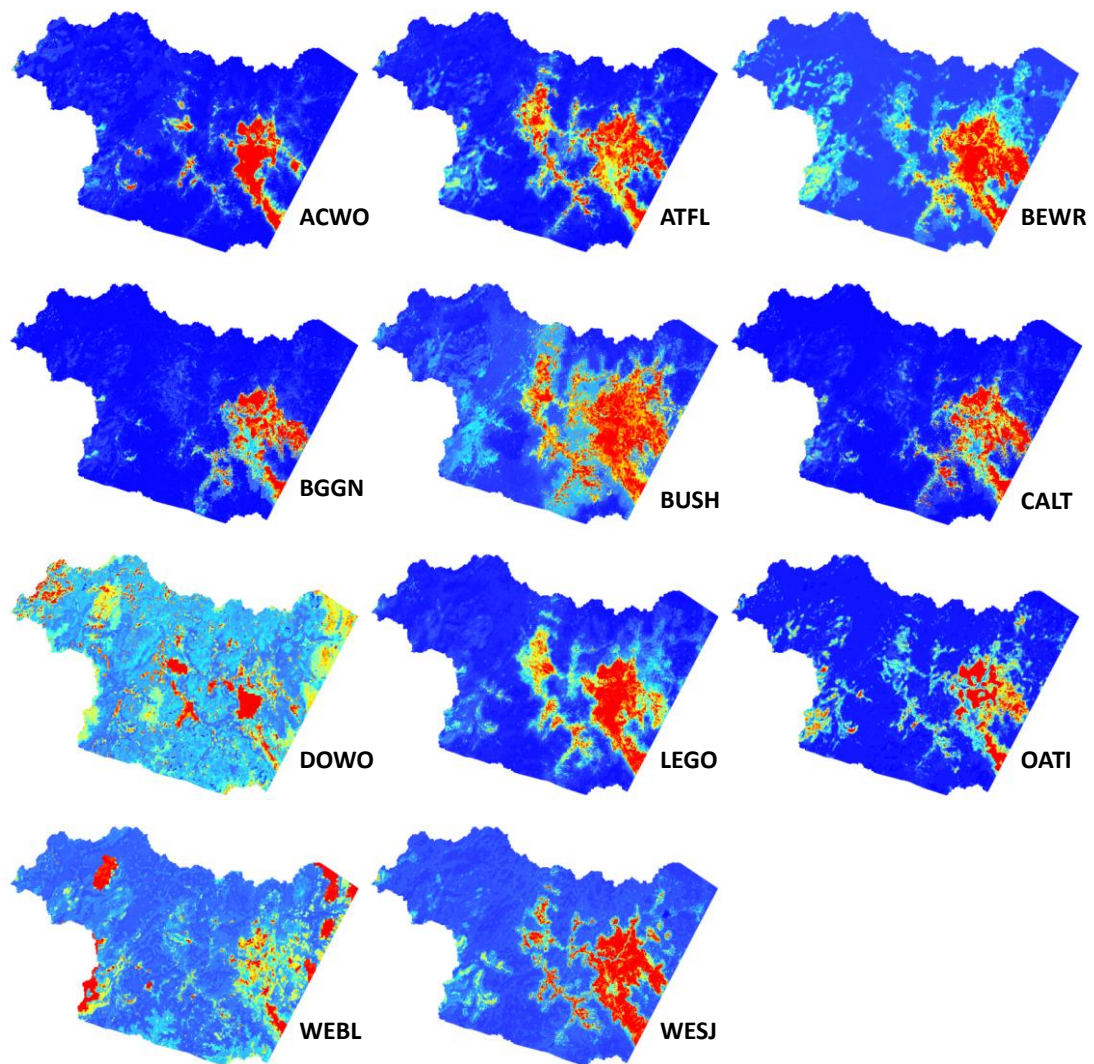


Figure 2.3. Predicted avian species richness maps within the Rogue Basin, Oregon for two species subsets and both SDM stacking methods used. Darkest red areas indicate areas of highest possible species richness, and areas of dark blue indicate areas of lowest possible richness.

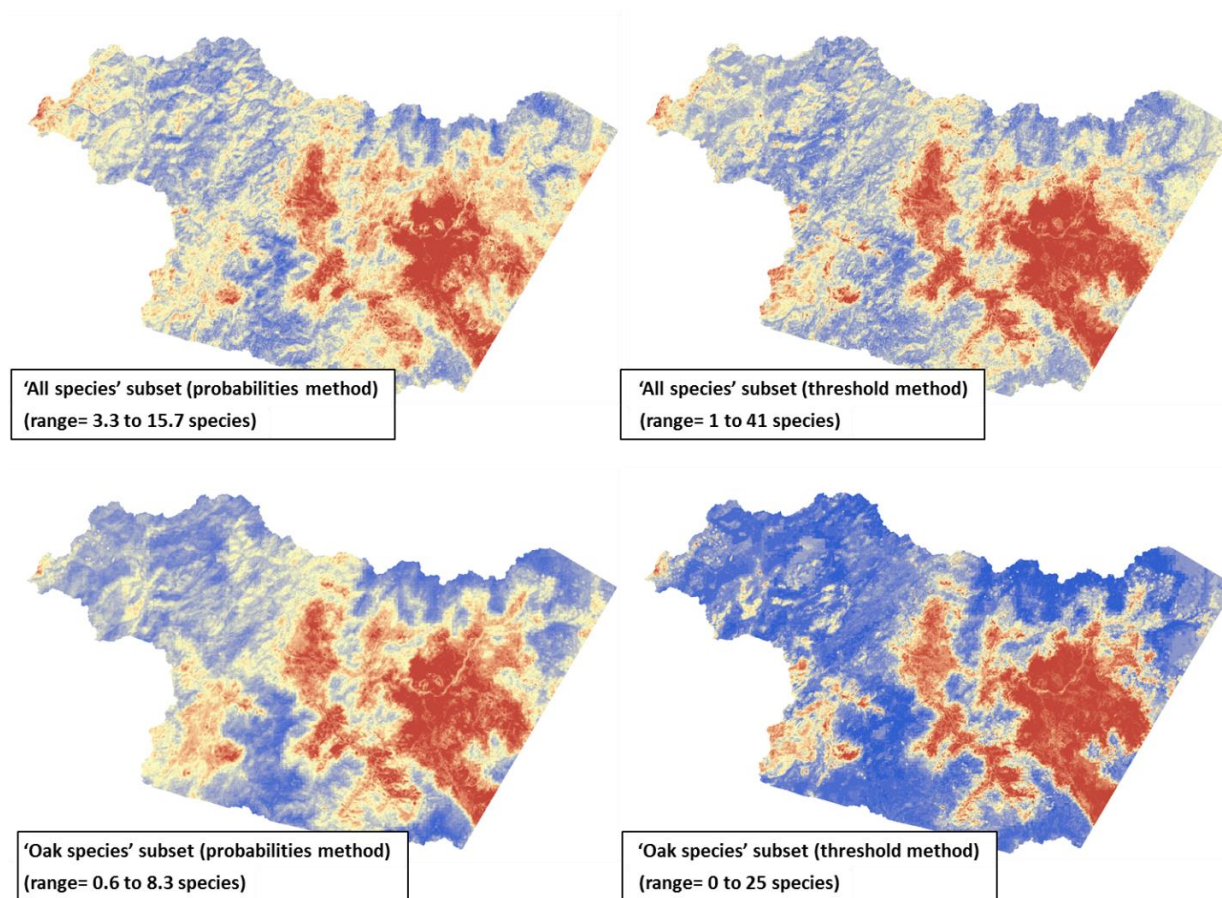


Figure 2.4. Standardized regression coefficients for effects of local (150m) and landscape (10,000m) habitat amount on species richness for the ‘probabilities’ (A) and ‘threshold’ (B) stacking methods, in four species subsets: ‘all species’ (48 spp), ‘oak species’ (25 spp), ‘all species - high performance’ (AUC >0.8) (8 spp), ‘all species - high performance’ (AUC >0.8) (6 spp). Habitat amount variables were relativized by standard deviation. Error bars represent 2 SEs for each coefficient. P-values for terms within each model (i.e., within each bar color) are denoted as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

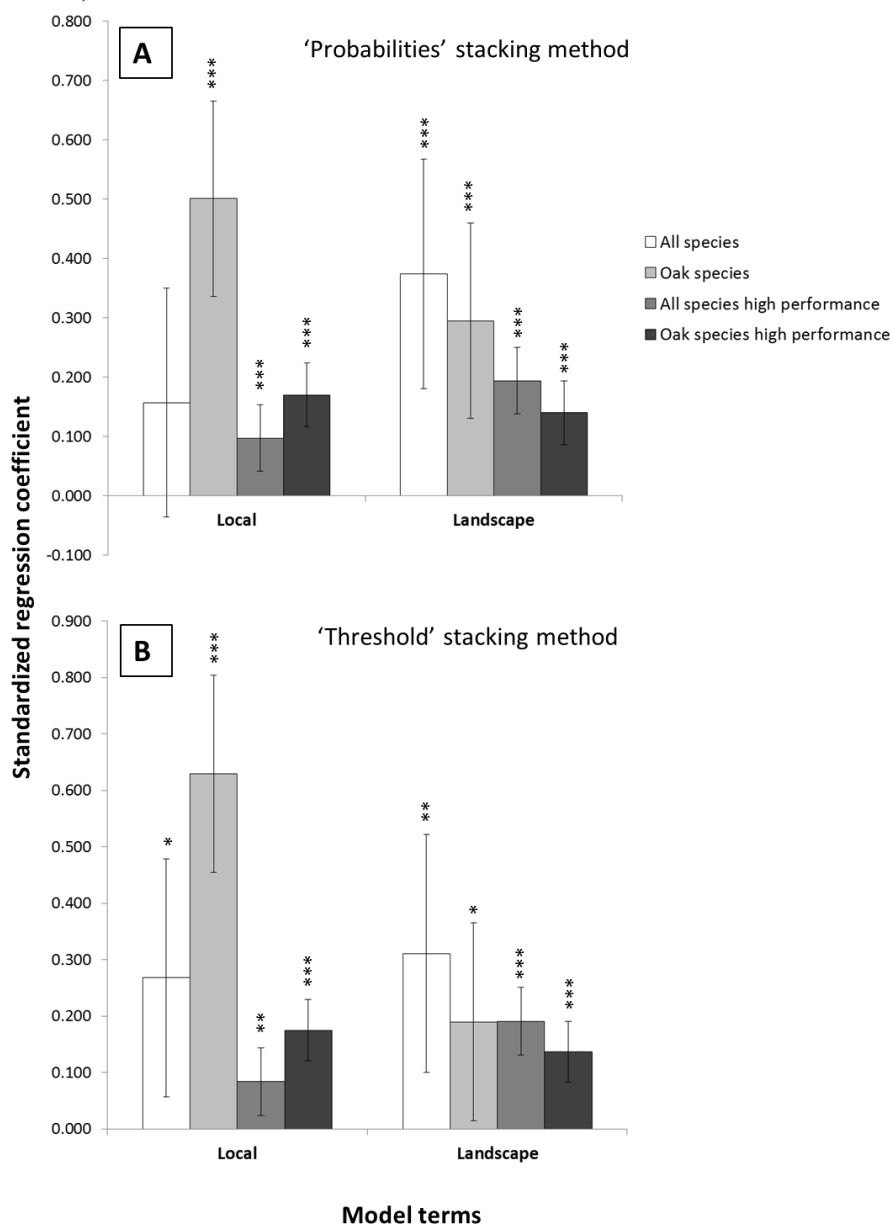
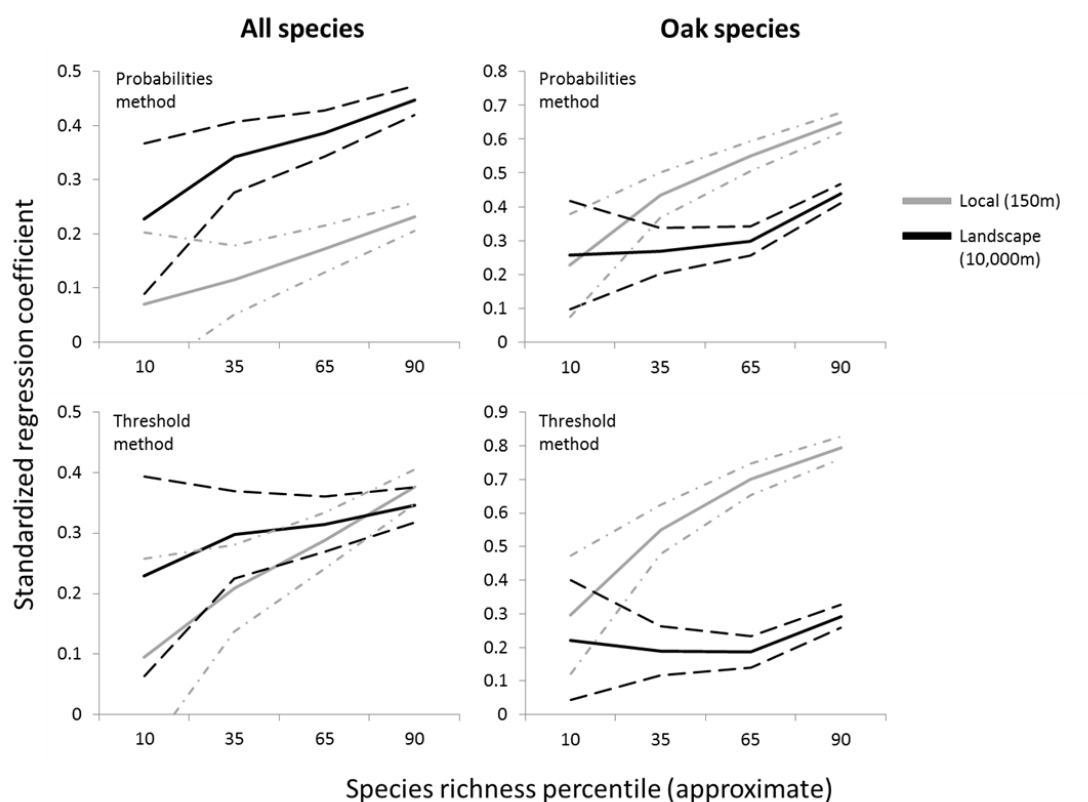


Figure 2.5. Results of quantile regression analysis, for ‘all species’ and ‘oak species’, and using both stacking methods (‘probabilities’ and ‘threshold’). Quantile regression examined changes in relationships between the response (i.e. local observed species richness) and the predictor variables (i.e. metrics for local vs. landscape habitat amount) along four percentile of the response. Solid lines indicate change in standardized regression coefficients for each predictor across each percentile of the response. Dashed lines represented the standard error around the regression coefficient at each percentile.



Appendices

2A. Appendix A Table 1. Names and descriptions of vegetation types targeted by a 2011 study of avian communities within oak vegetation types of the Rogue Basin, Oregon. Text is taken directly from USGS National Gap Analysis Program (GAP) GIS land cover metadata (<http://gapanalysis.usgs.gov/gaplandcover/>).

Vegetation Type Name	Description (from GAP land cover metadata)
OAK SAVANNAH, WOODLAND AND FOREST TYPES	
East Cascades Oak-Ponderosa Pine Forest and Woodland	"Forests and woodlands at or near lower treeline in foothills of the eastern Cascades in Washington and Oregon within 65 km (40 miles) of the Columbia River Gorge and in the Columbia Plateau ecoregion. Elevations range from 460 to 1920 m. Most occurrences of this system are dominated by a mix of Oregon white oak and ponderosa pine or Douglas-fir. Isolated, taller ponderosa pine or Douglas-fir over Oregon white oak trees characterize parts of this system. The understory may include dense stands of shrubs or, more often, be dominated by grasses, sedges or wildflowers. Shrub layers may including antelope bitterbrush, basin big sagebrush, black sagebrush, and green rabbitbrush. Understories are generally dominated by herbaceous species, especially grasses. Mesic sites have an open to closed sod-forming grasses and grass-like plants such as pinegrass, Geyer's sedge, Ross' sedge, long-stolon sedge, or blue wild rye."
Mediterranean California Mixed Oak Woodland	"Mixed oak woodlands from southwestern Oregon and southwestern Oregon, with Oregon white oak and California black oak. Occasionally other hardwoods, including Canyon live oak or madrone can be important, but conifers are not as important or common in this hardwood forest and woodland system. The understory in good condition areas are usually native perennial grass or deciduous shrubs (poison oak or snowberry), but introduced annual grasses have become dominant in most stands. Chaparral shrubs such as buckbrush or sticky manzanita are often present as well."
North Pacific Oak Woodland	"This ecological system is limited to the southern portions of the North Pacific region. It occurs primarily in the Puget Trough and Willamette Valley but trickles down into the Klamath ecoregion and into California. The woodlands and forests are dominated by Oregon white oak, and are found on dry, predominantly low-elevation sites and/or sites that experienced frequent presettlement fires. Many places are being invaded by Douglas-fir or other conifers with fire suppression. Pacific madrone is also not uncommon. Plant life under the tree canopy was historically composed of native grasses but are now mostly composed of non-native (introduced from other continents) grasses, as well as poison oak, snowberry or ferns."

Vegetation Type Name	Description (from GAP land cover metadata)
Willamette Valley Upland Prairie and Savanna	"This grassland system is known only to the Puget Trough and Willamette Valley area. They are rare, dry, upland prairies and savannas found in the valleys and foothills of western Washington and Oregon. Dominated by native bunchgrasses and diverse wildflowers, often with a few open and scattered trees of Oregon white oak, Douglas-fir or Ponderosa pine. In Washington & British Columbia prairies can be found on glacial outwash areas, while in Oregon they are on deep soils and were maintained by native Indian burning. Without regular burning, more and more trees would come in and shade out the prairie sun-loving wildflowers. Much of these prairies have been converted to agriculture or developed for housing."
OAK/CHAPARRAL TYPES	
California Montane Woodland and Chaparral	"A mix of montane chaparral shrubs and open forest and savanna found in the mountains. The trees are variable, usually pine or cypress, but occasionally fir or oak, but never becoming an actual forest, usually a very open woodland or savanna. Chaparral shrubs include many species with leathery, evergreen leaves and in the north some deciduous shrubs. Trees tend to have a scattered open canopy or can be clustered, over a usually continuous dense shrub layer. Trees can include Jeffrey pine, white fir, California red fir, western white pine, sugar pine, Coulter pine, knobcone pine, tecate cypress, Cuyamaca cypress, and Piute cypress. Typical sclerophyllous chaparral shrubs include pinemat manzanita, greenleaf manzanita, Eastwood's manzanita, mountain whitethorn, pinemat, Kern River buckbrush, tobacco-brush, and Sierran chinkapin."
Northern and Central California Dry-Mesic Chaparral	"This open chaparral shrubland is found inland from maritime chaparral up to 1500 m 4550 feet in elevation, in interior valleys and their margins, from northern California through the northern end of the Central Valley and north into Oregon. A mix of drought deciduous and evergreen chaparral species, including common chamise, buckbrush, several manzanita species, California flannelbush, bushmallow, bush poppy, and stingaree-bush. In Oregon, it is characterized by buckbrush and manzanita, usually with bunchgrass understories. These chaparral shrublands usually occur in and around larger patches of oak savannas, woodlands and mixed hardwood - conifer woodlands. Fires are intense, the shrubs reseed after fire, so it is considered a fire-adapted shrubland."
MIXED CONIFER AND OAK/HARDWOOD Types	

Vegetation Type Name	Description (from GAP land cover metadata)
Mediterranean California Dry-Mesic Mixed Conifer Forest and Woodland	"Dry mixed conifer forests and woodlands, usually with Douglas-fir codominant with sugar pine, incense cedar, and/or Ponderosa pine. In the transverse ranges of southern California, incense cedar can be codominant with white fir in this system, but further north white fir is an indicator of the moist-mesic mixed conifer system. These forests and woodlands were fire maintained ecosystems, mostly now found on ridgetops, south and west-facing slopes, Evergreen and deciduous hardwoods can occur in the understory, but if these make up even 20% of the canopy they are classified as a different system. The understory is variable, usually with deciduous shrubs, evergreen shrubs and wildflower present."
Mediterranean California Lower Montane Black Oak-Conifer Forest and Woodland	"These are mixed oak - conifer forests and woodlands, found in the valley bottoms, valley margins and canyon and foothill slopes of northwestern California and southwestern Oregon. Ponderosa pine is usually present with one or more oaks, most commonly California black oak, Oregon white oak, canyon live oak or interior live oak. In many stands, Douglas-fir can occur as well, or replace much or all of the ponderosa pine. The stands often have shrubby understories with chaparral shrubs, or can be grassy, with native perennial grasses or introduced annual grasses."
Mediterranean California Mixed Evergreen Forest	"This ecological system occurs from the Santa Cruz Mountains, California, north into southwestern Oregon throughout the outer and middle Coast Ranges. It occurs just inland of the redwood belt. It also occurs in southern California in more mesic, protected, cooler sites of the Transverse and Peninsular ranges. Characteristic trees include Douglas-fir, canyon live oak, tanoak, Pacific madrone, California laurel, and golden chinkapin. On the eastern fringe of this system, in the western Siskiyou, other conifers occur such as ponderosa pine and Port Orford-cedar. In southern California (Transverse and Peninsular ranges), bigcone Douglas-fir replaces Douglas-fir but co-occurs with canyon live oak and sometimes coast live oak. Incense-cedar is occasional. In the southern portion of the range, tanoak, Pacific madrone, California laurel, and golden chinkapin become less important or are absent. Historic fire frequency was higher than for redwood forests, occurring (every 50-100 years)."
North Pacific Dry Douglas-fir-(Madrone) Forest and Woodland	"This system is most common in the Puget Trough - Willamette Valley ecoregion but also occurs in adjacent ecoregions. These woodlands are fairly dry conifer forests dominated by Douglas fir, often with madrone or Oregon white oak, but rarely with other conifers present. Historically this was a widespread, fire maintained type, which has moved to occupy areas that were formerly prairies and oak savannas. These sites are too dry and warm or have been too frequently and extensively burned to have more than small amounts of western hemlock or western red-cedar. Pacific madrone is favored by high-severity fires on sites where it occurs, and Douglas-fir can be locally eliminated by logging and hot fire or repeated high-severity fires. Incense-cedar is absent."

Vegetation Type Name	Description (from GAP land cover metadata)
North Pacific Lowland Mixed Hardwood- Conifer Forest and Woodland	"This lowland mixed hardwood - conifer forest system occurs throughout the Pacific Northwest. These forests are composed of large conifers, including douglas-fir, western red-cedar, grand fir, western hemlock, and/or sitka spruce, with deciduous hardwood trees present and usually codominant, such as bigleaf maple, oregon white oak, red alder, cascara false buckthorn, and pacific dogwood. Under the tree canopy are many deciduous shrubs such as vine maple, beaked hazelnut and pacific poison-oak, but evergreen shrubs, including salal and dwarf oregon-grape, ferns and wildflowers such as redwood sorrel, can be dominant."

2B. Appendix A Table 2. Summary of membership in analysis subsets for 48 Rogue Basin forest bird species. “High performance” refers to species whose SDMs scored AUC greater than or equal to 0.8 when evaluated with independent presence/absence data.

Common name	Code	All species	Oak species	All species high performance	Oak species high performance
Acorn Woodpecker	ACWO	X	X		
American Goldfinch	AMGO				
American Robin	AMRO	X			
Ash-throated Flycatcher	ATFL	X	X	X	X
Black-capped Chickadee	BCCH	X	X		
Bewick's Wren	BEWR	X	X		
Blue-gray Gnatcatcher	BGGN	X	X		
Brown-headed Cowbird	BHCO	X			
Black-headed Grosbeak	BHGR	X	X		
Brown Creeper	BRCR	X			
Black-throated Gray Warbler	BTYW	X	X		
Bullock's Oriole	BUOR	X			
Bushtit	BUSH	X	X		
California Towhee	CALT	X	X	X	X
Cassin's Vireo	CAVI	X	X		
Chestnut-backed Chickadee	CBCH	X		X	
Chipping Sparrow	CHSP	X	X		
Dark-eyed Junco	DEJU	X			
Downy Woodpecker	DOWO	X	X	X	X
Dusky Flycatcher	DUFL	X			
Hermit Warbler	HEWA	X			
House Wren	HOWR	X	X		
Hutton's Vireo	HUVI	X	X		
Lazuli Bunting	LAZB	X	X		
Lesser Goldfinch	LEGO	X	X		
MacGillivray's Warbler	MGWA	X			

Common name	Code	All species	Oak species	All species high performance	Oak species high performance
Mourning Dove	MODO	X			
Nashville Warbler	NAWA	X	X		
Northern Flicker	NOFL	X			
Oak Titmouse	OATI	X	X	X	X
Orange-crowned Warbler	OCWA	X			
Pacific-slope Flycatcher	PSFL	X			
Purple Finch	PUFI	X	X		
Red-breasted Nuthatch	RBNU	X			
Rufous Hummingbird	RUHU	X			
Spotted Towhee	SPTO	X	X		
Steller's Jay	STJA	X			
Townsend's Warbler	TOWA	X		X	
Tree Swallow	TRES	X			
Warbling Vireo	WAVI	X			
White-breasted Nuthatch	WBNU	X	X		
Western Bluebird	WEBL	X	X	X	X
Western Scrub-Jay	WESJ	X	X	X	X
Western Tanager	WETA	X	X		
Western Wood-Pewee	WEWP	X	X		
Wilson's Warbler	WIWA	X			
Wrentit	WREN	X			
Yellow-rumped Warbler	YRWA	X			

2C. Appendix A Table 3. ROC cut points calculated independently for each species, to convert probability of occurrence to presence/absence for analysis.

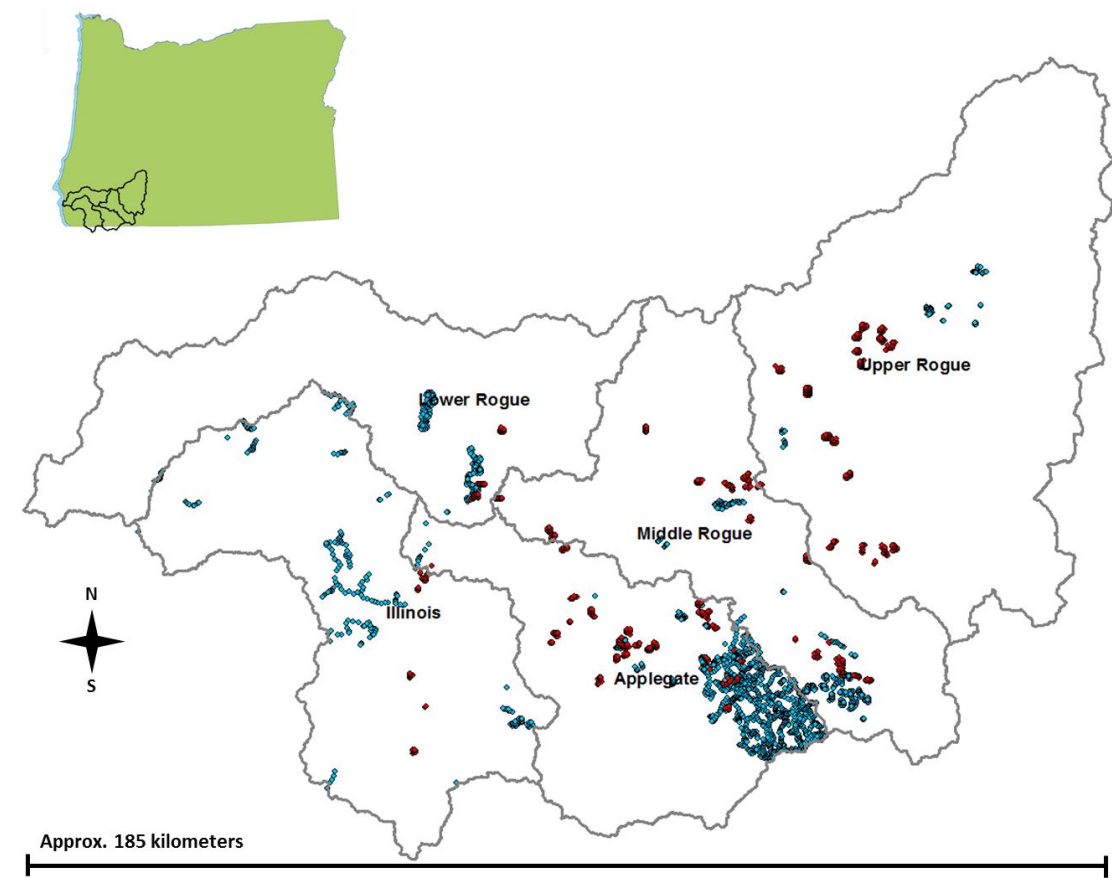
Common name	Code	ROC cut point
Acorn Woodpecker	ACWO	0.0096235
American Goldfinch	AMGO	0.1686270
American Robin	AMRO	0.0833485
Ash-throated Flycatcher	ATFL	0.0121505
Black-capped Chickadee	BCCH	0.0270410
Bewick's Wren	BEWR	0.0316265
Blue-gray Gnatcatcher	BGGN	0.0143250
Brown-headed Cowbird	BHCO	0.1608630
Black-headed Grosbeak	BHGR	0.4150895
Brown Creeper	BRCR	0.2152135
Black-throated Gray Warbler	BTYW	0.2456455
Bullock's Oriole	BUOR	0.0950120
Bushtit	BUSH	0.0452335
California Towhee	CALT	0.0183870
Cassin's Vireo	CAVI	0.1474080
Chestnut-backed Chickadee	CBCH	0.1126400
Chipping Sparrow	CHSP	0.1287220
Dark-eyed Junco	DEJU	0.4535310
Downy Woodpecker	DOWO	0.0304945
Dusky Flycatcher	DUFL	0.1493845
Hermit Warbler	HEWA	0.1846760
House Wren	HOWR	0.2575950
Hutton's Vireo	HUVI	0.0376600
Lazuli Bunting	LAZB	0.1417570
Lesser Goldfinch	LEGO	0.0601415
MacGillivray's Warbler	MGWA	0.5011330
Mourning Dove	MODO	0.0943605
Nashville Warbler	NAWA	0.1545845

Common name	Code	ROC cut point
Northern Flicker	NOFL	0.1598845
Oak Titmouse	OATI	0.0118920
Orange-crowned Warbler	OCWA	0.0326725
Pacific-slope Flycatcher	PSFL	0.2307585
Purple Finch	PUFI	0.1379270
Red-breasted Nuthatch	RBNU	0.4053645
Rufous Hummingbird	RUHU	0.0705300
Spotted Towhee	SPTO	0.1090265
Steller's Jay	STJA	0.2532065
Townsend's Warbler	TOWA	0.0154445
Tree Swallow	TRES	0.1352180
Warbling Vireo	WAVI	0.2022600
White-breasted Nuthatch	WBNU	0.0114110
Western Bluebird	WEBL	0.0104210
Western Scrub-Jay	WESJ	0.0511060
Western Tanager	WETA	0.3881645
Western Wood-Pewee	WEWP	0.3063265
Wilson's Warbler	WIWA	0.2436210
Wrentit	WREN	0.0525040
Yellow-rumped Warbler	YRWA	0.0332170

2D. Appendix A Table 4. Comparison of correlation (adjusted R^2 from linear regression) between estimated habitat amounts at a local scale (150m) and three landscape scales (2,000m, 5,000m, and 10,000m).

Scale comparison	Stacking method	Correlation (R^2)
150m vs 2,000m	probabilities	0.7814
150m vs 5,000m	probabilities	0.4831
150m vs 10,000m	probabilities	0.329
150m vs 2,000m	threshold	0.8234
150m vs 5,000m	threshold	0.6075
150m vs 10,000m	threshold	0.4386

2E. Appendix A Figure 1. Map of model training and evaluation point count locations within the Rogue Basin, with sub-basins labeled. Training data were collected at blue points, evaluation data at red points. Location of the Rogue Basin within the State of Oregon is shown on the green state locator map.



CHAPTER 3: THE IMPLICATIONS OF LAND OWNERSHIP FOR MODELED AVIAN SPECIES RICHNESS AND HABITAT DISTRIBUTION WITHIN OAK VEGETATION TYPES OF SOUTHWESTERN OREGON

Abstract

Effective conservation prioritization must consider both ecological value and socio-political constraints. Spatially explicit investigations of the implications of land tenure are rare, and are challenged by the difficulty of exploring species diversity and land use patterns at appropriately fine resolutions and broad spatial scales. I used ‘stacked’ species distribution models (S-SDMs) based on remotely sensed environmental data to estimate distribution of individual species habitat suitability and species richness at fine (30 x 30 m) resolutions for 48 bird species across the Rogue Basin of southwestern Oregon. I also examined a subset of 25 avian species highly associated with threatened Oregon white oak and California black oak (*Quercus garryana* and *Q. kelloggii*) vegetation types. Estimated local mean species richness of oak-associated birds in private non-industrial (PNI) ownerships was approximately double that within any of four other public and private ownership types. This result may be driven by disproportionate PNI ownership of regionally limited oak cover types, and/ or by hypothesized variation in management goals and activities among owners which influence local vegetation structure. Additionally, four of the five owners were estimated to support relatively high regional levels of suitable habitat for various oak-associated and declining bird species. These findings validate current engagement of private landowners, but also suggest the importance of multi-owner collaboration, in bird-focused conservation of Rogue Basin oak ecosystems. I also suggest that S-SDM approaches have broad potential to improve effective targeting of ownerships in regional conservation efforts.

Introduction

Effective prioritization, conservation, and restoration of areas with high ecological value is a major topic of concern in conservation biology (Moilanen et al. 2009). “Spatial conservation prioritization” describes a group of methodologies for evaluation of environmental planning problems (such as conservation area site selection) in a quantitative and explicitly spatial manner (Ferrier and Wintle 2009). Although the processes of prioritization and selection are often constrained and challenged by land ownership, and involve political, ecological, and financial challenges, conservation priority areas are often mapped on the basis of ecological value, without sufficient regard for socio-political or economic considerations (Ferrier and Wintle 2009). Land ownership type can be of great importance to the distribution of threatened biota and systems (Lovett-Doust et al. 2003, Ortega-Huerta and Kral 2007), however research explicitly examining the relationship between patterns of ownership and species diversity or species distributions is rare.

Recent work suggests the potential for ownership types within the same region to have significantly different vegetation structure, due to the legacy effects of differing owner values, management objectives, and management techniques employed (Stanfield et al. 2002, Schaich and Plieninger 2013). In the Coast Range of Oregon, divergent stand structure between private and public ownerships may result from policy mandates unique to each owner, related to policies regarding rare species or timber management (Spies et al. 2007). Bias in the holdings of certain vegetation types may also be an artifact of concentration of ownership along elevation gradients within Oregon (Burnett et al. 2007). The convergence of historical placement and current management may result in particular landowners disproportionate supporting certain species or biological community; indeed, the U.S. Fish and Wildlife Service has estimated that the majority of most ESA listed species’ habitat is on private lands (Polasky 2008).

Management practices that drive differences in local vegetation structure have the potential to scale up to affect patterns of regional ecosystem services (Schaich and Plieninger 2013) and species diversity (Jones et al. 2012), underscoring the usefulness of evaluating biological diversity patterns in the context of ownership in applied conservation efforts. Understanding the ecological implications of land ownership may help to determine the consequences of conservation and restoration efforts (Lovett-Doust et al. 2003, Ortega-Huerta and Kral 2007, Spies et al. 2007). In some cases, it may be possible to take advantage of turnover in vegetation structure or biodiversity across ownership types to achieve “complementarity” of conservation projects at broad scales (i.e., maximizing representation of different portions of a region’s biodiversity across multiple conservation areas) (Ferrier and Wintle 2009). In this sense, it would be important to establish whether diversity is ‘redundant’ (i.e., very similar) or ‘additive’ (i.e., relatively distinct) across owners to determine whether conservation efforts would be best be focused on one highly diverse ownership versus multiple owners who together represent a large part of the regional diversity. Additionally, such research may help identify opportunities for conservation project implementation and cost-effectiveness related to ownership and other socio-economic and socio-political factors (Knight et al. 2009).

Avian species as conservation surrogates

Breeding Bird Survey data for Oregon indicate that many common bird species, particularly associated with broadleaf vegetation, are experiencing state-level declines (Betts et al. 2010, Altman 2011). The State of the Birds Report for 2013 (NABCI 2013) identifies private landowners as being responsible for the majority of extant oak vegetation types in the Western U.S., as well as for the majority of the distributions of many oak-associated bird species. Additionally, State of the Birds 2011 notes that distributions for all western forest bird species combined are split approximately evenly between private and public lands (NABCI 2011). These

continent-scale analyses suggest a critical need for region-specific information on the relationships between land ownership and diversity distributions to guide on-the-ground management of threatened bird populations.

Avian species are often highly sensitive and responsive to land cover changes, due to strong associations with vegetation structure and composition (MacArthur and MacArthur 1961). It has been proposed that land birds may act as a surrogate for other vertebrate biodiversity in monitoring efforts (Hutto 1998), and response of birds has been used to evaluate the ecological effects of forest management such as fuels reduction treatments (Seavy et al. 2008). Forest birds are highly vagile and responsive to vegetation change (Cahall et al. 2013) and relatively easy to study, so are of potential value for use in monitoring and assessing the success of management actions (Ralph et al. 1995, Alexander et al. 2007). The benefits of using birds to monitor and assess conservation efforts may be applied to the challenges of site prioritization across ownership boundaries and at large scales. Region-specific and long-term bird monitoring datasets are available for many regions (e.g. (Swatantran et al. 2012, Shirley et al. 2013).

Modeling species distributions

Species distribution models (SDMs) may be used in conservation prioritization to examine differences in individual species habitat suitability among entities (e.g., landowners) in a region of interest (Elith and Leathwick 2009a). These relationships can also be investigated for whole groups or assemblages of species using a “predict first, assemble later” (Ferrier and Guisan 2006) or “stacked” SDM (S-SDM) method in which multiple SDMs are combined for predictions of total or selected richness (Ferrier et al. 2009). SDMs can make use of sparse species observation data and underlying geographic or environmental variables to interpolate predictions of species distribution or habitat suitability across an entire landscape or region (Elith and Leathwick 2009a, 2009b), and so for example could be useful for estimating richness

in private ownerships where survey data are often limited (Hilty and Merenlender 2003). Recent advances in species distribution modeling using remote sensing technology (Swatantran et al. 2012, Shirley et al. 2013) holds particular promise for this type of application. The fine resolution of modern remote sensing (e.g. 30x30 m for Landsat reflectance data) enables spatial prioritization work to be done at scales and resolutions that are relevant to on-the-ground management and land-use patterns, thus improving their potential efficacy (Ferrier and Wintle 2009).

A number of authors have used direct modeling of species richness or of distributions of select focal species to examine the ecological implications of ownership on biodiversity for purposes of conservation planning (McComb et al. 2007, Ortega-Huerta and Kral 2007, Spies et al. 2007), though such studies are still uncommon. The use of combined or ‘stacked’ SDMs (S-SDMs) for large species pools has been increasingly used to study distributions of regional richness (e.g., (Pineda and Lobo 2009) but, to my knowledge, has not yet been applied to investigation of richness patterns in the context of land ownership. S-SDMs approaches are conceptually attractive as they embrace a ‘species-centered’, or ‘continuum’ (Fischer and Lindenmayer 2006) perspective, in which individual species’ habitats are modeled according to unique relationships to environmental gradients. Compared with direct modeling of species richness, which does not integrate this complexity, S-SDMs could present a powerful and flexible way to prioritize conservation areas according to both ecological value and socio-political considerations.

Conservation and land ownership in oak systems of the Rogue Basin, Oregon

Oak ecosystems of the Rogue Basin in southwest Oregon are an excellent example of the challenges and importance of cross-ownership conservation and restoration. Oak systems dominated by Oregon white oak (*Quercus garryana*) are an important component of Pacific Northwest (PNW) ecology and biodiversity. Many species from multiple taxa (including birds, reptiles, and invertebrates) unique to this

region are considered obligate or highly dependent on oak vegetation types (Altman 2011, Altman and Stephens 2012). Since the mid-1800's, oak systems in the PNW have experienced great losses in quality and extent due to many diverse and interacting factors, including displacement of native people and their management systems, fire suppression, land clearing for agriculture, and development related to increasing human populations (Schindel et al. 2013). Cover types broadly characterized as oak savannah, oak woodland/forest, and oak chaparral are particularly important to oak-associated species in this region and are of high conservation concern (Altman 2011, Altman and Stephens 2012). It is estimated that approximately 10% of pre-settlement oak vegetation throughout the PNW remains (Harrington and Devine 2006). Within the Klamath Mountains Ecoregion, which includes the Rogue Basin, 65% of remaining oak vegetation is in private ownership (Altman and Stephens 2012).

Research questions and objectives

In this chapter I will address the following questions: 1) Is richness of oak-associated bird species additive or redundant among landowners, and 2) Do different landowners support differing levels of suitable habitat for individual oak-associated bird species? My objective is to assess the degree to which the richness and habitat distribution of relatively common oak-associated species may be correlated with land ownership in southern Oregon. Total species richness per se may be a dubious goal for conservation prioritization (e.g., if richness estimates include non-native or widely distributed generalists). However, a 'selected' richness estimate of species associated with vegetation types of conservation concern (such as Rogue Basin oak-associated avian species) may be a useful and biologically relevant way to begin the process of identifying areas of high ecological value to inform conservation efforts.

I expect that those owners holding relatively larger amounts of oak savannah, oak woodland, and oak-chaparral vegetation (i.e., oak vegetation types that are limited on this landscape), will have higher levels of both oak-associated bird species richness

and individual species habitat. If this sort of variation in oak types occurs, I also expect that avian species richness and amount of suitable habitat for individual species will be additive among Rogue Basin landowners; that is, there will be evidence that individual owners may support distinct components of the regional avian diversity. Alternatively, if all Rogue Basin landowners are similar in terms of vegetation structure and composition, and hence in their ability to provide habitat for avian species, then I expect to find redundancy across owners; that is, there will be evidence for similar levels of species richness and individual species suitable habitat among owners.

I focus on the five primary owners of forest lands in this region: the Bureau of Land Management (BLM), the United States Forest Service (USFS), the State of Oregon (State), private industrial, and private non-industrial. Ownership relationships with richness and suitable habitat will be tested using SDMs created for 48 prevalent oak- and deciduous-vegetation associate bird species. I focus my analysis specifically on a nested subset of this species group, comprised of 25 oak-associated species of high management relevance in this region (Altman 2011, Altman and Stephens 2012). The SDMs used in this study were developed using a “continuum” approach (Fischer and Lindenmayer 2006) in which the occurrence of each species was uniquely modeled on the basis of important environmental gradients related to habitat use: breeding season vegetation cover (from 30x30m Landsat land cover data), climate variables relevant to breeding birds and vegetation development, and elevation (as an indirect proxy for other habitat characteristics and processes not captured by land cover or climate). The results of this research will increase the understanding of the ecological implications of ownership patterns in the Rogue Basin, and improve effective targeting of ownerships for regional oak-focused conservation action.

Methods

Study area

I collected data on bird distributions in the Rogue Basin, or the Rogue River Watershed, located in southwest Oregon. The Rogue Basin is composed of five subbasins (or HUC8 watersheds: the Upper, Lower, and Middle Rogue; the Applegate; and the Illinois), and drains into the Pacific Ocean. The Basin is part of the Klamath Mountains ecoregion, at the convergence of the Western Cascades and the Coast Range, and contains the cities of Grants Pass (42.4389° N, 123.3283° W), Ashland (42.1914° N, 122.7008° W), and Cave Junction (42.1667° N, 123.6469° W). According to Oregon Geospatial Enterprise Office (GEO; <http://www.oregon.gov/DAS/CIO/GEO>) landowner data, USFS is the largest of the five landowner considered in this study (331,140 ha), followed by private non-industrial (284,223 ha), and BLM (274,456 ha), private industrial (124,430 ha), and finally State of Oregon (5,574 ha).

This region is characterized by complex topography, with elevation ranging from sea level to approximately 2,300 m. The Rogue Basin is characterized by spatially heterogeneous vegetation types which include prairies, riparian systems, shrub fields, and forest types dominated by a number of coniferous and deciduous tree species with varying amounts of canopy cover. The climate is Mediterranean-type with cool, wet winters (precipitation in the form of both rain and snow), and hot, dry summers (Myers et al. 2000). Mean monthly precipitation ranges from 5.85 ml (July) to 849 ml (December), and mean monthly temperatures from -4.41 °C (December) and 33.29 °C (July; PRISM Climate Group, <http://www.prism.oregonstate.edu>). This region is additionally part of the California Floristic Province biodiversity hotspot (Myers et al. 2000).

The oak-dominated vegetation types of the Rogue Basin are considered the most ecologically diverse in the Pacific Northwest (Altman and Stephens 2012).

Oregon white oak (*Quercus garryana* Dougl.) and California black oak (*Quercus kelloggii* Newb.) are the primary oak species within the Basin, but canyon live oak (*Quercus chrysolepis* Liebm.) can also be found, particularly in the southwest portion of the Basin. The three primary oak species are dominant or important in a wide range of vegetation types, including oak savannah, oak woodland, oak chaparral, mixed oak-conifer. A number of conifer species (e.g., Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), ponderosa pine (*Pinus ponderosa* Dougl.), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and incense cedar (*Calocedrus decurrens* Torr.) and other hardwood tree species (e.g., bigleaf maple (*Acer macrophyllum* Pursh), Oregon ash (*Fraxinus latifolia* Benth.), Pacific madrone (*Arbutus menziesii* Pursh) (USDA, NRCS 2013) are also found in these vegetation types in varying degrees of dominance. Individuals of all three oak species are variable in form, depending on site soil and climate conditions. They may occur in shrub-form in dry conditions, such as in south facing chaparral fields, as tall thin trees where light is limited such as in foothill oak woodlands or mixed-conifer forests, or as large, wide-trunked trees with spreading limbs on sites with abundant light and moisture such as in lowland savannahs (Altman and Stephens 2012).

Species distribution models

My general approach followed three major steps. First, I generated spatial predictions of distribution for 48 avian species in the Rogue Basin. This step required using bird detection/non-detection data (henceforth referred to as “occurrence”) from a training dataset along with a suite of spatial predictor variables (i.e., remotely sensed land cover, and modeled climate and elevation data) to develop species distribution models (SDMs) for all species. Predicted values from these models were used as an index of ‘habitat suitability’ for each species. Second, I used SDMs to map each species’ distribution across the study area and summed, or ‘stacked’ these maps to

provide quantitative estimates of species richness across the Basin. I used these variables to compare patterns of estimated species richness and individual species habitat suitability among Rogue Basin landowners. Finally, I evaluated the ability of stacked SDMs (S-SDMs) versus a direct model for species richness to predict observed richness from an independent evaluation dataset.

SDM response variables

Occurrence data from avian point counts collected across the Rogue Basin from 2000 to 2011 by the Klamath Bird Observatory (KBO) and Redwood Science Lab were used as response variables for SDMs. Point count transects were established along gradients of elevation and vegetation cover, with individual points spaced at 150 - 250 m to limit redetection of individual birds (Shirley et al. 2013). Counts were conducted between 5:30 and 10:30 am between late May and early July to coincide with hours of peak forest bird activity during the main portion of the breeding season, using 5-minute fixed- and variable-radius point count methodologies (Ralph et al. 1993, Stephens et al. 2010). In fixed radius point counts, there is a set maximum distance radius from the observer (e.g., 100 m) within which detected birds are recorded, while in variable-radius surveys there is no set distance. All birds detected by sight or sound were recorded, along with detection type (e.g., visual or auditory) and estimated distance in meters to each bird. Flyovers, or non-territorial individuals who are detected moving over the point but not using the local vegetation, were noted and excluded from analysis. These point count locations are often visited across multiple years and sometimes several times per year. For the purposes of species distribution modeling, data from a single visit and a single year were randomly selected for each point count location. Data were constrained to all auditory and visual detections (with the exception of flyovers) occurring within 50 m of point count locations, and those which fell within the Oregon portion of Rogue Watershed and the

boundaries imposed by land cover variables, hereafter the “study area” (Appendix B, Figure 1). This resulted in a dataset of 2,612 sample points that I used in SDMs.

SDM evaluation and testing

I collected bird species presence/absence data in a 2011 point count study focused on oak vegetation types within the Rogue Basin. I used these data for evaluation of SDMs for the current study, and in construction of linear models testing the relationship between species richness and local versus landscape habitat amount (Chapter 2). I used aerial photography, landowner data, and Gap Analysis Program (US Geological Survey 2011; <http://gapanalysis.usgs.gov/gaplandcover/>) land cover data in a Geographic Information System (GIS) to identify 55 sample areas (each containing 5 to 16 point count locations) containing oak savannah, oak woodland, oak chaparral, or mixed oak/conifer/hardwood vegetation types across the Rogue Basin (Appendix B, Table 1). The points count locations (n=627) used in this analysis were constrained to the same study area boundaries applied to training data. Each of these point count locations were surveyed once, using a methodology identical to that used to collect data used in model training, described above (Ralph et al. 1993, Stephens et al. 2010), except that only variable-radius surveys were used. Only detections within 50 m of point count locations were used in model evaluation and testing for habitat amount relationships (Appendix B, Figure 1).

Accessibility to potential sampling areas was limited to public ownerships (e.g., BLM, USFS, City of Ashland) and individual private properties and for which permission to survey had been granted and public road access was available. While the sampling design was thus influenced by accessibility, an effort was made to sample as evenly as possible across the vegetation types described in Appendix A, Table 1. However access issues did limit the ability to survey in oak savannah, woodland, and chaparral types (primarily existing on private lands), resulting in an approximately 4-

fold greater number of survey points falling within mixed oak/hardwood-conifer types than in oak savannah, woodland, and chaparral.

SDM predictor variables

Three types of data representing conditions important to forest bird distributions (land cover, climate, and elevation) were used as predictors in SDMs. Landsat Thematic Mapper (TM) imagery with a 30 x 30 m pixel resolution, corresponding to the year of data collection for each point within the model training dataset, were used as continuous land cover variables. Images were acquired from USGS (US Geological Survey, EROS center 1982); <http://earthexplorer.usgs.gov/>). A cosine-Theta (COST) correction was applied to each image to minimize noise from atmospheric conditions, according to the process in (Kennedy et al. 2007). Landsat images are collected in the form of 170 km (north-south) by 183 km (east-west) “scenes”, each with a unique Path/Row identification, and each containing 7 spectral bands corresponding to different portions of the light spectrum. Two Landsat scenes (Path/Row 46/30 and 46/31) collected on the same day were merged to create single large scenes for each year of point count data collection which covered the majority of the Rogue Basin study area. I chose to exclude adjacent scenes due to potential error resulting from differences in reflectance values associated with data collection on different days, resulting in a slight truncation of the study area boundary in the northeast portion of the Basin.

I selected relatively cloud-free Landsat scenes from the months of July and August, which allowed reflectance data to be relevant to the timing of the study species’ breeding period as well as to the vegetation growing season. As clouds could not be avoided altogether, I applied cloud masks developed using Vegetation Change Tracker from (Huang et al. 2010) to exclude cloudy pixels from analysis. For all non-infrared Landsat TM bands (i.e., 1, 2, 3, 4, and 7) the means and standard deviation of reflectance values were averaged at radii of 150 m, 500 m, 1000 m, and 2000 m at

each pixel using a moving window analysis in GIS (following (Shirley et al. 2013)). This process resulted in 48 predictor variables (mean and SD for each of six bands), represented as 48 30 x 30 m grids of mean and SD values. I acquired climate variables from the PRISM Climate Group at Oregon State University (<http://www.prism.oregonstate.edu>), in the form of 800 x 800 m grids of month-by-month means of temperature and precipitation data from years 1981 to 2010, the most relevant range of climate means available. I selected a total of 6 variables describing the minimum and maximum precipitation (July and December, respectively), minimum and maximum temperature (December and July, respectively), and mean precipitation and temperature for June (corresponding to mid-breeding season for Rogue Basin forest bird species). Finally, I included elevation as a predictor using a 30 x 30 m digital elevation model (DEM; <http://www.oregon.gov/DAS/CIO/GEO>)

Data analysis

Species distribution models

Boosted regression tree (BRT) models (Friedman et al. 2000, Friedman 2001) were used to analyze the relationship between bird occurrence (from the training dataset) and environmental variables (land cover, climate, and elevation variables). BRTs have been increasingly used and tested in ecological applications (Elith and Graham 2009, Benito et al. 2013). Shirley et al. (2013) demonstrated that BRTs are well suited to predicting distribution of forest birds as a function of continuous Landsat TM data. Rather than attempt to fit a single parsimonious model, BRTs add a “boosting” method to a traditional regression tree methodology to improve model accuracy; beginning with a single regression tree, new trees are added iteratively in a forward, stagewise fashion that minimizes loss of predictive performance (Elith et al. 2008). BRTs can be used with a variety of response distribution types, and do not require linear relationships, removal of outliers, or data transformation.

I constructed SDMs using BRT for the 48 bird species that were most prevalent within the 2011 oak-focused point count dataset (Table 1), and which represent a regional pool of species that are expected to occur within the full range of Rogue Basin oak vegetation types. I fit all BRT models using the package ‘dismo’ in R (R Development Core Team 2008), with additional source code from Elith et al. (2008, Appendix). For first runs, the user-controlled model parameters of ‘learning rate’ (*lr*), ‘tree complexity’ (*tc*), and ‘bag fraction’, were those suggested in Elith et al. (2008) and validated for use in forest bird distribution models in Shirley et al. (2013). However, *lr* was adjusted slightly on an individual species basis where necessary to optimize the number of trees (*nt*) produced (with a goal of at least 1000 trees), with *tc* being adjusted in tandem with *lr* for optimization of *nt* as suggested in Elith et al. (2008; Table 2).

Using the packages ‘raster’ and ‘dismo’ in R, I extrapolated individual species BRT models for each of the 48 study species to predicted probability of occurrence across the study area on a 30 x 30m pixel basis. Predictions were fitted using climate data (temperature and precipitation means for June, July, and December) and elevation grids identical to those used in BRT models. Because the final goal of the analysis was to predict species richness at the locations of the 2011 oak-focused point count study, I selected 2011 Landsat data for land cover variables in the extrapolations, using means and SDs of reflectance values for the six spectral bands as in BRT models.

Estimation of Rogue Basin bird species richness

I used an SDM stacking method (S-SDM) to convert predictions of occurrence for individual species to a prediction of species richness across the Basin. S-SDM has been increasingly employed for examination of potential species richness for purposes such as conservation area assessment (Benito et al. 2013). A number of different distribution modeling and stacking methods may be employed, and several studies have assessed the various benefits and drawbacks of stacking S-SDMs richness

predictions using either summed raw probabilities versus threshold methods that reduce probabilities to presence or absence of each species (Wilson et al. 2005, Pellissier et al. 2013). Although continuous probability of occurrence predictions may be informative in S-SDMs for some applications, it is often necessary to convert continuous predictions to binary presence/absence predictions for species diversity or community analysis (Pellissier et al. 2013). In this study, the goal of estimating and analyzing differences in species richness and individual species prevalence among Rogue Basin landowners, necessitated the use of a ‘threshold’ method for SDM stacking.

I selected an objective posteriori probability cutpoint at which to determine presence/absence of each species for the ‘threshold’ method. I calculated cutpoints using the “youden” method (or “Youden’s J statistic) in the R package ‘pROC’. The “youden” method maximizes the sum of the specificity and sensitivity of the ROC curve, and is recommended by (Liu et al. 2005) for SDMs. I then reclassified the 30 x 30 m prediction grids for each species to ‘present’ or ‘absent’ based on the unique cutpoint for that species (Appendix B, Table 2). Finally, I summed all reclassified grids for a prediction of total species richness at each pixel across the study area.

I created three species subsets to examine potential differences in species richness as a function of landowner relationships within the entire selected species pool and in those species that are highly specialized on oak vegetation, as well as to assess potential influence of high-performing models on test results. These subsets were the following: all 48 study species (‘all species’), 25 highly oak-associated species selected from Altman and Stephens (2012) (‘oak species’), and 8 species with highest AUC values ($AUC > 0.8$) when independently evaluated with the 2011 oak-focused point count dataset (‘all species - high performance’) (Appendix B, Table 3). For each subset, the above process of stacking SDMs to create gridded estimates of species richness was applied for a total of three Basin-wide estimates of species richness distribution.

Model evaluation

I evaluated prediction success of SDMs in several ways. First, for each individual species model, area under the receiver operating characteristic curve (AUC) and its standard error were calculated within the model training data using a ten-fold cross validation procedure in the package ‘dismo’ (Elith et al. 2008). AUC essentially represents the probability of correct classification of true versus false positives, and is a standard way of evaluating the discriminatory power of SDMs (Lobo et al. 2008, Elith and Graham 2009). Second, AUC was used to evaluate the performance of each model in predicting species occurrence from the independent 2011 oak-focused point count survey of the Rogue Basin, using the R package ‘pROC’ (Table 2). Third, I evaluated the success of S-SDMs in predicting observed species richness within the 2011 evaluation dataset. I used linear regression to examine and compare correlations between observed species and predicted species richness from 1) S-SDMs and 2) the direct BRT model of species richness. Finally, I examined the relationship between elevation and observed species richness within the evaluation dataset using linear regression to further inform interpretation of results.

High-quality predictions of species richness are necessary for meaningful management recommendations, however studies explicitly comparing efficacy of S-SDMs versus ‘macroecological model’ (MEM) approaches (in which species richness is modeled directly based on environmental predictors) are rare (Dubuis et al. 2011). Dubuis et al. (2011) found that threshold-based S-SDMs overpredicted plant species richness but had a higher correlation with observed richness compared to an MEM. To evaluate my S-SDM richness predictions, I constructed a direct MEM of species richness within the training dataset as a function of the same land cover, climate, and elevation predictors used in individual species models. The MEM was constructed using the same BRT technique as was used for SDMs, using the package ‘dismo’ in R (R Development Core Team 2008), with additional source code from Elith et al (2008,

Appendix). The user-controlled parameter of lr and tc were set at 0.01 and 5, respectively.

Local and regional species richness among owners

I subsetting landowner spatial data in GIS (<http://www.oregon.gov/DAS/CIO/GEO>) to include only the five key landowners of interest, which accounted for approximately 97% of the study area. To test for patterns in species richness, I then sampled the entire study area using a systematic 500 m grid in GIS with a random start point (for total of 40,739 sample points). I extracted data for landowner identity and species richness in each of the three species subsets to all 500 m grid sample points.

To test the statistical hypothesis that there is no difference in the average local species richness across owners, I used ANOVA and Tukey HSD post-hoc pair wise comparisons in R with estimated species richness as a response variable, and land ownership as a predictor. Although differences in the ‘all species’ and ‘oak species’ analysis groups were of primary interest, I also tested for differences in the ‘all species - high performance’ group to determine sensitivity of the results to SDM prediction success.

In addition to examining differences in mean local (i.e., sample point-level) richness across owners, I compared landowners in their potential to support the entire suite of species in each subset within the entirety of their Rogue Basin holdings. Comparing species richness across landowners with different total amounts of land (or in this case, differences in total ownership of oak vegetation areas) is problematic because species richness is known to increase log-linearly with area (Preston 1962). Therefore to test the hypothesis of differences in regional species richness among owners, I created species accumulation curves (SACs) in the package ‘BiodiversityR’. The 500 m grid of sample points was randomly sampled within each ownership type for occurrence of individual species, progressively summing the number of unique

species encountered, with species counted once. While similar to a species-area curve, species accumulation curves differ in that they allow visual comparison of the amount of area required to obtain saturation in species richness across a region (the Rogue Basin) and among groups (the five key landowners).

Values for mean richness across landownerships could potentially be misleading as they could mask important differences in distributional area of particularly high or low species richness across the regional. For this reason, I also calculated and compared the total area within four species richness intervals for each ownership. Intervals for ‘all species’ subset were: 1-10, 11-20, 21-30, and 31-41 species (1 being the lowest and 41 being the highest value for any ‘all species’ richness pixel in any ownership). Intervals for ‘oak species’ subset were: 0-5, 6-12, 13-19 and 20-25 species (0 being the lowest and 25 being the highest value for any ‘oak species’ richness pixel in any ownership).

Individual species distributions among owners

To examine differences in Basin-wide distribution of individual oak-associated bird species habitat suitability by owner, I summed the total area classed as ‘present’ for each species (from species richness grids) in the ‘oak species’ subset and compared results among the five key ownerships. I compared these results with total pixels classed as ‘present’ for the ‘all species - high performance’ species to check for sensitivity to high-performing models. And finally, to look for particularly conservation-relevant patterns in individual species by Rogue Basin ownership, I completed a similar analysis for 19 species within the ‘all species’ subset that are identified as significantly declining in Oregon according to 50 year Breeding Bird Survey (BBS) trends (Sauer et al. 2012). BBS counts are conducted yearly along randomly selected roadside routes between late May and early July by skilled observers, using a three-minute fixed radius (400 m) point count methodology. Trend

data are derived using a hierarchical Bayesian model, described in Sauer and Link (2011).

Land ownership and vegetation type

To inform results for species richness and habitat suitability among owners, I used GEO landowner data and USGS Gap Analysis Program (GAP; <http://gapanalysis.usgs.gov/gaplandcover/>) land cover data in GIS (ESRI 2011. ArcGIS Desktop: Release 10) to estimate the total hectares of vegetation types potentially important to oak-associated birds owned by the five Rogue Basin owners. Total hectares held by each owner was calculated for each of 14 GAP land cover types in which one or more of the three oak species (i.e., *Q. garryana*, *Q. kelloggii*, and *Q. chrysolepis*) are considered dominant or important (Appendix B, Table 1). Of the 14 vegetation types examined, 12 had been targeted in the 2011 Rogue Basin oak-focused point count study, and 2 were not available for that effort but were present in the Basin and included in this analysis. I additionally grouped these vegetation types into three major vegetation categories (oak savannah, woodland, and forest; oak/chaparral; and mixed conifer and oak/hardwood) and compared total area in each category across owners.

Results

Land ownership and vegetation type

According to GAP vegetation models, BLM and USFS are the first- and second-largest owners of vegetation in the three major oak categories (i.e., oak savannah/woodland, oak chaparral, and mixed oak/hardwood/conifer), with approximately 219,000 ha and 196,000 ha respectively. Private non-industrial owners are the third largest, with approximately 167,000 ha (approximately 219,000 ha and 196,000 ha respectively; Table 3). However, private non-industrial ownership account

for ~64% combined ownership of the oak savannah/woodland and the oak chaparral vegetation categories, the highest of any owner. BLM holds the second-highest percentage of combined oak savannah/woodland and oak chaparral categories at 19%, and USFS the third-highest at ~11% (Table 3). These two major vegetation categories generally describe those types considered most important to highly oak-associated species in the Rogue Basin (Altman and Stephens 2012). BLM ownerships contain ~33% of the mixed conifer and oak/hardwood types in the region, compared to USFS' ~30% and private non-industrial's ~25%. State and private industrial owners do not have large amounts of land of any given vegetation type, with State containing ~0.5% to ~2% and private industrial containing ~3% to ~13% of the three major vegetation categories (Table 3).

Model evaluation

Prediction success for species distribution models (SDMs) was generally high for within-model tests on the training dataset (i.e., cross-validation), with a mean AUC of approximately 0.80 (SD = 0.08; Table 2). A total of 45 species had prediction accuracies > 0.7 to 0.935, (>0.7 is considered a threshold for good discriminatory power; (Hosmer and Lemeshow 2005), and three species had AUC values between 0.6 and 0.7. In an SDM stacking study of butterfly communities, Pellissier et al. (2013) determined that inclusion of low-AUC models (<0.6) into S-SDMs did not alter correlations between predicted and observed species richness. Based on this, I chose to retain species with AUC between 0.6 and 0.7 for my estimation and analysis of bird species richness. AUC was ≥ 0.8 (the threshold for excellent prediction success) for 26 species. Prediction success within the evaluation dataset was lower and more variable, with a mean AUC of approximately 0.66 (SD = 0.11). Of the 48 species, 18 had AUC ≥ 0.7 , and only 8 species had AUC over 0.8 (i.e. the 'all species - high performance' analysis subset; Appendix B, Table 3).

There was a positive and statistically significant correlation between observed species richness (from 2011 the evaluation dataset) and predicted species richness from S-SDMs for both ‘all species’ ($F(1, 625)=29.76$, $p<0.0001$) and ‘oak species’ ($F(1, 625)=109.8$, $p<0.0001$). Explanatory power of species richness from S-SDMs was low for ‘all species’ ($R^2=0.04$) and slightly higher for ‘oak species’ ($R^2=0.15$). In contrast, the MEM (i.e., species richness modeled directly by BRT) was not correlated with observed ‘all species’ richness ($R^2= -0.001$, $F(1, 625)=0.06$, $p=0.80$), but was correlated with ‘oak species’ richness’ ($F(1, 625)=66.66$, $p<0.0001$), with low explanatory power ($R^2=0.09$).

Local and regional species richness among owners

Unique patterns were evident in individual species distributions (Figure 2). S-SDMs for ‘all species’ and ‘oak species’ showed very similar patterns of estimated richness across the Rogue Basin (Figure 3). I found a statistically significant relationship between mean species richness and landowner identity in ‘all species’ ($R^2=0.41$, $F(4, 40733)=7063$, $p<0.0001$) in ‘oak species’ subsets ($R^2=0.43$, $F(4, 40733)=7590$, $p<0.0001$) at the level of the 500 m grid sample points private non-industrial owners contained significantly and markedly higher mean richness at 500 m grid sample point locations than any other landowner for both subsets (Figure 4). USFS consistently had the lowest local mean species richness across all species subsets (Figure 4). All pairwise comparisons were statistically significant for ‘oak species’, and all but two were statistically significant for ‘all species’ (‘BLM - State’ and ‘PI - State’; Table 4). Results for ‘all species - high performance’ were very similar overall ($R^2=0.42$, $F(4, 40733)=7310$, $p<0.0001$), but contained the most non-statistically significant pairwise comparisons (Table 4). However, the pattern of significantly higher estimated mean species in private non-industrial than other ownership (Figure 4, Table 4) was maintained in ‘all species - high performance’,

indicating that results for the primary subsets had not been biased by inclusion of low-performing SDMs.

At the scale of the entire study region, all land-ownerships contained all of the species examined, with the exception of one species (blue-gray gnatcatcher) missing from State ownership. Further, species accumulated with area at very similar rates; the slopes of SACs for ‘all species’ and ‘oak species’ were very similar (Figure 5A & 5B) and curves for these owners consistently acquired every possible species in each subset within 150 to 800 random points (equivalent to 3,750 to 20,000 hectares). State ownership had only one species less than total possible landscape-level richness in both ‘all species’ and ‘oak species’ subsets. Similar patterns were evident in the ‘all species - high performance’, though State accumulated equal richness to other landowners in this subset (Figure 5C).

There were marked differences among landowners in terms of the amount of area in species richness intervals for the ‘all species’ and ‘oak species’ subsets (Figure 6A). Private non-industrial owners held the largest total area in the two highest richness intervals for both subsets. Within the ‘all species’ subset, private non-industrial had more than 300% more area than the next-highest owner (BLM) in the 21-30 species interval, and roughly 1300% more area in the 31-41 species interval than the next highest owner (BLM). There was a very similar pattern for the two highest species richness intervals in the ‘oak species’ subset. Private non-industrial accounted for approximately 70% of the area estimated to exist in the two highest richness intervals for oak-associated species (between 13 and 25 species; Figure 6B). In both subsets, USFS was the largest owner of the lowest species richness interval, and was also the largest owner of the second-lowest richness interval for ‘all species’. In all three of these lower richness intervals, BLM was the second-largest owner. Total area of ownership by private industrial was relatively low in the two lowest richness intervals for both subsets, and was very low in the two highest intervals for both

subsets. State-owned land was very low in every interval for both subsets (Figures 6A & 6B).

Individual species distributions among owners

Private non-industrial owners held the most land in the Rogue Basin study area classed as ‘present’ for 21 of the 25 ‘oak species’, although for several of these species, there was nearly an equivalent amount held by another owner (Figure 7). For 13 species, the difference was substantial, with approximately half of the total area classed as ‘present’ within private non-industrial ownership (e.g ACWO, LAZB, and WEWP; see Table 1 for species codes). For most ‘oak species’, either BLM or USFS held the second- and third-highest positions for total area classes as ‘present’. USFS had highest ownership of habitat for 4 ‘oak species’, though most of these had nearly equivalent levels of suitable habitat in another ownership. The pattern was slightly more variable for the 19 species identified as significantly declining in Oregon according to BBS 50 year trends (Figure 8). Within this group, 12 species had highest area classed as ‘present’ in private non-industrial ownership and 6 were highest in USFS ownership; however habitat area was nearly equal in USFS and private non-industrial for 3 of these species. One declining species (MacGillivray’s warbler) was highest in BLM ownership (Figure 8). For both of the above subsets, private industrial land had consistently lower suitable habitat for most species, though approaching that of the USFS and BLM for some species, while habitat amount was consistently very low in State ownership. The eight ‘all species - high performance’ species showed patterns very similar to both of the above subsets; suitable habitat for five species was highest in private non-industrial ownership, and for each of these, at least half of the area classed as ‘present’ occurred on private non-industrial land (Figure 9). Habitat for the remaining three species was highest in USFS ownership for ‘all species - high

performance’, and consistent with patterns of ‘all’ and ‘oak’ subsets, habitat for all species was generally lower on private industrial and very low in State ownership.

Discussion

My results indicate the importance of land tenure to avian species richness in the Rogue Basin. Overall, non-industrial private landowners seemed to contribute highly both to species richness, and to the total amount of habitat for individual oak-associated species. This study therefore provides evidence that current efforts to engage private landowners in bird-focused oak vegetation conservation and restoration are well-placed and critical. However, suitable habitat for oak-associated and declining species was broadly distributed among ownerships, with high concentrations for certain species predicted within all but State land. This finding suggests that broad-scale multi-ownership collaboration would likely be most fruitful for maintenance of the full suite of oak-associated bird diversity in the Basin. This study also demonstrates the utility of fine-resolution species distribution models (SDMs) in examining associations between land tenure and species richness and individual species’ habitat distribution in a quantitative and spatially-explicit manner.

Distribution of species richness and individual species habitat

My first research objective was to determine whether avian species richness may be additive or redundant across the key land ownership types examined (BLM, USFS, State, private industrial, private non-industrial). My results for species accumulation curves, mean richness, and richness intervals together suggest two key findings: 1) in general, all ownerships may provide some amount of habitat for nearly all of the study species in both the ‘all species’ and ‘oak species’ subsets, and 2) private non-industrial ownership may support the highest levels of both site-level

species richness and may additionally contain much greater areas of high species richness than any other owner.

Species accumulation curves (SACs) notably indicated that each of the five landowners examined may be capable of supporting each of the 48 study species somewhere in the Rogue Basin (with the exception of one species missing from State land; Figure 5), which might indicate some redundancy of richness across the owners at the scale of the entire study area. However, private non-industrial owners showed a striking increase in mean species richness at the level of random sample points - at least double that of any other owner for each species subset examined (Figure 7). Nearly identical results for 'all species - high performance' species did not suggest that this analysis was sensitive to SDM predictive performance. Thus, ownership appears to be highly additive on a site-by-site basis, with a given private non-industrial site contributing more species than a site within any other ownership. Additionally, private non-industrial owners held the greatest absolute amount of land in the two highest species richness intervals for 'all species' and 'oak species' - at least 4.5x that of any other owner (Figure 6). So while each landowner can potentially represent each species across the entire study area, avian species richness in the Rogue Basin may be most heavily concentrated on lands in private non-industrial ownership.

I also sought to determine whether the five key Rogue Basin landowners may support different levels of habitat amount for individual bird species. Results for estimated area classed as 'present' for individual species in each of the five ownerships clearly pointed to the importance of private non-industrial ownership. This ownership was the primary holder of suitable habitat for the majority of 'oak species', and held at least half of the suitable habitat estimated to exist in the Rogue Basin for more of these species than any other owner (Figure 7). However, ownership by BLM, USFS, and in some cases private non-industrial owners were also important contributors of suitable habitat for various 'oak species' and should not be disregarded. USFS and BLM contributed more highly to suitable habitat of 19 species

predicted by BBS trend data to be significantly declining in Oregon, particularly for species such as chestnut-backed chickadee (CBCH) and MacGillivray's warbler (MGWA; Figure 8) which may use oak cover types but are not highly associated with them. In general, these results appear to support national-scale analyses in the 2011 and 2013 State of the Birds Reports (NABCI 2011, NABCI 2013) that note the responsibility of both private and public owners in supporting populations of western forest bird species. My results additionally seem to be consistent with the emphasis placed on private owners for conservation of species associated with oak and other deciduous tree-dominated forests in these documents. However, these results also indicate that public lands contribute heavily to landscape-level suitable habitat for individual oak-associated species in the Rogue Basin.

Mechanisms for landowner relationships to species richness and distribution

A number of potential mechanisms exist for the estimated differences in both species richness and individual species distributions among owners. First, it is well-documented that lower elevation oak vegetation sites in the Rogue Basin are primarily in private ownership (Schindel et al. 2013). Elevation can be a strong predictor of bird species richness (Rahbek 1997), and may relate to productivity gradients which are hypothesized to drive global and regional diversity (Gaston 2000); however I did not find a strong relationship between elevation and observed species richness at evaluation points in this study. Although mean elevation of private non-industrial is the lowest of all the owners (Appendix B, Table 4), overall mean elevation differences among owners do not appear consistent with striking differences in mean species richness at random sample points between private non-industrial and all other owners (Appendix B, Table 4; Figure 4).

It may be that climate or other conditions associated with elevation results in the vegetation concentrated in private non-industrial lands being of higher quality or

productivity for oak-obligate and oak-associated bird species. The disproportionately large combined percentage of the oak savannah/woodland and oak chaparral vegetation categories (Table 3) estimated by GAP vegetation models to be held by private non-industrial owners (approximately 64%) might be evidence of this pattern in the Rogue Basin. Additionally, private non-industrial ownerships do appear to have distinctive average climatic conditions (Appendix B, Table 4), with drier and colder winter conditions, and drier and warmer summer conditions relative to other owners. Overall, these results suggest the possibility that greater holdings of particular oak vegetation types by non-industrial owners within a particular range of climatic conditions may contribute to predicted patterns of higher point-level mean species richness, greater concentration of area within high richness intervals, and generally higher total area of suitable habitat of oak-associated species.

In addition to historic settlement patterns resulting in disproportionate ownership of high-value oak vegetation by private non-industrial owners, differences in management goals and activities that alter vegetation structure may also contribute to predicted differences in richness and suitable habitat among owners. Research in the Oregon Coast Range has suggested that ownership may contribute to variation in vegetation structure and composition after controlling for environmental conditions (Stanfield et al. 2002, Spies et al. 2007). Stanfield et al. (2007) proposed that such patterns could arise from differences in management goals and activities among owners. (Fischer and Bliss 2008) found that the goals and values of private owners of oak areas in the Coast Range led to highly variable management activities across owners, which included both active and passive management for disparate outcomes such as low intensity timber extraction and biodiversity conservation. These activities are likely similar, but perhaps less consistent and homogenous across parcels than would be expected within individual public ownerships or for commercial timber producers (Spies et al. 2007).

If similar diversity and variability of management goals and activities among owners exists in the Rogue, and if it tends to produce higher levels of vegetation heterogeneity both within private parcels and among private non-industrial and other owners, it could be hypothesized that 1) increased predicted species richness within private non-industrial ownership might be due in part to increased vegetation heterogeneity both locally within parcels and regionally among parcels and 2) that this effect could be operating above and beyond underlying environmental site differences. I conducted a preliminary examination of this question by comparing the mean reflectance values and their standard deviations from Landsat TM band data as a proxy for land cover heterogeneity, but did not find any indication of clear differences among landowners (Appendix B, Figure 2). Comprehensive research examining the management goals and activities of private non-industrial and other owners related to current oak vegetation structure has not been conducted in the Rogue Basin, and would likely shed light on the drivers of some of the patterns observed in this study.

My results from Chapter 2 suggest that a combination of local and landscape habitat effects contribute to species richness and habitat suitability patterns among owners. In Chapter 2, I found that while estimated local-scale (150 m) and landscape-scale (10,000 m) habitat amount were both positive predictors of richness for the ‘oak species’ subset, local habitat amount was 1.5 - 3x more important than landscape habitat amount. This result suggests that differences in local habitat structure caused by differing management among landowners or inherent site conditions could be central to determining the level of oak-associated bird species richness that can be supported at any given site. However, influences to local richness by dispersal from regional species pools (Ricklefs 1987) and broad-scale environmental filtering of species (Tscharntke et al. 2012) are also supported by the results I report in Chapter 2, suggesting that ownership context within 10,000 m of any given site might be a partial determinant of local richness. For example, a private non-industrial parcel embedded within USFS property might tend to have lower richness of oak species than the same

parcel surrounded by other private non-industrial property, due to decreased levels of suitable habitat in the surrounding USFS-owned land. This is a key point given the complex nature of land ownership patterns in the Basin (see map, Figure 1). Other studies have suggested that the potential for suitable habitat to support avian species at a local site may be dependent on landscape context of that site (Bakker et al. 2002, Ribic et al. 2009). In the Rogue Basin, work to determine the effects of “ownership context” on local richness after controlling for similarities among neighboring parcels due to environmental conditions could aid the understanding of how stand-level conservation projects might be influenced by surrounding ownerships.

Accumulation rates for SACs were similar across owners, though with consistently higher rates for private non-industrial ownership across the three species subsets examined (Figure 5). This result could point to ‘area effect’ as a main driver for the importance of private non-industrial ownership (Preston 1962, Fahrig 2013), i.e., that this ownership contains more oak vegetation than any other, and thus should be expected to contain higher levels of basin-wide suitable habitat and richness of oak-associate bird species. However, USFS had a distinctly lower rate of accumulation of oak-associated species than any other owner, despite having the third largest percentage of basin-wide oak savannah/woodland and oak-chaparral vegetation (~11%). If all areas classed by GAP models as oak savannah/woodland and oak-chaparral are identical in quality for the oak-associated bird species examined, the species should be expected to accumulate at rates consistent with owners’ holdings of these vegetation types. This result might point to additional mechanisms for differences in richness among owners, related to hypotheses discussed above: 1) differences in management activities might alter the structure of a given vegetation type across owners (Stanfield et al. 2002); 2) the landscape context of ownerships might vary, impacting the ability of species to disperse due to observed differences in cover type in each ownership (Table 3); or 3) modeled vegetation types might not be a good proxy for occurrence of birds on this study, as was suggested in Cushman et al.

(2008), and hence may not provide accurate expectations for oak-associated species richness among owners.

Implications for management

My results consistently point to lands in private non-industrial ownership as being most likely to 1) support higher numbers of oak-associated bird species at a given location within the Rogue Basin, 2) contain more area potentially conducive to high levels of species richness, and 3) contain highest total area of suitable habitat for a given individual oak-associated bird species. Each of these findings supports current emphasis on the role of private non-industrial owners as key players in conservation of Rogue Basin oak vegetation types and their associated avian species (NABCI 2013). Oak-associated bird species are associated with vegetation and landscape conditions that are quickly disappearing in the Basin and elsewhere in the PNW (Altman 2011, Schindel et al. 2013), and there is increasing evidence for the presence of landscape-level habitat thresholds below which forest bird populations show reduced occupancy rates (Betts et al. 2010, van der Hoek et al. 2013). Betts et al. (2010) identified thresholds for a number of the ‘oak species’ (e.g., black-headed grosbeak and lazuli bunting) associated with amount of early-seral broadleaf vegetation in the landscape. Additionally, extirpations (e.g. of Lewis’ woodpecker; Altman 2011) and declines (e.g. of oak titmouse; Rich et al. 2004) of oak-obligate bird species in the Rogue Basin suggest the potential of habitat thresholds for other oak-obligate avian species. Particularly in this scenario, the high levels of estimated ‘oak species’ richness and individual species’ habitat suitability estimated for private non-industrial owners presents an opportunity to make positive contributions toward the maintenance of these species in the region.

Finally, results from SACs indicating that diversity might be redundant at the level of the entire Rogue Basin do not preclude the importance of each individual

forest owner for maintenance of the entire suite of species examined here. Higher relative proportions of suitable habitat for specific oak-associated and declining avian species on USFS and BLM lands indicate that ownership in the basin is complementary in terms of supporting bird diversity. In other words, each ownership type examined might contribute uniquely to sustaining regional populations (Ferrier and Wintle 2009). These ownerships in many cases also contributed substantial amounts of habitat for species that had their primary habitat area on private non-industrial land. Such results suggest that conservation efforts should not focus solely on private non-industrial lands to the exclusion of other owners. Mandates and explicit goals to maintain biodiversity exist for public owners (e.g., BLM, USFS) (McComb et al. 2007, Spies et al. 2007) but also city and county owners that were not examined in this study. Thus, it is important that harvest, fuels reduction, and grazing practices on public lands be critically evaluated in their potential effect to bird populations through manipulation of vegetation structure. Additionally, the role of private industrial owners in providing early seral habitat for hardwood-associated bird species has gained recent attention, particularly with such cover types in decline on public lands (Betts et al. 2010). Private industrial lands, though containing a small percentage of total amount of Rogue Basin oak vegetation and lacking large amounts of area within high species richness intervals, were nonetheless associated with relatively high amounts of suitable habitat for a number of oak-associated species (e.g., black-headed grosbeak, house wren, and western tanager) and declining species (e.g., black-throated gray warbler, dark-eyed junco, and MacGillivray's warbler). Together, these results highlight the importance of multi-owner participation for highest retention of avian species habitat across the Rogue Basin.

Study limitations

It has become increasingly clear that accounting for imperfect detection via occupancy modeling in the analysis of point count data can have dramatic influences on values for observed richness used as model response variables (Jones et al. 2012). Current occupancy modeling tools allow probability of detection to be incorporated into a species habitat model, but require linear relationships between the response and the predictors (Jones et al. 2011). My decision to use BRT to model species habitat suitability, based on its ability to fit complex and non-linear relationships between species occurrence and variables such as Landsat TM spectral data, precluded the use of occupancy modeling.

Although SDMs provide a unique and powerful way to quantify and visualize patterns of richness and ownership, error in model predictions (Elith and Graham 2009) cautions a conservative interpretation of the results. Additionally, AUC scores for some individual SDMs were below the threshold for what is considered a “good” model (i.e. $AUC < 0.7$; (Hosmer and Lemeshow 2005)). However, comparison between ‘all species’ (which included all models) and ‘all species- high performance’ (which included only model with $AUC > 0.8$) did not reveal major inconsistencies in the results. Second, it is well recognized that threshold-based S-SDMs, such as those used here, while useful in their ability to retain species identities and provide simple binary metrics for habitat suitability, tend to over-estimate species richness (Dubuis et al. 2011). Hence, it is important to view species richness and suitability estimates as indices for these parameters, rather than absolute values. Additionally, I would urge caution in the application of the results to management action due to the relatively low explanatory power of both threshold- and summed probabilities-based S-SDMs in predicting observed richness of oak-associated species at a 30 x 30 m pixel resolution ($R^2 = 0.15$). However, it is interesting to note that the species-centered S-SDM approach outperformed a direct model of oak-associated species richness at this fine

resolution ($R^2=0.09$). Biological processes may be differently modeled by the MEM and S-SDM techniques, a hypothesis which requires further examination in the context of this study.

Finally, I did not account for source-sink dynamics in the estimation of habitat suitability, though this has been implicated as a potentially important driver of individual species population viability within neighboring habitat areas (Bonnot et al. 2013). Simple presence or absence of a species at a sample location does not necessarily equate to high quality habitat (Jones 2001). High presence may be observed in “ecological traps”, areas where environmental cues are decoupled from habitat quality resulting in high mortality or low reproductive success (Battin 2004). Because neither adult survivorship nor reproductive output were measured, it cannot be ruled out that areas modeled as ‘suitable habitat’ based on point count data did not in part represent ecological traps. Further work is needed to determine whether areas predicted to be suitable habitat represents sources or sinks for oak-associated birds and whether source-sink dynamics differ across ownerships.

Conclusions

In this study, use of S-SDMs produced continuous spatial predictions of the association of avian species richness with land ownership across the Rogue Basin. By explicitly modeling individual species perceptions of habitat and merging them for continuous species richness estimates, S-SDMs allowed me to investigate the implications of ownership to individual oak-associated species and to local assemblages. In future conservation prioritization work in this region, this technique might prove a useful way to assess and prioritize ecological value in the context of on-the-ground management and land use patterns at a fine resolution that is relevant to both. Use of quantitative spatial models in general has the potential to increase the understanding of the ecological implications of ownership patterns in the Rogue

Basin, and improve effective targeting of ownerships for regional oak-focused conservation action.

A primary conclusion of this research is that the private non-industrial landowners of the Rogue Basin may have the greatest opportunity to contribute positively to maintaining populations of oak-associated bird species. Strong evidence for high richness and individual species habitat suitability validate recent efforts, such as by the Central Umpqua-Mid Klamath Oak Habitat Conservation Project (North American Bird Conservation Initiative, U.S. Committee 2013), to engage private non-industrial owners in oak conservation and restoration. A focus on common bird species associated with threatened oak cover types might provide a means for positive landowner engagement, though more region-specific work must be done to determine the most effective mechanisms and incentives for private non-industrial landowners. Another main conclusion is that each of the key Rogue Basin landowners has an opportunity to contribute to regional oak and avian conservation efforts. The regional complementarity of these ownerships in the Basin suggests that the most effective conservation efforts will be done in a way that maximizes the contribution of each owner to maintenance of oak ecosystems and their dependent biota.

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Tables

Table 3.1. Common names, scientific names, and AOU four letter codes for 48 species used in species distribution models for the Rogue Basin, Oregon. Species are those oak or deciduous vegetation associated species that were most prevalent in a 2011 Rogue Basin oak-focused point count study.

Common name	Scientific name	Code
Acorn Woodpecker ^{2,6}	<i>Melanerpes formicivorus</i>	ACWO
American Goldfinch	<i>Spinus tristis</i>	AMGO
American Robin	<i>Turdus migratorius</i>	AMRO
Ash-throated Flycatcher ^{2,6}	<i>Myiarchus cinerascens</i>	ATFL
Black-capped Chickadee ^{4,6}	<i>Poecile atricapillus</i>	BCCH
Bewick's Wren ^{2,4,6}	<i>Thryomanes bewickii</i>	BEWR
Blue-gray Gnatcatcher ^{4,6}	<i>Poliophtila caerulea</i>	BGGN
Brown-headed Cowbird	<i>Molothrus ater</i>	BHCO
Black-headed Grosbeak ⁶	<i>Pheucticus melanocephalus</i>	BHGR
Brown Creeper ⁵	<i>Certhia americana</i>	BRCR
Black-throated Gray Warbler ^{5,6}	<i>Dendroica nigrescens</i>	BTYW
Bullock's Oriole ³	<i>Icterus bullockii</i>	BUOR
Bushtit ^{2,6}	<i>Psaltiriparus minimus</i>	BUSH
California Towhee ^{4,6}	<i>Pipilo crissalis</i>	CALT
Cassin's Vireo ⁶	<i>Vireo cassinii</i>	CAVI
Chestnut-backed Chickadee	<i>Poecile rufescens</i>	CBCH
Chipping Sparrow ^{2, 6}	<i>Spizella passerina</i>	CHSP
Dark-eyed Junco	<i>Junco hyemalis</i>	DEJU
Downy Woodpecker ^{2, 3, 6}	<i>Picoides pubescens</i>	DOWO
Dusky Flycatcher	<i>Empidonax oberholseri</i>	DUFL

Common name	Scientific name	Code
Hermit Warbler ⁵	<i>Dendroica occidentalis</i>	HEWA
House Wren ^{2, 6}	<i>Troglodytes aedon</i>	HOWR
Hutton's Vireo ^{5, 6}	<i>Vireo huttoni</i>	HUVI
Lazuli Bunting ⁶	<i>Passerina amoena</i>	LAZB
Lesser Goldfinch ^{4, 6}	<i>Spinus psaltria</i>	LEGO
MacGillivray's Warbler	<i>Oporornis tolmiei</i>	MGWA
Mourning Dove	<i>Zenaida macroura</i>	MODO
Nashville Warbler ^{2, 4}	<i>Vermivora ruficapilla</i>	NAWA
Northern Flicker	<i>Colaptes auratus</i>	NOFL
Oak Titmouse ⁴	<i>Baeolophus inornatus</i>	OATI
Orange-crowned Warbler ⁵	<i>Vermivora celata</i>	OCWA
Pacific-slope Flycatcher ⁵	<i>Empidonax difficilis</i>	PSFL
Purple Finch ⁶	<i>Carpodacus purpureus</i>	PUFI
Red-breasted Nuthatch	<i>Sitta canadensis</i>	RBNU
Rufous Hummingbird ⁵	<i>Selasphorus rufus</i>	RUHU
Spotted Towhee	<i>Pipilo maculatus</i>	SPTO
Steller's Jay	<i>Cyanocitta stelleri</i>	STJA
Townsend's Warbler	<i>Dendroica townsendi</i>	TOWA
Tree Swallow ³	<i>Tachycineta bicolor</i>	TRES
Warbling Vireo	<i>Vireo gilvus</i>	WAVI
White-breasted Nuthatch ^{2, 6}	<i>Sitta carolinensis</i>	WBNU
Western Bluebird ^{5, 6}	<i>Sialia mexicana</i>	WEBL
Western Scrub-Jay ⁶	<i>Aphelocoma californica</i>	WESJ
Western Tanager ⁶	<i>Piranga ludoviciana</i>	WETA
Western Wood-Pewee ^{2, 6}	<i>Contopus sordidulus</i>	WEWP

Common name	Scientific name	Code
Wilson's Warbler ⁵	<i>Wilsonia pusilla</i>	WIWA
Wrentit ^{3, 4}	<i>Chamaea fasciata</i>	WREN
Yellow-rumped Warbler	<i>Dendroica coronata</i>	YRWA

¹ Grassland/savannah focal species, Altman 2000; ² Oak woodland focal species, Altman 2000;
³ Riparian focal species, Altman 2000; ⁴ Chaparral focal species, Altman 2000; ⁵ Conifer forest focal species, Altman 1999; ⁶ Oak focal species, Altman and Stephens 2012

Table 3.2. Summary of BRT model parameters (*lr* and *tc*), results for within-model cross validation training (AUC and SE), and results for model prediction to independent evaluation data (AUC) for 48 Rogue Basin forest bird species.

Common name	Learning rate (lr)	Tree complexity (tc)	CV AUC (within-model cross validation)	CV SE (within-model cross validation)	AUC (2011 evaluation data)
Acorn Woodpecker	0.001	5	0.872	0.022	0.72
American Goldfinch	0.0005	5	0.84	0.046	0.70
American Robin	0.001	5	0.736	0.012	0.46
Ash-throated Flycatcher	0.001	5	0.884	0.02	0.82
Black-capped Chickadee	0.001	5	0.859	0.021	0.52
Bewick's Wren	0.001	5	0.896	0.012	0.77
Blue-gray Gnatcatcher	0.001	5	0.935	0.013	0.75
Brown-headed Cowbird	0.001	5	0.816	0.014	0.63
Black-headed Grosbeak	0.005	5	0.788	0.011	0.56
Brown Creeper	0.001	5	0.72	0.014	0.72
Black-throated Gray Warbler	0.005	5	0.852	0.014	0.55
Bullock's Oriole	0.001	5	0.882	0.023	0.78
Bushtit	0.001	5	0.761	0.02	0.78
California Towhee	0.001	5	0.929	0.007	0.87
Cassin's Vireo	0.001	5	0.729	0.016	0.54
Chestnut-backed Chickadee	0.001	5	0.712	0.011	0.82
Chipping Sparrow	0.001	5	0.859	0.021	0.70
Dark-eyed Junco	0.005	5	0.739	0.011	0.52
Downy Woodpecker	0.0003	5	0.669	0.064	0.84
Dusky Flycatcher	0.001	5	0.824	0.02	0.52
Hermit Warbler	0.005	5	0.853	0.008	0.60
House Wren	0.005	5	0.811	0.014	0.63
Hutton's Vireo	0.001	5	0.7	0.044	0.55
Lazuli Bunting	0.005	5	0.814	0.012	0.65
Lesser Goldfinch	0.001	5	0.852	0.017	0.72
MacGillivray's Warbler	0.005	5	0.745	0.021	0.66

Common name	Learning rate (lr)	Tree complexity (tc)	CV AUC (within-model cross validation)	CV SE (within-model cross validation)	AUC (2011 evaluation data)
Mourning Dove	0.001	5	0.787	0.019	0.51
Nashville Warbler	0.005	5	0.813	0.01	0.55
Northern Flicker	0.001	5	0.649	0.028	0.46
Oak Titmouse	0.0005	5	0.9	0.026	0.82
Orange-crowned Warbler	0.001	5	0.826	0.032	0.61
Pacific-slope Flycatcher	0.001	5	0.77	0.016	0.70
Purple Finch	0.001	5	0.768	0.024	0.60
Red-breasted Nuthatch	0.001	5	0.772	0.015	0.57
Rufous Hummingbird	0.001	5	0.656	0.033	0.61
Spotted Towhee	0.005	5	0.84	0.009	0.67
Steller's Jay	0.001	5	0.689	0.021	0.54
Townsend's Warbler	0.0005	5	0.637	0.089	0.85
Tree Swallow	0.001	5	0.927	0.015	0.69
Warbling Vireo	0.001	5	0.741	0.023	0.64
White-breasted Nuthatch	0.001	5	0.756	0.057	0.65
Western Bluebird	0.0005	8	0.721	0.073	0.86
Western Scrub-Jay	0.001	5	0.896	0.009	0.82
Western Tanager	0.005	5	0.768	0.013	0.53
Western Wood-Pewee	0.005	5	0.821	0.015	0.58
Wilson's Warbler	0.001	5	0.801	0.029	0.65
Wrentit	0.001	5	0.845	0.027	0.76
Yellow-rumped Warbler	0.005	5	0.834	0.011	0.48

Table 3.3. Summary of vegetation type holdings by five key Rogue Basin land owner types. Vegetation types are from the National Gap Analysis Program (GAP) land cover database.

Vegetation Type (GAP)	Area owned (Hectares)				
	BLM	USFS	State	Private non-industrial	Private industrial
Total area held (all vegetation types present in the RogueBasin)	274456.26	331140.33	5574.42	284223.15	124430.22
East Cascades Oak-Ponderosa Pine Forest and Woodland	1583.28	26.82	14.40	2866.41	172.53
Mediterranean California Mixed Oak Woodland	2570.49	1000.26	12.24	9189.09	140.22
North Pacific Oak Woodland	4516.20	365.04	176.49	24367.50	689.49
Willamette Valley Upland Prairie and Savanna	636.03	59.67	50.22	6773.31	474.30
OAK SAVANNAH, WOODLAND AND FOREST TOTAL	9306.00	1451.79	253.35	43196.31	1476.54
Percent of the total area held by all owners	16.71	2.61	0.45	77.57	2.65
California Montane Woodland and Chaparral	4469.58	2480.40	49.68	1863.90	868.41
California Xeric Serpentine Chaparral*	10.26	0.54	0.36	3.42	0.00
Klamath-Siskiyou Xeromorphic Serpentine Savanna and Chaparral*	511.47	4298.49	18.09	1142.01	39.15
Mediterranean California Mesic Serpentine Woodland and Chaparral*	241.92	302.31	1.08	228.69	0.81
Northern and Central California Dry-Mesic Chaparral	1372.68	606.24	72.72	4755.78	565.65
OAK/CHAPARRAL TOTAL	6605.91	7687.98	141.93	7993.80	1474.02
Percent of the total area held by all owners	27.64	32.16	0.59	33.44	6.17
Mediterranean California Dry-Mesic Mixed Conifer Forest and Woodland	29905.11	19868.13	96.93	5824.08	21581.82

Vegetation Type (GAP)	Area owned (Hectares)				
	BLM	USFS	State	Private non-industrial	Private industrial
Mediterranean California Lower Montane Black Oak-Conifer Forest and Woodland	84856.14	15877.62	701.10	82190.07	26721.09
Mediterranean California Mixed Evergreen Forest	63074.25	137562.57	920.70	12447.36	18827.10
North Pacific Dry Douglas-fir-(Madrone) Forest and Woodland	24026.85	11437.83	461.16	14801.76	8122.77
North Pacific Lowland Mixed Hardwood-Conifer Forest and Woodland	992.97	2552.31	2.16	518.40	966.06
MIXED CONIFER AND OAK/HARDWOOD TOTAL	202855.32	187298.46	2182.05	115781.67	76218.84
Percent of the total area held by all owners	34.72	32.05	0.37	19.81	13.04
TOTAL OAK, OAK CHAPPARAL, OR MIXED OAK-CONIFER	218767.23	196438.23	2577.33	166971.78	79169.40
Percent of total area held by all owners	32.95	29.59	0.39	25.15	11.92

*vegetation type was not included in 2011 oak-focused point count survey

Table 3.4. Results for pairwise comparisons (Tukey's HSD) of mean species richness between landowners for each of three species subsets (PNI = Private non-industrial, PI = Private industrial).

Species subset	Adjusted			Owner comparisons	Mean difference	Adjusted	
	F	R ²	P-value			95% CI	p-value
All species	7063	0.41	<0.0001	BLM - PI	-0.30	(-0.57, -0.17)	0.031
				BLM - PNI	9.71	(9.49, 9.92)	< 0.0001
				BLM - State	0.14	(-0.94, 1.22)	0.997
				BLM - USFS	-2.49	(-2.70, -2.28)	< 0.0001
				PI - PNI	10.00	(9.72, 10.28)	< 0.0001
				PI - State	0.43	(-0.66, 1.53)	0.819
				PI - USFS	-2.20	(-2.47, -1.92)	< 0.0001
				PNI - State	-9.57	(-10.65, -8.49)	< 0.0001
				PNI- USFS	-12.20	(-12.40, -11.99)	< 0.0001
USFS - State	-2.63	(-3.70, -1.55)	< 0.0001				
Oak species	7590	0.43	<0.0001	BLM - PI	-0.66	(-0.88, -0.43)	< 0.0001
				BLM - PNI	8.18	(8.00, 8.36)	< 0.0001
				BLM - State	1.09	(0.22, 1.97)	0.006
				BLM - USFS	-1.93	(-2.10, -1.76)	< 0.0001
				PI - PNI	8.84	(8.62, 9.06)	< 0.0001
				PI - State	1.75	(0.87, 2.64)	< 0.0001
				PI - USFS	-1.27	(-1.49, -1.05)	< 0.0001
				PNI - State	-7.09	(-7.96, -6.21)	< 0.0001
				PNI- USFS	-10.11	(-10.28, -9.94)	< 0.0001
USFS - State	-3.02	(-3.89, -2.15)	< 0.0001				
All species - high performance	7310	0.42	<0.0001	BLM - PI	-1.00	(-1.15, -0.84)	0.439
				BLM - PNI	5.50	(5.38, 5.62)	< 0.0001
				BLM - State	0.53	(-0.07, 1.12)	0.984
				BLM - USFS	-1.03	(-1.15, -0.92)	< 0.0001
				PI - PNI	6.49	(6.34, 6.64)	< 0.0001
				PI - State	1.52	(0.92, 2.12)	0.874
				PI - USFS	-0.04	(-0.19, 0.11)	0.006
				PNI - State	-4.97	(-5.56, -4.38)	< 0.0001
				PNI- USFS	-6.53	(-6.64, -6.41)	< 0.0001
USFS - State	-1.56	(-2.15, -0.97)	0.358				

Figures

Figure 3.1. Map of ownership and oak vegetation categories (GAP) in the Rogue Basin, Oregon.

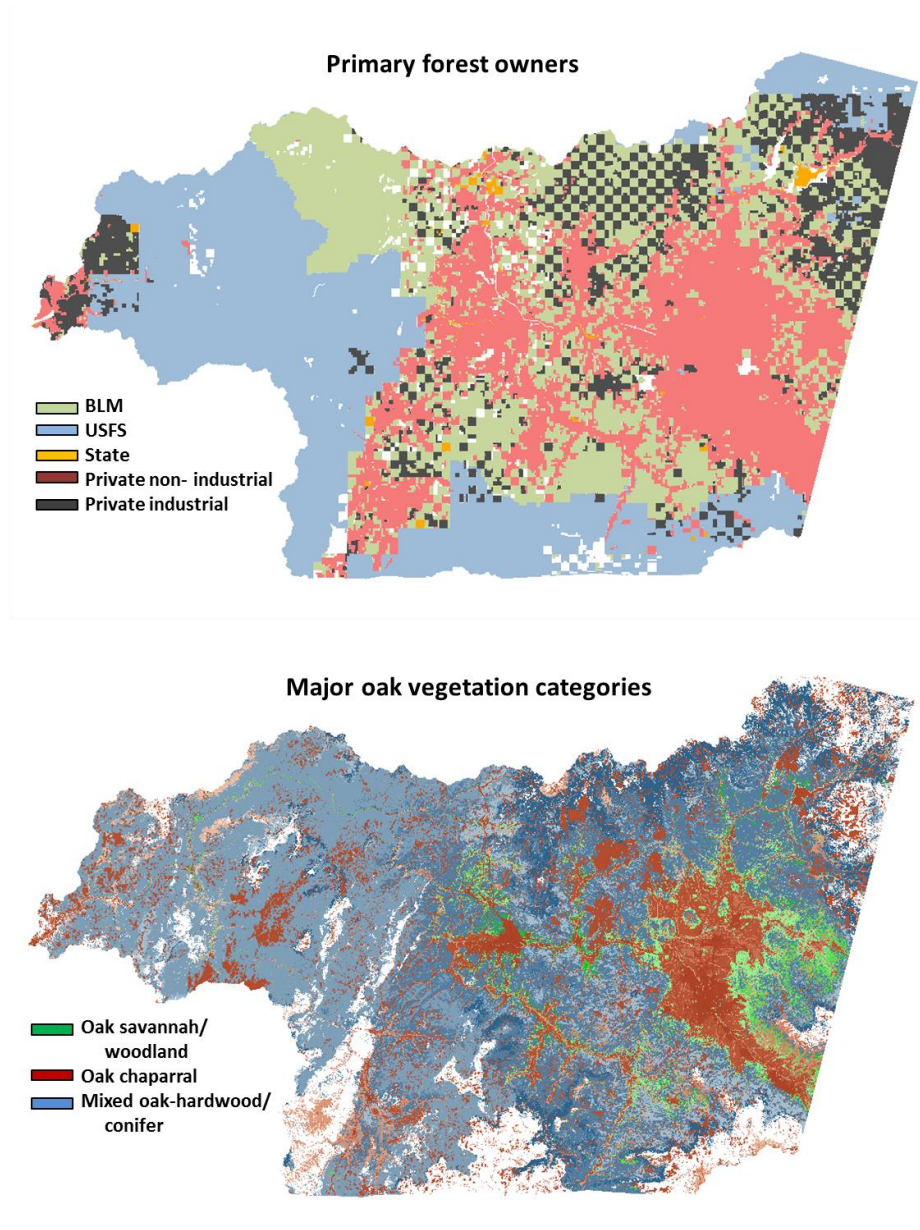


Figure 3.2. Species distribution maps (30 x 30 m resolution) within the Rogue Basin, Oregon for 11 oak-associated species with the most strongly-performing SDMs (AUC >0.7 tested against independent evaluation data). Species depicted are a smaller subset of the ‘oak species’ analysis subset. Darkest red areas indicate areas of highest probability of occurrence, and areas of dark blue indicate areas of lowest probability of occurrence. Species code definitions are in Table 1.

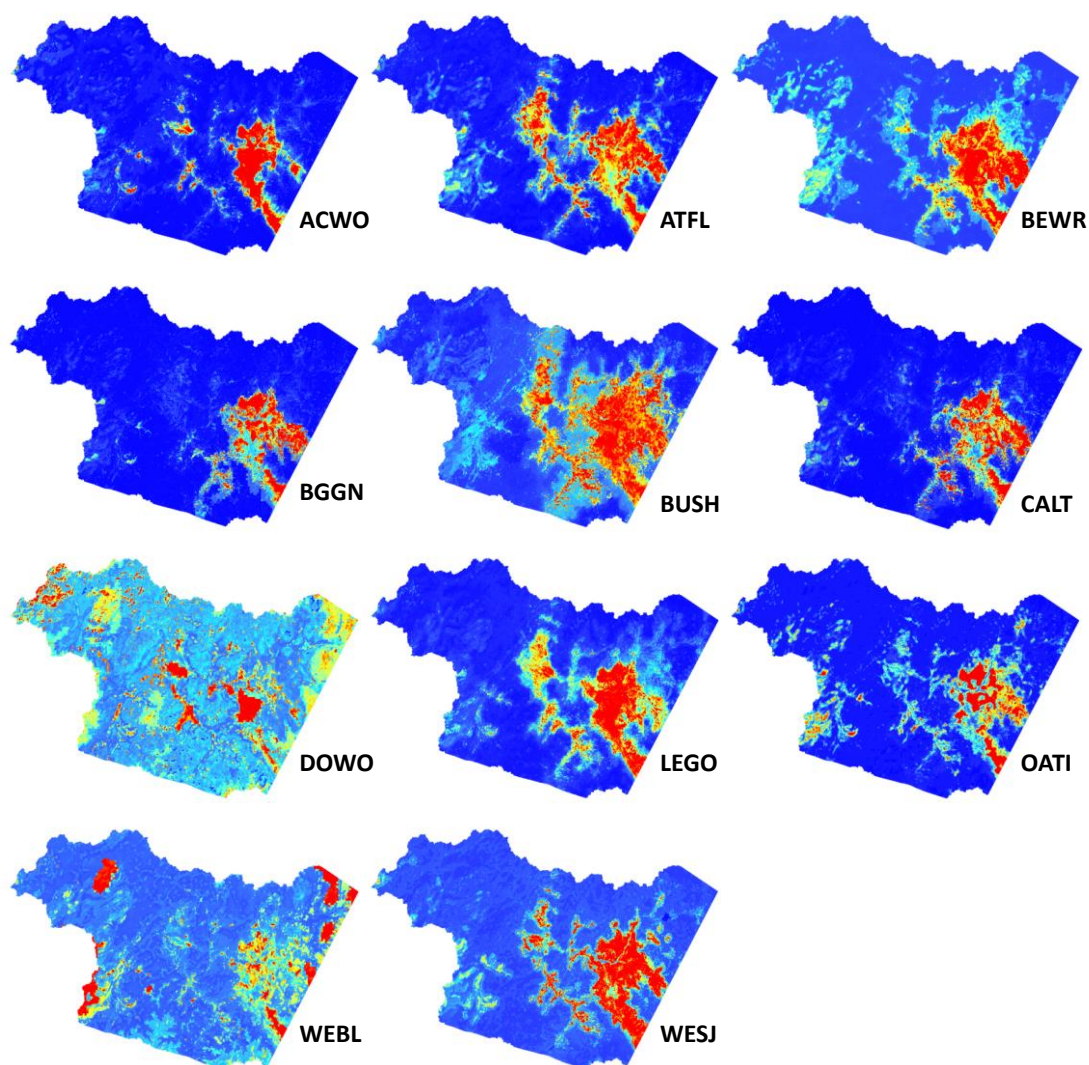


Figure 3.3. Predicted avian species richness maps within the Rogue Basin, Oregon for the two primary species subsets ('all species' and 'oak species') using a 'threshold' SDM stacking method. Darkest red areas indicate areas of highest possible species richness, and areas of dark blue indicate areas of lowest possible richness.

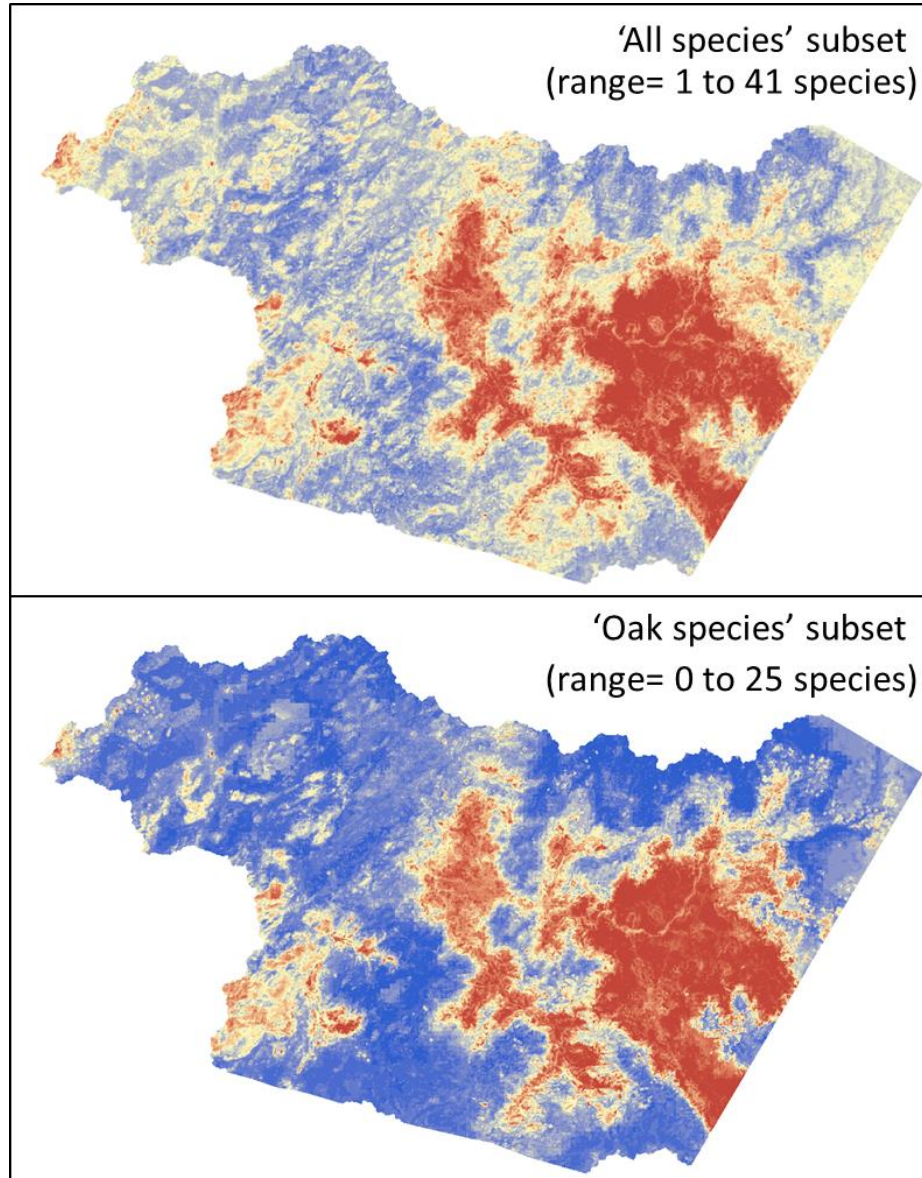


Figure 3.4. Mean species richness among the five key Rogue Basin landowners, compared among the three species analysis subsets: A) all species, B) oak-associated species, and C) all species - high performance (AUC >0.8) tested with independent evaluation data. (PNI = Private non-industrial, PI = Private industrial).

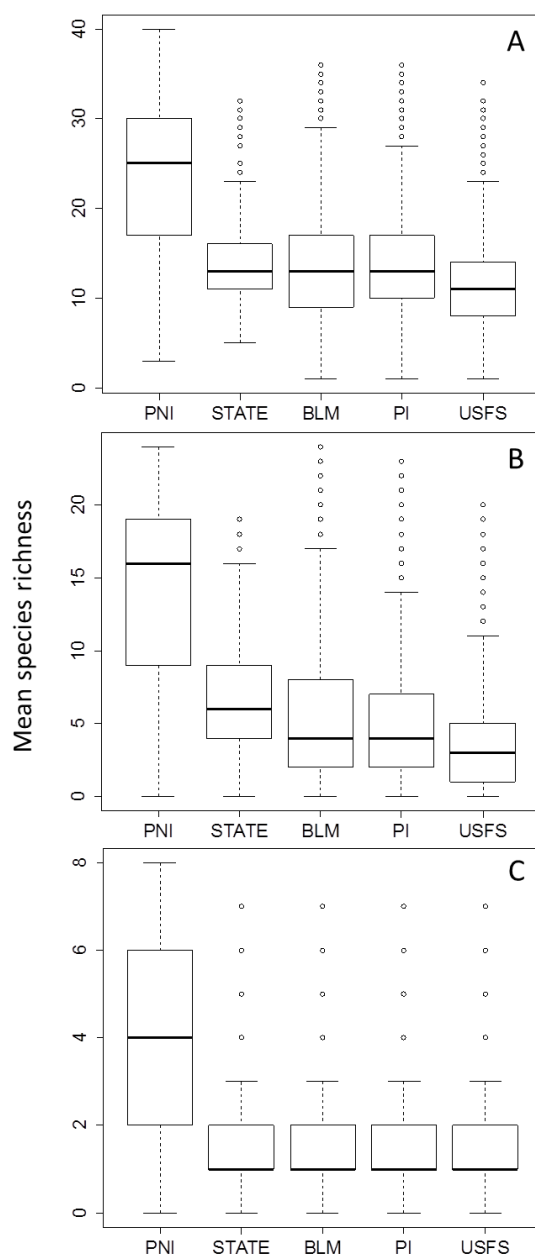


Figure 3.5. Species accumulation curves for five Rogue Basin landowners, compared among the three species analysis subsets: A) all species, B) oak-associated species, and C) all species - high performance models (AUC >0.8) tested with independent evaluation data. 100 sample points is equivalent to 2,500 ha.

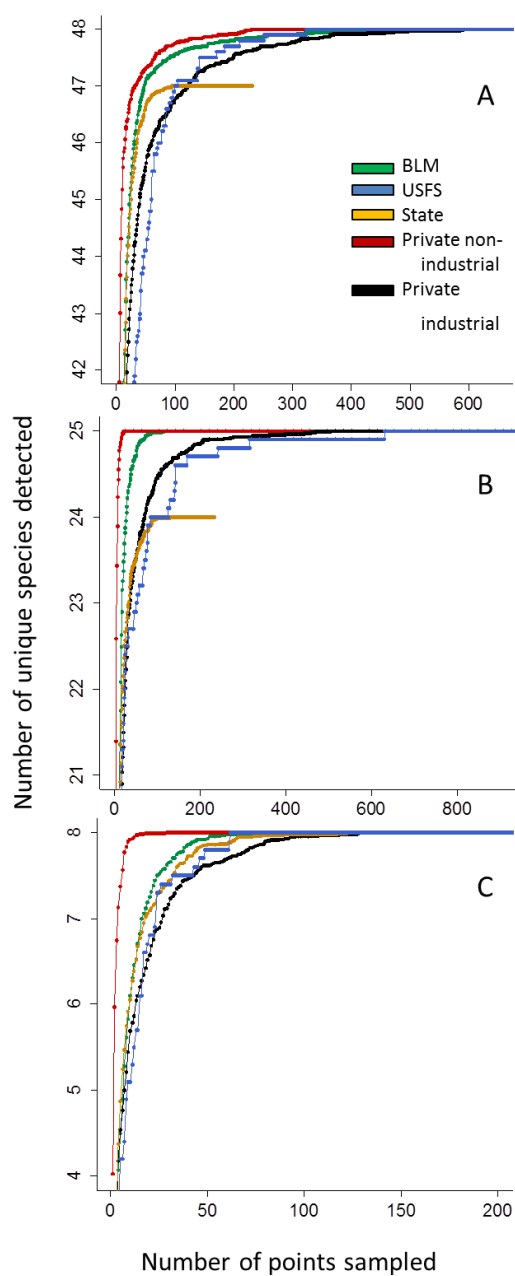


Figure 3.6. Comparison of total area within species richness intervals for five Rogue Basin landowners, compared among two species analysis subsets: A) all species, and B) oak-associated species.

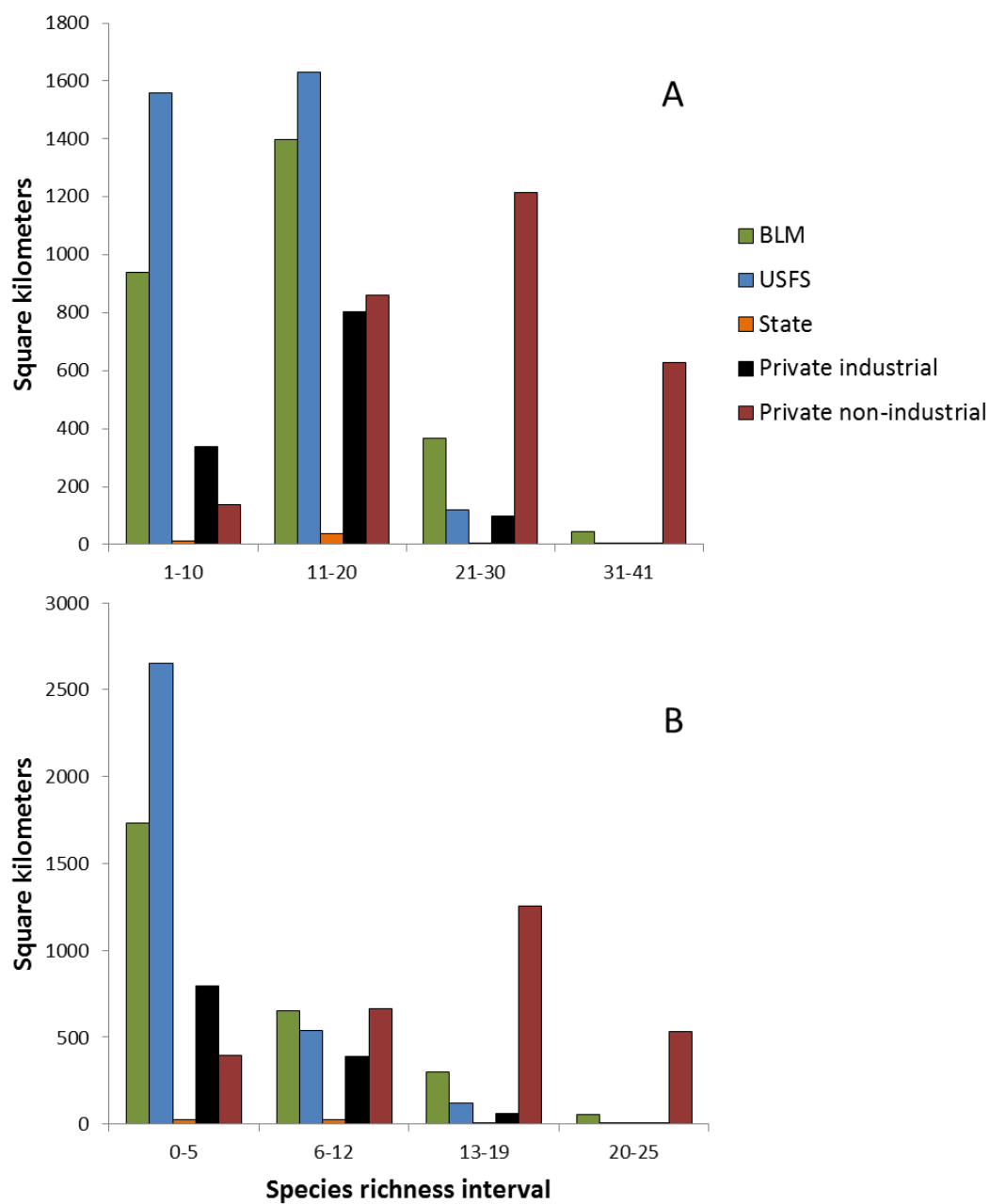


Figure 3.7. Total area classified as ‘present’ for the analysis subset of oak-associated species, compared among five Rogue Basin landowners. See Table 1 for species code definitions.

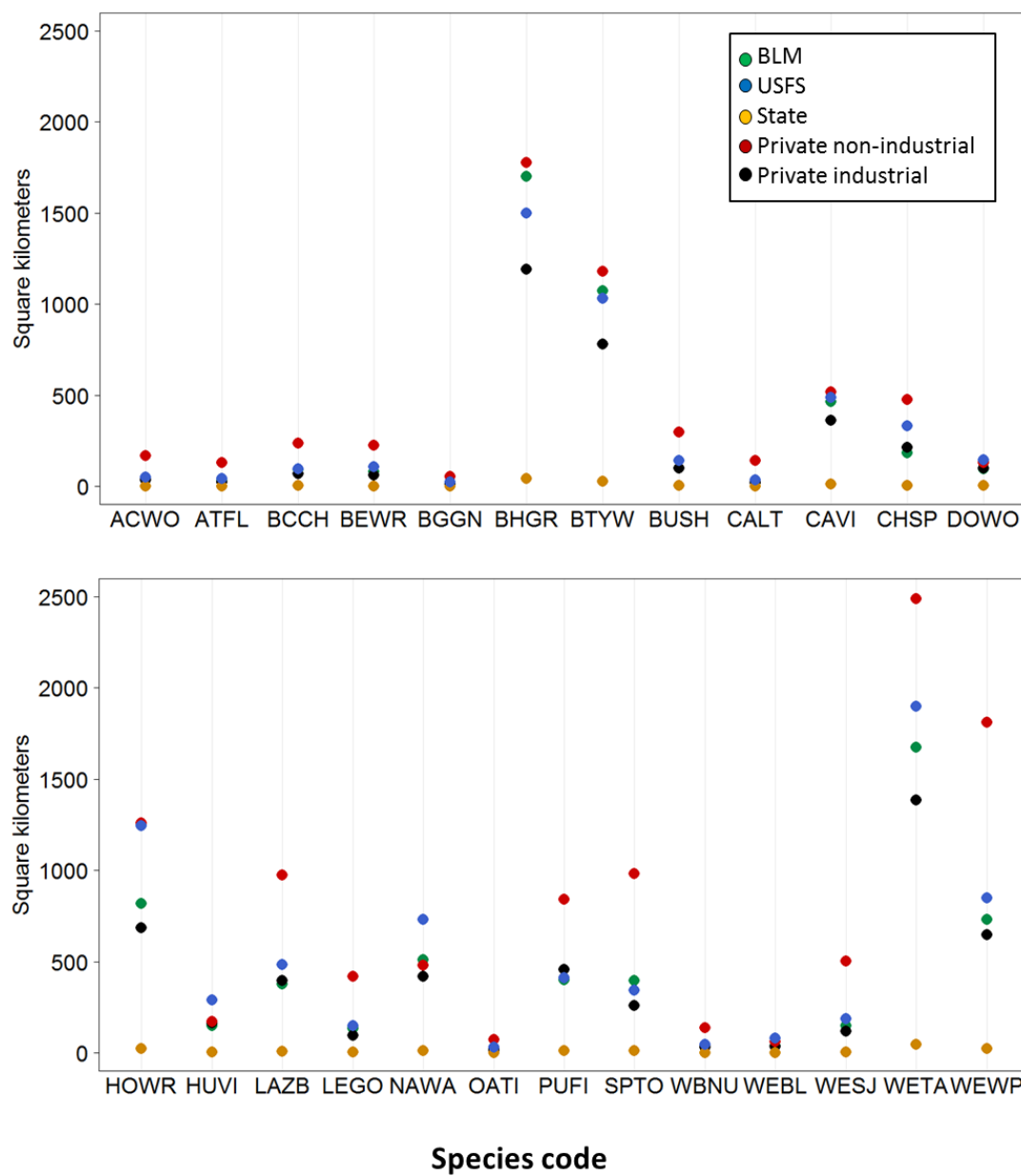


Figure 3.8. Total area classified as ‘present’ for the 20 species showing significant declines in the state of Oregon according to Breeding Bird Survey (BBS) trends, compared among five Rogue Basin landowners. See Table 1 for species code definitions.

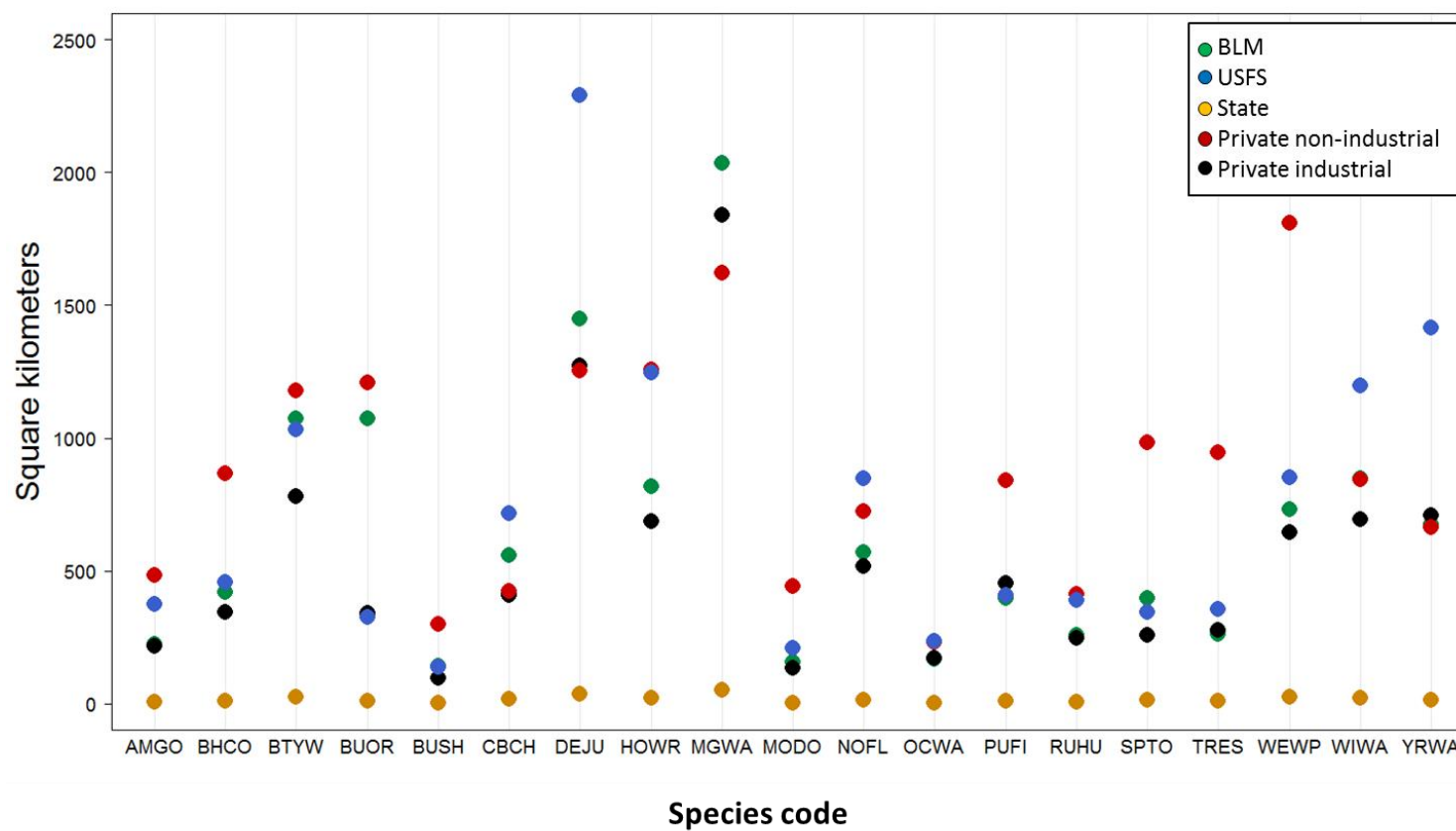
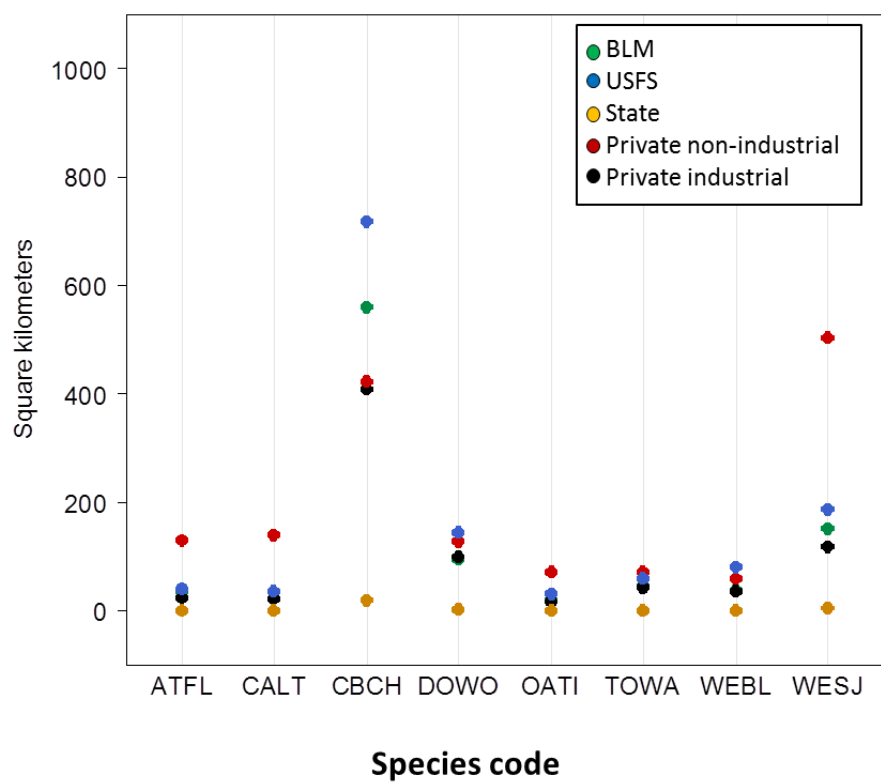


Figure 3.9. Total area classified as ‘present’ for the analysis subset of species with high AUC models ($AUC > 0.8$) tested with independent evaluation data, compared among five Rogue Basin landowners. See Table 1 for species code definitions.



Appendices

3A. Appendix B Table 1. Names and descriptions of vegetation types targeted by a 2011 study of avian communities within oak vegetation types of the Rogue Basin, Oregon.

Vegetation Type Name	Description (from GAP land cover metadata)
OAK SAVANNAH, WOODLAND AND FOREST TYPES	
East Cascades Oak-Ponderosa Pine Forest and Woodland	"Forests and woodlands at or near lower treeline in foothills of the eastern Cascades in Washington and Oregon within 65 km (40 miles) of the Columbia River Gorge and in the Columbia Plateau ecoregion. Elevations range from 460 to 1920 m. Most occurrences of this system are dominated by a mix of Oregon white oak and ponderosa pine or Douglas-fir. Isolated, taller ponderosa pine or Douglas-fir over Oregon white oak trees characterize parts of this system. The understory may include dense stands of shrubs or, more often, be dominated by grasses, sedges or wildflowers. Shrub layers may including antelope bitterbrush, basin big sagebrush, black sagebrush, and green rabbitbrush. Understories are generally dominated by herbaceous species, especially grasses. Mesic sites have an open to closed sod-forming grasses and grass-like plants such as pinegrass, Geyer's sedge, Ross' sedge, long-stolon sedge, or blue wild rye."
Mediterranean California Mixed Oak Woodland	"Mixed oak woodlands from southwestern Oregon and southwestern Oregon, with Oregon white oak and California black oak. Occasionally other hardwoods, including Canyon live oak or madrone can be important, but conifers are not as important or common in this hardwood forest and woodland system. The understory in good condition areas are usually native perennial grass or deciduous shrubs (poison oak or snowberry), but introduced annual grasses have become dominant in most stands. Chaparral shrubs such as buckbrush or sticky manzanita are often present as well."
North Pacific Oak Woodland	"This ecological system is limited to the southern portions of the North Pacific region. It occurs primarily in the Puget Trough and Willamette Valley but trickles down into the Klamath ecoregion and into California. The woodlands and forests are dominated by Oregon white oak, and are found on dry, predominantly low-elevation sites and/or sites that experienced frequent presettlement fires. Many places are being invaded by Douglas-fir or other conifers with fire suppression. Pacific madrone is also not uncommon. Plant life under the tree canopy was historically composed of native grasses but are now mostly composed of non-native (introduced from other continents) grasses, as well as poison oak, snowberry or ferns."

Vegetation Type Name	Description (from GAP land cover metadata)
Willamette Valley Upland Prairie and Savanna	"This grassland system is known only to the Puget Trough and Willamette Valley area. They are rare, dry, upland prairies and savannas found in the valleys and foothills of western Washington and Oregon. Dominated by native bunchgrasses and diverse wildflowers, often with a few open and scattered trees of Oregon white oak, Douglas-fir or Ponderosa pine. In Washington & British Columbia prairies can be found on glacial outwash areas, while in Oregon they are on deep soils and were maintained by native Indian burning. Without regular burning, more and more trees would come in and shade out the prairie sun-loving wildflowers. Much of these prairies have been converted to agriculture or developed for housing."
OAK/CHAPARRAL TYPES	
California Montane Woodland and Chaparral	"A mix of montane chaparral shrubs and open forest and savanna found in the mountains. The trees are variable, usually pine or cypress, but occasionally fir or oak, but never becoming an actual forest, usually a very open woodland or savanna. Chaparral shrubs include many species with leathery, evergreen leaves and in the north some deciduous shrubs. Trees tend to have a scattered open canopy or can be clustered, over a usually continuous dense shrub layer. Trees can include Jeffrey pine, white fir, California red fir, western white pine, sugar pine, Coulter pine, knobcone pine, tecate cypress, Cuyamaca cypress, and Piute cypress. Typical sclerophyllous chaparral shrubs include pinemat manzanita, greenleaf manzanita, Eastwood's manzanita, mountain whitethorn, pinemat, Kern River buckbrush, tobacco-brush, and Sierran chinkapin."
Northern and Central California Dry-Mesic Chaparral	"This open chaparral shrubland is found inland from maritime chaparral up to 1500 m 4550 feet in elevation, in interior valleys and their margins, from northern California through the northern end of the Central Valley and north into Oregon. A mix of drought deciduous and evergreen chaparral species, including common chamise, buckbrush, several manzanita species, California flannelbush, bushmallow, bush poppy, and stingaree-bush. In Oregon, it is characterized by buckbrush and manzanita, usually with bunchgrass understories. These chaparral shrublands usually occur in and around larger patches of oak savannas, woodlands and mixed hardwood - conifer woodlands. Fires are intense, the shrubs reseed after fire, so it is considered a fire-adapted shrubland."
MIXED CONIFER AND OAK/HARDWOOD Types	

Vegetation Type Name	Description (from GAP land cover metadata)
Mediterranean California Dry-Mesic Mixed Conifer Forest and Woodland	"Dry mixed conifer forests and woodlands, usually with Douglas-fir codominant with sugar pine, incense cedar, and/or Ponderosa pine. In the transverse ranges of southern California, incense cedar can be codominant with white fir in this system, but further north white fir is an indicator of the moist-mesic mixed conifer system. These forests and woodlands were fire maintained ecosystems, mostly now found on ridgetops, south and west-facing slopes, Evergreen and deciduous hardwoods can occur in the understory, but if these make up even 20% of the canopy they are classified as a different system. The understory is variable, usually with deciduous shrubs, evergreen shrubs and wildflower present."
Mediterranean California Lower Montane Black Oak-Conifer Forest and Woodland	"These are mixed oak - conifer forests and woodlands, found in the valley bottoms, valley margins and canyon and foothill slopes of northwestern California and southwestern Oregon. Ponderosa pine is usually present with one or more oaks, most commonly California black oak, Oregon white oak, canyon live oak or interior live oak. In many stands, Douglas-fir can occur as well, or replace much or all of the ponderosa pine. The stands often have shrubby understories with chaparral shrubs, or can be grassy, with native perennial grasses or introduced annual grasses."
Mediterranean California Mixed Evergreen Forest	"This ecological system occurs from the Santa Cruz Mountains, California, north into southwestern Oregon throughout the outer and middle Coast Ranges. It occurs just inland of the redwood belt. It also occurs in southern California in more mesic, protected, cooler sites of the Transverse and Peninsular ranges. Characteristic trees include Douglas-fir, canyon live oak, tanoak, Pacific madrone, California laurel, and golden chinkapin. On the eastern fringe of this system, in the western Siskiyou, other conifers occur such as ponderosa pine and Port Orford-cedar. In southern California (Transverse and Peninsular ranges), bigcone Douglas-fir replaces Douglas-fir but co-occurs with canyon live oak and sometimes coast live oak. Incense-cedar is occasional. In the southern portion of the range, tanoak, Pacific madrone, California laurel, and golden chinkapin become less important or are absent. Historic fire frequency was higher than for redwood forests, occurring (every 50-100 years)."
North Pacific Dry Douglas-fir-(Madrone) Forest and Woodland	"This system is most common in the Puget Trough - Willamette Valley ecoregion but also occurs in adjacent ecoregions. These woodlands are fairly dry conifer forests dominated by Douglas fir, often with madrone or Oregon white oak, but rarely with other conifers present. Historically this was a widespread, fire maintained type, which has moved to occupy areas that were formerly prairies and oak savannas. These sites are too dry and warm or have been too frequently and extensively burned to have more than small amounts of western hemlock or western red-cedar. Pacific madrone is favored by high-severity fires on sites where it occurs, and Douglas-fir can be locally eliminated by logging and hot fire or repeated high-severity fires. Incense-cedar is absent."

Vegetation Type Name	Description (from GAP land cover metadata)
North Pacific Lowland Mixed Hardwood- Conifer Forest and Woodland	"This lowland mixed hardwood - conifer forest system occurs throughout the Pacific Northwest. These forests are composed of large conifers, including douglas-fir, western red-cedar, grand fir, western hemlock, and/or sitka spruce, with deciduous hardwood trees present and usually codominant, such as bigleaf maple, oregon white oak, red alder, cascara false buckthorn, and pacific dogwood. Under the tree canopy are many deciduous shrubs such as vine maple, beaked hazelnut and pacific poison-oak, but evergreen shrubs, including salal and dwarf oregon-grape, ferns and wildflowers such as redwood sorrel, can be dominant."

3B. Appendix B Table 2. ROC cut points calculated independently for each species, to convert probability of occurrence to presence/absence for analysis.

Common name	Code	ROC cut point
Acorn Woodpecker	ACWO	0.0096235
American Goldfinch	AMGO	0.1686270
American Robin	AMRO	0.0833485
Ash-throated Flycatcher	ATFL	0.0121505
Black-capped Chickadee	BCCH	0.0270410
Bewick's Wren	BEWR	0.0316265
Blue-gray Gnatcatcher	BGGN	0.0143250
Brown-headed Cowbird	BHCO	0.1608630
Black-headed Grosbeak	BHGR	0.4150895
Brown Creeper	BRCR	0.2152135
Black-throated Gray Warbler	BTYW	0.2456455
Bullock's Oriole	BUOR	0.0950120
Bushtit	BUSH	0.0452335
California Towhee	CALT	0.0183870
Cassin's Vireo	CAVI	0.1474080
Chestnut-backed Chickadee	CBCH	0.1126400
Chipping Sparrow	CHSP	0.1287220
Dark-eyed Junco	DEJU	0.4535310
Downy Woodpecker	DOWO	0.0304945
Dusky Flycatcher	DUFL	0.1493845
Hermit Warbler	HEWA	0.1846760
House Wren	HOWR	0.2575950
Hutton's Vireo	HUVI	0.0376600
Lazuli Bunting	LAZB	0.1417570
Lesser Goldfinch	LEGO	0.0601415
MacGillivray's Warbler	MGWA	0.5011330
Mourning Dove	MODO	0.0943605
Nashville Warbler	NAWA	0.1545845

Common name	Code	ROC cut point
Northern Flicker	NOFL	0.1598845
Oak Titmouse	OATI	0.0118920
Orange-crowned Warbler	OCWA	0.0326725
Pacific-slope Flycatcher	PSFL	0.2307585
Purple Finch	PUFI	0.1379270
Red-breasted Nuthatch	RBNU	0.4053645
Rufous Hummingbird	RUHU	0.0705300
Spotted Towhee	SPTO	0.1090265
Steller's Jay	STJA	0.2532065
Townsend's Warbler	TOWA	0.0154445
Tree Swallow	TRES	0.1352180
Warbling Vireo	WAVI	0.2022600
White-breasted Nuthatch	WBNU	0.0114110
Western Bluebird	WEBL	0.0104210
Western Scrub-Jay	WESJ	0.0511060
Western Tanager	WETA	0.3881645
Western Wood-Pewee	WEWP	0.3063265
Wilson's Warbler	WIWA	0.2436210
Wrentit	WREN	0.0525040
Yellow-rumped Warbler	YRWA	0.0332170

3C. Appendix B Table 3. Summary of membership in analysis subsets for 48 Rogue Basin forest bird species

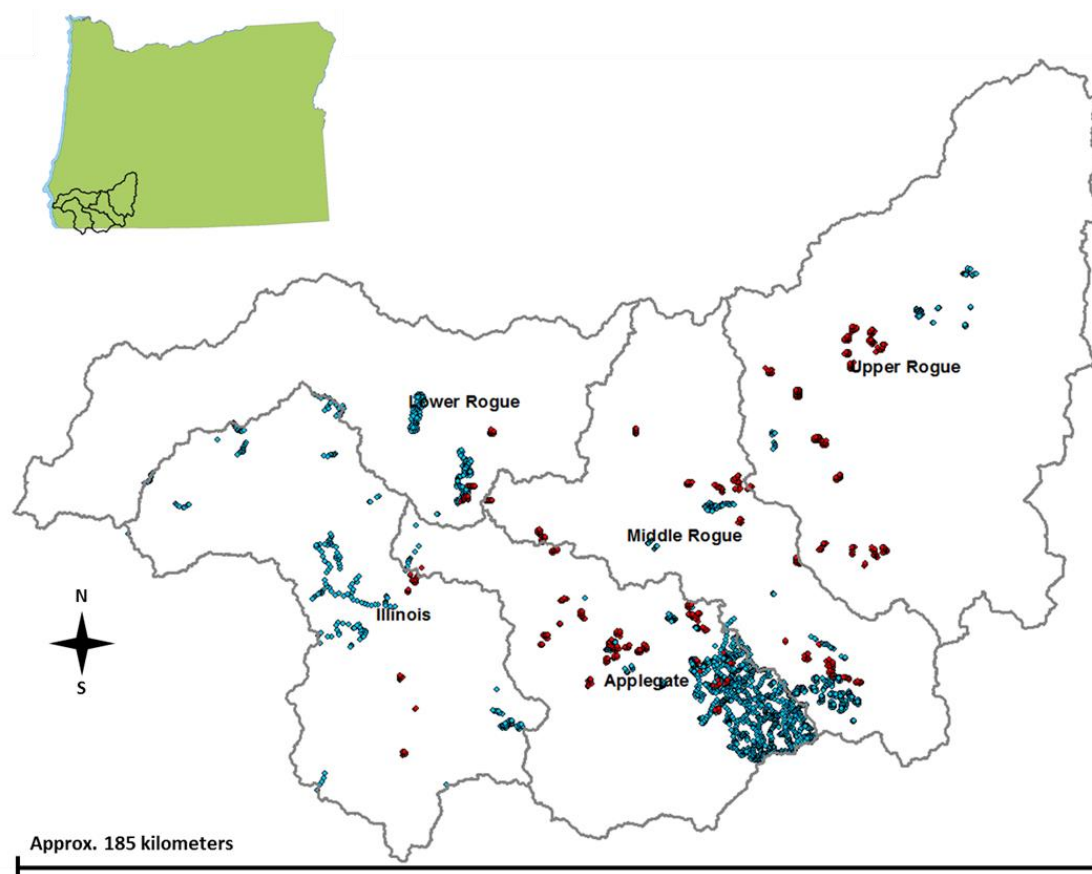
Common name	All species subset	Oak species subset	High performance (AUC >0.8)
Acorn Woodpecker	X	X	
American Goldfinch			
American Robin	X		
Ash-throated Flycatcher	X	X	X
Black-capped Chickadee	X	X	
Bewick's Wren	X	X	
Blue-gray Gnatcatcher	X	X	
Brown-headed Cowbird	X		
Black-headed Grosbeak	X	X	
Brown Creeper	X		
Black-throated Gray Warbler	X	X	
Bullock's Oriole	X		
Bushtit	X	X	
California Towhee	X	X	X
Cassin's Vireo	X	X	
Chestnut-backed Chickadee	X		X
Chipping Sparrow	X		
Dark-eyed Junco	X		
Downy Woodpecker	X	X	X
Dusky Flycatcher	X		
Hermit Warbler	X		
House Wren	X	X	
Hutton's Vireo	X	X	
Lazuli Bunting	X	X	
Lesser Goldfinch	X	X	
MacGillivray's Warbler	X		
Mourning Dove	X		

Common name	All species subset	Oak species subset	High performance (AUC >0.8)
Nashville Warbler	X	X	
Northern Flicker	X		
Oak Titmouse	X	X	X
Orange-crowned Warbler	X		
Pacific-slope Flycatcher	X		
Purple Finch	X	X	
Red-breasted Nuthatch	X		
Rufous Hummingbird	X		
Spotted Towhee	X	X	
Steller's Jay	X		
Townsend's Warbler	X		X
Tree Swallow	X		
Warbling Vireo	X		
White-breasted Nuthatch	X	X	
Western Bluebird	X	X	X
Western Scrub-Jay	X	X	X
Western Tanager	X	X	
Western Wood-Pewee	X	X	
Wilson's Warbler	X		
Wrentit	X		
Yellow-rumped Warbler	X		

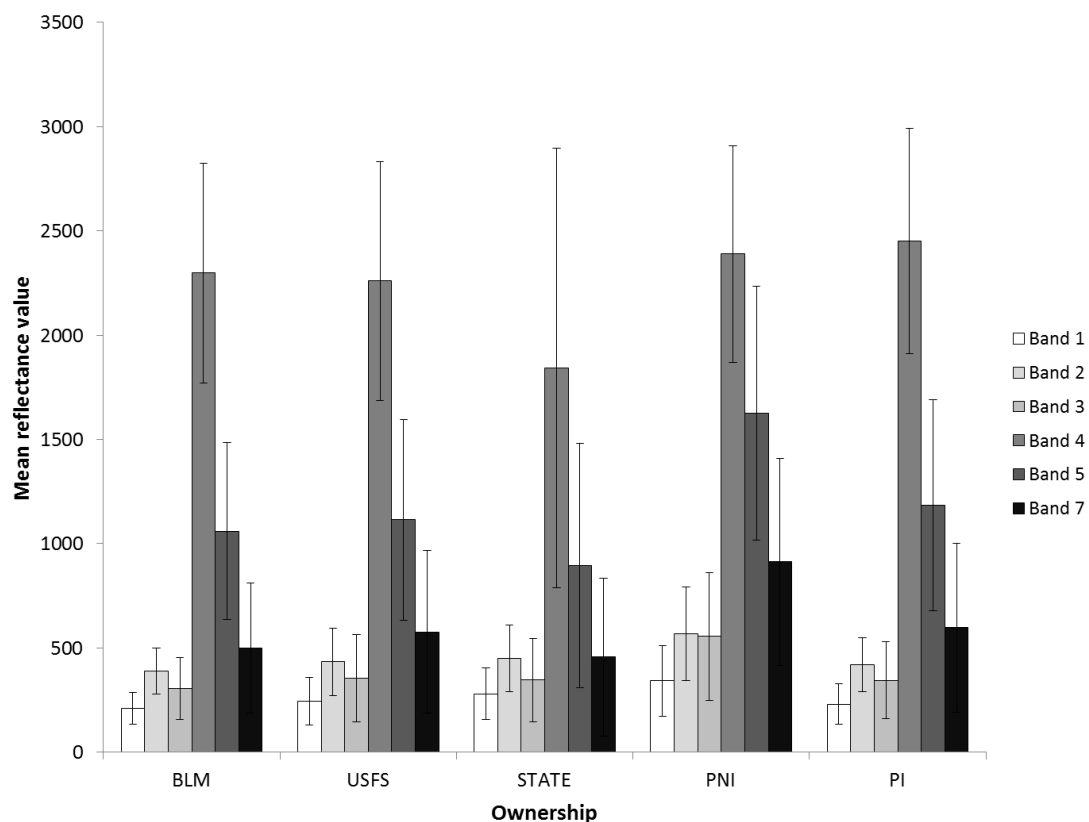
3D. Appendix B Table 4. Examination of means and standard deviations (SD) of elevation and key climatic variables used in species distribution modeling among five Rogue Basin landowners. Means were calculated based on values for each variable at 500 m grid sample point locations.

	Elevation (meters)		December precip. (ml)		July precip. (ml)		December temp. (C)		July temp. (C)	
	(mean)	(SD)	(mean)	(SD)	(mean)	(SD)	(mean)	(SD)	(mean)	(SD)
BLM	787.226	254.845	211.808	75.442	11.827	3.254	0.028	1.034	28.806	2.205
STATE	629.319	287.611	216.197	114.702	10.493	3.547	0.002	1.387	29.643	2.314
USFS	891.016	385.172	371.331	145.875	13.975	4.133	0.543	1.667	27.697	2.511
Private non-industrial	536.906	214.403	163.917	74.624	10.365	2.762	-0.257	0.982	30.893	1.933
Private industrial	803.684	279.475	247.270	122.814	14.077	3.683	-0.052	1.837	28.119	2.152

3E. Appendix B Figure 1. Map of model training and evaluation point count locations within the Rogue Basin, with sub-basins labeled. Training data were collected at blue points, evaluation data at red points. Location of the Rogue Basin within the State of Oregon is shown on the green state locator map.



3F. Appendix B Figure 2. Examination of means and standard deviations (SD) of reflectance values for all non-infrared Landsat TM bands within each of five primary land ownership types in the Rogue Basin, Oregon (PNI = Private non-industrial, PI = Private industrial). Error bars represent one SD from the mean.



CHAPTER 4: CONCLUSION

In this thesis, my objectives were to 1) examine potential influences of habitat amount at multiple scales on local bird species richness, and 2) examine the degree to which the richness and habitat distribution of relatively common oak-associated species may be correlated with five primary ownership types in southern Oregon. I focused on 48 forest bird species, including a nested pool of 25 highly oak-associated species (the ‘all species’ and ‘oak species’ subsets, respectively), within threatened Oregon white oak and California black oak (*Quercus garryana* and *Q. kelloggii*) vegetation types in the Rogue Basin of southwest Oregon. I used a ‘continuum’-based ‘stacked’ species distribution model (S-SDM) approach to estimate habitat suitability, species richness, and indices of multi-scale habitat amount for use in both investigations. In Chapter 2, I tested the relative importance of local-scale versus landscape-scale habitat amount, as well as broad-scale spatial aggregation, to local avian species richness in the two nested species pools. I additionally assessed differences in these relationships using two S-SDM methods: ‘probabilities’, in which raw SDM probability of occurrence values were summed across all pixels, and ‘thresholds’, in which a posteriori ROC cutpoint was applied uniquely to each species before stacking. In Chapter 3, I examined 1) whether oak-associated bird species richness might be additive or redundant among landowners and 2) whether landowners may support differing levels of suitable habitat for individual oak-associated bird species.

In Chapter 2, habitat amount, plus a spatial autocorrelation term, explained approximately 18 - 31% of the variation in local species richness at fine (30 x 30 m) resolutions in linear models. I found evidence for greater importance of estimated landscape-scale habitat to local (i.e., territory level) richness of the large pool of 48 forest birds. The ‘probabilities’ method showed a high relative importance for

landscape and no statistically significant support for local habitat amount, while there was evidence for lower effect of local- than landscape-level habitat using the ‘threshold’ method’. In contrast, there was evidence that local-scale habitat may be considerably more important than landscape-scale habitat amount for the nested subset of 25 highly oak-associated birds, with a 1.5-fold increase in effect size for *local* using the ‘probabilities’ method and a 3-fold increase using the ‘threshold’ method. However, the effect size for landscape habitat amount influence on ‘oak species’ richness was similar to the effect size for ‘all species’, suggesting that landscape context was still important to local richness of oak-associated avian species

Results for the ‘all species’ pool appears to support the “regional species pool” hypothesis (Ricklefs 1987, Zobel 1997), which posits that availability of habitat at the regional level is of primary importance to determine which species can disperse to a local site, above and beyond local conditions (Tscharntke et al. 2012). Alternately, for the oak-associated species, effect sizes for habitat amount indicated that a site’s local quality for multiple species is more important to local assembly than the capacity for those species to disperse through the landscape. Results for the oak-associated species subset may support mechanistic hypotheses for local richness related to local site conditions, such as the “vegetation heterogeneity” hypothesis which posits an overriding importance of local habitat quality and structure over landscape context (MacArthur and MacArthur 1961, Tews et al. 2004). These differences in relationships suggest potential differences in the degree to which fine- and broad-scale processes influence local community assembly, depending on the species pool considered.

The larger, ‘all species’ pool included species that utilize, but are not highly associated with oak- and other hardwood-dominated cover types, as well as species highly associated with coniferous forest (e.g., hermit warbler and brown creeper). This divergent species group may reveal the over-arching importance of broad-scale habitat

availability to eventual filtering of the regional species pool to the local site. Belmaker and Jetz (2012) noted the importance of testing multi-scale habitat relationships for all species potentially able to disperse to a site, regardless of each species' association with particular cover types. This has remained unexplored empirically, possibly due to the challenge of estimating useful habitat amount parameters for groups of species with disparate habitat associations (Fahrig 2013). I proposed and tested one potential method for dealing with this complexity, but relatively low explanatory power of habitat amount (~ 18% explained variation in local richness for both S-SDM methods) does suggest that many other unmeasured factors may have strong influences on local richness for species with high variation in habitat associations. Further work is required to test the applicability of this approach in other regions, biological systems, and taxa.

The results for the subset of 25 oak-associated species imply that focus on improving habitats via conservation or restoration of oak vegetation types in the Rogue Basin should prioritize maximizing the quality of stand-level conditions over maintaining high levels of landscape-level habitat connectivity. Decreased sensitivity to landscape context by specialists was suggested in a meta-analysis by (Prugh et al. 2008), and has additionally been hypothesized for avian species adapted to naturally fragmented oak vegetation types in the PNW (Altman and Stephens 2012). Percent variance in local oak-associated species richness explained by habitat amount models was almost double that for the 'all species' subset (~30-31%, both stacking methods), but was still lower than explanatory power for forest bird richness in other studies (Saab 1999, Rahbek and Graves 2001, White and Hurlbert 2010, Belmaker and Jetz 2012). It would be interesting to further examine the potential causes of this variation in explanatory power, which for example could be related to higher overall model quality for 'oak species' or differences in habitat amount sensitivities among generalist versus specialist species (Mitchell et al. 2001, Prugh et al. 2008). The generality of the

approach applied in this research should be examined in other contexts, particularly to determine whether patterns of decreased importance of landscape processes in habitat specialists in forested landscapes can be supported elsewhere using S-SDM techniques.

In Chapter 3, species accumulation curves (SACs) indicated that each of the five landowners examined (USFS, BLM, State, private non-industrial, and private industrial) may, in general, be capable of supporting each of the 48 study species somewhere within the Rogue Basin. However, private non-industrial ownership consistently emerged as highly important to oak-associated species. This ownership was most likely to 1) support higher oak-associated species richness at a given location, 2) contain more area within the Rogue Basin potentially conducive to high levels of species richness, and 3) contain the highest total area of suitable habitat for a given individual oak-associated bird species. Estimates from S-SDMs also indicated high proportions of suitable habitat for a number of avian species on USFS, BLM, and private industrial lands, particularly species predicted by BBS trend data to be declining in Oregon, such as dark-eyed junco and MacGillivray's warbler (Sauer et al. 2012). USFS ownership was also more important for habitat of several species considered associated with conifer forests (Hutton's vireo, western bluebird, and Wilson's warbler; Altman 1999). Hence, while richness was 'redundant' among owners for the entire suite of species regionally (i.e., each species might be expected to occur somewhere within a particular ownership), ownership is perhaps also 'additive' to species richness regionally. In other words, each ownership type examined might contribute uniquely to sustaining regional populations by providing habitat for different parts of the avian species pools examined.

These results have two key implications for management of bird species diversity in the Rogue Basin. First, this research validates current efforts to engage private landowners in conservation and restoration projects targeting high-value oaks

vegetation areas and their associated avian biota. It also confirms a recent nationwide assessment (North American Bird Conservation Initiative, U.S. Committee 2013) pointing to private landowners as having the greatest potential to positively impact populations of bird species reliant on oak and other hardwood-dominated vegetation types. Second, despite the clear importance of private non-industrial lands, my results point to the importance of multi-owner collaboration in conservation of common Rogue Basin oak species. Unlike private non-industrial owners, public owners are subject to policies and mandates which seek to maintain ecosystem function and native biodiversity (Spies et al. 2007). Additionally, unique management regimes on private industrial lands may provide habitat for early seral vegetation that is increasingly rare in Oregon, and of particular importance to many declining forest bird species (Betts et al. 2010). Patterns in individual species' habitat distributions suggest that effective and consistent implementation of biodiversity-related policies by public owners, and consideration of biodiversity impacts by private industrial owners, might be a great benefit to the populations of these species regionally.

A key contribution of this research was the use of fine-resolution, 'continuum'-based S-SDM methods to examine avian species richness, habitat amount, and land ownership in a forested landscape. I tested richness-habitat amount relationships in the Rogue Basin using two S-SDM methods in order to assess the relative efficacy of both, with particular interest in a summed probabilities approach which remains little explored in the literature (Wilson et al. 2005, Dubuis et al. 2011). I also used species richness estimates from S-SDMs to explore a facet of the ecological implications of land ownership for a large region, contributing a novel approach for an important but rarely examined topic in conservation research (Spies et al. 2007, Ferrier and Wintle 2009).

In Chapter 2, I found that the summed probabilities approach for S-SDMs performed similarly to a more traditional threshold-based method in tests of relative

importance of multi-species habitat amount. As individual species perceive habitat as gradients of suitability across a landscape (Fischer and Lindenmayer 2006), the summed probabilities approach may be more biologically realistic and more flexible than threshold-based approaches that are reliant on the patch/matrix paradigm of habitat. The S-SDM approach used in this research might be valuable to future investigations of habitat amount relationships which seek to incorporate the complexity of species' habitat gradients. However, further research should examine the causes and consequences of low-performance ($AUC < 0.7$) individual species models in S-SDMs, as well as the implications and generality of relatively low (~18%-31%) model explanatory power for various species groups estimated in this study.

Both the probabilities- and threshold-based S-SDMs performed better in predicting observed local species richness at 2011 evaluation sites than a direct macroecological model (MEM) of species richness using BRT model method and environment predictors identical to those used in SDMs. Threshold-based S-SDMs in particular should be expected to overestimate species richness (Dubuis et al. 2011), and so estimated values should be taken as an index rather than an absolute prediction. However, my S-SDMs did suggest richness and individual species habitat patterns which were generally consistent with what might be expected, given the total holdings of oak vegetation by each owner basin-wide. Overall, my research demonstrates the utility of fine-resolution, regional-scale S-SDMs in examining associations of land tenure with species richness and individual species' habitat distribution in a quantitative and spatially-explicit manner. Such approaches may have broad applicability in more effective targeting of ownerships for regional conservation efforts.

In summary, results from Chapter 2 reveal potential differences in the degree to which fine- and broad-scale processes influence local community assembly, depending on the species pool considered. Next, Chapter 3 results suggests that

ownership type may be of importance to species habitat and richness distributions, and effective conservation efforts should consider the contribution of each owner to maintaining threatened ecosystems and their dependent biota. Finally, my results provide evidence for the utility of S-SDM approached in estimating fine-resolution, multi-species habitat amount metrics that embrace the unique ways in which individual co-existing species perceive and utilize habitat.

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