Amount of chaparral habitat at the landscape scale influences site level occupancy for three chaparral-associated bird species

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Blue-gray Gnatcatcher
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Abstract

To offset oak ecosystem loss and reduce the risk of severe wildfire, oak restoration in Oregon and California prioritizes protecting large oak trees and reducing the risk of high severity fire. Chaparral, a drought-tolerant plant community comprised of hard-leaved woody shrubs that do not require periodic wildfire to persist, is a common and natural understory in oak ecosystems, but is often removed to meet oak restoration goals. Wildlife often respond to restoration and management at multiple scales, making landscape-scale considerations an important component of restoration design, yet restoration practitioners lack information on how chaparral-associated bird occupancy may change following chaparral removal at local and landscape scales, in part because chaparral is difficult to map at large scales. To identify how chaparral-associated birds respond to habitat amount at local and landscape scales and inform restoration planning, we use recently developed 'species-centered' distribution models for five chaparral-associated species as a proxy for chaparral habitat amount. Using an independent dataset, we tested for occupancy of chaparral-associated birds in response to chaparral habitat amount at local (150m) and landscape (10000m) scales. Our results indicate that Blue Gray Gnatcatcher and California Towhee occupancy was predicted by an interaction of local and landscape habitat amount, Bewick's Wren occupancy was predicted by landscape habitat amount, and we found no effect of habitat amount on Lazuli Bunting occupancy. Our results suggest that when chaparral removal is warranted, chaparral species occupancy in retained patches following chaparral removal will be higher in landscapes where chaparral is abundant in a 10,000m radius.

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Introduction

Oak woodland, chaparral, and prairie ecosystems are some of the most biologically diverse in the Pacific Northwest; yet oak habitats have declined by as much as 90% in the last 150 years (Vesely and Rosenberg 2010, Oregon Department of Fish and Wildlife (ODFW) 2016). In southern Oregon and northern California these ecosystems were historically maintained by a mixed-severity fire regime (Oregon Department of Fish and Wildlife (ODFW) 2016), resulting in a mosaic of habitats. In addition to habitat loss, a century of fire suppression has further degraded oak woodland and chaparral ecosystems by shifting the fire regime. The likelihood of high severity fires burning in the region's remaining oak woodlands has increased, particularly as a result of conifer tree encroachment (Oregon Department of Fish and Wildlife (ODFW) 2016). Oak-associated bird species have declined as habitat has been reduced or degraded, making oak habitat restoration a conservation priority (Rosenberg et al. 2016).

To offset oak ecosystem loss and reduce the risk of severe wildfire, oak restoration in Oregon and California prioritizes protecting large oak trees and reducing the risk of high severity fire (Hosten et al. 2006). However, chaparral, a drought-tolerant plant community comprised of hard-leaved woody shrubs that do not require periodic wildfire to persist, is a common and natural understory in oak ecosystems (Halsey 2007). Due to concern that chaparral may contribute to high severity fire, chaparral is often removed in an effort to meet restoration goals.

Restoration goals should include maintaining adequate chaparral in other areas to meet diverse needs of oak and chaparral-associated wildlife species, requiring trade-offs in restoration planning to ensure a gradient of vegetation structure and composition (Hosten et al. 2006). When removal of chaparral is warranted to meet the needs of oak restoration objectives, it is also important to evaluate approaches to chaparral removal, including the specific removal techniques (Alexander et al. 2007, Seavy et al. 2008), patch size requirements of wildlife species (Stephens and Gillespie *in review*), and the amount and distribution of chaparral retention across landscapes to best meet additional restoration goals, such as promoting healthy habitat for wildlife.

Wildlife often respond to habitat conditions at multiple scales (Ricklefs 1987, Sisk et al. 1997). While local habitat availability is necessary for species occupancy, local habitat management can fail when ecological conditions at larger scales are not considered (Jorgensen et al. 2014). Landscape-scale processes (i.e., beyond the typical home range of an individual) can influence species occupancy through habitat selection cues, life-history expression, predation risk, or dispersal. Local and landscape land cover often interact to drive processes that predict habitat use (Buler et al. 2007), and landscape structure has been identified as important in predicting local bird species abundance in managed landscapes (McGarigal and McComb 1995). Thus landscape-scale processes may contribute to wildlife management success by limiting habitat use in fragmented landscapes and/or by enhancing habitat use in sites where surrounding habitat is most abundant. Given the likelihood that following local management activities, the occupancy of remaining chaparral vegetation by focal bird species may be affected by the surrounding landscape, restoration planning requires information concerning how bird species may respond to habitat availability at multiple scales.

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Still, the information needed for determining priority of restoration sites and practices is limited, in part because the mechanisms which may predict species response to management at local and landscape scales are complex and can be unpredictable in novel ecological conditions created by anthropogenic land-use change (Robertson and Hutto 2006). Unfortunately, information concerning how species respond to habitat conditions at scales beyond local vegetation composition is challenging to obtain (Jones 2011), and may be difficult to summarize in a way that is useful for restoration or conservation planning for multiple species (Poiani et al. 2000). Moreover, it remains logistically challenging to make decisions which take landscape-scale habitat into account, because sufficiently fine-resolution maps of specific habitat features are challenging to obtain at the scale of typical management or restoration projects (Betts et al. 2006*b*). For example, in oak ecosystems, restoration requires planning for a gradient of vegetation community types, including oak forest, oak woodlands, oak-chaparral, and oak savanna, each of which may support different wildlife species. Thus, habitat requirements for chaparral-associated species must be considered in oak restoration planning in order to balance the needs of multiple species simultaneously. When some chaparral removal is necessary to meet oak restoration objectives, understanding the scale at which species respond may be useful for prioritizing sites for chaparral retention across landscapes to achieve wildlife objectives. Specifically, more information is needed to determine how chaparral-associated birds may respond to chaparral removal as a gradient of oak woodland habitats are restored across southern Oregon and northern California.

Practitioners have historically relied on information gathered from wildlife surveys to guide future and ongoing restoration and management decisions. Bird species in particular are highly mobile and respond quickly and consistently to changes in vegetation structure and composition, thus acting as indicators of management successes or failures (Hutto 1998, Carignan and Villard 2002). For example, occupancy of focal bird species has been successfully applied to evaluate the efficacy of different chaparral removal treatments (Alexander et al. 2007, Seavy et al. 2008), and patch area sensitivity for chaparral-associated species (Stephens and Gillespie, in review). A study in oak-chaparral has demonstrated that key chaparral-associated bird species may be more likely to occupy large patches of chaparral (Stephens and Gillespie, in review). Inferences from two case-studies suggest that shrub associated bird species such as Bewick's Wren and Wrentit may be less abundant in treatment plots which remove large areas of chaparral with mechanical mastication techniques (Seavy and Alexander 2008), versus hand-piled removal techniques to remove smaller patches of chaparral (Alexander et al 2007). Although these studies can inform decision-making regarding the chaparral patch retention area and techniques used in chaparral reduction, the scale is limited to local responses, which may fail to address how landscape-scale habitat availability may influence local bird species occupancy.

Species distribution models (SDMs) use wildlife survey data and spatially-explicit landcover and climatic variables to predict species occurrence across a geographic range, and are increasingly used by management agencies for conservation planning (Guisan et al. 2013). Importantly, SDMs have the potential to predict ecological species-habitat relationships while incorporating meaningful ecological relationships which may operate at multiple spatial scales (Elith and Leathwick 2009). Recently, in an effort to reduce uncertainty and error associated

with classified landcover layers in distribution modeling, which can bias definitions of habitat because they rely on human-defined general classifications of landcover and vegetation type, ecologists have explored the application of unclassified remote sensing imagery in species distribution models (Shirley et al 2013) to create so-called "species-centered" habitat distribution models (Betts et al 2014). Unlike other species distribution models that restrict species habitat definitions to previously defined vegetation cover classes, species-centered modeling recognizes that habitat is a species-specific concept and defines habitat on a continuum of probability of occupancy. Because species-centered distribution maps define habitat based on actual predictions of species occurrence rather than human-delineated vegetation classifications, they have potential to be used as a relatively fine-scale proxy for defining habitat across landscapes (Betts et al 2014). Using species distributions for chaparral-associated bird species may be an opportunity to define chaparral habitat at local and landscape scales.

Here, we used species distribution models (SDMs) for a suite of focal chaparral-associated bird species (Blue-gray Gnatcatcher (*Polioptila caerulea*) (Vroman 2003), Bewick's Wren (*Thryomanes bewickii*) (Peck 2003), California Towhee (*Melozone crissalis*) (Tutland 2003), Lazuli Bunting (*Passerina amoena*) (Dowlan 2003), and Wrentit (*Chamaea fasciata*) (Hunter 2003) to predict their probability of occurrence across a regional management area in southern Oregon and northern California. We then used a summed or "stacked" (S-SDM) method to calculate an index of chaparral habitat amount at both local and landscape scales. Our objectives were to 1) determine whether a calculated index of local and landscape chaparral habitat amount can predict occupancy of focal chaparral-associated bird species, and 2) if so, identify the relative importance of local- and landscape-scale habitat amount on local occupancy of a suite of focal chaparral-associated bird species.

Methods

We modeled species distributions in the Klamath Mountains ecoregion in southern Oregon and northern California (US EPA 1996). The area is defined by the Klamath and Siskiyou mountain ranges, incorporating portions of the Klamath, Rogue, and Umpqua river watersheds (US EPA 1996).

Survey data

Species presence/absence from point count bird monitoring data collected from 2000 to 2016 for the Klamath Bird Monitoring Network (Alexander et al. 2004., Alexander 2011) was used as the response (or 'training') data in distribution models for five chaparral-associated bird species (Table 1). Counts were conducted within four hours of sunrise between mid-May and early-July to coincide with hours of peak forest bird activity during the main portion of the breeding season, using 5-minute variable-radius point count methodology (Ralph et al. 1993, Stephens et al. 2010). If locations were surveyed more than once, we randomly selected one survey to include in the model training dataset. We truncated surveys to only individuals that were detected within a 75m radius in order to optimize bird detections while minimizing the possibility of Type II error (i.e., false absences). The final dataset used to develop models included 6055 unique survey locations from surveys in years 2000 to 2015. We reserved all

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point counts conducted in 2016 (263 unique locations) as an independent data set for testing species response to multi-scale habitat amount (see below).

Predictor variables

To overcome the challenges of incomplete or incorrect classification for chaparral vegetation types across our study region, we used temporal median composites (Ruefenacht 2016) of unclassified Landsat 5 Thematic Mapper (L5 TM), Landsat 7 Enhanced Thematic Mapper (L7 EMT+) , and Landsat 8 Operational Land Imager (L8 OLI) imagery as land cover predictor in focal species SDMs (following Shirley et al. 2013). All the Landsat images were acquired from USGS (http://landsat7.usgs.gov/index.php). Landsat images are taken globally on a 16-day cycle, and are collected in the form of 170 km x 183 km overlapping scenes with a 30m^2 pixel resolution. Because each Landsat scene contains a certain percentage of pixels that may unusable due to cloud cover or some other disturbance, composites of all available Landsat scenes in a given area across a given time period have the benefit of providing a more spatially continuous, cloud-free, and overall more robust image for ecological modeling than the image from any one date could provide (White et al. 2014, Ruefenacht 2016).

For compositing, we selected all available Landsat scenes that directly covered the study area or overlapped with scenes covering the study area, and which fell within the greenup-to-senescence period of June 1 to October 15 (identified with an NDVI profile) for each of the years in which point count training data were collected (2000 through 2015). All scenes were atmospherically corrected using LEDAPS (Ruefenacht 2016, Masek et al 2012) and cloudy pixels were removed using CFMask (USGS 2016). Finally, for all non-infrared Landsat bands (1, 2, 3, 4, 5 and 7) the median value of each pixel from the available images (minus the pixels excluded by the cloud mask) was found, and used as the final pixel values in the composite images (Ruefenacht 2016). The performance of median composites has been shown to be comparable to other compositing methods for use in ecological modeling (Ruefenacht 2016).

L5 TM data were used in composites for years 2000 through 2011. L7 ETM+ data were used for 2012, as L5 was decommissioned in 2011. Because L7 used a similar sensor to that used in L5, reflectance data from these two Landsat missions is compatible. The 2012 L7 data were impacted by the failure of the Scan Line Correcter (SLC), which left regular 'no data' gaps in 22% of each scene collected by L7; this issue is referred to as 'SLC-off'. SLC-off-impacted (i.e., 'no data') pixels were excluded from the calculation of the median pixel values. The compositing took advantage of overlapping L7 scenes to fill in some of the missing pixel values. However, due to the large proportion of each image affected by SLC-off, a very small proportion of pixels in the final composite may have had no valid observation. While it is possible to interpolate values from surrounding valid pixels to fill in SLC-off data gaps, we chose not to do this to avoid the potential model error associated with creating synthetic pixel values. Additionally, many SLC-off areas filled in by overlapping adjacent scenes have values appreciably different than surrounding pixels, creating visible stripes in the final composite. Due to the relatively small number of L7 scenes available from which to create composites for 2012, any great phenological differences between images used to calculate medians for areas affected versus not affected by SLC-off are apparent. To validate the use of L7 composites in distribution models, we visually inspected images where the SLC-off pixels reduced the data

available in the composite to ensure there were no apparent data gaps, and further verified the relative negligible impact of the SLC-off images by running a series of test models with and without the 2012 data, verifying that the model performance and relative weight of the predictor variables did not differ as a result of variance introduced by the SLC-off pixels.

For years 2013 - 2016, data from Landsat 8 Operational Land Imager (L8 OLI), which launched in 2013, were used to create composites; this avoided data issues inherent in SLC-off L7 images from this period. Because L8 uses a different sensor than previous Landsat missions, it was necessary to 'harmonize' the L8 reflectance data to make it compatible with that from L5 and L7. For each L8 image in the study area, using the closest least cloudy L7 image as a reference, pseudo invariant pixels between the two images were found, a reduced major axis regression model was developed band-by-band between each L8 image and L7 reference pair, and finally the regression coefficient was applied to reflectance values of each band in each L8 image to harmonize them to the L7 values (Roy et al. 2016). Buyantuyev et al. (2007) suggested that because reduced major axis regression does not assume that the independent variable was measured without error (unlikely in the case of remote sensing of ecological systems), it may be preferred to ordinary least squares regression for harmonizing of remote sensing products. For all non-infrared bands (1, 2, 3, 4, 5 and 7) we calculated means and standard deviation of reflectance values from the composite Landsat images at radii of 150, 500, 1,000, and 2,000 meters using a moving window analysis in GIS to capture the influence of land cover at multiple scales relevant to bird habitat use and life-history (following Shirley et al. 2013). We associated mean and SD values to each point count location to corresponding to the year the data at each location were collected.

We used 800m resolution climate raster layers from the PRISM Climate Group at Oregon State University, which provide spatially referenced monthly climatic conditions calculated as 30-year means from 1981 to 2010 (OSU 2011). We used a total of seven climate variables: mean July precipitation (annually the lowest precipitation mean for this region), mean December precipitation (annually the highest precipitation mean for this region), maximum July temperature (annually the highest mean temperature for this region), minimum December temperature (annually the lowest mean temperature for this region), and June mean precipitation, minimum temperature, and maximum temperature (corresponding to mid-breeding season for bird species in our study region). We resampled raster layers to a 30m resolution to correspond to the resolution of the land cover variables. Finally, we extracted elevation data for all survey locations from a 30m resolution DEM to (USGS 2016).

Species distribution model development

We developed species distribution models using data from 2000-2015. We used boosted regression trees (BRT) to develop a series of individual predictive species distribution models for bird species within the study area (Elith et al. 2008). BRTs have been increasingly used and tested in ecological applications (Elith and Graham 2009, R Core Team 2015, Benito et al. 2013), and are powerful in that they model both non-linear relationships and interactions among predictors, can be used with a variety of response distribution types, and allow for a large number of predictor variables without overfitting. We fit all BRT models using the package 'dismo' in R (R Core Team 2015), with additional source code from Elith et al (2008).

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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). When necessary, lr was adjusted slightly for some species to optimize the number of trees produced (with a goal of at least 1000 trees, as recommended by Elith et al 2008). We evaluated the predictive success for each model by examining the area under the receiver operator curve (AUC) created by the internal ten-fold cross validation procedure in package 'dismo' (Elith et al 2008). We used a 0.7 AUC threshold to evaluate model performance, which is a standard threshold for reliable species distribution models (Lobo et al. 2008, Elith and Graham 2009).

Calculating "habitat amount"

We used a 'stacked' SDM (S-SDM) method to convert probability of occurrence for all five focal species (Blue-gray gnatcatcher, Bewick's wren, California Towhee, Lazuli bunting, and Wrentit) into a single metric representing habitat amount for all five species. Although other bird species will utilize oak-chaparral habitat, we selected these species assuming they were the most frequently and reliably associated with chaparral in this region, so as to calculate a relatively conservative representation of chaparral habitat amount. We summed probability values for all species on a pixel-by-pixel basis across the study area. While 'threshold' S-SDM methods are often used to generate species richness values for community analysis (Pellissier et al. 2013), threshold and summed probability S-SDM methods have been found to perform similarly for predicting local species richness in our study region (Halstead 2013). As a continuous metric for chaparral species was more relevant for determining chaparral habitat amount at local and landscape scales, we deemed summed probability of occurrence more appropriate for our analysis (Betts 2007, Betts et al. 2014). Although there are other bird species known to use chaparral patches in oak/chaparral vegetation communities, we limited our species list to focal species known to be closely associated with chaparral vegetation types, in order to ensure a consistent and conservative chaparral habitat amount metric across the study region (Fahrig 2013). We used Landsat composite images for 2016 so as to have a habitat amount value for the year in which we were testing independent survey points for the analysis of species occupancy in response to local and landscape habitat amount (see below). We used a moving window analysis on the stacked SDM which summarized the mean chaparral habitat amount value at a 150m radius (relevant to the home-range size of our focal species), and at three different radii (2,000m, 5,000m, and 10,000m) representing 'landscape' scale radii that have been found in other studies to be meaningful predictors of bird occupancy (following Betts et al 2006), restoration success (Crouzeilles and Curran 2016), and also relevant to typical management and restoration units for oak chaparral habitat.

Testing species responses to multi-scale habitat amount

We tested the ability of S-SDM-defined local and landscape 'habitat amount' to predict the occupancy of four focal chaparral-associated bird species (Blue-gray gnatcatcher, Bewick's wren, California Towhee, Lazuli bunting) in the independent survey dataset from 2016 with survey points not included in species distribution development. Due to insufficient sample size, we were unable to test occupancy of Wrentit. We associated chaparral habitat amount at 150, 2,000, 5,000, and 10,000 to independent presence/absence data collected in 2016 using

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identical methods to those described above. We determined correlation between local habitat amount and landscape amount at 2,000, 5,000, and 10,000m (Table 1), and subsequently selected the average habitat amount at 10,000m radius to serve as the landscape habitat amount because it was the least correlated with local habitat amount at 150m radius. We used a series of general linear models (GLMs) with a binomial distribution and a logit link to test for occupancy of each of the four focal species, using habitat amount at local (150m radius) and landscape (10,000m radius) plus an interaction as predictor variables. We grand-mean scaled each habitat amount metric to one standard deviation (i.e. 150m and 10,000m radii) to aid in model convergence and allow direct comparison of effect sizes (Gelman 2008). We checked for multicollinearity in each model by calculating a variance inflation factor (VIF) for model predictors (Zurr 2007).

Because spatial autocorrelation in ecological studies can violate statistical assumptions about independence in a dataset (Legendre 1993), and failing to account for spatial autocorrelation can lead to overestimation of habitat effects (Betts et al 2006), we tested for spatial autocorrelation in the GLM model residuals. We calculated an autocovariate term for each individual species model. We used package 'ncf' (Bjornstad 2016) to test for spatial autocorrelation in the residuals of each model, using a lag distance of 0.0025 decimal degrees (250m), the minimum distance between survey points in the dataset. We determined the distance at which there was significant spatial autocorrelation for each model, and developed an autocovariate term to account for spatial autocorrelation at that scale using package "spdep" and added it to all linear models (following Betts et al. 2009) (Table 1). We performed a subsequent post-hoc test on the residuals of the updated models to confirm that adding the autocovariate term reduced the influence of spatial autocorrelation.

Results

The five focal chaparral bird species distribution models had high cross-validation prediction success, with a mean AUC of 0.822 (Table 1); all were at or above the desired 0.7 AUC threshold. The summed probability of occurrence for all five focal species resulted in a chaparral habitat amount metric for the Klamath Mountains Ecoregion (Figure 1).

For GLMMs testing the ability of chaparral habitat amount to predict the occupancy of four focal bird species, the spatial autocorrelation term was significant for all species (Table 3). After controlling for the effects of spatial autocorrelation, we found significant effects of landscape habitat amount in three of four focal species (Blue-gray Gnatcatcher, California Towhee, and Bewick's Wren, Table 3). For Blue-gray Gnatcatcher and California Towhee, occupancy was associated with a negative interaction of local and landscape habitat amount (Table 3, Figure 2A, B). We found no relationship between local habitat amount and Bewick's Wren occupancy, but occupancy was higher as landscape habitat amount increased (Figure 2C). We found no significant effect of local and landscape habitat amount on Lazuli Bunting occupancy.

Discussion

We found that an interaction of local and landscape habitat amount defined by an S-SDM of five focal chaparral bird species predicted local occupancy for Blue-gray Gnatcatcher

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and California Towhee, and landscape habitat amount predicted local occupancy of Bewick's Wren; we found no effect of local or landscape habitat amount on Lazuli Bunting occupancy. Our results suggest that our defined proxy for 'chaparral habitat' successfully predicted local and landscape habitat associations of some, but not all, chaparral-associated birds.

In a previous study of patch size requirements for chaparral associated birds, Bewick's Wren, California Towhee, and Lazuli Bunting were significantly sensitive to patch area, exhibiting higher probability to occupy patches larger than 2ha (Stephens and Gillespie, in review). The results from the current study add to the previous results for California Towhee, suggesting that in addition to local patch size, landscape-area chaparral amount facilitates California Towhee occupancy in our study region. Yet while Blue-gray Gnatcatcher did not exhibit significant patch-area sensitivity in the previous study (Stephens and Gillespie, in review), Blue-gray Gnatcatcher occupancy did demonstrate significant positive relationships with both local and landscape scales in this study, suggesting that Blue-gray Gnatcatcher may be more likely to occupy patches when landscape-scale habitat amount is high.

While our results show that increasing habitat amount at both the local and landscape scale increase occupancy for California Towhee and Blue-gray Gnatcatcher, we also found a significant negative interaction term. In both models, as landscape habitat amount increases, the relationship between local occupancy and local habitat amount changes. Both occupancy models demonstrate that at higher landscape habitat amounts, the probability of occupancy at lower local habitat amounts is higher, yet at very high local habitat amounts, the probability of occupancy at different landscape habitat amounts is similar (Figure 2A, 2B).

In particular, the contrast between the two studies highlights the importance of considering factors in the landscape which may influence patch occupancy at local scales. For example, our results suggest that as chaparral amount increases at the landscape scale, the amount of local habitat needed for occupancy of Blue-gray Gnatcatcher decreases. Therefore, it is possible that the influence of abundant chaparral on the landscape reduced the effect of local patch size on Blue-gray Gnatcatcher occupancy in the previous field study (Stephens and Gillespie 2016, in review).

Spatial autocorrelation was significant in all species models, highlighting the importance of considering spatial autocorrelation in examination of results and interpreting predictions from species distribution models (Betts et al. 2006a). It is also important to note that numerous biotic and abiotic process can contribute to spatial autocorrelation (Legendre 1993), some of which have implications for local and landscape scale processes which may drive species occupancy. For example, spatial distribution of ecologically-meaningful habitat characteristics (predator communities, vegetation composition, etc) plays an important role in species distributions and is unevenly distributed across landscapes. Thus by adding an autocovariate term to the models and reducing the variance associated with spatial autocorrelation *per se*, we were able to identify important overarching relationships between species occupancy and local and landscape habitat amount independent of spatial autocorrelation. Still, it is important to note that adding a spatial autocorrelative term to the models may in fact have reduced our ability to test for some local and landscape-scale processes which are often spatially correlated, and could potentially explain our failure to find significant effects of local and landscape habitat amount on Lazuli Bunting occupancy.

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Similar to other recent studies (Shirley et al 2013, Halstead 2013, Betts et al 2014), our results demonstrate the utility of using stacked "species-centered" models to estimate spatially-explicit habitat availability for focal species (Betts et al. 2006). Using species-centered definitions of habitat reduces bias and potentially heightens precision for quantifying habitat amount compared to models that use vegetation layers, as species distribution models can predict habitat features and species occupancy more reliably than traditional classified land cover layers (Betts et al 2014). In addition, using raw Landsat data to parameterize species distribution models improves species-centered distribution models by bypassing human-delineated vegetation layers altogether, avoiding some of the possible errors inherent in landcover classification. Still, while this approach provides more accurate predictions of species occurrence (Betts et al. 2014), it can be challenging to translate multiple species distributions into meaningful recommendations for practitioners focused on the management of a particular vegetation type. By stacking multiple species distributions for focal species with similar habitat associations across a region, we were able to examine species response to a proxy for local and landscape habitat amount. Using relatively fine-scale and continuous species-centered habitat amount values in this study provided predictions of local and landscape-scale habitat relationships that may have been difficult to determine using coarse-scale delineated vegetation layers (e.g. from the USGS National Gap Analysis Program), which do not delineate oak-chaparral habitat specifically (https://gapanalysis.usgs.gov/).

For the three species that exhibited landscape-scale sensitivity in this study, factors beyond local chaparral removal may need to be considered when planning for management actions which affect habitat for chaparral associated birds. Blue-gray Gnatcatcher, Bewick's Wren, and California Towhee were all more likely to occupy sites with more landscape habitat amount. That the probability of local occupancy changes as landscape-scale habitat amount increases is consistent with other studies examining thresholds in songbird occupancy as a function of habitat amount at a large radius. Forest songbirds fail to occupy local habitat patches when the summed probability of occupancy is low in a 2000m radius (Betts et al. 2007), and species associated with early-seral broadleaf habitat exhibited a threshold in local occurrence when broad-leaf forest was limited in the surrounding landscape (i.e., a 2,000m radius) (Betts et al. 2010). While we did not examine thresholds in occupancy in this study, we did find a significant effect of the interaction of local and landscape habitat amount for two of our focal species, suggesting that the amount of habitat available at the landscape scale is especially relevant to local occupancy when local habitat amount is limited (Figure 2A-B).

Considering landscape context is an important, but often overlooked, component of restoration design. Our results suggest that when chaparral removal is warranted, chaparral species occupancy in retained patches following chaparral removal will be higher in landscapes where chaparral is abundant in a 10,000m radius. Our results are consistent with studies in other ecological systems that have demonstrated that amount of habitat at the landscape scale is positively correlated to site level restoration success in riparian (Gardali and Holmes 2011) and forest (Crouzeilles and Curran 2016) habitats. Prioritizing chaparral retention in landscapes with more chaparral may thus offer restoration practitioners more flexibility and provide the greatest likelihood of providing adequate chaparral for bird species following oak restoration projects.

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Tables

Table 1. AUC (area under the receiver operator curve) results from boosted regression (BRT) models for five focal chaparral-associated bird species. AUC ranges from 0-1; values above 0.7 are considered acceptable for reliable predictions of species occurrence (Elith et al 2008).

Species	Species Code	AUC (SE)
Blue-gray Gnatcatcher	BGGN	0.899 (0.006)
Bewick's Wren	BEWR	0.922 (0.007)
California Towhee	CALT	0.905 (0.013)
Lazuli Bunting	LAZB	0.84 (0.007)
Wrentit	WREN	0.835 (0.009)

Table 2. Correlation matrix (R^2) between local habitat amount (150m) and landscape habitat amount calculated at three separate radii.

Scale comparison (m)	Correlation (R^2)
150 v 2000	0.822
150 v 5000	0.761
150 v 10000	0.688

Table 3. Results from GLMs examining the influence of local and landscape habitat amount for each of four focal species. "Space" are parameter results for the spatial autocovariate term that was included in the model to reduce the variance associated with spatial autocorrelation. See Table 1 for species code definitions.

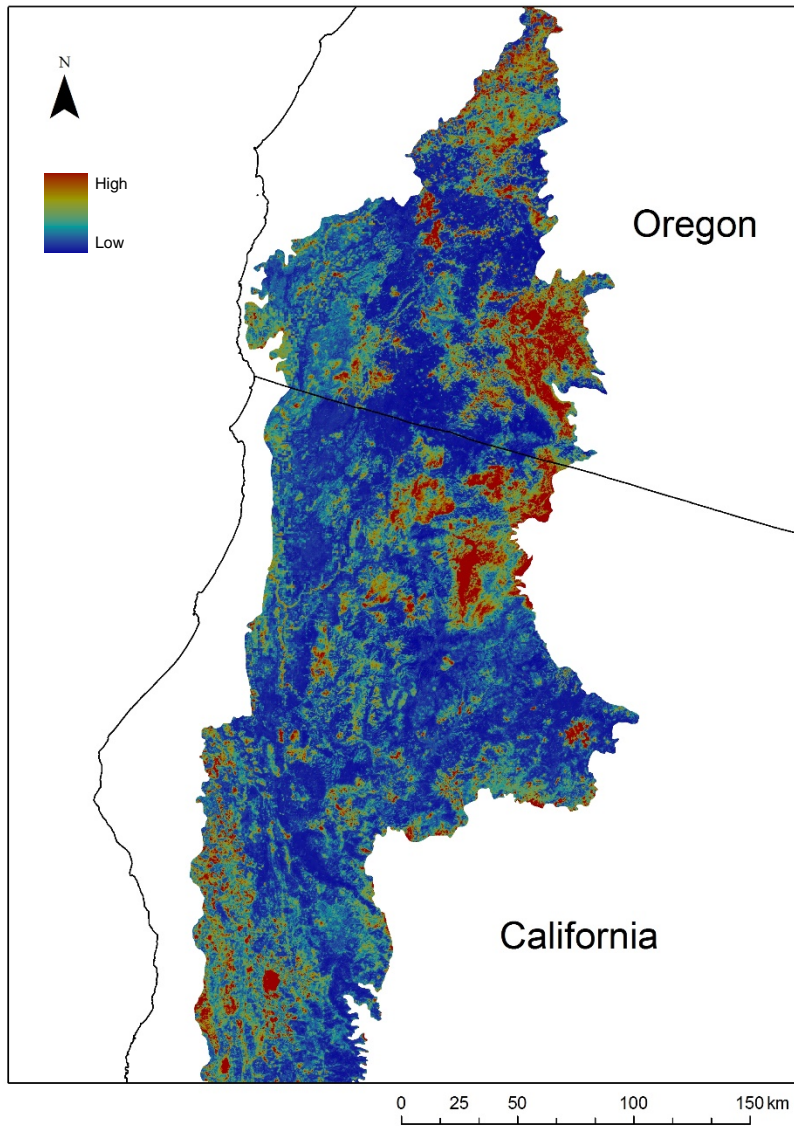|	BGGN		BEWR		CALT		LAZB	
	β (se)	p	β (se)	p	B(se)	p	β (se)	p
Intercept	-1.36 (0.17)	**<0.001**	-0.81 (0.19)	**<0.001**	-2.19 (0.45)	**<0.001**	-0.19 (0.16)	0.25
Local	0.33 (0.25)	0.20	0.44 (0.26)	0.11	1.23 (0.43)	**<0.01**	0.19 (0.20)	0.34
Landscape	0.55 (0.25)	**<0.05**	0.91 (0.27)	**<0.01**	1.50 (0.51)	**<0.01**	0.02 (0.19)	0.92
Local x Landscape	-0.78 (0.32)	**<0.05**	-0.50 (0.32)	0.12	-1.46 (0.55)	**<0.01**	-0.37 (0.21)	0.07
Space	2.37 (0.85)	**<0.01**	-0.01 (0.78)	0.98	5.30 (2.02)	**<0.01**	3.12 (0.62)	**<0.001**

Figures

Figure 1. Predicted species-centered chaparral habitat amount based on summed probability of occurrence for five chaparral associated focal species across the Klamath Mountains Ecoregion. Color scale ranges from blue (lowest habitat amount) to red (highest habitat amount).
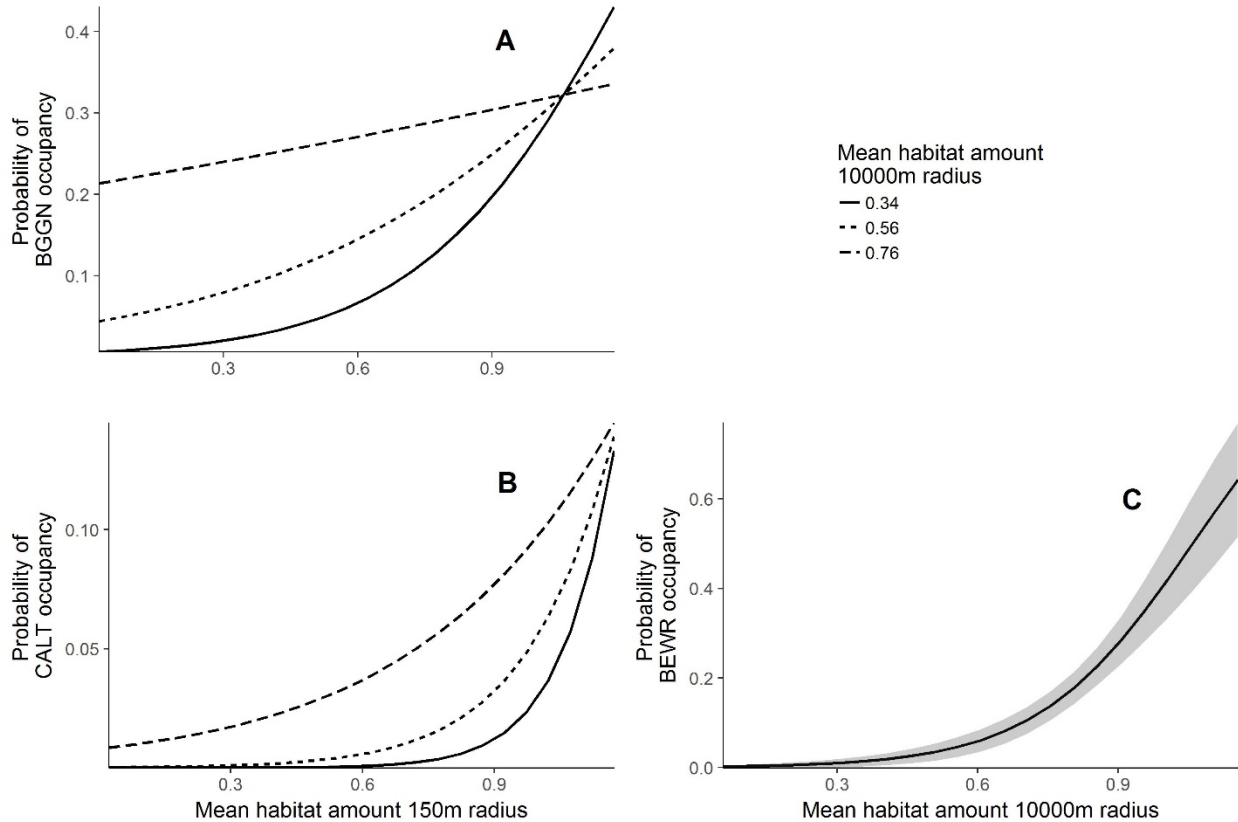
Figure 2. Probability of local occupancy (within 75m of a survey point) of focal chaparral associated birds according to mean 'habitat amount' metric calculated from a stacked species distribution model. BGGN and CALT occupancy was predicted by an interaction between local habitat amount (150m radius) and landscape habitat amount (10,000m radius) (A-B). BEWR occupancy was predicted by landscape habitat amount (C). Lines and shaded areas represent predicted probability with 95% confidence intervals from each model. In A and B, for ease of comparison landscape habitat amount is shown at the median (0.56), and first and third quantile (0.34, 0.76) in the dataset, and confidence intervals are not included. See Table 1 for species code definitions.