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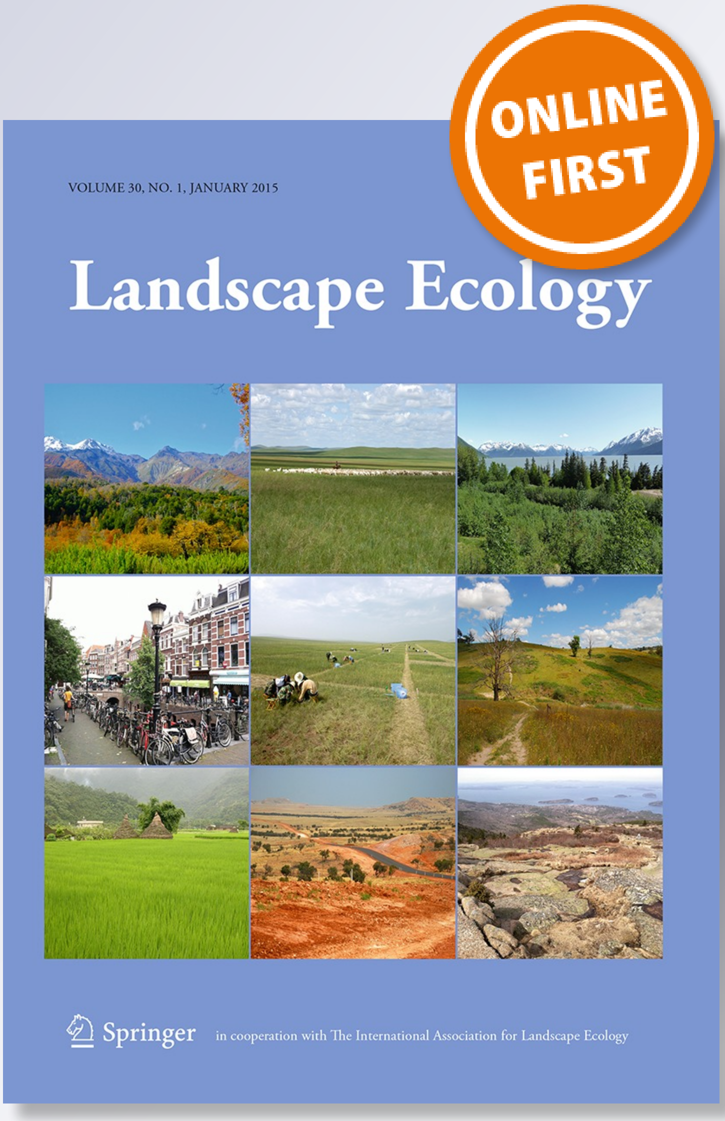

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RESEARCH ARTICLE

Relative influence of local and landscape factors on bird communities vary by species and functional group

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Abstract
Introduction Both fine scale patterns of vegetation and coarser scale landscape patterns affect bird community composition, but the relative importance of these two sets of patterns tends to be context dependent, varying by location and taxonomic group. Here, we explore the relative roles of landscape pattern and stand structure and composition in defining bird communities in 44 remnant oak stands in the Willamette Valley, Oregon. We focused on: (1) whether bird communities are influenced more by landscape (matrix and patch) patterns or stand composition and structure, and (2) in what contexts each of these spatial scales are more important. Specifically, we focused on how different groups of bird species (functional groups, synanthropic and non-synanthropic species, and individual species) were differentially influenced by landscape and more local patterns.
Methods We conducted point counts to determine avian abundance, richness and evenness and categorized birds into functional groups based on diet and foraging tactics. We then used canonical correspondence analysis and generalized linear models to analyze overall community patterns, functional group diversity, synanthropic and non-synanthropic species diversity and individual species' abundances.
Results Both local and landscape factors significantly influenced each group of avian species for every measure of diversity we tested, but their relative importance varied markedly. Local factors explained four times more variance than landscape factors for overall species diversity, whereas for functional groups, landscape factors explained one quarter to ten times the variance of local factors, depending on the group. For example, landscape factors were five times more important for the *corvidae* omnivores and ten times more important for the flycatchers than were local factors. By contrast, local factors were twice as important for seed eaters, frugivores and ground foragers, and bark foragers than were landscape patterns. We found the same high variability for individual species.
Conclusion We conclude that the relative contribution of factors at different scales to the structuring of bird communities (as with the effects of so many other ecological processes and patterns) strongly depends on context—in this case, the specific group of species being considered.

Keywords Avian · Birds · Matrix · Scale · Functional groups · Habitat · Community composition

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Introduction

Many forest birds throughout the US are in decline (Robbins et al. 1989; Butcher and Niven 2007). These declines have been attributed, in part to the loss, fragmentation and degradation of habitat (Askins and Philbrick 1987; Robinson et al. 1995). Although many studies have linked birds with specific aspects of vegetation and landscape patterns, researchers and managers still have a relatively rudimentary understanding of many of the factors that structure avian communities. One critical gap in this understanding is the degree to which bird communities are structured by local patterns of vegetation structure and composition versus landscape scale patterns and how these impacts change across different landscapes or for different communities.

It has long been known that ecological niches of many species can be defined by the structure and composition of vegetation (Grinnell 1917). For example, structural height diversity—the vertical complexity of vegetation—is a well-recognized driver of avian species diversity (MacArthur and MacArthur 1961; Moss 1978). Only more recently has it been established that birds respond to landscape patterns (e.g., Freemark et al. 1995; Hawrot and Nieme 1996). Initial studies predominantly focused on how patch size, shape and isolation influence species, populations and communities. However, area and isolation by themselves are often poor predictors of occupancy, and after patch area, the surrounding matrix often explains much of the variation in the composition of various wildlife communities (Prugh et al. 2008).

Although it is now well established that birds respond to both local vegetation structure and landscape patterns, it is far less clear whether the factors at one of these levels of organization are more important for explaining avian diversity or structuring communities than the factors at the other—and if so, under what conditions and for what groups of species that differential influence exists. For example, some studies find that local environmental factors are more influential in structuring avian communities (e.g., Roberts 2001; Fletcher and Hutto 2008) whereas others conclude that landscape factors are dominant drivers (e.g., Smith and Wachob 2006). Still others find that both local and landscape factors influence avian communities to varying degrees (e.g., Hodgkison et al. 2007).

Here, we investigate the degree to which local and landscape factors affect avian communities in the threatened Oregon white oak (*Quercus garryana*) savannahs and woodlands of the Willamette Valley, Oregon. Less than one percent of the historical oak communities remain and the remnant stands are scattered throughout the valley in relatively isolated patches or in the foothills of the Cascade and Oregon Coast Ranges (Noss et al. 1995). We explored patterns at three spatial scales for four groups of birds using multiple response variables. We assessed the relative influence of local, within patch variables (such as the number of tree stems and foliage height diversity), landscape patch variables (such as area and perimeter) and landscape matrix variables (such as percentage of surrounding area that is agricultural or developed land). We focused on avian diversity and composition of the entire bird community, of synanthropic and non-synanthropic species, of functional groups and of several individual species of concern.

Methods

Study area and site selection

The Willamette Valley covers approximately over 31,000 km^2 and is bounded by the Columbia River in the north, the Calapooya Mountains in the south and the crests of the Oregon Coast Range and Cascade Range in the west and east, respectively (Fig. 1).

The oak savannahs and woodlands within the Willamette Valley are predominantly on privately owned lands. Because of access issues, we chose sites opportunistically. We identified 103 survey points in 75 sites (oak patches), all strategically located within a 2 h drive of each other to maximize the number of sites visited per day within the short breeding season (Fig. 1). Sites ranged in size from roughly 596 to 401,729 m^2. Thirty-three sites (44 %) were located on private lands and 42 sites (56 %) on public lands. By under-sampling private lands, it is possible, if private lands differ significantly from public lands, that the results of our study are more representative of the drivers of bird community composition on public lands and are not as representative of the Willamette Valley as a whole. We define a site or oak "patch" as a distinct cluster of oak savannah (between 10 and 50 % tree cover) or woodland (greater than 50 % tree cover) containing at least 50 % *Q. garryana* (Garry oak) and/or *Quercus kelloggii* (California black oak) trees. All

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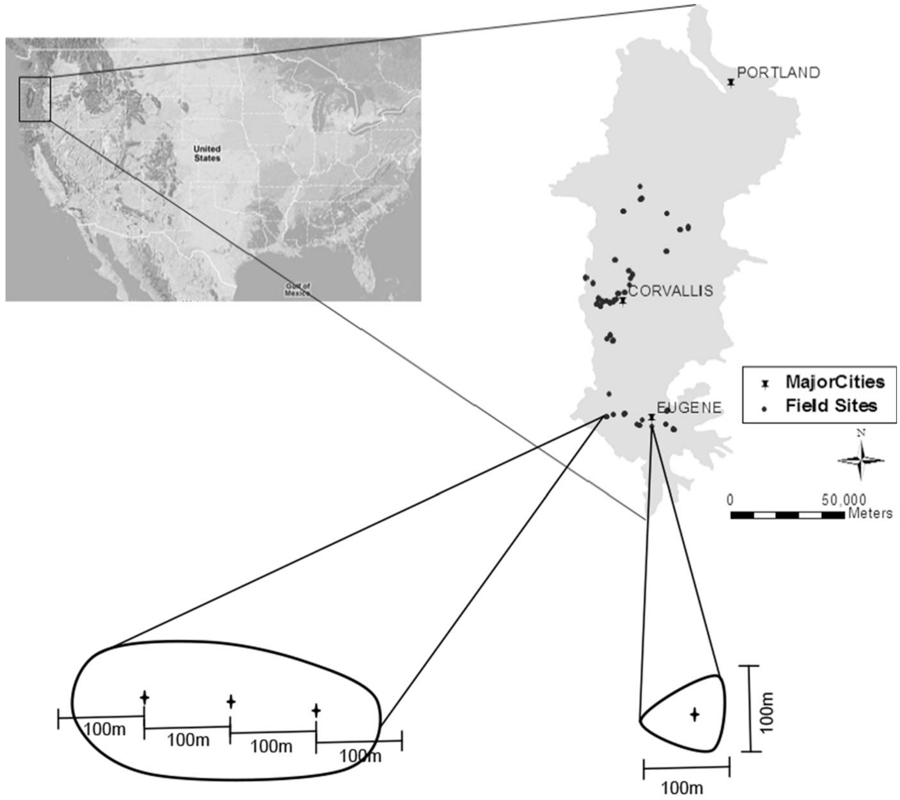

Fig. 1 Willamette Valley River Basin, Oregon, USA (*left*) and *inset* of field sites in the Willamette Valley (*right*)

Large site (greater than 100 m in at least one direction) – as many points as can fit within site 100 m from each other and edge of patch.

Small site – only one point per site, approximately in the center of the patch.

sites were dominated by these two oak species (>50 % oak) and were located in non-riparian areas.

Avian surveys

We conducted 50-m fixed-radius point-count surveys at 103 sample points (points) in the 75 sites, based on the methods described in Bibby et al. (2000) and Huff et al. (2000). Each location was visited four times over two years, two times per year during the breeding season of 15 May–8 July 2010 and 2011. We used a single observer for all sites in both years. All point counts were conducted between 0.5 h prior to and 4.25 h after sunrise. For each point, we recorded all birds identified by sight or sound during a 10-min period. Nocturnal species, raptors and birds that were flying over or through a site were noted but not further analyzed. Birds circling above the canopy and using the site were included in our analyses (e.g., swallows foraging above the canopy). Counts were not conducted in heavy rain or strong wind. We recorded the location (measured with a GPS) of each point.

To explore the impact of sampling intensity on detection, we visited a subset of 10 of the 75 sites 6–9 times (Supplementary Table 2). We chose these sites because they harbored a relatively large percentage of all bird species detected in the study (as assessed in the first couple of visits in year 1). We detected 52 of 68 species (76 % of all bird species in our study) in the subset over the two seasons. Every species detected in the subset of ten sites was detected a minimum of 44 % of the time. Because we visited all sites in our study more than 2.3 times (=1/0.44), we had a relatively high probability of detection at all 75 of our sites in four visits.

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The patchy nature of our habitat precluded using variable distance estimators and calculating detectability across distance (as opposed to through time as a result of sampling intensity). We assumed detection rates were comparable to similar bird studies in the region conducted in patchy habitats. In those studies, detection was greater than 90 % for 50-m fixed areas (Marzluff 2014). Because our fixed radius was a very small area, which, for some sites corresponded to the boundaries of the patch, detection should have been unaffected by vagaries of the landscape (Marzluff 2014).

Within each site, we located one to four points at which the point counts were conducted. Where the breadth of a site exceeded 100 m in at least one dimension, multiple counts were done, spaced at least 50 m apart, maximizing total possible points within each site while minimizing double-counting of birds across points (Fig. 1). For sites smaller than 10,000 m^2 (or with widths less than 100 m in any direction), a single point was located at approximately the center of the site (Fig. 1). To address sampling intensity bias, we evaluated our sites for significant, positive correlations between richness and number of sampling points per site and found a positive correlation with increased sampling intensity ($r = 0.85$, $P < 0.01$). To address this issue, for all sites with more than one point per site, we averaged richness across points and then across samples. Averaging across points eliminated sampling intensity bias ($r < 0.01$, $P > 0.98$). Thus, sites served as our experimental units for all analyses.

Local habitat characteristics

We selected local patch variables and applicable plot sizes based on a literature search of variables important to avian diversity (e.g., MacArthur and MacArthur 1961; James and Shughart 1970; Hagar and Stern 2001). We estimated canopy cover by averaging four densitometer readings at 0°, 90°, 180° and 270°, 1 m from the estimated centermost tree. We estimated average canopy height in the patch using a laser rangefinder. We counted the number of snags (standing dead trees) and fallen logs within a 0.04-ha circle centered on the point count. We counted the number of trees of each species within the same plot and placed them into one of seven size classes based on their diameter at breast height (dbh); <2.5, 2.5–8, 8–15, 15–23, 23–38, 38–60 and >60 cm. We calculated the total number of seedling (dbh <2.5 cm), sapling ($2.5 < \text{dbh} < 8$ cm) and large (dbh >8 cm) oak, non-oak deciduous, coniferous and total tree species. We estimated the percentage of ground covered by grasses or forbes, bare soil or litter, impervious surface and water within a 0.01-ha circle. Within the same plot, we estimated the percentage of the understory covered by tree saplings and the percentage covered by *Rhus diversiloba* (poison oak) and *Rubus discolor* (Himalayan blackberry)—the main invasive understory species in our sites. For each point, we counted the number of nest boxes (many sites were on private land and a few sites contained artificial nest boxes), noted the presence of recent tree harvest, cow and/or sheep grazing and estimated the percentage of impervious area and water within 50 m of the point.

Height diversity was measured based on the methods in Moss (1978). Using a ruler and a laser rangefinder for each vegetation layer, we measured the minimum, the maximum and the mode of vegetation heights at all points as well as the percentage of the modal vegetation covered at the center of the point and at four random points within 50 m of the center point. These layers included one or more ground cover, understory (shrub) and canopy (tree) layer.

Landscape characteristics

We used a Trimble Juno (GPS + handheld computer) and a TruPulse 360B Rangefinder installed with ArcPad 7.1.1 to map patch perimeters. Areas, perimeters, core areas and the ratios of area to perimeter were calculated for each patch using Hawth tools (Beyer 2006) in ArcGIS, v.9.3.1 (Environmental Systems Resource Institute, ESRI 2009). To assess the composition of the surrounding matrix, we used 425-m radius (small buffer) and 701-m radius (large buffer) digital plots, based on known territory sizes for bird species found in our sites (Poole 2005). Within each buffer, we calculated the percentage of the area covered by oaks, other trees, development, agriculture, and all "other" land cover (roads, water, bare ground, etc.) from a 30-m resolution land-cover layer (NatureServe 2005) with 81 % overall fuzzy accuracy and a 59 % deterministic accuracy (Jensen 2004).

Because some of our landscape-level plots overlapped in space, they were not totally independent. To increase their independence, we reduced overlap of the

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digital sample plots for our sites by eliminating 31 of our original sites. The remaining 44 sites had a maximum overlap of 25 % for small buffers and 30 % for large buffers. This resulted in mean overlaps of 3 and 6 % for small and large buffers, respectively. This also likely reduced any spatial autocorrelation across our sites. However, to specifically address the issue of potential spatial autocorrelation, we tested the residuals from all of our models using the Mantel test. The test found no spatial autocorrelation for overall bird richness, abundance or evenness with an alpha value of 0.05.

Data analyses

For each site, we computed three measures of avian diversity—abundance, richness and evenness. Mean relative abundance, calculated as the mean number of individual birds detected per site, per survey, has been shown to be preferable to other metrics of abundance (Hepinstall et al. 2008). We calculated richness as the mean number of species for each point over all visits, averaged for all points at the site. We calculated evenness using the Shannon Index for diversity.

We grouped bird species into functional groups based on each species' foraging habitat, behavior and food preferences (Ehrlich et al. 1988; Poole 2005) (Supplementary Table 3). Using the Cluster Package, Agnes method in R v.2.14.1 (R Development Core Team 2010; Oksanen 2014), we grouped species based on a hierarchical cluster analysis using Euclidean distance and the unweighted pair-group method using arithmetic averages with standardized variables having a zero mean and unit variance (e.g., Jaksić and Medel 1990). This process resulted in a dendrogram depicting potential cluster groups. Twenty functional groups were identified and used in subsequent analyses (Supplementary Table 3). We defined species as being synanthropic or non-synanthropic based on established lists in the literature (Johnston 2001; Donnelly and Marzluff 2006).

Canonical correspondence analysis (CCA)

We examined the effects of the local, patch and matrix factors on overall avian community structure using CCA in the Vegan Package in R (Oksanen 2011; Oksanen et al. 2011). CCA is a direct ordination technique that arranges sites and species along environmental gradients. We chose this approach because it can be used with large, complex data sets without preprocessing, it does not produce the arch effect found in other ordination techniques, it can handle rare species and it produces quantified effects of environmental variables on sites and species (Ter Braak 1986; Palmer 1993).

We reduced our list of candidate explanatory variables to six local and six landscape variables by excluding obviously correlated variables and variables with relatively uniform distributions across sites (Supplementary Table 4). We used a combined forward and backward stepwise model building approach in CCA in conjunction with Monte Carlo permutation tests (1,000 random permutations) to determine which of these environmental factors explained a significant amount of variation in the species communities across sites and which spatial scales (local, patch or matrix) were most influential.

We performed CCA and partial CCA on the overall bird community, on synanthropic and non-synanthropic groups of species separately and on species split into their functional groups. Partially constrained CCA allowed us to separate out the effect of one set of variables (e.g., local effects) after removing the effects of another set (e.g., landscape effects). Hence, we determined local, patch, matrix and shared (e.g., matrix and patch) effects for all of our sets of avian species.

Generalized linear models

We built generalized linear models (GLMs) to analyze the effects of local, patch and matrix variables on richness and abundance of all species, the richness and abundance of synanthropic and non-synanthropic species, the richness and evenness of our 20 functional groups, the abundance of each functional group and the abundance of four key species of concern. Three additional species of concern that we identified were found in fewer than 10 % of our sites, precluding the use of GLMs for these species. We used GLMs because our preliminary analyses showed no complex relationships, our data were continuous, and distributions were best approximated by or could be transformed to have normal distributions.

We constructed all possible models excluding interactions among variables. We used the R function "glmulti" and specified the family as Gaussian. We did not include interactions because we were

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interested in the basic influence of the main variables and comparing landscape and local characteristics, rather than interactions among the variables.

For the GLMs, we reduced our set of explanatory variables from the original list (Supplementary Table 4) by excluding one of any two explanatory variables exceeding a pairwise Spearman correlation of $|0.8|$ to limit collinearity (Riitters et al. 1995; Bollmann et al. 2005). Spearman correlations are nonparametric and best suited for our analyses. We arcsine-transformed all proportion data and used the square root transformation with variance stabilizing properties for all Poisson distributed data (Zar 1998). All GLM models were constructed in R.

We identified the best fit models by using the small sample size Akaike's information criterion ($\mathrm{AIC_c}$) to rank all candidate models (Akaike 1973; Burnham and Anderson 2002). We identified the lowest $\mathrm{AIC_c}$ ($\mathrm{AIC_{cmin}}$) as the best model and any models having an $\mathrm{AIC_c}$ of $\mathrm{AIC_{cmin}} - 2$ as viable alternatives (Burnham and Anderson 2002). We used R^2 (1 minus the residual deviance divided by the null deviance) values to evaluate model fit (Supplementary Table 5). We also used GLMs to partition the variation explained by local, landscape and shared local and landscape factors on the richness, evenness and abundance of birds for the groups described above. For analyses in which the null model was a viable model using the $\mathrm{AIC_c}$ criteria described above, we did not calculate the variation in avian diversity explained by local, landscape and shared (a combination of) local and landscape factors.

Results

We identified 5,840 birds of 74 species in our 75 sites (4,990 birds of 68 species after removing raptors, nocturnal species and birds flying over the sites). Of the 74 avian species identified, we classified 45 as synanthropic species and 29 as non-synanthropic (Supplementary Table 1). We identified seven sensitive and/or oak-associated bird species from the literature to be further analyzed—Acorn Woodpeckers (*Melanerpes formicivorus*), Anna's Hummingbirds (*Calypte anna*), Chipping Sparrows (*Spizella passerine*), Western Bluebirds (*Sialia mexicana*), Western Meadowlarks (*Sturnella neglecta*), Western Scrub Jays (*Aphelocoma californica*) and White-breasted Nuthatches (*Sitta carolinensis*) (Huff et al. 2005; Altman 2011).

An analysis of annual variation established that our results were not affected by yearly variation; hence we grouped all species data by sites for both years. An analysis of small versus large buffers showed no difference in results; hence we show all results for small buffers only. Mantel tests on the model residuals showed no spatial autocorrelation for overall bird richness, abundance or evenness with an alpha of 0.05.

We found that both local and landscape factors significantly influenced each group of avian species for every measure of diversity we tested, but their relative importance varied considerably. The variation explained by landscape factors ranged from one quarter to ten times as important as local factors. For each response variable and each bird group we analyzed, the composition of the surrounding matrix explained more variance than did patch variables. For overall bird diversity, patch variables were not significant. However, some groups and individual species were influenced by the size and shape of the patch and those influences differed among response variables as well.

Overall bird community and diversity

The results of the CCA on the total bird community showed that the composition of the local vegetation structure (local factors) was similar in importance to patch size, shape and surrounding matrix (landscape factors) in defining overall community structure (Fig. 2). At the landscape level, however, the surrounding matrix, which accounted for approximately 12 % of the explained variation, was much more important than patch area or perimeter, which together accounted for just 3.5 % of the variation (Figs. 2, 3). Together, all environmental factors explained 35.4 % of the variation in community structure (Fig. 2).

Our step-wise model building using CCA for the whole bird community corroborates the results of the overall CCA (Table 1). The amount of surrounding development and non-oak forests, as well as three local variables, contributed to the overall avian community structure. Monte Carlo permutation tests (1,000 random tests) found these five variables to be significant ($P < 0.10$). Patch variables of area and perimeter were not significant for organizing overall bird community structure ($P > 0.10$).

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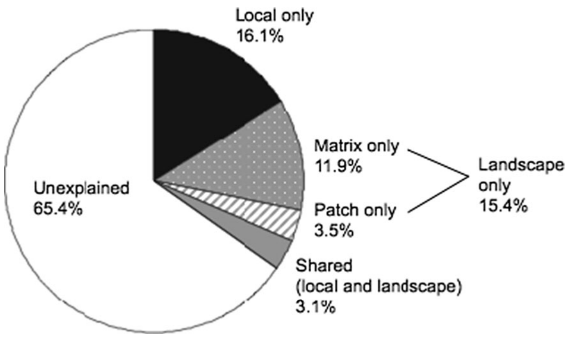

Fig. 2 Variation explained by local (*solid black*), landscape (*grey patterns*) and shared local and landscape (*solid grey*) factors for overall bird community structure. Landscape factors include both patch (*striped grey*) and matrix (*dotted grey*) variables

Our GLMs indicated similar impacts of local and landscape factors on overall avian richness and abundance (Table 2). Local and matrix variables each influenced both richness and abundance of the overall bird community in our oak patches. Richness was associated with height diversity, total number of stems, canopy cover, canopy height, amount of surrounding development and total number of large stems. Abundance was associated with the amount of surrounding agriculture, the amount of surrounding oak, canopy height, the total number of large stems and canopy cover. Although both local and landscape factors influenced richness and abundance, local factors were more important for richness (local explained 20 % of variance vs. just 5 % explained by landscape) than abundance (local and landscape factors were equally important; Table 2). In addition, area was not significant for either total species richness or abundance. All viable models are shown in Supplementary Table 6.

Synanthropy

Similar to our results for the entire bird community, landscape factors and patch-level factors were roughly equally important in structuring the community of synanthropic birds. Not surprisingly, GLMs showed that surrounding development and agriculture positively affected synanthropic birds, whereas the area of surrounding oak forest in the matrix was negatively correlated with synanthropic bird richness and abundance (Supplementary Table 5). Contrary to the

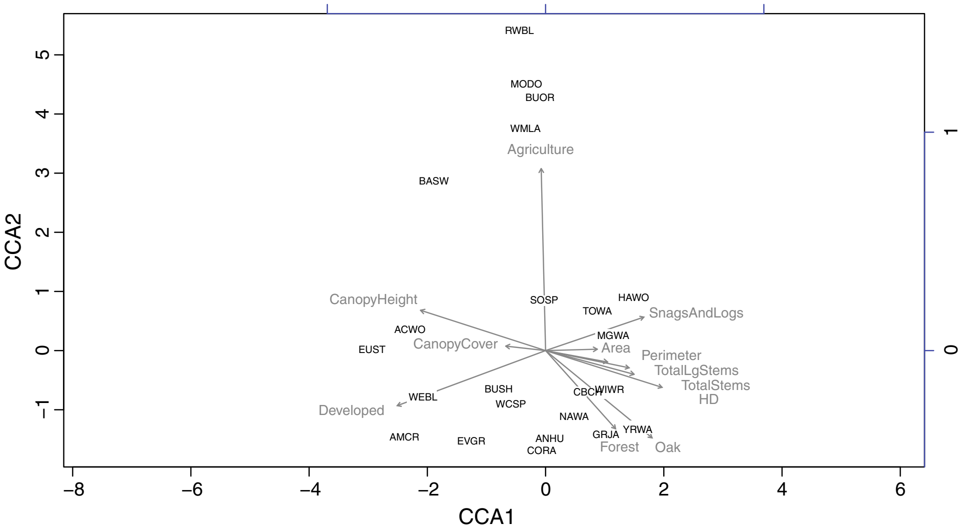

Fig. 3 Location of species scores defined by the first two axes of the canonical correspondence analysis (CCA) for overall bird community composition during the 2010–2011 avian breeding seasons in the Willamette Valley, Oregon. Environmental metrics are represented by *arrows* and text (*HD* height diversity) and species by their codes (*RWBL* Red winged Blackbird, *MODO* Mourning Dove, *BUOR* Bullock's Oriole, *WMLA* Western Meadowlark, *BASW* Barn Swallow, *SOSP* Song Sparrow, *TOWA* Townsend's Warbler, *HAWO* Hairy Woodpecker, *MGWA* McGillivray's Warbler, *CBCH* Chestnut-backed Chickadee, *NAWA* Nashville Warbler, *WIWR* Winter Wren, *YRWA* Yellow Warbler, *GRJA* Gray Jay, *ANHU* Anna's Hummingbird, *CORA* Common Raven, *WCSP* White-crowned Sparrow, *BUSH* Bushtit, *EVGR* Evening Grosbeak, *AMCR* American Crow, *EUST* European Starling, *ACWO* Acorn Woodpecker, *WEBL* Western Bluebird)

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Table 1 Summary statistics for the overall species canonical correspondence analysis (CCA) obtained from Monte Carlo significance tests and a step-wise CCA approach

Variable codes	F	P	Eigenvalue	Explained variance (%)
Developed (%)[b]	3.053929	0.01	0.186	7
Canopy height (m)[a]	1.673039	0.08	0.102	4
Total stems (#)[a]	1.592758	0.09	0.0971	4
Forest (%)[b]	1.423526	0.09	0.0868	3
Total large stems (#)[a]	1.404972	0.1	0.0857	3
Snags and logs (#)[a]	1.318787	0.14	0.0804	3
Oak (%)[b]	1.197904	0.3	0.0730	3
Perimeter (m)[b]	1.197283	0.24	0.0730	3
Canopy cover (%)[a]	1.109018	0.34	0.0676	2
HD (#)[a]	0.936969	0.71	0.0571	2
Ag (%)[b]	0.813851	0.68	0.0496	2
Area (ha)[b]	0.679916	0.93	0.0415	2
Total				35.4

CCA explained 35.4 % of the total variation in 68 bird species

[a] Patch (local) variables

[b] Landscape variables

effects on overall bird diversity and synanthropic community structure, area had a positive effect on synanthropic bird abundance (Supplementary Table 5) and landscape factors (11 % of the explained variance) played a slightly larger role than local factors (7 %; Table 2).

Landscape factors were much less important for non-synanthropic birds; 20 % of the variation explaining non-synanthropic avian community composition was attributed solely to local variables, compared to 11 % explained by landscape variables alone. Only 2.5 % of the variation was attributed to patch size and shape. Monte Carlo permutation tests in CCA revealed no significant landscape variables. Because the null model was considered a viable model, we did not evaluate the GLMs for non-synanthropic species richness or abundance (all viable models listed in Supplementary Table 6).

Functional group diversity

Using CCA to examine community structure based on functional groups produced results that were similar to those based on the CCA conducted using species. We found that local and landscape factors were approximately equally important in defining functional community composition, and patch size and shape contributed little to the community composition of functional groups. Nonetheless, there were some differences between species and functional groups when we modeled the potential drivers of functional group evenness and abundances. For example, area was a significant determinant of functional group evenness (Supplementary Tables 3, 5) and of the abundance of several functional groups. Of the five functional groups containing more than a single species and having only viable models that did not include the null model, three groups were influenced by area along with local vegetation and surrounding matrix variables (Supplementary Tables 3, 5).

Using GLMs to partition the magnitude of the effects that local, landscape and shared local and landscape factors had on richness, evenness and abundance, we found striking differences in the factors that influenced different functional groups. Landscape factors were five times more important for the *corvidae* omnivores and ten times more important for the flycatchers, whereas local factors were twice as important for the group of seed eaters, frugivores and ground foragers and the group of bark foragers (Table 2). We also note that the groups influenced by area were also the groups more affected by local factors than landscape factors (and vice versa; Table 2, Supplementary Table 5).

Species of concern

We found differences in the effects that local vegetation, patch shape and size, and the surrounding matrix had on the abundances of the individual species of concern. Although local vegetation characteristics and surrounding matrix most influenced community structure for the seven species of concern (Fig. 3), area did have an effect

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Table 2 Variation explained by local, landscape and shared local and landscape variables determined through generalize linear models for all bird groups analyzed

Scope	Diversity indicators	Local only (%)	Landscape only (%)	Shared (%)
Overall	Richness	**20**	5	1
	Abundance	**16**	**16**	4
Non-synanthropic	Richness	–	–	–
	Abundance	–	–	–
Synanthropic	Richness	–	–	–
	Abundance	7	**11**	3
Functional diversity	Richness	–	–	–
(where only functional group is listed, the abundance of that group was evaluated)	*Corvidae* omnivores	8	**38**	0
	Seed eaters, frugivores, ground foragers	**16**	8	2
	Bark foragers	**12**	6	0
	Flycatchers	3	**28**	0
	Foliage gleaners	**19**	14	0
	Vireos, sparrows, warblers	–	–	–
	Hummingbirds	–	–	–
	Swallows	–	–	–
	Evenness	**17**	11	0
Acorn Woodpecker	Abundance	**18**	8	5
Chipping Sparrow	Abundance	2	**13**	0
Western Scrub Jay	Abundance	3	**19**	0
White-breasted Nuthatch	Abundance	**18**	14	6

The level (local or landscape) that affects diversity more is highlighted in bold print. Variation is not provided where the null model is a viable model ($AIC_c = AIC_{cmin} \pm 2$; see Supplementary Table 5 for these values)

on the abundance of one species, the Chipping Sparrow (Supplementary Table 5). Higher Chipping Sparrow abundances were also associated with lower surrounding development, taller average canopy height, fewer total stems and a larger patch size. Both Western Scrub Jays and Chipping Sparrows were more influenced by landscape variables than by local variables, although Western Scrub Jays were only affected by the matrix surrounding the patch, not the size of the patch itself (Table 2; Supplementary Tables 5, 6). As expected, the Acorn Woodpecker, an oak dependent species, was more than twice as dependent on local environmental factors than the composition of the matrix surrounding the patch, and was unaffected by the size of the patch. The White-breasted Nuthatch was approximately equally affected by local and landscape variables, but not influenced by patch size.

Discussion

Although it is not surprising that different groups of birds respond differently to environmental patterns at different spatial scales, it is striking how much the relative contribution of local- and landscape-level factors varied across groups. Whereas local and landscape factors were approximately equally important in defining overall community structure and driving abundance (Fig. 2; Table 2), local factors were four times more important in predicting overall species richness (Table 2). Landscape factors were 5–10 times more important in explaining the abundance of *corvidae* omnivores (5 times), flycatchers (10 times), Western Scrub Jays (6 times) and Chipping Sparrows (6.5 times), whereas local factors were approximately twice as important to the abundance of seed eaters, frugivores and ground foragers, bark foragers, and Acorn Woodpeckers (Fig. 4).

Overall diversity

The difference we observed in factors associated with overall species richness and abundance is likely attributed to the types of species found in each patch and the way they use their environment, as well as the overall structure of oak forests in the Willamette

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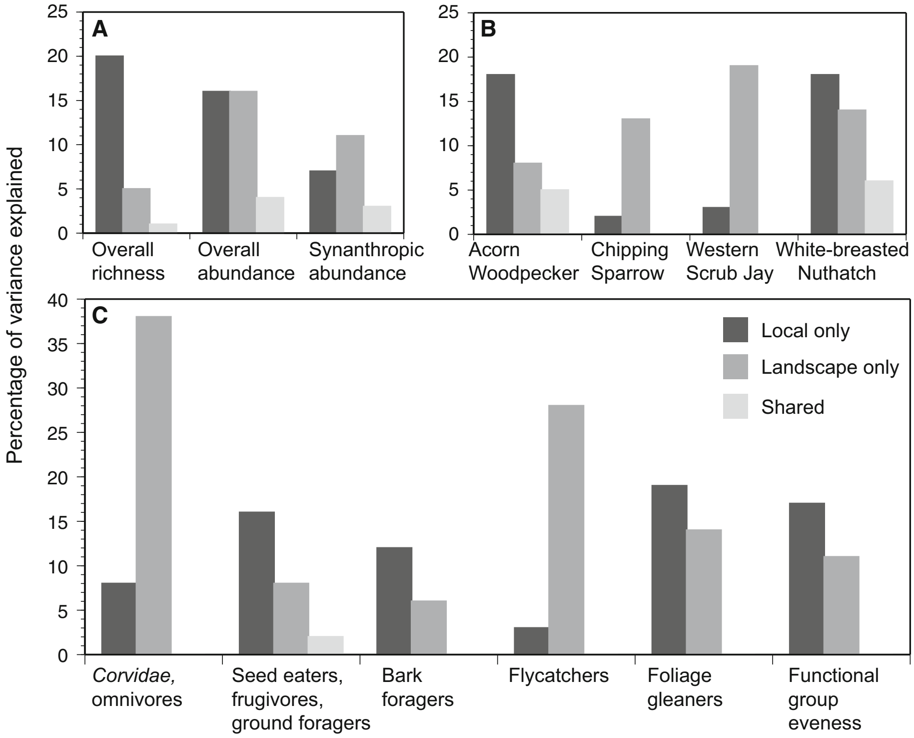

Fig. 4 Variation in **a** the overall bird community, **b** the abundance of specific species of concern, and **c** functional group abundance explained by local, landscape and shared local and landscape variables resulting from a set of generalize linear models. Groups and species for which the null model was a viable model ($AIC_c = AIC_{cmin} \pm 2$) are not represented

Valley. Surrounding agriculture and development bring more common species like American Crows (*Corvus brachyrhynchos*) and European Starlings (*Sturnus vulgaris*) that are often found in larger groups, but potentially fewer rare species or species found in smaller numbers, like many warblers, vireos and woodpeckers. Thus, the human-dominated landscapes surrounding some of our sites increase the total abundance of avian species within the encircled oak patches but not the total richness in those patches, as other researchers have found (Andrén 1994). Local factors, conversely, contribute to a more diverse community within the patch, increasing available habitat (e.g., through increased height diversity) for a number of less common species. Our data support these claims. For example, we found large numbers of European Starlings, Band-tailed Pigeons (*Patagioenas fasciata*) and Red-winged Blackbirds (*Agelaius phoeniceus*) at sites within a mainly agricultural matrix. In addition, patches in the Willamette Valley are relatively small and may not vary enough in size for patch size to be as influential as local characteristics. This may be an important factor for conservation planners to consider. In a highly fragmented landscape like the Willamette Valley, in which remaining patches are relatively small, factors other than patch area are likely be more important drivers of avian diversity.

Functional bird communities and individual species

It is also striking how consistently the nature of the matrix played a larger role in structuring the bird communities and individual species distributions than did patch characteristics. The stronger impact of matrix variables relative to local variables, as well as the lack of influence of patch size on some functional groups and individual birds, depends on the degree to which a species is a habitat or food specialist or generalist. Bender et al. (1998) and Prugh et al. (2008) found that generalists and omnivores are less likely to be influenced by the size of the patch. The Western Scrub Jay and every species in the *corvidae* omnivore

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group are all generalists and omnivores (Ehrlich et al. 1988; Poole 2005) and, as expected, unaffected by the size of the patch (Andrén 1994) but highly influenced by the composition of the surrounding matrix (Table 2). These species are likely unaffected by the size of the oak patches because they forage, nest and live not only in oak forests but also in other forests, agricultural and urban areas (Andrén 1994). The flycatcher group was also unaffected by patch area and mainly dependent on the surrounding matrix (Table 2). These birds depend on open areas for foraging (Fitzpatrick 1981; Poole 2005), and the identified positive relationship with agriculture in the surrounding matrix reflects this (Supplementary Table 5). In addition, all of the birds in each of these two functional groups as well as the Western Scrub Jay are larger birds with larger territory sizes (Ehrlich et al. 1988; Poole 2005) that likely extend beyond the size of many of our patches. These birds likely perceive each patch as only a fraction of their oak habitat, because their large territory size includes other patches as well (Wiens 2008).

In contrast to the larger generalists and omnivores, the group of seed eaters, frugivores and ground foragers and the group of bark foragers, as well as the Acorn Woodpecker and the White-breasted Nuthatch are all influenced more by local variables than landscape variables (Table 2). These birds are all specialists—eating fruits, seeds or acorns or gleaning insects from the tree bark (Ehrlich et al. 1988; Poole 2005). They rely more on local habitat characteristics to provide the specialized food they require (Table 2). Species in the specialist guilds are also more restricted to the oak patches they inhabit (Andrén 1994) and are, therefore, more affected by the size of the patch. Other researchers have also found patch size and local habitat variables are the most important predictors of the richness of avian forest specialists (Fernández-Juricic 2004).

Approach and limitations

We note that many of our R^2 values are low. We have much more confidence in our ordination analyses which explained a lot more of the variance (34.6 %) than the GLMs, whose R^2 values ranged from 3.82 to 47.4 %. Exceptions include overall abundance (26.2 %), *corvidae* omnivores (47.4 %), and White-breasted Nuthatch abundance (27.4 %). For many of the models that explained less than 20 % of the variance, there were clearly other variables that factored into bird richness, abundance and/or evenness. However, our analyses comparing scales are not affected by the magnitude of the variance explained. We acknowledge that we could not evaluate every variable in our analyses and only evaluated those variables listed in Table 1.

Although we tried to be objective using the literature as a guide, we acknowledge that our results could have differed if different characteristics were used to describe functional groups, or the synanthropies of species were defined differently. We also acknowledge that our species of concern are site specific and may not be “sensitive” species in other habitats or locations. Additional work on grouping species into different functional guilds may provide further insight into what characteristics of different avian species require specific vegetative characteristics, a larger patch size or a less fragmented landscape. However, these data will likely only strengthen our conclusions.

Although we selected a set of variables that had been identified in multiple studies as influencing bird abundance and richness, we undoubtedly did not capture all of the factors that determine species presence or abundance at a given site. In particular, we did not specifically attempt to measure connectivity. Our measure of the amount of oak woodland in the surrounding landscape was likely a reasonable measure of connectivity for many species in our study that have larger home ranges, but it may have been a poor measure for species less likely to move through agriculture or conifer forests. Thus, we may have underestimated the impact of the matrix—in terms of connectivity or the lack there of—on the distribution of some species with smaller home ranges and/or species that avoid agriculture and conifer forests.

Implications for conservation

If urban and agricultural development in the Willamette Valley continues, it is likely that the remaining oak patches will continue to shrink and the surrounding matrix will become more uniform. As this study shows, despite the caveats addressed above, these changes may lead to the loss of some species of concern like the Chipping Sparrow, some functional groups like the bark foragers and the seed and fruit dispersers, and perhaps, a degree of ecosystem

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functionality as a result (Sekercioglu 2006). Retaining avian diversity by expansion of current oak forest reserves as well as land-use planning or conservation easements on adjacent lands may be important for a fully functioning, healthy ecosystem with a diversity of avian species (Sekercioglu 2006). If development does not account for oak forest retention or expansion, populations of species of concern will likely decrease while generalists and omnivores increase, causing a loss in ecosystem functionality with effects yet to be fully realized (Sekercioglu 2006).

Although this study focused on oak woodlands and savannahs of the Willamette Valley in Oregon, results from our research can be applied to other landscapes. As shown above, many factors are associated with the community of avian species found in habitats with differing local vegetation, patch size and shape and surrounding matrices, but specific factors and spatial scales affect certain species, synanthropic species and foraging guilds more than others. Depending on the specific conservation needs of an ecosystem, directing studies to focus on these types of explicit guilds, species or response variables will help improve the efficiency of future wildlife conservation efforts.

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