

# Urban landscape matrix affects avian diversity in remnant vegetation fragments: Evidence from the Phoenix metropolitan region, USA

Jennifer Litteral · Jianguo Wu

Published online: 5 July 2012  
© Springer Science+Business Media, LLC 2012

**Abstract** Biodiversity conservation in urban areas has become increasingly important as cities have expanded to cover larger proportions of landscapes across the world. The careful planning of habitat reserves within urbanized areas has the potential to make significant contributions to regional biodiversity. We surveyed the passerine community in 15 habitat reserves within the Phoenix metropolitan region and explored the relationships between community composition and urban land uses surrounding the reserves. Diversity of different guilds was affected in substantially different ways by reserve characteristics and surrounding urban land use. Guilds responded to land use at all three scales included in the study – 200 m, 1000 m and 2500 m. The responses of four guilds, synanthropic, non-synanthropic, insectivore and feeding generalist, were well predicted by the factors considered here. Reserve characteristics (area, shape, isolation), particularly area, had effects on all four of these guilds with non-synanthropic and insectivore species responding positively to area, while synanthropic and feeding generalist species responded negatively. Land use type surrounding the reserves had significant effects on all of these guilds, except for feeding generalists. High density, high diurnal activity land uses decreased diversity, while medium density, low diurnal activity uses increased the diversity of some guilds, particularly insectivores, probably by providing supplemental habitat. This study provides new evidence from an arid urban landscape that not only reserve characteristics, but also surrounding urban land use should be considered during conservation planning, especially if non-synanthropic or insectivore species are among the targeted species.

**Keywords** Urban ecology · Habitat fragmentation · Avian · Nesting guilds · Feeding guilds · Urban land use · Habitat reserve · Synanthropy

---

J. Litteral (✉)  
School of Life Sciences, Arizona State University, P.O. Box 874601, Tempe, AZ 85287-4601, USA  
e-mail: jlitteral@alumni.wfu.edu

J. Wu  
School of Life Sciences & School of Sustainability, Arizona State University, P.O. Box 874601, Tempe, AZ 85287-4601, USA

## Introduction

Urbanization drastically changes landscapes, increasing patch density, decreasing average patch size, and increasing the juxtaposition of highly contrasting patches (Luck and Wu 2002). These changes in landscape structure result in habitat loss and fragmentation which in turn affect biodiversity and ecosystem processes in urban areas (Saunders et al. 1991; Grimm et al. 2008; Buyantuyev and Wu 2009, 2010; Wu 2009). Landscapes are comprised of mosaics of patch types that have differing values to any given focal taxon (Estades and Temple 1999; McGarigal and McComb 1995). In urban regions, patch types used for planning are often human-defined land use and land cover types. Therefore, it is important to understand how these people centric constructs affect biodiversity. In urban habitats, many species of birds are quite adept at utilizing urban resources and other species at least commonly pass through these habitats, still others avoid urban areas entirely (Chace and Walsh 2004; Johnston 2001). Thus, it seems important to examine not only the classic island biogeography variables (MacArthur and Wilson 1967), but also variables that characterize the nature of the urban matrix, while studying the effects of habitat fragmentation and urbanization on birds (Estades and Temple 1999; Wiens 1995). The importance of patches of various urban land use types as either supplemental habitats or barriers for birds, however, is not well understood in arid environments.

There is evidence that both the degree of urbanization and type of urban land use changes the composition of avian communities (Marzluff 2001; Clergeau et al. 2006; Blair 2001; Germaine et al. 1998; Stratford and Robinson 2005; Parsons et al. 2003; Tait et al. 2005; Recher and Seventy 1991). However, most urban studies have been conducted in forest-or woodland-type landscapes. Comparatively little work has been conducted in urban systems in a landscape as arid as the Sonoran Desert. In one other study conducted in an arid system (Tucson, Arizona, USA), it was found that housing density, percent paved area and area of open exotic cover were each significantly correlated with native breeding bird and non-native bird species richness, negatively and positively, respectively (Germaine et al. 1998). A comparable Phoenix study found that land use type in general was not very useful for predicting individual species abundances, but that golf course area and structure were important determinants of the abundance of some native species (Hostetler and Knowles-Yanez 2003).

We categorized bird species observed in native habitat reserves within the Phoenix metropolitan region into guilds based upon life history characteristics (Table 1). We hypothesized that guilds' negative relationships with land use types surrounding the reserves indicate that those types act as hostile edges which birds are less likely to cross when adjacent to desert habitat fragments (Warren et al. 2005), serving to further isolate the reserves, or that those types in some way reduce habitat quality within the reserve by increasing disturbance and edge effects (Hodgson et al. 2007; Rodewald and Vitz 2005; Fernandez-Juricic 2001). Positive relationships suggest that those types provide some type of supplemental habitat that the species within the guilds may use for extra resources, or move through towards other habitat patches (Kristan et al. 2003).

Since birds chose habitat hierarchically at multiple spatial scales (Hostetler and Holling 2000), we took a multi-scale approach to investigate how urbanization-driven land use change specifically might affect the bird diversity of remnant habitat reserves in the Phoenix metropolitan region. While there is a debate on the relative importance of local (Fletcher and Hutto 2008) or landscape-level factors (Stratford and Robinson 2005; Melles et al. 2003; Bentley and Catterall 1997), what is consistent in almost all studies is that factors on multiple scales together determine bird diversity (Mitchell et al. 2006; Garden et al. 2006).

**Table 1** All species observed more than once during the study were included in the calculations of species density. Each species was assigned a guild based upon synanthropy, nesting habits, feeding habits and migratory behavior. In the table below, these guild identities are abbreviated as follows: synanthropic (S), non-synanthropic (NS), shrub/tree/cactus nesting (STC), cavity-nesting (CAV), ground-nesting (GR), crevice and cliff-nesting (CC), nest parasite (P), feeding generalist (G), insectivore (I), frugivore (F), Seed-eating (SE), carnivorous (C), nectivore (N), migratory (M) and resident (R). European starlings were not analyzed with any nesting guild because of their extreme opportunism in nest site selection using caves, houses, natural crevices, cavities and cliffs (CC\*). These designations were assigned based on species abstracts in the Arizona Breeding Bird Atlas (Corman and Wise-Gervais 2005)

Species	Guild Membership			
	Synanthropy	Nesting Habits	Feeding Habits	Migratory Behavior
Abert's Towhee	S	STC	S	R
Anna's Hummingbird	S	STC	N	R
Ash-throated Flycatcher	NS	CAV	I	M
Audubon's Warbler	S	STC	G	M
Bewick's Wren	NS	CAV	I	R
Black-headed Grosbeak	NS	STC	G	M
Black-chinned Hummingbird	S	STC	N	M
Black-tailed Gnatcatcher	NS	STC	I	R
Black-throated Sparrow	NS	STC	G	R
Blue-gray Gnatcatcher	NS	STC	I	M
Brewer's Blackbird	S	STC	G	M
Brewer's Sparrow	NS	STC	G	M
Brown-crested Flycatcher	NS	STC	I	M
Brown-headed Cowbird	S	P	S	R
Cactus Wren	S	STC	G	R
Cliff Swallow	S	CC	I	M
Common Raven	S	STC	C	R
Costa's Hummingbird	NS	STC	N	M
Curve-billed Thrasher	S	STC	I	R
Dusky-capped Flycatcher	NS	CAV	I	M
European Starling	S	CC*	G	R
Gambel's Quail	S	GR	S	R
Gilded Flicker	NS	CAV	I	R
Gila Woodpecker	S	CAV	I	R
Gray Flycatcher	NS	STC	I	M
Great-tailed Grackle	S	STC	G	R
Green-tailed Towhee	NS	STC	S	M
House Finch	S	STC	G	R
House Sparrow	S	CAV	G	R
Inca Dove	S	STC	F	R
Ladder-backed Woodpecker	NS	CAV	I	R
Lesser Goldfinch	S	STC	G	R
Loggerhead Shrike	NS	STC	C	R
Mourning Dove	S	STC	F	R
Northern Mockingbird	S	STC	G	R
Northern Rough-winged Swallow	S	CC	I	M

**Table 1** (continued)

Species	Guild Membership			
	Synanthropy	Nesting Habits	Feeding Habits	Migratory Behavior
Orange-crowned Warbler	NS	GR	G	M
Phainopepla	NS	STC	F	M
Rock Wren	NS	CC	I	R
Say's Phoebe	NS	CC	I	R
Slate-colored Junco	S	GR	G	M
Verdin	S	STC	G	R
Violet-green Swallow	NS	CC	I	M
White-crowned Sparrow	NS	STC	G	M
White-winged Dove	S	STC	F	R
Wilson's Warbler	NS	STC	I	R
Yellow-eyed Junco	S	GR	G	R

The Phoenix metropolitan region provides an ideal area to study the effects of urbanization on birds in habitat reserves in arid ecosystems due to several areas, deemed too steep for building, that were established as habitat reserves while the city was built. Based on field survey of passerine birds in 15 habitat reserves in the area, we explored the relationships between species diversity and reserve characteristics and urban land uses surrounding the reserves. Since the habitats within the remnant habitat reserves in this area are relatively homogeneous, our study was focused on the influence of factors at larger scales, within 200 m to 2500 m surrounding the boundaries of focal habitat reserves.

## Methods

### Study area

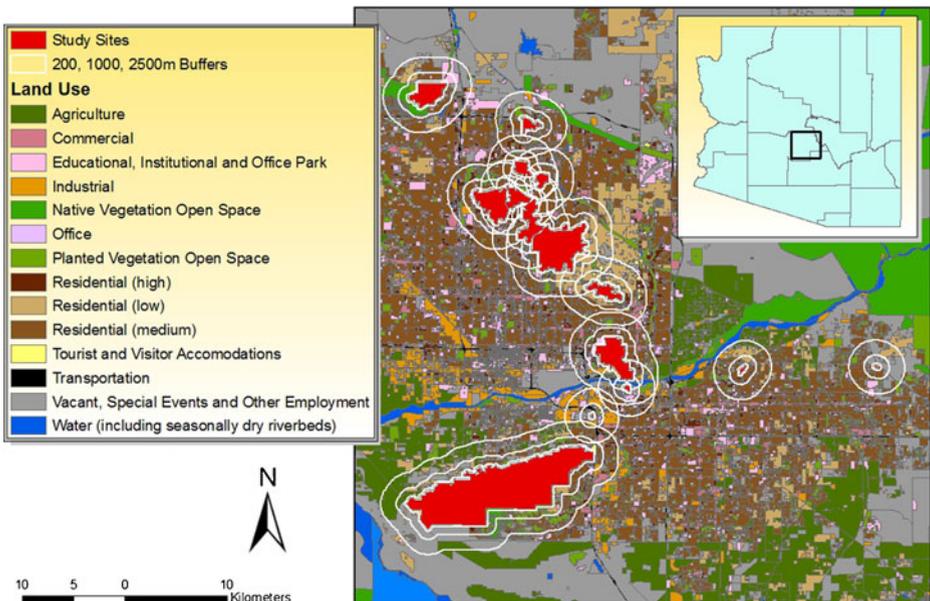
The Phoenix metropolitan region is a rapidly urbanizing area that contains more than a dozen large (>10 ha) native vegetation remnant reserves. The study was conducted in the Phoenix metropolitan region, Arizona, USA (population >4 million) on 15 mountain reserves with remnant desert vegetation. The Phoenix metropolitan region is the 14<sup>th</sup> largest metropolitan area in the United States and has the second fastest growth rate. The population increased by 45.3% between 1990 and 2000 (U.S. Census Bureau 2001).

While some data have been recorded, the avian community in these reserves has never before been comprehensively surveyed (Stiles 2006). Historically, the region was a mixture of Upland and Lower Sonoran desert vegetation with a few riparian corridors (Brown 1994). The increase in the human population and associated urban development in the region have been found to be highly correlated with each other, both increasing exponentially since 1912 (Jenerette and Wu 2001; Luck and Wu 2002). While much of the urban growth involved the conversion of land from open desert to agriculture, then agriculture to urban use, more recently the trend has been towards direct desert to urban conversion (Jenerette and Wu 2001), which has a greater impact on desert habitat availability for desert birds.

The reserves in this study range in size from 6.2 to 6664.6 ha and have roughly the same floristic composition as the outlying undisturbed desert that surrounds the metropolitan region, although the relative abundances of some species and exact species composition are different (Stiles 2006). All of the reserves can be considered Sonoran desert habitats with Arizona Upland vegetation and have no perennial water sources (Brown 1994). This habitat type is dominated by shrubs and small trees including creosote (*Larrea tridentata*), triangle-leaf bursage (*Ambrosia deltoidea*), brittlebush (*Encelia farinosa*), saltbush (*Atriplex* ssp.), mesquite (*Prosopis* ssp.) and palo verde (*Parkinsonia* ssp.). Summer temperatures regularly reach into the 40–45°C range and winter temperatures rarely go below freezing. Annual rainfall is generally between 200 and 425 mm and comes in the form of late summer monsoons and more dispersed winter rains (Brown 1994).

All of the reserves are completely surrounded by flat, developed areas (Fig. 1). Since most populated areas of Phoenix are dominated by irrigated, often mesic vegetation, the boundaries of these fragments represent not only legal boundaries, but also ecological ones. The populated parts of the city have such a different water regime and are dominated by so many non-native species; they are much more similar woodland ecosystems, than the native desert.

All but one of the fragments is publicly owned (City of Phoenix, City of Tempe, City of Mesa or Maricopa County) and principally used for recreation. The remaining fragment (Buttes Resort) is on the property of a privately owned resort.



**Fig. 1** Urban land uses in the Phoenix metropolitan area were categorized into 14 types that the authors predicted would be relevant to passerines. These types were derived from data compiled by the Maricopa Association of Governments (Maricopa Association of Governments MAG 2000). The focal native desert habitat reserves (and the point count sites within them) were all surrounded by urban land uses. The percentage of each land use type within 200-, 1000-, and 2500-m buffers around each reserve were calculated using ArcGIS 9.2 (ESRI 1999–2006)

## Sampling

We took a stratified random sampling approach to assess avian species diversity. Stiles (2006) mapped the dominant vegetation in the reserves in this study. One randomly placed sampling point was established for each vegetation type per reserve. These vegetation types are similar in vegetative structure, but have different species abundances. This method produced 42 points total, with between 1 and 5 points placed in each fragment depending on the number of dominant vegetation types found there (Fig. 1). Fifteen minute point counts were completed at each site using standard Central Arizona Phoenix—Long Term Ecological Research (CAP-LTER) project protocol (Katti 2000). Species were assumed to have equal detection probabilities due to a lack of dense vegetation and minimal noise in the study sites themselves. This assumption is common to studies of desert and urban bird communities (Germaine et al. 1998; Donnelly and Marzluff 2004; Chapa-Vargas and Robinson 2006; Mills et al. 1989; Green and Baker 2003). These counts were completed at each point giving a total of four counts conducted over two breeding seasons in consecutive years (April 2007, May 2007, April 2008 and May 2008).

## Quantification of the landscape pattern

Fourteen of the original fifteen reserves were retained for the analysis. Buffalo Ridge was determined to be an outlier and a qualitative assessment showed that land use at this particular site has changed significantly through extensive urban development between 2000, when the land use data were collected, and 2007–2008, when the avifaunal data were collected. Five key reserve characteristics and 14 land use types were calculated using ArcGIS 9.2 and used as predictors for the statistical analysis (Fernandez-Juricic 2000; ESRI 1999–2006). Five predictors were used to quantify reserve characteristics (1) log (area), (2)  $D_i$ , (3) distance to outlying desert, (4) distance to next fragment and (5) time since isolation. The log of area was used to achieve normality for the regression analysis.  $D_i$  is an indicator of the shape of an area and indicates its deviation from a perfect circle. If  $D_i$  is higher, the shape of the patch is more complex leading to a higher edge to area ratio. The three metrics—distance from the focal reserve to the outlying desert, the distance from the focal reserve to the next desert habitat fragment, and the time since the focal reserve was isolated from the outlying desert were used to measure isolation. The locations of outlying deserts and habitat fragments were determined based on existing land use data (Maricopa Association of Governments MAG 2000). Outlying desert was defined as any contiguous area categorized as passive open space or vacant of 50,000 hectares or more. Habitat fragments were defined as any passive open space within the metropolitan area that is as large as the smallest reserve included in the study (6.2 hectares) or larger. A series of historical land use maps from the CAP-LTER were used to determine the time since isolation (Maricopa Association of Governments MAG 2000; Moritz et al. 1998). For reserves isolated for more than 33 years, time since isolation was approximated to the nearest 20 years based on available land use maps categorized from aerial photography. The precision of more recently isolated reserves was approximately 5 years due to more frequently available remote sensing data.

The landscape matrix surrounding each reserve was also quantified based on land use maps (Maricopa Association of Governments MAG 2000). Created for a variety of planning purposes, the Maricopa Association of Governments (MAG) (2000) data had 42 land use types. To make the data more suitable for our study, we aggregated the original 42 land use types into 14 types more reasonably reflective of distinctions relevant to passerines (Table 2).

**Table 2** The codes used to refer to various land use types and definitions of those types are listed below. These land use types were derived from existing land use maps developed for a variety of planning purposes (Maricopa Association of Governments MAG 2000)

Land UseType Code	Land Use Type Description
LC1	Tourist and visitor accommodations including hotels, motels and resorts
LC2	Low density residential (<1/5–2 dwelling units per acre)
LC3	Medium density residential (2–10 dwelling units per acre)
LC4	High density residential (10 - >15 dwelling units per acre)
LC5	Vacant, airports, special events
LC6	Commercial
LC7	Schools, institutions, community centers, office park/campuses
LC8	Active open space (irrigated), developed parks, cemeteries, golf courses
LC9	Office
LC10	Transportation, roads, railroads
LC11	Passive (undeveloped and un-irrigated) open space, desert preserves, open desert
LC12	Agriculture
LC13	Naturally occurring water, seasonally dry riverbeds, man-made water structures
LC14	Industrial

Three buffers of 200, 1000 and 2500 meter diameters were placed around each reserve using ArcGIS 9.2 (Fig. 1) (ESRI 1999–2006). Each of these scales was found to be significant in previous studies of urban birds (Germaine et al. 1998; Stratford and Robinson 2005; Melles et al. 2003; Stefanov 1998; Mortberg 2001). The proportion of area of each buffer covered by each of the 14 land use types was then calculated. These calculations resulted in three sets of land use type predictors, one set for each buffer size.

### Rarefaction

The stratified random sampling design used to assess avian species richness created samples of unequal sizes for different fragments. To avoid skewing the results through passive sampling effects (Hostetler and Knowles-Yanez 2003), the species richness of each fragment was standardized by sampling effort in a rarefaction process (Haila et al. 1993; Colwell 2005).

This yielded a measure called species density which is often considered more useful in a conservation context, than raw species richness because area available for conservation is generally limited (Sanders 1968). Each visit to each point count location within a fragment was considered a repeated sample of that fragment when constructing the species accumulation curves. Species accumulation curves were constructed for each fragment based on how many new species were observed in a given sample that was not observed in previous samples. Curves were then smoothed by repeated random re-sampling of samples without replacement with 1000 randomization runs using EstimateS software (Gotelli and Colwell 2001).

Rarefied species density was also obtained for a number of guilds (subsets of the community). These values included synanthropic species density, non-synanthropic species density, density of migratory species and density of resident species. There were five categories for both the nesting and feeding guilds, however, for each, three groups had less

than ten representatives and no representatives were observed in many reserves. However, cavity nesting species, tree/shrub/cactus nesting species, insectivore species and feeding generalist species each had enough representatives to be input into the rarefaction algorithm. Each species was included in one guild based on synanthropy, one guild based on feeding habits, one guild based on nesting habits and one guild based on migratory habits (Table 1). Guild groupings were made based upon species accounts published in the Arizona Breeding Bird Atlas (Corman and Wise-Gervais 2005). Moran's I and Geary's  $c$  correlograms of the variables showed little evidence of spatial autocorrelation, so traditional statistics were employed for analysis.

### Principal components analysis

We reduced the 14 land cover classifications at each scale to their first three principal components, and then used Akaike's Information Criterion (AIC) to determine the best combination of these 8 predictors (five site characteristics and three principal components at each scale) to describe the responses of the guilds at each scale. Three principal components for each scale were retained. Since there is evidence that all of the calculated predictors may reasonably have an effect on species density, all models that included combinations of these three principal components and the five site characteristics were calculated for each scale. Adjusted  $r^2$  was calculated to determine the goodness-of-fit for the regression models. For those responses with best fit models  $r^2$  values above 0.65, Akaike weight ( $w_i$ ) was used for selecting the those models which make up a 95% confidence set of models for that response. This set is made up of the best fit models in order of lowest AIC where the sum of  $w_i$  equals at least 0.95 (Bozdogan 1987; Burnham and Anderson 1998).

## Results

A total of 48 passerine species were observed during the two breeding seasons included in the study. We divided the community into two groups based upon their ability to thrive in proximity to human settlement (synanthropy). Twenty-three species were assigned to the synanthropic guild, 25 species in the non-synanthropic guild. We also divided the community based on migratory behavior with 22 in the migratory guild, and 26 in the resident guild. We also divided the community into several nesting and feeding guilds, however only two guilds from each division contained enough members to be retained for analysis. The two nesting guilds retained for analysis were cavity-nesters, including nine species, and tree/shrub/cactus-nesters, including 29 species. The two feeding guilds retained for analysis, insectivores and generalists included 18 species per guild (Table 1).

### Principal components analysis

First, we reduced the 14 land cover classifications (Table 2), at each scale, to their first three principal components. Then, we used AIC to determine the best combination of eight predictors: the five site characteristics and the three principal components. This analysis was completed separately for each scale. The first three principal components captured 62.4%, 65.4% and 68.1% of the variation at the 200 m, 1000 m, and 2500 m scales, respectively. Because of the high amount of variation explained, we only retained the first three PCs for further analysis. The loadings on the principal component axes are given in Table 3.

**Table 3** The eigenvectors show the loadings on each of the principal components axes. These loadings represent the degree to which the original variables are correlated with the principal components and whether the correlation is direct or inverse. Eigenvectors of greater than 0.3 have been made bold to highlight particularly important variables

Land Use Type	Eigenvectors								
	PC1-200	PC2-200	PC3-200	PC1-1000	PC2-1000	PC3-1000	PC1-2500	PC2-2500	PC3-2500
LC1	<b>0.462</b>	-0.141	0.080	<b>0.386</b>	-0.150	0.221	0.220	-0.151	<b>-0.491</b>
LC2	0.076	-0.205	0.025	0.018	<b>-0.401</b>	-0.021	-0.067	<b>-0.317</b>	<b>-0.463</b>
LC3	<b>-0.347</b>	-0.093	<b>-0.426</b>	<b>-0.367</b>	0.072	0.123	<b>-0.308</b>	<b>0.369</b>	-0.032
LC4	-0.206	0.263	0.284	-0.180	0.279	<b>0.367</b>	0.108	<b>0.354</b>	0.147
LC5	<b>0.500</b>	-0.018	0.090	0.205	-0.124	<b>-0.500</b>	0.013	<b>-0.427</b>	0.291
LC6	-0.206	<b>0.327</b>	<b>0.329</b>	-0.115	<b>0.497</b>	0.150	0.102	<b>0.434</b>	0.058
LC7	0.114	<b>0.483</b>	-0.088	0.218	<b>0.388</b>	-0.298	<b>0.389</b>	-0.071	0.268
LC8	-0.076	-0.107	<b>0.564</b>	0.055	-0.250	0.201	-0.095	-0.158	<b>0.369</b>
LC9	0.197	<b>0.462</b>	-0.046	<b>0.417</b>	0.120	0.238	<b>0.418</b>	0.116	-0.204
LC10	-0.069	0.186	-0.098	<b>0.417</b>	0.129	0.218	<b>0.429</b>	0.102	-0.003
LC11	-0.241	-0.085	<b>0.474</b>	-0.174	0.057	0.189	-0.216	<b>0.319</b>	0.025
LC12	<b>0.390</b>	-0.209	0.119	0.135	-0.274	-0.022	-0.059	-0.295	0.244
LC13	-0.063	0.043	-0.193	0.156	<b>0.375</b>	<b>-0.423</b>	0.291	0.014	<b>0.348</b>
LC14	0.222	<b>0.455</b>	0.027	<b>0.396</b>	0.096	0.283	<b>0.420</b>	0.040	-0.054

At the 200 m scale, PC1 [200] represented various kinds of semi-developed open space including tourist areas and resorts (LC1), vacant areas and airports (LC5), and agricultural fields and pastures (LC12). Negative medium density residential (LC3) also loaded heavily on this axis. PC2 [200] was loaded with land uses characterized by a high density of buildings and a lot of diurnal activity such as commercial (LC6), industrial (LC14), school and institutional (LC7) and office (LC9). PC3 [200] was characterized by both passive (native desert) (LC11) and active (planted and irrigated) (LC8) open spaces. It was also positively associated with commercial (LC6) land use and negatively associated with medium density residential (LC3), just as PC1 [200].

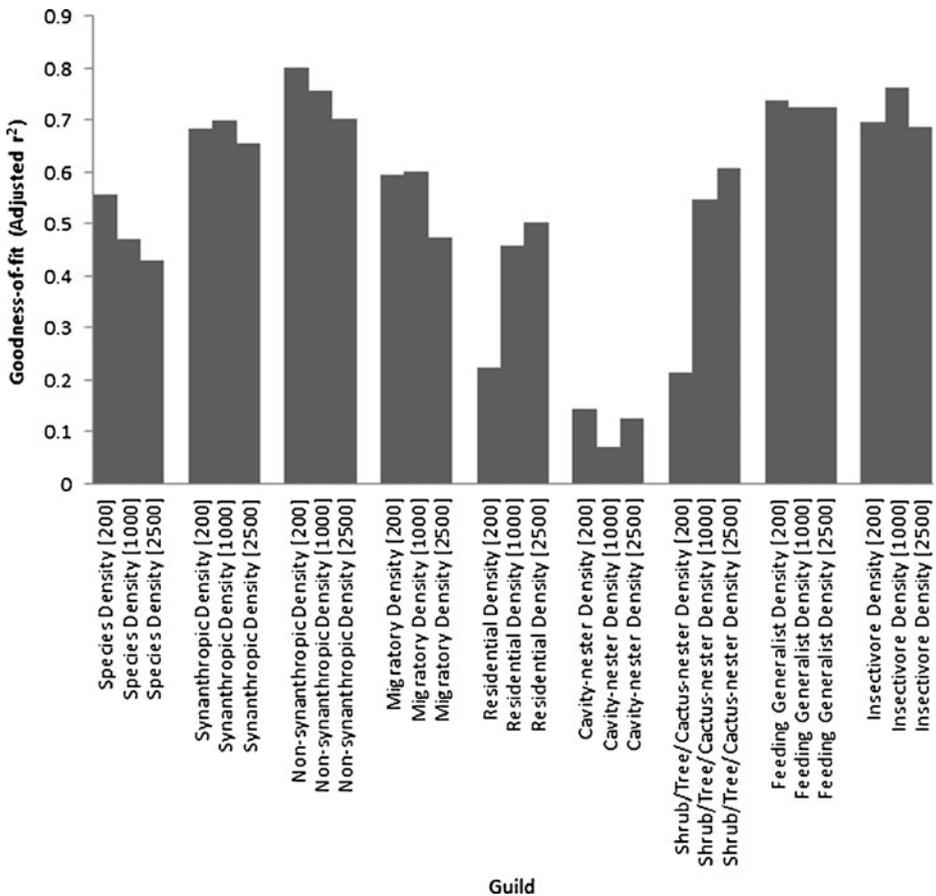
At the 1000 m scale, PC1 [1000] was positively associated with various non-residential land uses such as office (LC9), transportation (LC10), industrial (LC14), and tourist areas and resorts (LC1). As with PC1 [200] and PC3 (200), there was a prevalent negative association with medium density residential (LC3). PC2 [1000] was similar to PC2 [200], and dominated by commercial (LC6) and school and institutional (LC7) uses. Open water (LC13) also loaded heavily on this axis. PC3 [1000] was characterized by a strong negative loading of vacant areas and airports (LC5) and water (LC13), which are areas of low building density, and a positive loading of high density residential (LC2).

At the 2500 m scale, PC1 [2500] was very similar to PC1 (1000). The loadings on PC2 [2500] were more widely dispersed and difficult to interpret, but residential land uses (LC2, LC3 and LC4) weighed more heavily on this axis than any of the others. PC3 [2500] was characterized by low density uses, showing negative associations with tourist areas and resorts (LC1) and low density residential (LC2) areas and positive association with active open space (LC8) and water (LC13), both areas where there is an artificial water subsidy provided to the ecosystem.

## Regression analysis

The best fit models for the diversity of each guild at each scale are presented in [Appendix A](#). The adjusted  $r^2$  is a measure of the goodness of fit of each model and Akaike weight ( $w_i$ ) is a relative measure, based on AIC, which represents the probability that of all the possible models, the model indicated is the true model for the data.

The adjusted  $r^2$  values for the guilds defined by synanthropy and feeding habits were particularly high, so these models were investigated further (Fig. 2). The 95% confidence set of models, based upon  $w_i$ , are presented for these variables in [Appendix A](#). When enough of the best fit models are included so that cumulative  $w_i$  is equal to or greater than 0.95, there is a 95% chance that the true model is among the models in the 95% confidence set. If a predictor is included in all models in the 95% confidence set, we can have 95% confidence that the variable is part of the true model (Bozdogan 1987; Burnham and Anderson 1998). We focused on these variables to understand the relationships between parts of the community defined by synanthropy and feeding habits and reserve and landscape characteristics.



**Fig. 2** The figure shows the goodness-of-fit, as measured by adjusted  $r^2$ , for the best fit models for overall species diversity and the diversity of each guild at each scale. The guilds best described by the models presented are synanthropic, non-synanthropic, feeding generalist and insectivore guilds

In almost all confidence sets, area was among these variables (Appendix A). For synanthropic density, this relationship was negative at all scales. Conversely, it was positive for non-synanthropic density at all scales but 1000m, where area was not among the variables present in all models in the 95% confidence set (Appendix A). Similarly, the relationship with area was positive in all models in the 95% confidence sets for insectivore density at all scales and negative in all models in the 95% confidence sets for feeding generalist density, except at the 1000m scale (Appendix A).

The relationship with distance to next fragment was negative in all models in the 95% confidence set for non-synanthropic density at the 2500m scale and positive in all models in the 95% confidence sets for feeding generalist density at all scales (Appendix A). Positive time since isolation and negative  $D_i$  were also present in all models in the 95% confidence set for non-synanthropic density at the 2500m scale (Appendix A).

At least one PC axis was a significant predictor at the 95% confidence level for the density of species in guilds based on synanthropy at all scales. For synanthropic density these were negative PC2 [200] at the 200 m scale, negative PC1 [100] and negative PC2 [1000] at the 1000 m scale, and negative PC1 [2500] at the 2500 m scale. For non-synanthropic density, they were negative PC2 [200] at the 200 m scale, negative PC2 [1000] and positive PC3 [1000] at the 1000 m scale, and positive PC3 [2500] at the 2500 m scale (Appendix A). Insectivore density was significantly affected by many PC predictors which included negative PC1 [200], negative PC2 [200] and negative PC3 [200] at the 200 m scale, negative PC1 [1000] and negative PC2 [1000] at the 1000 m scale and only negative PC1 [2500] at the 2500 m scale (Appendix A). On the other hand, no PC variables were present in all models in the 95% confidence set to describe feeding generalist density at any scale (Appendix A).

## Discussion

### Major findings

Our study showed that bird species diversity in habitat reserves in the Phoenix metropolitan region was influenced by factors on multiple spatial scales, with no specific scale standing out as the most influential across guilds (Fig. 2). This result provides new support from an arid ecosystem for the hypothesis that passerines use multiple scales in habitat selection (Hostetler and Holling 2000; Bentley and Catterall 1997; Garden et al. 2006). All guilds were more consistently influenced by reserve characteristics than land use, but land use did prove to be significantly influential to certain guilds (Table 4).

The models of several guilds did not predict the guild responses well enough to merit further interpretation (Fig. 2). While this was expected for the models intended to predict overall species diversity, due to the wide diversity of life histories of species included there, it is surprising that urbanization was not more predictive of diversity for those guilds based on residency. In a similar study conducted in the bushland of Queensland, Australia, among bushland-dependent species, residency was the best predictor of a species response to isolation of a habitat fragment through urbanization (Bentley and Catterall 1997). Furthermore, in North America, studies have repeatedly found neotropical migrants, as a guild, to be particularly sensitive to urbanization (Stratford and Robinson 2005; Melles et al. 2003; Mitchell et al. 2006). Further research that considers residents and migratory species that are habitat specialist and habitat generalists separately may shed further light on the dynamics of these guilds.

**Table 4** The diversity of guilds defined by feeding habits and synanthropy were especially well predicted by reserve characteristics and land use types, as indicated by adjusted  $r^2$  (Adj.  $r^2$ ) values above 0.65. According to the information theoretic approach, the Akaike weight ( $w_i$ ), represents the possibility that of all possible models the model in question is the true model. When adding the  $w_i$  of the best models (as determined by lowest AIC value), we can be 95% confident that the true model is within the set when the sum of all  $w_i$  values within the set are greater than or equal to 0.95 (Bozdogan 1987). The predictors below are those that are present in every model in the 95% confidence set for each guild and scale below

Guild	Scale (m)	Predictors
Synanthropic Density	200	- log (Area), - PC2 [200]
Synanthropic Density	1000	- log (Area), + Time Since Isolation, - PC1 [1000], - PC2 [1000]
Synanthropic Density	2500	- log (Area), - PC1 [2500]
Non-synanthropic Density	200	+ log (Area), - PC2 [200]
Non-synanthropic Density	1000	- PC2 [1000], + PC3 [1000]
Non-synanthropic Density	2500	+ log (Area), - Distance to Next Fragment, + Time Since Isolation, - $D_i$ , + PC3 [2500]
Insectivore Density	200	+ log (Area), + Time Since Isolation, - PC1 [200], - PC2 [200], - PC3 [200]
Insectivore Density	1000	+ log (Area), + Time Since Isolation, - PC1 [1000], - PC2 [1000]
Insectivore Density	2500	+ log (Area), - PC1 [2500]
Feeding Generalist Density	200	- log (Area), - Distance to Outlying Desert, + Distance to Next Fragment, - $D_i$
Feeding Generalist Density	1000	- Distance to Outlying, + Desert Distance to Next Fragment, - $D_i$
Feeding Generalist Density	2500	- log (Area), - Distance to Outlying Desert, + Distance to Next Fragment, - $D_i$

## The effects of reserve characteristics

### *Synanthropy*

Unsurprisingly, the diversity of guilds defined by synanthropy were well predicted by variables associated with urbanization (Table 4, Appendix A). The guilds defined by synanthropy (synanthropic and non-synanthropic) showed significant and opposite relationships with reserve area. Non-synanthropic species showed area sensitivity. The negative log of fragment area was part of all models within the 95% confidence set for synanthropic models at all scales, while the positive relationship with the log of fragment area was included in the 95% confidence set of all models for the non-synanthropic guild at the 200 and 2500 meter scales (Table 4, Appendix A).

Time since isolation had a weaker, but still significant effect on the synanthropic group. The longer a fragment has been surrounded by urban land uses, the more synanthropic species have colonized it (Table 4, Appendix A). Distance to next fragment was significantly negatively related to non-synanthropic density, suggesting that the less distance there is to cross between fragments, the more non-synanthropic species have colonized it (Table 4, Appendix A). While both of these relationships are exactly what would be predicted by the theory of island biogeography, it is surprising that no significant relationship exists between non-synanthropic density and the distance to the outlying desert (MacArthur and Wilson 1967). This lack of a significant relationship

suggests that populations of non-synanthropic species populations within the reserves are not dependent on populations in the outlying desert as source populations. Future research comparing the genetics of populations of birds in the outlying desert to their desert remnant counterparts could provide important information about whether the outlying desert continues to act as a source for desert remnant populations or whether these populations are self-sustaining.

### Feeding habits

The guilds defined by feeding habits tell a somewhat different story. We still found strong area sensitivity among insectivores (Table 4, Appendix A), which is consistent with an urban bird studies in semi-arid Australian landscapes which found small insectivores to be absent from urban and suburban land use types (Parsons et al. 2003) and declining in a native habitat fragment, similar to the ones in this study (Recher and Seventy 1991). There was a weaker negative relationship with area among feeding generalists, however, distance to the outlying desert does play a role in the density of the feeding generalist guild (Table 4, Appendix A). Overall, the results from this set of guilds is more difficult to understand. Insectivore density showed a positive relationship with time since isolation, which is the opposite of what we would expect from a guild which seems more sensitive to urbanization based on its area requirements. We hypothesize this may be due to increased water subsidies in the urban areas surrounding the fragments in fragments that have been enveloped by urbanization longer, leading to increased insect populations during certain times of the year. Insect populations in Phoenix do seem to be less affected by seasonal fluctuations in land use types characterized by more intense urbanization (Cook and Faeth 2006). This is supported by the result that insectivore diversity seemed to be more dependent on the nature of the urban landscape surrounding the fragments than other guilds, as evidenced by it having more significant relationships with the land use types than any other guild considered here (Table 4, Appendix A).

Feeding generalist density, in contrast, showed no dependence on the nature of the urban landscape (Table 4, Appendix A). All significant relationships with the diversity of this guild were with reserve characteristics. However, these relationships were somewhat puzzling, especially the negative relationship with distance to outlying desert paired with the positive relationship with distance to next fragment. Both variables are measures of degree of isolation. The positive relationship with distance to next fragment may be a statistical artifact, since this variable was highly influenced by three sites, Camelback Mountain, Buttes Resort and Park of Canals, but further research will be required to determine whether it is indicative of an actual ecological phenomenon.

### Effects of the urban matrix

#### *Synanthropy*

Both the synanthropic and non-synanthropic guilds were affected by the landscape in the same way at the 200-meter scale, the only significant relationship was a negative one with PC2 [200] (Table 4, Appendix A). It is likely that the noise and activity of the high density, high diurnal use land uses that characterize PC2 [200] (Table 3) drove down the density of all species, even those synanthropic ones that may cope well with lower intensity human land uses. However, at larger scales, the guilds' responses were more divergent (Table 4, Appendix A).

## Feeding habits

While feeding generalists, as a group, were not affected at all by the nature of the landscape matrix, the insectivore guild was affected by the land uses at all three scales (Table 4, Appendix A). At the smallest scale this guild responded negatively to all PC axes, representing negative relationships with almost all land uses. However, medium density residential loaded strongly and negatively on both PC1[200] and PC3[200], meaning it had a positive effect on insectivore density (Table 3). At the 1000-meter scale, the negative relationship with PC1[1000] and PC2 [1000] represents a negative relationship with areas of high diurnal activity (Table 2, Table 3). The positive relationship with medium density residential, which was apparent at the 200-meter scale, persisted at the 1000-meter and 2500-meter scales, indicating this low density, low diurnal activity area likely provides supplementary habitat for insectivores. The negative responses at the 2500-meter scale were similar to the 1000-meter scale, as well (Table 4, Appendix A).

## Conclusion

The results of our study are consistent with other studies of birds in urban habitat fragments in less arid systems in that there are unique and strong relationships between the diversity of certain guilds and reserve area (Biamonte et al. 2010; Catterall et al. 1998; Parsons et al. 2006), but the relationship between diversity and isolation was less strong than in other studies (Fernandez-Juricic 2000; Cook and Faeth 2006; Platt and Lill 2006). The importance of the matrix was consistent with studies completed in forested landscapes. There is evidence from forest systems that even in relatively pristine habitat reserves, surrounding matrix types affect bird diversity within the reserve (Estades and Temple 1999; Donnelly and Marzluff 2004; Marzluff 2005). Studies have shown various effects of the landscape matrix on bird species habitat reserves (Renjifo 2001; Dunford and Freemark 2005; Wethered and Lawes 2005; Hamer et al. 2006). Wethered and Lawes (2005) found that smaller reserves were significantly more species rich, and the species-area relationship was much weaker, in a plantation matrix than a grassland matrix indicating that the plantation matrix was more porous to certain forest species, just as medium density residential appears to be more porous to species sensitive to urbanization in the present study (Table 4, Appendix A). In the Seattle metropolitan region the relationship of bird species richness to reserve size was affected by the degree of urbanization that surrounded a native vegetation reserve. Habitat reserves within low density urban and forested matrices have higher diversity of habitat specialist species than habitat reserves of similar sizes in more disturbed matrices (Donnelly and Marzluff 2004; Wethered and Lawes 2005; Donnelly and Marzluff 2006).

While this study provides strong support that, like in less arid urban landscapes, not only reserve characteristics but also the nature of the urban mosaic affects the diversity of at least certain guilds of birds, more data would have allowed a more thorough investigation of the dynamics of this community. For example, a similar study in Queensland, Australia found significant differences in bird communities affected by urbanization based on seasonality (Catterall et al. 1998). This was especially true for migratory species. If we had been able to collect enough avifaunal data, over a longer timeframe, we would have been able to do separate analyses for summer and winter communities. A future study incorporating these analyses might produce models better able to predict the responses of resident and migratory guilds. Some species, too, may respond most strongly to scales much smaller than patch or reserve size. Local habitat variables, specific to the sites within the reserves where the point counts were

taken were not considered in this study. While they are similar on a broad scale, fine differences may have significant effects on the diversity of some guilds, particularly those defined by nesting. The question as to whether landscape level or habitat level variables are more important has been explored in various urban bird studies. Future research that incorporates habitat variables in arid urban landscapes could shed more light on this phenomenon.

This study demonstrates that type of urbanization, not only the degree, has an effect on diversity within habitat fragments in arid urban landscapes (Table 4, Appendix A). For urban planners these results mean that not only the size, but also the urban land types surrounding urban reserves within a radius of at least up to 2500 m are important depending on the target species. If planners intend to use reserves to protect non-synanthropic and insectivorous species that do not thrive in other urban land uses, these reserves should be as large as possible and close to land use types that enhance the diversity of these guilds.

### Appendix A

**Table 5** The diversity of guilds defined by feeding habits and synanthropy were especially well predicted by reserve characteristics and land use types, as indicated by adjusted  $r^2$  (Adj.  $r^2$ ) values above 0.65. According to the information theoretic approach, the Akaike weight ( $w_i$ ), represents the possibility that of all possible models the model in question is the true model. When adding the  $w_i$  of the best models (as determined by lowest AIC value), we can be 95% confident that the true model is within the set when the sum of all  $w_i$  values within the set are greater than or equal to 0.95(Bozdogan 1987). The models above are the 95% confidence sets of models for the diversity of synanthropic, non-synanthropic, feeding generalist and insectivore guilds at each scale

	Predictors	Adj. $r^2$	$w_i$	$\sum w_i$
Synanthropic Density (200)	- log (Area)+Time Since Isolation - PC1 [200] - PC2 [200] - PC3 [200]	0.6853	0.129	
	- log (Area) - Distance to Outlying Desert+Time Since Isolation - PC1 [200] - PC2 [200] - PC3 [200]	0.6771	0.101	0.23
	- log (Area) - Distance to Outlying Desert+Time Since Isolation - PC1 [200] - PC2 [200]	0.673	0.099	0.329
	- log (Area)+Time Since Isolation - PC1 [200] - PC2 [200]	0.6633	0.096	0.425
	- log (Area) - Distance to Outlying Desert+Time Since Isolation - $D_i$ - PC1 [200] - PC2 [200] - PC3 [200]	0.6602	0.077	0.502
	- log (Area) - Distance to Next Fragment+Time Since Isolation - PC1 [200] - PC2 [200] - PC3 [200]	0.6614	0.073	0.575
	- log (Area) - PC1 [200] - PC2 [200]	0.63	0.065	0.64
	- log (Area) - Distance to Outlying Desert - PC2 [200]	0.6214	0.055	0.695
	- log (Area) - PC1 [200] - PC2 [200] - PC3 [200]	0.6349	0.055	0.75
	- log (Area)+Time Since Isolation - $D_i$ - PC1 [200] - PC2 [200] - PC3 [200]	0.6461	0.053	0.803
	- log (Area) - PC2 [200]	0.5993	0.052	0.855
	- log (Area) - PC2 [200] - PC3 [200]	0.6167	0.050	0.905
	- log (Area)+ $D_i$ - PC1 [200] - PC2 [200]	0.6286	0.048	0.953
	Synanthropic Density (1000)	- log (Area)+Time Since Isolation - PC1 [1000] - PC2 [1000]	0.6981	0.377
- log (Area) - Distance to Next Fragment+Time Since Isolation - PC1 [1000] - PC2 [1000]		0.6717	0.176	0.553
- log (Area)+Time Since Isolation - PC1 [1000] - PC2 [1000] - PC3 [1000]		0.6691	0.167	0.72

**Table 5** (continued)

	Predictors	Adj. $r^2$	$w_i$	$\sum w_i$	
Synanthropic Density (2500)	- log (Area)+Time Since Isolation - $D_i$ - PC1 [1000] - PC2 [1000]	0.6607	0.140	0.86	
	- log (Area) - Distance to Outlying Desert+Time Since Isolation - PC1 [1000] - PC2 [1000]	0.6606	0.140	1	
	- log (Area) - Distance to Next Fragment - PC1 [2500] - PC2 [2500]	0.6555	0.163		
	- log (Area)+Time Since Isolation - PC1 [2500] - PC2 [2500]	0.6445	0.131	0.294	
	- log (Area)+Time Since Isolation - PC1 [2500] - PC2 [2500] PC3 [2500]	0.6371	0.095	0.389	
	- log (Area) - Distance to Next Fragment+Time Since Isolation - PC1 [2500] - PC2 [2500]	0.6369	0.094	0.483	
	- log (Area) PC1 [2500] - PC2 [2500]	0.6134	0.094	0.577	
	- log (Area) - Distance to Next Fragment - PC1 [2500]	0.6066	0.084	0.661	
	- log (Area) - Distance to Outlying Desert+Time Since Isolation - PC1 [2500] - PC2 [2500]	0.6256	0.076	0.737	
	- log (Area) - Distance to Next Fragment $D_i$ - PC1 [2500] - PC2 [2500]	0.6229	0.072	0.809	
	- log (Area) - Distance to Outlying Desert Distance to Next Fragment - PC1 [2500]	0.6083	0.066	0.875	
	- log (Area) - Distance to Next Fragment - PC1 [2500] - PC2 [2500] - PC3 [2500]	0.6164	0.064	0.939	
	- log (Area) - Distance to Outlying Desert - Distance to Next Fragment - PC1 [2500] - PC2 [2500]	0.6131	0.061	1	
	Non-synanthropic Density (200)	+ log (Area) - $D_i$ - PC2 [200]	0.8006	0.273	
		+ log (Area) - $D_i$ - PC1 [200] - PC2 [200]	0.7872	0.134	0.407
+ log (Area) - $D_i$ - PC2 [200]+PC3 [200]		0.7851	0.126	0.533	
+ log (Area) - PC2 [200]+PC3 [200]		0.7763	0.124	0.657	
+ log (Area) - Distance to Outlying Desert - $D_i$ - PC2 [200]		0.7807	0.100	0.757	
+ log (Area)+Distance to Next Fragment - $D_i$ - PC2 [200]		0.7802	0.100	0.857	
Non-synanthropic Density (1000)	+ log (Area) - PC2 [200]	0.7603	0.098	0.955	
	+ Distance to Next Fragment - PC2 [1000]+PC3 [1000]	0.7586	0.196		
	- Distance to Outlying Desert - Distance to Next Fragment - PC2 [1000]+PC3 [1000]	0.7524	0.126	0.322	
	+ log (Area) - Time Since Isolation - PC2 [1000]+PC3 [1000]	0.7491	0.115	0.437	
	- Time Since Isolation - PC2 [1000]+PC3 [1000]	0.7323	0.095	0.532	
	+ log (Area) - PC2 [1000]+PC3 [1000]	0.7276	0.084	0.616	
	+ log (Area) - Distance to Next Fragment - PC2 [1000]+PC3 [1000]	0.7368	0.083	0.699	
	- Distance to Next Fragment - Time Since Isolation - PC2 [1000] +PC3 [1000]	0.7357	0.080	0.699	
	+ log (Area) - Distance to Outlying Desert - $D_i$ - PC2 [1000]+PC3 [1000]	0.739	0.073	0.852	
	- Distance to Next Fragment - PC1 [1000] - PC2 [1000]+PC3 [1000]	0.7323	0.073	0.925	
Non-synanthropic Density (2500)	- Distance to Next Fragment - $D_i$ - PC2 [1000]+PC3 [1000]	0.732	0.073	0.998	
	+ log (Area) - Distance to Next Fragment+Time Since Isolation - $D_i$ +PC3 [2500]	0.703	0.426		

**Table 5** (continued)

	Predictors	Adj. $r^2$	$w_i$	$\sum w_i$
	+ log (Area) - Distance to Outlying Desert - Distance to Next Fragment+Time Since Isolation - $D_i$ +PC3 [2500]	0.676	0.217	0.643
	+ log (Area) - Distance to Next Fragment+Time Since Isolation - $D_i$ - PC1 [2500]+PC3 [2500]	0.6673	0.180	0.823
	+ log (Area) - Distance to Next Fragment+Time Since Isolation - $D_i$ - PC2 [2500]+PC3 [2500]	0.6665	0.177	1
Insectivore Density (200)	+ log (Area)+Time Since Isolation - PC1 [200] - PC2 [200] - PC3 [200]	0.6969	0.334	
	+ log (Area) - Distance to Outlying Desert+Time Since Isolation - PC1 [200] - PC2 [200] - PC3 [200]	0.6853	0.241	0.575
	+ log (Area) - Distance to Outlying Desert+Time Since Isolation - $D_i$ - PC1 [200] - PC2 [200] - PC3 [200]	0.6638	0.164	0.739
	+ log (Area)+Time Since Isolation - $D_i$ - PC1 [200] - PC2 [200] - PC3 [200]	0.6584	0.135	0.874
	+ log (Area) - Distance to Next Fragment+Time Since Isolation - PC1 [200] - PC2 [200] - PC3 [200]	0.6549	0.126	1
Insectivore Density (1000)	+ log (Area)+Time Since Isolation - PC1 [1000] - PC2 [1000]	0.7624	0.380	
	+ log (Area) - Distance to Next Fragment+Time Since Isolation - PC1 [1000] - PC2 [1000]	0.7436	0.188	0.568
	+ log (Area)+Time Since Isolation - $D_i$ - PC1 [1000] - PC2 [1000]	0.735	0.149	0.717
	+ log (Area) - Distance to Outlying Desert+Time Since Isolation - PC1 [1000] - PC2 [1000]	0.7336	0.143	0.86
	+ log (Area)+Time Since Isolation - PC1 [1000] - PC2 [1000] - PC3 [1000]	0.7328	0.140	1
Insectivore Density (2500)	+ log (Area) - Distance to Next Fragment+Time Since Isolation - PC1 [2500] - PC2 [2500]	0.6855	0.117	
	+ log (Area) - Distance to Next Fragment - PC1 [2500] - PC3 [2500]	0.6706	0.101	0.218
	+ log (Area) - Distance to Next Fragment+Time Since Isolation - PC1 [2500]	0.6675	0.095	0.313
	+ log (Area) - Distance to Outlying Desert Distance to Next Fragment - PC1 [2500] - PC2 [2500] - PC3 [2500]	0.6782	0.094	0.407
	+ log (Area)+Time Since Isolation - PC1 [2500] - PC2 [2500]	0.6637	0.088	0.495
	+ log (Area) - Distance to Outlying - Desert Distance to Next Fragment+Time Since Isolation - PC1 [2500]	0.6591	0.067	0.562
	+ log (Area) - Distance to Next Fragment+Time Since Isolation - PC1 [2500] - PC3 [2500]	0.6483	0.054	0.616
	+ log (Area) - Distance to Next Fragment - PC1 [2500]	0.6252	0.053	0.616
	+ log (Area)+Time Since Isolation - PC1 [2500] - PC2 [2500] - PC3 [2500]	0.6476	0.053	0.722
	+ log (Area) - Distance to Next Fragment - PC1 [2500] - PC2 [2500] - PC3 [2500]	0.6457	0.051	0.773
	+ log (Area) - Distance to Next Fragment+Time Since Isolation - PC1 [2500] - PC2 [2500] - PC3 [2500]	0.6458	0.048	0.821
	+ log (Area)+Time Since Isolation - PC1 [2500]	0.6187	0.047	0.868
	+ log (Area) - Distance to Next Fragment+Time Since Isolation - $D_i$ - PC1 [2500] - PC2 [2500]	0.6431	0.045	0.913

**Table 5** (continued)

	Predictors	Adj. $r^2$	$w_i$	$\sum w_i$
	+ log (Area) - Distance to Outlying Desert+Time Since Isolation - PC1 [2500] - PC2 [2500]	0.638	0.044	0.957
	+ log (Area) - Distance to Outlying Desert - Distance to Next Fragment+Time Since Isolation - PC1 [2500] - PC2 [200]	0.6408	0.043	1
Feeding Generalist Density (200)	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$ - PC1 [200]	0.7355	0.289	
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$	0.7248	0.261	0.55
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - Time Since Isolation - $D_i$	0.7008	0.122	0.672
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$ - PC1 [200] - PC2 [200]	0.701	0.115	0.787
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$ - PC1 [200] - PC3 [200]	0.6978	0.107	0.894
	- log (Area) - Distance to Outlying Desert - Distance to Next Fragment+Time Since Isolation - $D_i$ - PC1 [200]	0.6977	0.106	1
Feeding Generalist Density (1000)	- log (Area) - Distance to Outlying+Desert Distance to Next Fragment - $D_i$	0.7248	0.170	
	- log (Area) - Distance to Outlying+Desert Distance to Next Fragment - $D_i$ - PC1 [1000]	0.7206	0.129	0.299
	- log (Area) - Distance to Outlying+Desert Distance to Next Fragment - Time Since Isolation - $D_i$ - PC2 [1000]	0.7227	0.127	0.426
	- Distance to Outlying Desert+Distance to Next Fragment - Time Since Isolation - $D_i$ - PC2 [1000] - PC3 [1000]	0.7184	0.114	0.54
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$ - PC2 [1000]	0.7115	0.103	0.643
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - Time Since Isolation - $D_i$	0.7008	0.080	0.723
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - Time Since Isolation - $D_i$ - PC2 [1000] - PC3 [1000]	0.6988	0.077	0.8
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$ - PC1 [1000] - PC2 [1000]	0.7004	0.074	0.874
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$ - PC1 [1000] - PC3 [1000]	0.6938	0.063	0.937
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$ - PC3 [1000]	0.6906	0.063	1
Feeding Generalist Density (2500)	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$	0.7248	0.298	
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$ - PC1 [2500] - PC2 [2500] - PC3 [2500]	0.7115	0.182	0.48
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$ - PC2 [2500]	0.7014	0.141	0.621
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - Time Since Isolation - $D_i$	0.7008	0.139	0.76
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$ - PC3 [2500]	0.696	0.125	0.885
	- log (Area) - Distance to Outlying Desert+Distance to Next Fragment - $D_i$ - PC1 [2500]	0.6924	0.115	1

## References

- Bentley JM, Catterall (1997) The use of bushland, corridors, and linear remnants by birds in Southeastern Queensland, Australia. *Conserv Biol* 11:1173–1189
- Biamonte E, Sandoval L, Chacon E, Barrantes G (2010) Effect of urbanization on the avifauna in a tropical metropolitan area. *Landscape Ecology*. In press
- Blair RB (2001) Creating a homogeneous avifauna. In: Marzluff JM, Bowman R, Donnelly R (eds) *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, pp 459–486
- Bozdogan H (1987) Model selection and Akaike's Information Criterion (AIC): The general theory and its analytical extensions. *Psychometrika* 52:345–370
- Brown DE (1994) *Biotic communities: Southwestern United States and Northwestern Mexico*. University of Utah Press, Salt Lake City
- Burnham KP, Anderson DR (1998) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York, NY
- Buyantuyev A, Wu J (2009) Urbanization alters spatiotemporal patterns of ecosystem primary productivity: A case study of the Phoenix metropolitan region, USA. *J Arid Environ* 73:512–520
- Buyantuyev A, Wu J (2010) Urban heat islands and landscape heterogeneity: linking spatiotemporal variations in surface temperatures to land-cover and socioeconomic patterns. *Landsc Ecol* 25:17–33
- Catterall CP, Kingston MB, Park K, Sewell S (1998) Deforestation, urbanisation and seasonality: Interacting effects on a regional bird assemblage. *Biol Conserv* 84:65–81
- Chace JF, Walsh JJ (2004) Urban effects on native avifauna: A review. *Landscape and Urban Planning* 74:46–69
- Chapa-Vargas L, Robinson SK (2006) Nesting success of a songbird in a complex floodplain forest landscape in Illinois, USA: Local fragmentation vs. vegetation structure. *Landsc Ecol* 21:525–537
- Clergeau P, Croci S, Jokimaki J, Kaisanlahti-Jokimaki M-L, Dinetti M (2006) Avifauna homogenisation by urbanisation: Analysis at different European latitudes. *Biol Conserv* 127:336–344
- Colwell R.K. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's Guide and application published at: <http://purl.oclc.org/estimates>
- Cook WM, Faeth SH (2006) Irrigation and land use drive ground arthropod community patterns in an urban desert. *Environmental Entomology* 35:1532–1540
- Corman T, Wise-Gervais C (eds) (2005) *Arizona Breeding Bird Atlas*. University of New Mexico Press, Albuquerque
- Donnelly R, Marzluff JM (2004) Importance of reserve size and landscape context to urban bird conservation. *Conserv Biol* 18:733–745
- Donnelly R, Marzluff JM (2006) Relative importance of habitat quantity, structure, and spatial pattern to birds in urbanizing environments. *Urban Ecosystems* 9:99–117
- Dunford W, Freemark K (2005) Matrix matters: Effects of surrounding land uses on forest birds near Ottawa, Canada. *Landsc Ecol* 20:497–511
- ESRI 1999–2006. ArcGIS, Release 9.2. Environmental Systems Research Institute, Redlands, California, USA.
- Estades CF, Temple SA (1999) Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine plantations. *Ecol Appl* 9:573–585
- Fernandez-Juricic E (2000) Bird community composition patterns in urban parks of Madrid: The role of age, size and isolation. *Ecol Res* 15:373–383
- Fernandez-Juricic E (2001) Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. *Biodivers Conserv* 10:1303–1316
- Fletcher RJ Jr, Hutto RL (2008) Partitioning the multi-scale effects of human activity on the occurrence of riparian forest birds. *Landsc Ecol* 23:727–739
- Garden J, McAlpine C, Peterson A, Jones D, Possingham H (2006) Review of the ecology of Australian urban fauna: A focus on spatially explicit processes. *Austral Ecology* 31:126–148
- Germaine SS, Rosenstock SS, Schweinsburg RE, Richardson WS (1998) Relationships among breeding birds, habitat, and residential development in Greater Tucson, Arizona. *Ecol Appl* 8:680–691
- Green DM, Baker MG (2003) Urbanization impacts on habitat and bird communities in a Sonoran desert ecosystem. *Landsc Urban Plan* 36:225–239
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 4:379–391
- Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. *Science* 319:756–760
- Haila Y, Hanski IK, Raivio S (1993) Turnover of breeding birds in small forest fragments: The "Sampling" colonization hypothesis corroborated. *Ecology* 74:714–725

- Hamer TL, Flather CH, Noon BR (2006) Factors associated with grassland bird species richness: The relative roles of grassland area, landscape structure, and prey. *Landscape Ecol* 21:569–583
- Hodgson P, French K, Major RE (2007) Avian movement across abrupt ecological edges: Differential responses to housing density in an urban matrix. *Landscape and Urban Planning* 79:266–272
- Hostetler M, Holling CS (2000) Detecting the Scales at which birds respond to structure in urban landscapes. *Urban Ecosystems* 4:25–54
- Hostetler M, Knowles-Yanez K (2003) Land use, scale, and bird distributions in the Phoenix metropolitan area. *Landscape and Urban Planning* 62:55–68
- Jenerette GD, Wu JG (2001) Analysis and simulation of land-use change in the central Arizona-Phoenix region, USA. *Landscape Ecol* 16:611–626
- Johnston RF (2001) Synanthropic Birds of North America. In: Marzluff JM, Bowman R, Donnelly R (eds) *Avian Ecology and Conservation in an Urbanizing World*. Kluwer Academic Publishers, Boston, pp 49–67
- Katti M. 2000. Bird Point Count, General Survey Protocol. Central Arizona Phoenix—Long Term Ecological Research Protocols, Phoenix, AZ, USA
- Kristan WB III, Lynam AJ, Price MV, Rotenberry JT (2003) Alternative causes of edge-abundance relationships in birds and small mammals of California coastal sage scrub. *Ecography* 26:29–44
- Luck M, Wu J (2002) A gradient analysis of urban landscape: A case study from the Phoenix metropolitan region, Arizona, USA. *Landscape Ecol* 17:327–339
- MacArthur RH, Wilson EO (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ
- Maricopa Association of Governments (MAG). 2000. Maricopa County land use map
- Marzluff JM (2001) Worldwide urbanization and its effects on birds. In: Marzluff JM, Bowman R, Donnelly R (eds) *Avian Ecology and Conservation in an Urbanizing World*. Kluwer Academic Publishers, Norwell, MA, pp 19–48
- Marzluff JM (2005) Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. *Urban Ecosystems* 8:157–177
- McGarigal K, McComb WC (1995) Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecol Monogr* 65:235–260
- Melles S, Glenn S, Martin K (2003) Urban bird diversity and landscape complexity: Species-environment associations along a multiscale habitat gradient. *Conservation Ecology* 7: online
- Mills GS, Dunning JB Jr, Bates JM (1989) Effects of urbanization on breeding bird community structure in southwestern desert habitats. *Condor* 91:416–428
- Mitchell MS, Rutzmoser SH, Wigley TB, Loehle C, Gerwin JA, Keyser PD, Lancia RA, Perry R, Reynolds CJ, Thill RE, Weih R, White D, Wood PB (2006) Relationships between avian richness and landscape structure at multiple scales using multiple landscapes. *For Ecol Manag* 221:155–169
- Moritz C, Hutchins J, Knowles-Yanez K, Bucchin M, McCartney PH, Redman CL (1998) Landuse Classification for 1912, 1934, 1955, 1975, and 1995 based available data including U.S. Soil Conservation Service air photos, USGS topographic maps, Glendale Historical Society, Salt River Project historical agricultural data, and Arizona Department of Water Resources historical agricultural data. CAP-LTER Dataset
- Mortberg UM (2001) Resident bird species in urban forest remnants; landscape and habitat perspectives. *Landscape Ecol* 16:193–203
- Parsons H, French K, Major RE (2003) The influence of remnant bushland on the composition of suburban bird assemblages in Australia. *Landscape and Urban Planning* 66:43–56
- Parsons H, Major RE, French K (2006) Species interaction and habitat associations of birds inhabiting urban areas of Sydney Australia. *Austral Ecology* 31:217–227
- Platt A, Lill A (2006) Composition and conservation value of bird assemblages of urban ‘habitat islands’: Do pedestrian traffic and landscape variables exert an influence? *Urban Ecosystems* 9:83–97
- Recher HF, Seventy DL (1991) Long term changes in the Relative Abundances of Birds in Kings Park, Perth, Western Australia. *Conserv Biol* 5:90–97
- Renjifo LM (2001) Effect of natural and anthropogenic landscape matrices on the abundance of subandean bird species. *Ecol Appl* 11:14–31
- Rodewald AD, Vitz AC (2005) Edge- and Area-Sensitivity of Shrubland Birds. *J Wildl Manag* 69:681–688
- Sanders H (1968) Marine benthic diversity: a comparative study. *Am Nat* 102:243–282
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological Consequences of Ecosystem Fragmentation: A Review. *Conserv Biol* 5:18–32
- Stefanov W (1998) Land cover classification for the CAP LTER study region using Landsat Thematic Mapper (TM) data for 1985, 1990, 1993 and 1998. CAP-LTER Dataset
- Stiles A (2006) Structure and distribution of Sonoran desert vegetation in metropolitan Phoenix, Arizona. Master’s Thesis, Arizona State University, Tempe, Arizona
- Stratford JA, Robinson WD (2005) Distribution of neotropical migratory bird species across an urbanizing landscape. *Urban Ecosystems* 8:59–77

- Tait CJ, Daniels CB, Hill RS (2005) Changes in species assemblages within the Adelaide metropolitan area, Australia, 1836–2002. *Ecol Appl* 15:346–359
- Bureau United States Census (2001) Ranking Tables for Metropolitan Areas: 1990 and 2000. Retrieved on November 22:2011
- Warren TL, Betts MG, Diamond AW, Forbes GJ (2005) The influence of local habitat and landscape composition on cavity-nesting birds in a forested mosaic. *For Ecol Manag* 214:331–343
- Wethered R, Lawes MJ (2005) Nestedness of bird assemblages in fragmented Afmontane forest: the effect of plantation forestry in the matrix. *Biol Conserv* 123:125–137
- Wiens JA (1995) Habitat fragmentation: island vs. landscape perspectives on bird conservation. pp. S97-S104
- Wu J (2009) Ecological dynamics in fragmented landscapes. In: Levin SA (ed) *The princeton guide to ecology*. Princeton University Press, Princeton, New Jersey, pp 438–444