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Avian response to urbanization in the arid riparian context of Reno, USA

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ABSTRACT

The difference between the urban and non-urban environment in arid landscapes can be quite distinct because of the large water and nutrient (along with many other) subsidies provided by human development. With these subsidies comes the potential to increase vertical structure and vegetation diversity over the natural landscape, creating artificial habitats. We assessed how birds were responding to urbanization in Reno, Nevada, USA (pop ~200,000), located in a semi-arid, "cold desert" climate. Despite a heavily developed core, we found that native richness increased as urbanization increased. Our analysis suggests that this pattern is driven by the Truckee River that flows through the city. Remnant riparian patches could combine with urban landscaping to effectively extend riparian habitat into the city. The role of urban riparian habitats for native bird conservation needs to be assessed as urbanization continues in arid regions.

1. Introduction

Urban ecosystems are unique combinations of socioeconomic factors, land use patterns and characteristics of the surrounding landscape. The impacts of urbanization on native avifauna have been documented in a wide variety of habitats, ranging from the Sonoran Desert (Green & Baker, 2003; Rosenberg, Terrill, & Rosenberg, 1987) to Mediterranean climates (Luther et al., 2008; Shwartz, Shirley, & Kark, 2008) to tropical regions (Acevedo & Aide, 2008; Hodgson, French, & Major, 2007; Suarez-Rubio & Thomlinson, 2009) to prairie systems (Atchison & Rodewald, 2006; Blair & Johnson, 2008; Pennington, Hansel, & Blair, 2008). While some reviews have made the case that urbanization generally results in reduced native and specialist species (Chace & Walsh, 2006), there is increasing evidence that the impact urban development has on avian diversity depends upon the landscape context (Rosenberg et al., 1987; Saab, 1999; Watson, Whittaker, & Freudenberger, 2005), surrounding human population (Fuller, Tratalos, & Gaston, 2009), scale of examination (Araujo, 2003; Hugo & Van Rensburg, 2008; Pautasso, 2007) and gradients present (Blair, 1996; Blair, 2004).

Loss of habitat is often the primary cause for reduced bird diversity in urban environments (Marzluff, Bowman, & Donnelly, 2001). In many urban environments, loss of vegetation structure leads to limited nesting and foraging habitat (Er, Innes, Martin, & Klinkenberg, 2005; Schlesinger, Manley, & Holyoak, 2008; Shochat, Warren, Faeth, McIntyre, & Hope, 2006), although habitat heterogeneity (Kennedy, Marra, Fagan, & Neel, 2010) and reduced native predators (Ryder, Reitsma, Evans, & Marra, 2010) may compensate for this effect. However, in arid and semi-arid regions, urban environments can experience increased vegetation abundance and structure (Emlen, 1974; Merola-Zwartjes & Delong, 2005; Rodríguez-Estrella, 2007) and higher net primary productivity (Buyantuyev & Wu, 2009; Imhoff et al., 2004). Studies that have assessed the response of birds to urbanization in arid environments have shown that presence of native vegetation (Germaine, Rosenstock, Schweinsburg, & Richardson, 1998) and maintenance of natural riparian areas (Green & Baker, 2003) help maintain high native avifauna richness.

The importance of riparian habitat for bird diversity in arid regions has been established both in natural landscapes (Saab, 1999) and in urban landscapes (Oneal & Rotenberry, 2009). While urbanization near natural riparian habitat can reduce native bird diversity (Luther et al., 2008; Rottenborn, 1999), urban riparian habitat, although altered, may still be important for regional biota (Schneider & Griesser, 2009; Seymour & Simmons, 2008). This close interface between riparian habitat and urbanization in an arid

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landscape has the potential to lead to reduced biodiversity, but can also lead to opportunities for conservation (Rosenberg et al., 1987).

The objective of this research is to determine how native bird abundance and distribution vary with urbanization in a semi-arid landscape. Specifically, we are interested in how the presence of a perennial river at the core of an urban environment influences avian species richness, abundance, and community composition. We use multivariate analysis to explore the relationship of riparian habitat and urbanization on native avifauna. In water-limited environments experiencing urban development, it is important to understand the ecological role of rivers and associated riparian habitats to better inform ecologically-based urban planning, especially where riparian areas are utilized by both wildlife and humans (Bark, Osgood, Colby, Katz, & Stromberg, 2009; Green & Baker, 2003; Urban, Skelly, Burchsted, Price, & Lowry, 2006).

2. Methods

2.1. Study area

Our Reno, Nevada study area is located on the western edge of the Great Basin at the foothills of the Sierra Nevada Mountains in the western United States (39°31′N, 119°48′W). Vegetation consists primarily of sagebrush steppe with cottonwood riparian woodland along the Truckee River. Temperatures are typical of a higher altitude (1600 m), semi-arid desert with a mean daily temperature of 10.7 °C (NOAA, 2010). Average annual precipitation is 184 mm, most of it falling in the form of snow in the winter months (WRCC, 2010). The Truckee River is fed almost entirely by snowmelt from the Sierra Nevada Mountains, and serves as the permanent water source for the metropolitan area, as it bisects Reno and adjoining Sparks, NV. Although Truckee River flows may become significantly reduced in the late summer, base flow for most of the year is approximately 8.5 cubic meters per second (USGS, 2010).

The city of Reno covers approximately 190 km^2 in the Truckee Meadows with an estimated population of 199,000 in 2004 when the fieldwork was completed (Hardcastle, 2010). Like many arid cities in the western U.S., much of the population growth has occurred in the previous 40 years, making most of the urban environment relatively young. Additionally, Reno is still considered a smaller city in the western U.S., but has the potential to double in population over the next 40 years (TMWA, 2010), making this an ideal place to study avian relationships in a smaller urban environment prior to its build out (Garaffa, Filloy, & Bellocq, 2009; Grimm, Grove, Pickett, & Redman, 2000). The relationship between Reno and the Truckee River is similar to many other semi-arid cities that have developed along a permanent water supply, making Reno a good location to study the dynamics of urban avian ecology in a smaller, semi-arid urbanized landscape.

2.2. Bird survey point counts

As an initial step in identifying potential habitats within the Reno study area, remnant habitat patches larger than 0.5 ha were digitized into a GIS using 3-m resolution, 24-bit color orthophotographs acquired from the National Agriculture Imagery Program (NAIP) in 2002. Images were segmented into polygons of maximum spectral and textural homogeneity using eCognition image processing software (version 4.0, Definiens Imaging, München, Germany). The software segments images into self-similar polygons based on user-defined scale, color, and shape parameters to highlight vegetation characteristics. The resulting 4355 polygons for all areas in and within 5 km of the urban boundary were manually photo-interpreted into one of the four vegetation types: coniferous forest, deciduous forest, riparian and upland/range. Vegetation categories were ground-truthed, but were used only to stratify point count locations. Although habitat type can be a good predictor of bird diversity (Heikkinen, Luoto, Virkkala, & Rainio, 2004), we used continuous habitat and vegetation data to better describe the influences of urbanization (Gustafson, 1998). Seventy-three point count locations, randomly located in the remnant habitat patches, were surveyed twice during the breeding season of 2004 (May–July), documenting birds visually and by call. Point counts were spaced at least 230 m apart to minimize the likelihood of double counting. Fifty meter radius point counts followed methodologies described by Ralph, Geupel, Pyle, Martin, and deSante (1993), consisting of 8 min observations after a 5-min calm down period. Bird locations within the 50 m radius were recorded in relation to the observer using estimated distances. All point counts were completed within 3 h after sunrise and counted only birds actively using the habitat (i.e. no flyovers were analyzed). Only species with >5 observations at >3 sites were included in the community analysis, while all birds were included in the richness and abundance analysis.

2.3. Environmental variables

There has been substantial debate over the relative importance of local (Luther et al., 2008; Oneal & Rotenberry, 2009) vs. landscape variables (Hedblom & Soderstrom, 2010; Suarez-Rubio & Thomlinson, 2009; Urbanova, 2009) for influencing avian distribution. Therefore, local and landscape variables describing anthropogenic and natural environmental influences were collected for each point count location (Table 1). Most local variables were collected in the field through vegetation surveys and observations of disturbances and focused on vegetation structure (Luther et al., 2008) and proximal anthropogenic disturbances (Oneal & Rotenberry, 2009). Tree layer and disturbance information was collected within 50 m, while shrub and herbaceous layers were sampled within a 20 m radius. Vegetation cover was visually estimated and calibrated by GRS densitometers, and tree density was tallied by diameter class. Landscape variables were derived in ArcGIS 9.1 (ESRI, Redlands, California) using multiple spatial analysis techniques with FragStats 3.3 software (McGarigal, Cushman, Neel, & Ene, 2002). To assess the scale dependence of avian response to urbanization (Oneal & Rotenberry, 2009), building and pavement cover within 100, 200, 300, 400, and 500 m circular buffers around the point counts were photo-interpreted from 1-m resolution, true-color NAIP imagery. All cover information was lumped into 10% bins (i.e. 1 = >0 to <10, 2 = 10–20, etc.). Distances from roads, arterials and highways, as well as road density were generated in ArcGIS using a detailed road coverage available from Washoe County GIS (http://www.co.washoe.nv.us/gis/datawarehouse.htm). Road density was calculated using the line density function in ArcGIS with a cell size of 10 m and search radius of 1000 m to ensure accurate density estimation. Distance from urban–rural boundary was generated for each point count location from the official City of Reno growth boundary, available at the Washoe County GIS site. FragStats was used to calculate patch shape and area to represent possible edge effects and describe the core area (Mason, Moorman, Hess, & Sinclair, 2007) as well as proximity and nearest neighbor index to represent isolation/connectivity effects (Fernandez-Juricic & Jokimaki, 2001; Nichol, Wong, Corlett, & Nichol, 2010) within a 10 km radius of each point count location. The 10 km search radius was chosen in order to incorporate all patches in the landscape, although patches very far away receive very little weight (McGarigal et al., 2002).

2.4. Species patterns

Species richness and relative species abundance patterns were modeled as Random Forests-derived classification and regression

Table 1
Description of environmental variables used to analyze bird distributions in Reno, NV. Local variables were primarily measured on site, while landscape variables were all generated with ArcGIS 9.1 (ESRI, Redlands, California) and FragStats 3.3 (McGarigal et al., 2002).

	Description
Local variables	
Distance to water	Distance to nearest water (m), measured from a shapefile of water bodies using GIS
Distance to trail	Distance to nearest visible undeveloped or developed trail (m), measured from a shapefile using GIS
Tree density	Overall tree density/ha, measured in the field
Tree density (5–25 cm DBH)	Smaller tree density/ha, measured in the field
Tree density >25 cm DBH	Larger tree density/ha, measured in the field
Shrub cover	Percent aerial cover from shrubs, measured in the field
Perennial grass cover	Percent aerial cover from perennial grasses, measured in the field
Annual grass cover	Percent aerial cover from annual grasses, measured in the field
Forb cover	Percent aerial cover from forbs, measured in the field
Vegetation diversity	Index: 1 for just trees up to 5 for all vegetation classes (trees, shrubs, perennial grass, annual grass and forbs) present
Pavement cover	Percent aerial cover from pavement, measured using aerial photographs in GIS
Trash cover	Percent aerial cover from trash, measured in the field
Disturbance index	Index: 1 for largely undisturbed to 4 for highly disturbed, measured in the field
People	Presence (1) or absence (0)
Dogs	Presence (1) or absence (0)
Landscape variables	
Distance from arterial road	Distance from nearest arterial road (m)
Distance from highway	Distance from nearest highway (m)
Distance from road	Distance from nearest road of any size (m)
Distance from Truckee	Distance from the Truckee River (m)
Distance from urban–rural boundary	Measured in meters. Negative values indicate distances outside of urban environment, positive indicate distance within urban environment. Large positive distances represent the habitats furthest within the urban boundary
Road density	Density (km/ha) of roads within 100, 200, 300, 400 and 500 m radii
Building cover	Percent cover within 100, 200, 300, 400 and 500 m radii
Pavement cover	Percent cover in 100, 200, 300, 400 and 500 m radii
Patch area	Continuous patch (ha)
Shape index	Calculated from FragStats using 10 km radius
Proximity index	Proximity to similar habitats, calculated from FragStats using 10 km radius
Nearest neighbor index	Distance to nearest habitat, calculated from FragStats using 10 km radius

trees in the program R using recursive partitioning. Classification and regression tree analysis (CART) is a non-parametric method that creates a decision tree by splitting data successively into increasingly homogeneous groups (nodes). The CART approach was chosen for its simplicity in interpretation and incorporation into a GIS, and its ability to represent hierarchical relationships and ecological thresholds. The ability to map biologically relevant thresholds in urban development is particularly important for regional planners, making CART a useful and intuitive method for this type of analysis (Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009). Recursive partitioning (RPART package in R) (Shannon, Province, & Rao, 2001) was used to minimize over-fitting. RPART allows v-fold cross-validation, which is useful for smaller datasets by deriving optimally sized classification trees based on validation (De'ath & Fabricius, 2000). This is done by dividing the dataset into 10 random subsets and excluding them one at a time from tree construction. The final tree is selected based on the tree with the smallest estimated error rate through that process. Additionally, because CART modeling is sensitive to the order and number of variables used as predictors, Random Forest models (Breiman, 2001; Peters et al., 2007) were used to identify the top environmental and urban variables that best explained the richness patterns. Random Forest works as a learning technique where bootstrap samples are used to construct many (in this case 500) classification or regression trees. For each tree, a random subset of variables is used, and the resulting tree is tested against data not used in the construction of the tree (called "out-of-bag" data). Random Forests then ranks the variables that are most often chosen to split the data. We used the top five variables identified by the Random Forests algorithm to develop RPART regression trees. Classification accuracy, number of observations per node, and residual mean difference are reported. Species richness was mapped in a GIS using the identified predictor thresholds from RPART trees.

2.5. Environmental gradient analysis

To better understand the underlying environmental gradients influencing native species distributions, nonmetric multidimensional scaling (NMS) ordinations in the software package PC-ORD 5.0 (McCune & Grace, 2002) were developed (Hudson & Bird, 2009; O'Dea & Whittaker, 2007; Vallejo, Aloy, & Ong, 2009). NMS is an indirect ordination method that has the least number of assumptions about the patterns of species distribution along environmental gradients. Euclidean distance was used to measure the multidimensional space between species. Because NMS requires the number of axes to be determined *a priori*, the first ordination was run using a 6-axis solution with a stability criterion of 0.00001, and 250 permutations each with real and randomized data. The final solution included the minimum number of axes that provided the lowest overall stress and instability. Corresponding environmental variables with a R^2 greater than 0.2 (McCune & Grace, 2002) were plotted as vectors to help interpret the environmental gradients responsible for shaping species distributions. Both native and exotic species were included in this analysis in order to better understand potential avian assemblages.

3. Results

3.1. Bird observations

A total of 56 species of birds were used for the diversity analyses, while only 35 were abundant enough to be used in the community-level ordination analyses (Table 2). All but three species counted were considered native. The Mourning Dove (*Zenaida macroura*) was the most abundant bird observed with 246 observations, while the House Finch (*Carpodacus mexicanus*) had 202 observations and Cliff Swallow (*Petrochelidon pyrrhonota*) had 188 observations.

Table 2
Total species list for all surveys collected in and around Reno in the summer of 2004, along with mean and standard deviation of their abundance. Species marked with '*' were observed only as flyovers, while '+' indicates non-songbirds that were excluded from all analyses. Bold fonts mark species seen at least 5 different times in at least 3 different point locations.

	Common name	Scientific name
	American Goldfinch	*Carduelis tristis*
+	American Kestrel	*Falco sparverius*
	American Robin	***Turdus migratorius***
*	Band-tailed Pigeon	*Patagioenas fasciata*
	Barn Swallow	***Hirundo rustica***
	Bewick's Wren	***Thryomanes bewickii***
	Black-billed Magpie	***Pica hudsonia***
	Black-chinned Hummingbird	***Archilochus alexandri***
	Black-headed Grosbeak	***Pheucticus melanocephalus***
	Black-throated Sparrow	*Amphispiza bilineata*
	Blue-gray Gnatcatcher	*Polioptila caerulea*
	Brewer's Blackbird	***Euphagus cyanocephalus***
	Brown-headed Cowbird	***Molothrus ater***
	Bullock's Oriole	***Icterus bullockii***
	Bushtit	*Psaltriparus minimus*
*	California Gull	*Larus californicus*
	California Quail	***Callipepla californica***
+	Canada Goose	*Branta canadensis*
	Cliff Swallow	***Petrochelidon pyrrhonota***
	Common Crow	***Corvus brachyrhynchos***
+	Common Merganser	*Mergus merganser*
	Common Nighthawk	*Chordeiles minor*
+	Cooper's Hawk	*Accipiter cooperii*
+	Double Crested Cormorant	*Phalacrocorax auritus*
	Downy Woodpecker	***Picoides pubescens***
	Empidonax spp	***Empidonax* spp.**
	European Starling	***Sturnus vulgaris***
*	Golden Eagle	*Aquila chrysaetos*
	Gray Flycatcher	*Empidonax wrightii*
+	Great Horned Owl	*Bubo virginianus*
	Hairy Woodpecker	*Picoides villosus*
	Horned Lark	*Eremophila alpestris*
	House Finch	***Carpodacus mexicanus***
	House Sparrow	***Passer domesticus***
	House Wren	***Troglodytes aedon***
+	Killdeer	*Charadrius vociferus*
	Lark Sparrow	*Chondestes grammacus*
	Lesser Goldfinch	***Carduelis psaltria***
	Lewis's Woodpecker	*Melanerpes lewis*
+	Mallard	*Anas platyrhynchos*
	Mountain Chickadee	***Poecile gambeli***
	Mourning Dove	***Zenaida macroura***
	Northern Flicker	***Colaptes auratus***
	Northern Mockingbird	***Mimus polyglottos***
	Northern Raven	*Corvus corax*
	Northern Rough-winged Swallow	*Stelgidopteryx serripennis*
	Orange-crowned Warbler	*Vermivora celata*
*	Prairie Falcon	*Falco mexicanus*
	Pygmy Nuthatch	*Sitta pygmaea*
	Red-breasted Sapsucker	*Sphyrapicus ruber*
+	Red-tailed Hawk	*Buteo jamaicensis*
	Red-winged Blackbird	***Agelaius phoeniceus***
	Rock Pigeon	***Columba livia***
	Rock Wren	***Salpinctes obsoletus***
	Rufous Hummingbird	*Selasphorus rufus*
	Say's Phoebe	*Sayornis say*
	Song Sparrow	***Melospiza melodia***
+	Spotted Sandpiper	*Actitis macularia*
	Spotted Towhee	***Pipilo maculatus***
	Steller's Jay	***Cyanocitta stelleri***
	Tree Swallow	***Tachycineta bicolor***
+	Turkey Vulture	*Cathartes aura*
	Vesper Sparrow	*Pooecetes gramineus*
	Violet-green Swallow	*Tachycineta thalassina*
	Warbling Vireo	***Vireo gilvus***
	Western Bluebird	*Sialia mexicana*
	Western Kingbird	*Tyrannus verticalis*
	Western Meadowlark	***Sturnella neglecta***
	Western Scrub Jay	***Aphelocoma californica***
	Western Tanager	***Piranga ludoviciana***
	Western Wood Pewee	***Contopus sordidulus***
+	White-faced Ibis	*Plegadis chihi*
	Wilson's Warbler	*Wilsonia pusilla*
	Yellow Warbler	*Dendroica petechia*

Total abundance was 2788 individuals, with 2149 of those birds being native species.

3.2. Native richness and abundance

Classification and regression tree results identified several key environmental influences that best describe native bird richness and abundance patterns. From Random Forests modeling, the top variables (in order of importance) for native species richness were: the distance from the Truckee River (−), patch area (−), mean height of shrubs (+), distance to nearest water (+), and distance from urban–rural boundary (+). The top variables for abundance (in order of importance) were: road density within a 500 m radius (+), patch area (−), distance to nearest road (−), distance from urban–rural boundary (+), and the presence/absence of trash (+). The most parsimonious CART model for native species richness only included distance from the Truckee River and patch area, while the final CART model for native bird abundance incorporated three variables: distance to nearest road, distance to urban–rural boundary and patch area (Fig. 1).

Native bird richness appears to be influenced primarily by distance to the Truckee River (Fig. 1(A)). According to the regression tree, the influence of the Truckee River can be visualized at three different levels. First there is a split at distances far from the river (3400 m), potentially accounting for the native bird species that are associated with shrub-dominated, rangeland habitats. Another split at 1600 m appears to highlight native generalist species. The final split occurs at 520 m from the river, representing the highest richness areas, and potentially riparian-specific species. Thus, this model shows decreased richness along a distance gradient from the Truckee River out into the rangeland (Fig. 2).

Native bird abundance appears to be influenced primarily by human-created environmental variables, in contrast to natural environmental variables for richness. The most influential predictor of native abundance is distance from nearest road, with closer distances yielding higher abundances (Fig. 1(B)). At distances from roads greater than 250 m, there are also relatively high abundances, especially in suburban habitats near the urban–rural boundary, both within and outside the urban environment. Smaller patches that are isolated from other habitats show high abundances. Larger habitat patches (greater than 4.5 ha) located close to roads are also predicted to have high native abundance.

3.3. Environmental gradients

NMS ordination results showed three potentially important gradients underlying avian assemblage structure in the greater Reno area, explaining a total of 78% of the overall variance (overall stress = 18.74; orthogonality = 100%). A single axis (Axis 2) explained 43% of the variance and described a gradient from locations that are deeply within the city limits, have a high road density, and are close to the Truckee River, to those that are far from the city limit, roads, or the Truckee River (Fig. 3(A) and (B)). Bird species with low scores on this axis included rangeland species such as Rock Wren (*Salpinctes obsoletus*), Western Meadowlark (*Sturnella neglecta*), and Black-blled Magpie (*Pica hudsonia*). Species with highest scores included riparian species such as Black-headed Grosbeak (*Pheucticus melanocephalus*), Downy Woodpecker (*Picoides pubescens*), Brewer's Blackbird (*Euphagus cyanocephalus*),

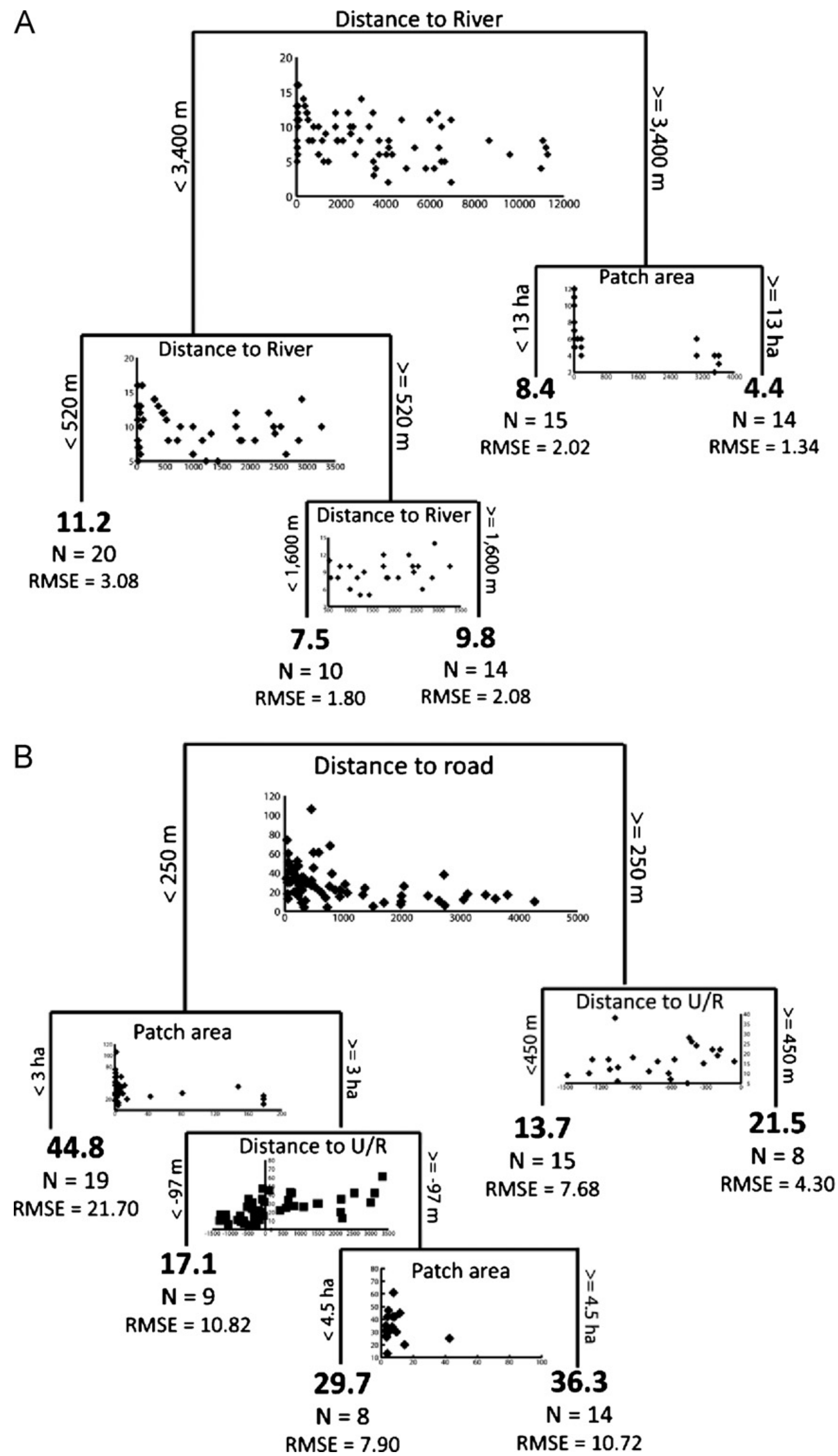

Fig. 1. CART models for native bird richness (A) and abundance (B) in urban Reno, NV. Each of the splits are labeled with the value of the variable used to make the split. Scatterplots show richness (A) and abundance (B) against the variables used in the splits. The mean response values are shown at the terminal nodes (in bold), along with the number of observations that follow the criteria and the root mean squared error. Native bird richness is highest in habitats close to the Truckee River, while native bird abundance is highest in smaller (patch area) habitats with lower road density in town. 41% of the variance is explained by the native bird richness tree, while 55% of the variance is explained by the native bird abundance tree.

Tree Swallow (*Tachycineta bicolor*), Black-chinned Hummingbird (*Archilochus alexandri*), and Bewick's Wren (*Thryomanes bewickii*) (Rich, 2002). This axis therefore describes a gradient of riparian influence that has a strong positive association with the urbanization gradient.

Axis 3 of the NMS ordination explained slightly over 20% of the overall variance and described a gradient of urban influence distinct from riparian effects (Fig. 3(B)). Environmental variables with strong correlations with this axis included building cover (positive correlation) and distance from arterial roads (negative correlation). Species with highest Axis 3 scores (i.e. "urban species") included Rock Pigeon (*Columba livia*), Red-winged Blackbird (*Agelaius phoeniceus*), European Starling (*Sturnus vulgaris*), House Sparrow (*Passer domesticus*), American Crow (*Corvus

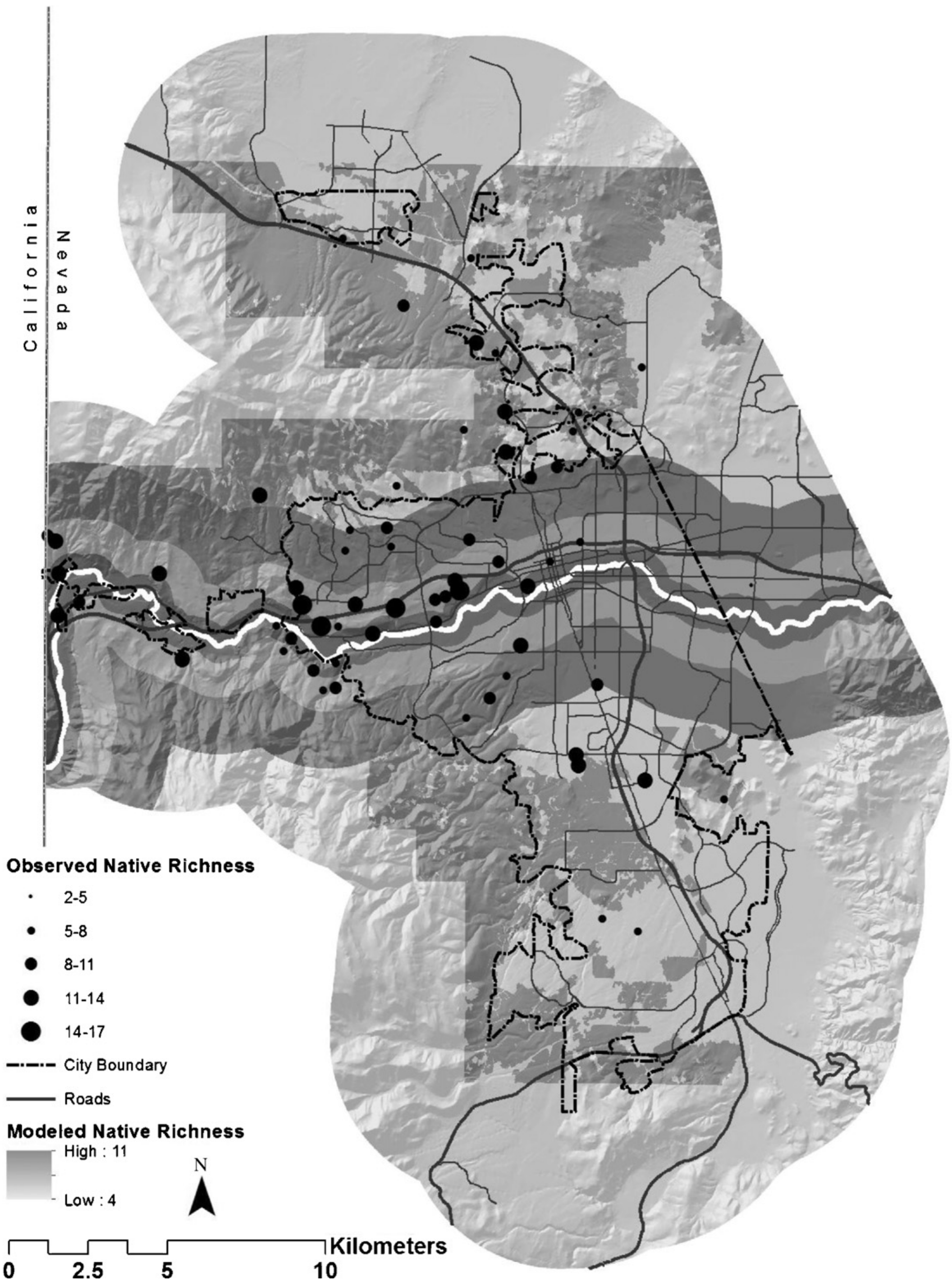

Fig. 2. Predicted native species richness in Reno, NV. Darker greys represent higher richness using thresholds identified in a CART analysis. Dashed line represents the urban–rural boundary for Reno. Highways and arterial roads are in light gray. Truckee River is the bold white line bisecting Reno. Black dots show native richness observed at each point count location. Native richness is influenced primarily by distance from the Truckee River, regardless of the presense of urbanization.

brachyrhynchos), Black-chinned Hummingbird (*Archilochus alexandri*), and Northern Mockingbird (*Mimus polyglottos*). Species with lowest Axis 3 scores (i.e. potential "wildland" species) included Warbling Vireo (*Vireo gilvus*), Western Wood Pewee (*Contopus sordidulus*), and Black-headed Grosbeak (*Pheucticus melanocephalus*). From this axis we can see some separation of the effects of urbanization and the effect of the Truckee River on native species.

NMS Axis 1 explained 14% of the overall variance, but was not significantly correlated with any of the measured environmental predictor variables (Fig. 3(A)). Species with highest Axis 1 scores included both rangeland and wetland species that share a proclivity for open areas, marshy areas, or sparse forest with large openings (e.g. Cliff Swallow, Red-winged Blackbird, Song Sparrow, *Empidonax* Flycatchers, Black-billed Magpie, and Northern Mockingbird). Species that require dense forest or are more common in higher-elevation coniferous forests in the foothills surrounding the urban area had lower scores (e.g. Mountain Chickadee, Western Tanager, and Common Crow). Axis 1 likely describes a gradient of forest vegetation that was not well captured by the measured tree density variables.

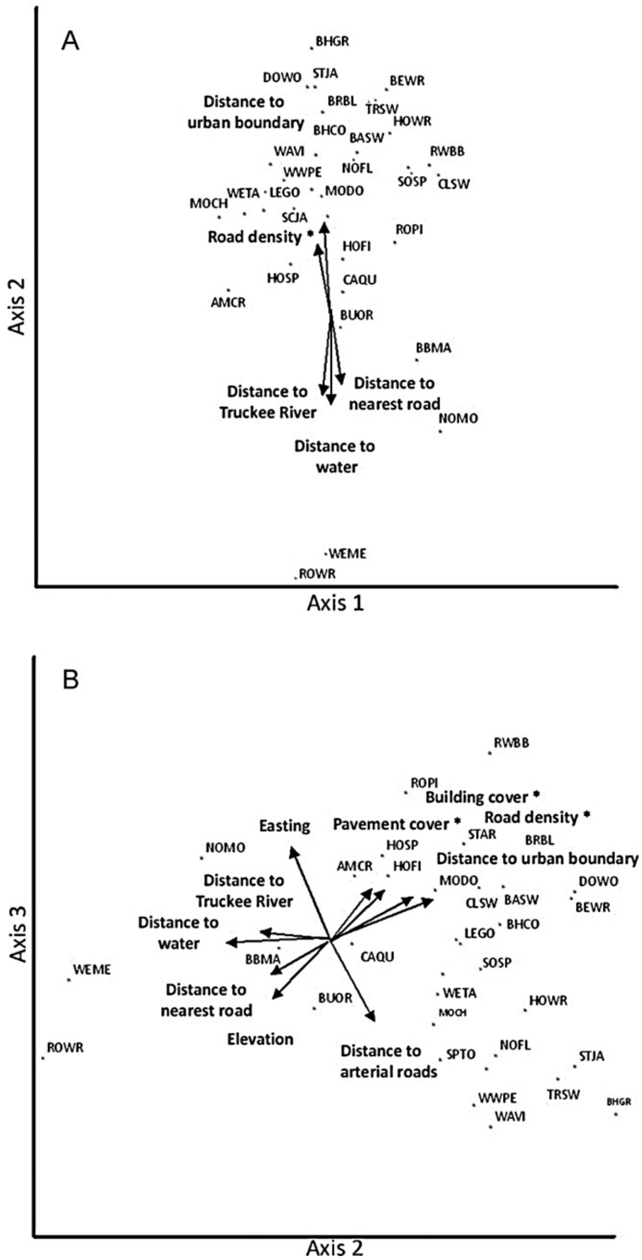

Fig. 3. Plot showing relative position of different birds found in Reno, NV in multi-dimensional space using non-metric multidimensional scaling (NMS). (A) NMS plot of axis 1 and 2 with environmental vectors as arrows. (B) NMS plot of axis 2 and 3 with environmental vectors as arrows. The length and direction of the environmental vectors indicate how well those variables can be used to explain the axis. Axis 1 had low correlation values to any of the measured environmental variables, while Axis 2 and Axis 3 hightlight the importance of the urban-Truckee River gradient and the Truckee River gradient separate of urbanization, respectively. Axis 2 and 3 best describe the avian communities present in Reno, NV, with riparian birds found in the lower left corner, urban riparian birds in the middle-right, and non-riparian rangeland birds on the far left. '*' indicates the variable was sampled within 500 m radius of point count.

The combination of Axes 2 and 3 most clearly describes avian assemblage structure in Reno and corroborates the key influences on avian species richness identified in the CART analysis (Fig. 3(B)). Western Meadowlark and Rock Wren stand out as indicator species of relatively undisturbed rangelands (Figs. 1 and 3(A) and (B)). Species of deciduous riparian forests that are less disturbed had species score centroids that correlate to habitats further from arterial roads, but close to the Truckee River (e.g. Warbling Vireo, Black-headed Grosbeak, Western Wood Pewee, Tree Swallow, and Steller's Jay). Species of urbanized riparian environments had species score centroids that placed them in habitats closer to roads and in areas with higher building and pavement cover, but still close to the Truckee River (e.g. Black-Chinned Hummingbird, Brewer's Blackbird, Red-winged Blackbird, Downy Woodpecker, and Bewick's Wren). Generalist species, including California Quail, Black-billed Magpie, House Finch, and American Robin, had low scores in both ordination axes. Predictor variables most influential for describing effects of urbanization on avian assemblage structure appear to be building cover, pavement cover, distance from nearest road, distance from the nearest arterial road, and distance from the urban boundary (Fig. 3).

4. Discussion

4.1. Native bird response to urbanization in an arid landscape

The Truckee River strongly influences spatial patterns of native richness in Reno, resulting in greater native bird richness within the most developed portion of Reno. While there are many studies that have found increasing species richness with increasing urbanization at regional or global scales (Araujo, 2003; Chiari, Dinetti, Licciardello, Licitra, & Pautasso, 2010; Hugo & Van Rensburg, 2008; Luck, 2007; Luck, Smallbone, Mcdonald, & Duffy, 2010; Moreno-Rueda & Pizarro, 2009), this study provides evidence of species richness increasing with human development at the city-wide scale. Similar to other studies, it appears that this pattern is strongly influenced by riparian habitat that has been maintained in an urban environment (Fletcher & Hutto, 2008; Hedblom & Soderstrom, 2010; Hugo & Van Rensburg, 2008; Miller, Wiens, Hobbs, & Theobald, 2003; Oneal & Rotenberry, 2009; Rodewald & Bakermans, 2006; Rosenberg et al., 1987). As with many semi-arid cities, urbanization is highest along portions of the Truckee River (Patten, 1998). In this study, native richness was highest immediately near the Truckee River, and at distances from 1600 to 3400 m from the river. The increased richness at intermediate distances supports the conclusions of many of the urban–rural gradient studies (Blair, 1996; Blair & Johnson, 2008; Chapman & Reich, 2007) as suburban development dominates the land use starting at 1 km from the Truckee River extending to the urban boundary. The increase in irrigation, vegetation structure, parks (Shwartz et al., 2008) and gardens (Doody, Sullivan, Meurk, Stewart, & Perkins, 2010) that accompany suburban development could be extending the riparian habitat into the city, possibly explaining the higher species richness at 1600–3400 m from the river. The increased richness immediately around the Truckee River, despite the intense urbanization present, suggests that remnant riparian habitat may reduce the negative effects of local urbanization on bird species richness in semi-arid habitats. Although we were unable to disentangle the covarying influences of increasing urbanization and presence of riparian habitat, it appears that riparian habitat is still an important factor in determining avian richness, even in urban landscapes (Oneal & Rotenberry, 2009).

Our findings corroborate previous research that calls for maintenance of riparian habitat for avian conservation (Green & Baker, 2003; Luther et al., 2008; Palmer & Bennett, 2006; Rodewald & Bakermans, 2006; Rottenborn, 1999; Saab, 1999). However, our results also identify certain bird species that may not respond so favorably to urbanization (most rangeland species, and a few disturbance-intolerant, riparian species). Additional consideration of larger-scale (gamma) diversity is necessary before concluding that semi-arid urban environments can play an important role in regional avian conservation. The possibility that remnant riparian patches act as sinks for regional avian diversity also needs to be further explored (Leston & Rodewald, 2006), especially when considering the increased abundance observed near roads in this analysis.

4.2. Planning implications

Improved urban planning based on locally focused environmental research is critical for reducing the negative impacts of urbanization on biodiversity (Grimm et al., 2000). The importance of urban green space and parks, specifically those focused around urban rivers, has been established on environmental (Atchison & Rodewald, 2006; Pennington et al., 2008) as well as socioeconomic (Acharya & Bennett, 2001; Chen & Jim, 2008; Kline, 2006) grounds. This research supports the call for better protection of river habitats and riparian corridors in semi-arid urban environments to promote bird conservation. Landscape features that promote native bird richness, such as distance from the Truckee River, best describe the observed native species richness patterns, suggesting that planners should focus on designating more parks and open space close to the Truckee River to protect remnant riparian habitat The observation that variables like road density and the presence of people did not negatively impact overall native richness suggests there may be a role for urban habitats in native bird conservation, though more research into survival and fitness of birds near these land uses is required before land use policies should be adopted.

4.3. Future research

Our Reno study area is fortunate in that riparian patches along the Truckee River have been protected as parks and other open space, even as the river flows through densely urbanized areas. Given the importance of rivers and their associated riparian forests to biota in arid environments, it would be useful to quantify how much and where urban riparian habitat exists. Likewise, research into the potential of suburban development in mimicking riparian habitat by creating water-rich, structurally diverse habitats will help in riparian bird conservation (Blair & Johnson, 2008).

The value of riparian areas in Reno has been recognized within the context of flood control, but the value as habitat for native fauna has yet to be quantified. Further research into how biodiversity varies along urban rivers, especially in varying levels of development and with different surrounding land use, is critical for improved management of urban riparian systems (Smith & Wachob, 2006). Likewise, research into the potential of urban landscape features to extend the distribution and connectivity of riparian habitat is needed, especially given the ability of planners to encourage tree plantings and zoning for various habitat variables (i.e. reduced road density or pavement cover).

5. Conclusion

The difference between the urban and non-urban environment in arid landscapes is distinct because of the large water subsidy provided by human development. This research has highlighted the importance of understanding the landscape context of a city in determining the potential response of native bird species to urbanization (Fletcher & Hutto, 2008; Luther et al., 2008). The strong effect of the Truckee River on avian richness patterns highlights the importance of riparian habitat in arid urban environments. Local ecological research is needed to provide regional planners with the best available data for designing urban landscapes, emphasizing the ecology of cities and not just ecology in cities (Grimm et al., 2000; McDonnell & Hahs, 2008). Ecologists, or ecologically trained planners, are best poised to understand the functional difference between the natural and urban environments, especially in arid environments where the difference is more than just a difference in land use, but a difference in water availability, ecological productivity and heterogeneity of habitat structure.

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