

Long-term effects of land-use change on bird communities depend on spatial scale and land-use type

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Abstract. Land-use transformation is one of the most important and pervasive ecological changes occurring across the Earth, but its long-term effects are poorly understood. Here, we analyze the effects of urban and agriculture development on bird biodiversity and community structure over a 16-yr study period. We found that long-term effects of land-use change are dependent on spatial scale and land-use type. At the regional scale, we found that gamma diversity (total number of species observed) declined by ~10% over time. At the landscape spatial scale, we found that beta diversity (uniqueness of bird communities) increased by ~16% over time. Additionally, the average contributions of urban riparian bird communities to beta diversity were generally the highest but declined by ~26% over the study period. Contributions of urban communities to beta diversity were generally the lowest but increased by ~10% over time. At the local scale, we observed different responses for different measures of alpha diversity. For bird species richness, temporal changes varied by land use. Species richness declined 16% at sites in desert riparian areas but increased by 21% and 12% at sites in urban and agricultural areas, respectively. Species evenness declined across all land uses, with some land uses experiencing more rapid declines than others. Our analysis of species groups that shared certain traits suggests that these community-level changes were driven by species that are small, breed onsite, and feed on insects, grains, and nectar. Collectively, our results suggest that biodiversity declines associated with land-use change predominate at the regional and local spatial scale, and that these effects can strengthen or weaken over time. However, these changes counterintuitively led to increases in biodiversity at the landscape scale, as bird communities became more unique. This has implications for conservation and management as it shows that the effects of land-use modification on biodiversity may be positive or negative depending on the spatial scale considered.

Key words: agriculture; alpha diversity; beta diversity; birds; desert; gamma diversity; land-use change; riparian; urban; urbanization.

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INTRODUCTION

Anthropogenic ecological change is pervasive in the Earth's ecosystems, as humans have changed the ecology of our entire planet (Ellis 2015).

One of the most important ways humans modify ecosystems is through the development of natural lands, turning natural landscapes into the farms and urban areas that support human populations (Grimm et al. 2008, Tylianakis et al. 2008, Kleijn

et al. 2009). As human populations continue to grow, biodiverse-rich natural lands are converted to agricultural and urban land uses to support this growth (Cincotta et al. 2000). In an analysis from 2001 to 2015, 21% of the 314 Mha of global forest loss was due to conversions of forest to agricultural land, with even greater proportions in regions associated with higher population growth (31% in Latin America and 92% in Africa; Curtis et al. 2018). Although urban lands cover only 2% of the Earth's surface, they host more than half of the world's human population (Grimm et al. 2008). Urban land development continues to increase, particularly in regions experiencing rapid growth such as China where the total urban land area doubled from 1990 to 2010 (Li et al. 2018). Understanding the ecological impacts of land conversion at multiple spatial and temporal scales is essential in order to manage lands to maintain ecosystem integrity and its associated ecological functions and ecosystem services.

Though the ecological changes produced by human land development can be dramatic, many aspects of an ecosystem remain in place. Ecosystem processes such as nutrient transformations, primary production and metabolism, and the trophic interactions that control energy flow through the food web still occur (Ellis 2015). Yet, anthropogenic land-use changes typically alter how these processes occur or which organisms perform them (Pickett et al. 2001). For example, one study showed gross primary productivity in stream ecosystems was higher in agricultural and urban areas than in natural reference streams across nine different geographical regions of the United States (Bernot et al. 2010). In another study on reptile communities in Caribbean islands, Jesse et al. (2018) observed that native species were most abundant in natural forests, while human-impacted sites were dominated by nonnative species. Further, the largest urban global database of multiple taxa observed that cities support regional biodiversity but at substantially lower densities compared with nonurban areas (Aronson et al. 2014). Human-modified ecosystems differ from their natural counterparts in many ways, though how these differences might change over time (e.g., strengthening or weakening) is less well known.

Long-term ecological studies are critical to understanding the temporal dynamics of global

environmental change on ecosystems. Indeed, we are now recognizing that long-term ecological studies have a disproportionate impact on science and policy relative to the amount of funding they receive (Hughes et al. 2017). Studies as part of a long-term stream monitoring program in the Hubbard Brook experimental forest helped discover acid rain as having broadscale environmental problem that alters biogeochemical processes in streams and forests (Likens et al. 1996), prompting an amendment to the U.S. Clean Air Act into address the issue. Likewise, long-term studies that remove top consumers or manipulate resource availability at the bottom of food webs have shown that these top-down and bottom-up effects can interact with temporal fluctuations in biotic and abiotic conditions in forests, deserts, lakes, and stream ecosystems (Brown et al. 2001, Carpenter et al. 2001, Power et al. 2008). Yet, most long-term studies have been conducted in natural ecosystems, so our understanding of long-term anthropogenic effects on ecosystems remains less clear.

Birds are a model system for studying the long-term responses of ecosystems to global environmental change. As mobile organisms that can move freely between habitats with a diverse suite of body size, feeding, and behavioral traits, bird community structure and composition can quickly change in response to environmental perturbations on short-time scales (Thorn et al. 2018). As long-lived vertebrates that may or may not adapt to changing conditions, population responses of individual species may not be consistent over longer time scales (Hardesty-Moore et al. 2018). Birds also perform a wide range of important ecosystem processes including pollination (Zanata et al. 2017), seed dispersal (Sekercioglu et al. 2004), and can also be important top-down controls on lower trophic levels (Gruner 2004). Thus, changes in bird community composition and structure have the potential to reverberate throughout ecosystems (Sekercioglu et al. 2004, Bregman et al. 2014). Long-term studies are showing that bird communities are changing across the globe in response to environmental change. For example, Stephens et al. (2016) used long-term data to document that bird species whose climate suitability has been increasing as a result of climate change are relatively more abundant in the United States and Europe.

Here, we present one of the first long-term studies of bird communities in both natural and anthropogenically modified ecosystems using bird survey data from the Central Arizona Phoenix Long-Term Ecological Research Program (CAP LTER). Phoenix, Arizona, United States, is situated within one of the dryland climates that make up 41% of the terrestrial biosphere (Reynolds et al. 2007), where two primary ecosystem types exist: uplands that typically lack trees and where vegetation is dominated by shrubs, succulents, or drought-resistant grasses; and lowland riparian and floodplain areas that border perennial, intermittent, and ephemeral streams and rivers which often harbor pioneer tree species. Riparian areas in the desert southwest are a critical habitat for bird conservation due to their importance as a migratory pathway (Skagen et al. 2005). Declines in bird communities in the southwestern United States have been reported in the desert in response to climate change (Iknayan and Beissinger 2018) and in riparian areas in response to recent large-scale biocontrol efforts to defoliate nonnative riparian vegetation (Darah and van Riper 2018) and to urbanization (Banville et al. 2017). And although previous work has investigated bird communities in urban areas in this region (Lerman and Warren 2011, Lerman et al. 2012, Warren et al. 2019), studies comparing long-term bird community dynamics in natural vs. anthropogenically modified habitats together are lacking.

We examined how bird biodiversity has changed over time across three different spatial scales: regional scale (gamma diversity), the landscape or metacommunity scale (beta diversity), and the local or site scale (alpha diversity). We compared

bird communities across five different land uses common in the region, two natural (desert and desert riparian) and three anthropogenically modified (urban, urban riparian, and agricultural). Based on previous studies in the region, we generated four predictions (Table 1): (1) Gamma diversity, the total number of species in the region, has declined over time following other studies finding bird declines globally and in the desert southwestern United States (Banville et al. 2017, Iknayan and Beissinger 2018, Spooner et al. 2018). (2) Beta diversity (uniqueness of individual bird communities within the landscape or metacommunity) has declined over time, as previous work has demonstrated that urbanization can homogenize communities in ways that should reduce beta diversity (Groffman et al. 2014, Murthy et al. 2016). (3) Local contributions to beta diversity (LCBD), which is the uniqueness of a given site relative to other communities in the landscape, should be highest in natural riparian areas due to unique taxa harbored by this ecosystem relative to other habitats in the landscape (Sabo et al. 2005). Local contributions to beta diversity will be lowest in anthropogenically modified land uses as they contain a nested subset (i.e., nonunique) of tolerant taxa also observed in natural land uses (Lerman and Warren 2011, Andrade et al. 2018). Moreover, we predicted that changes in LCBD for each land use over time would be different due to rapid declines in urban riparian bird species observed in this system (Banville et al. 2017). (4) Alpha diversity has declined over time in line with other studies showing global bird declines (Banville et al. 2017, Iknayan and Beissinger 2018, Spooner et al. 2018), and alpha diversity should

Table 1. Predictions for gamma diversity, beta diversity, Local contributions to beta diversity (LCBD), and alpha-diversity changes over time and differences between land uses.

Response variable	Time	Land use					Time × land use
		Ag	Des	Des Rip	Urb	Urb Rip	
Gamma diversity	–	NA	NA	NA	NA	NA	NA
Beta diversity	–	NA	NA	NA	NA	NA	NA
LCBD	0	–	0	+	–	+	Yes
Alpha diversity	–	0	0	+	0	+	Yes

Notes: Time is how a response variable changed over time. Abbreviations are Ag, agriculture; Des, desert; DesRip, desert riparian; Urb, urban; and UrbRip, urban riparian. + indicates an increase, – indicates a decrease, and 0 indicates no change over time or average value for land uses. Time × land use indicates if we predicted an interaction such that land-use effects changed over time. We indicate NA for when cannot make a prediction, as gamma diversity and beta diversity measure biodiversity across all the entire region ($n = 1$ per point in time) and not for a given land use.

be highest in riparian areas and lowest in urban, agriculture, and deserts (Lerman and Warren 2011, Murthy et al. 2016, Andrade et al. 2018). Taken together, our evaluation of these predictions provides a multi-scalar analysis of long-term anthropogenic impacts on the diversity and composition of a sentinel taxonomic group.

METHODS

Bird survey methods

The CAP LTER program surveys birds at many sites throughout the Phoenix, Arizona, United States, greater metropolitan area, and in the surrounding desert (Bateman et al. 2017). Trained observers recorded all birds seen and heard in point count surveys of birds using a 40-m fixed radius and completed all surveys under similar environmental conditions within four hours of sunrise. At each site, the observer remained quiet for 5 min and then recorded bird species and abundance for 15 min. Birds detected beyond the 40 m distance, or those that flew over the point, were not counted except for wide-ranging and wide-foraging species (i.e., birds of prey, waterfowl, and shorebirds). Three observers visited each site during each season, once during winter (end of December to mid-February) and once during spring (end of March to mid-May) for a total of six visits per site per year. Central Arizona Phoenix Long-Term Ecological Research Program bird surveys began in the year 2001 and continue to the present.

Data processing

For our time-series analysis, we processed the CAP LTER bird survey data to generate a temporally robust dataset. Some sites were not surveyed every year due to access issues, and some sites changed in land-use over time (e.g., several study sites originally on agricultural land were developed into new housing developments). We removed sites that did not contain data for a given year or if historical aerial/satellite imagery indicated that changes in land use had occurred. We also removed data for the year 2003 when no riparian sites were surveyed because we wanted to include riparian sites in our analysis. The final dataset consisted of 43 sites with both winter and spring bird surveys from 2001 to 2002 and from 2004 to 2016 (Fig. 1, Data S1). We used observer

field notes and historical aerial/satellite imagery to classify sites into one of five land-use categories: agriculture ($n = 4$), desert ($n = 13$ sites), desert riparian ($n = 5$), urban ($n = 16$), and urban riparian ($n = 5$).

Although there was some year-to-year consistency in individual observers, over the 16 yr study period some observers ceased working on the project and new observers were trained to replace them. Because the identity of observers did not remain consistent throughout the study period, it would be difficult to use observer identity as a covariate in our analyses since it would be confounded with the time period with which they were making observations. Additionally, in 10 of the 1290 sites, in at least one survey one or two of the three observations were missing, or in some cases there was one observation too many. To correct these inconsistencies, we collapsed our dataset by taking the mean abundance of bird taxa recorded at each site during each survey (one bird community species composition and abundance datum per site per survey). This yielded 1290 bird community data points ($43 \text{ sites} \times 15 \text{ yr} \times 2 \text{ seasons}$). Finally, previous analyses of CAP LTER bird community data have shown that winter and spring bird communities are distinct from each other (Banville et al. 2017). Many taxa reside in the region only in the winter as part of their nonbreeding winter range, and many reside in the region only in spring as passing migrants or as part of their summer breeding range. Accordingly, we treat the winter and spring bird community data as separate datasets.

We assessed how the biodiversity of bird communities changed over time at the regional, landscape, and local spatial scales. We measured gamma diversity (regional-scale biodiversity, data collected across all sites are pooled) as the total number of bird species recorded during surveys across all 43 sites during a given time point. We measured beta diversity (landscape-scale biodiversity, comparisons of the uniqueness of sites against each other) of the entire metacommunity (all 43 study sites) at each point in the time series (total beta diversity). We also calculated the contribution to beta diversity of each site (LCBD) and each species (species contribution to beta diversity). All beta-diversity calculations were made using the *adespatial* package in R software

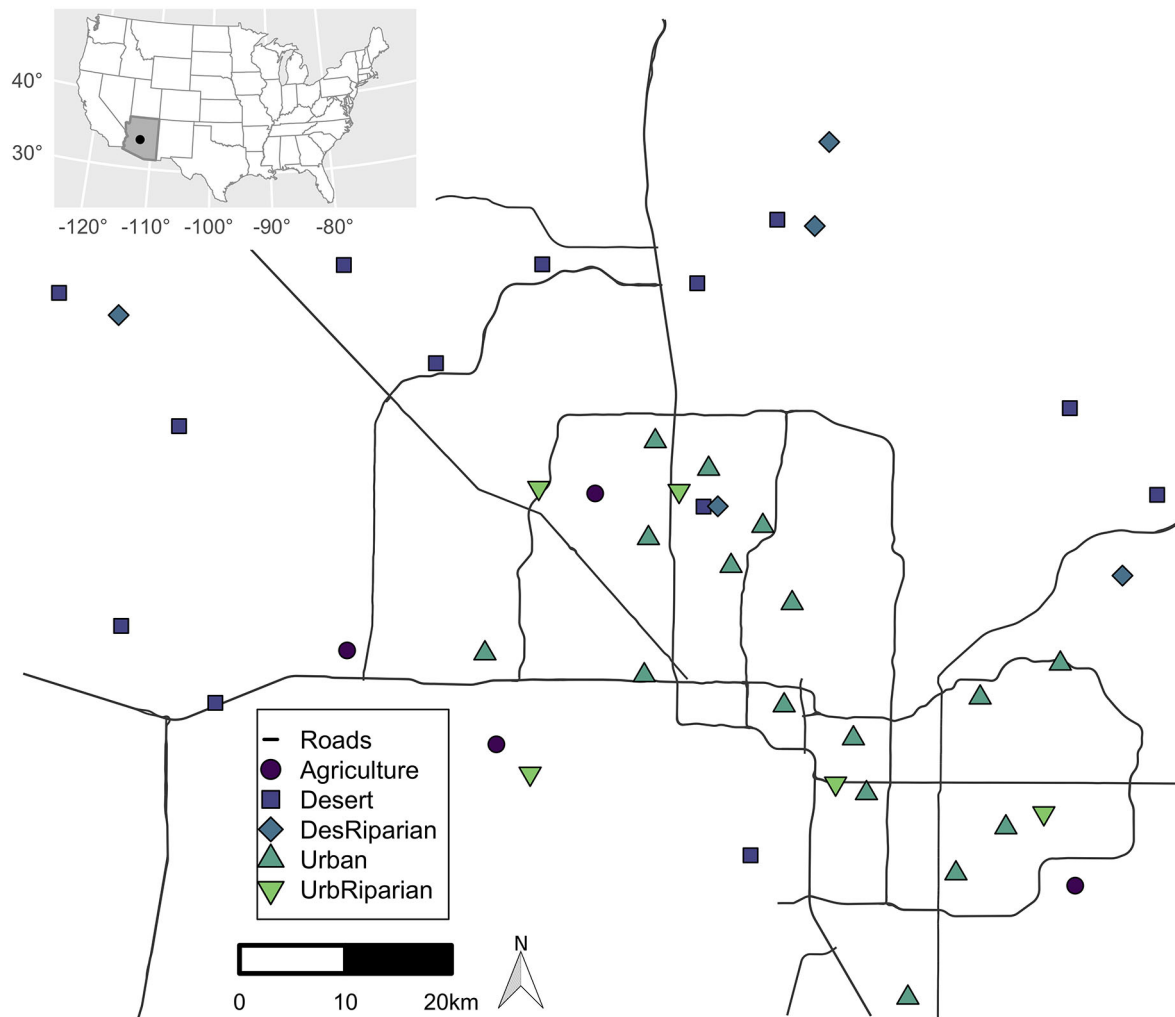


Fig. 1. Map of study sites. Inset map shows study area in the state of Arizona in the United States. Sites in each land use are a different shape and color (see legend).

and follow the methods described in Legendre and Cáceres (2013). To quantify local-scale biodiversity at each site at each point in the time series, we calculated two different measures of alpha diversity, species richness (S) and Pielou's evenness (J). Species richness and Pielou's evenness calculations were made using the *vegan* package in R software.

To investigate how biodiversity metrics changed over time and whether these changes varied by land use, we used general linear models with year as a continuous fixed variable, land use as a categorical fixed variable, and interaction term between them to see whether temporal trends varied by land-use type. However, for analyses

with gamma diversity and total beta diversity as response variables, we used simple general linear models (GLMs). Because gamma- and beta-diversity measurements are calculated across all sites in all land uses, we had only values per survey, so we used a general linear model with year as a continuous fixed variable as the single factor.

Since preliminary analyses indicated that bird communities have changed over time, we conducted an additional set of analyses to investigate which taxa were driving these community changes. We wanted to know whether changes in bird communities were due to increases/decreases in the ranges or abundances of certain taxa with specific sets of species traits. For all 219

taxa we observed, we compiled data on the following traits: (1) body size: maximum length (cm) and maximum weight (g); (2) diet: frugivore, granivore, plantivore, insectivore, nectar feeder, predator of terrestrial prey, predator of aquatic prey, and carrion feeder/scavenger (diet traits recorded as present or absent); and (3) species range: nonnative, onsite breeder, year-round resident, migrant only, summer breeder, and winter nonbreeder (range traits recorded as present/absent). For species that breed in the region, (4) life history: clutch size (number of eggs) and nesting behavior: tree, shrub, cavity, floating, burrow, cliff, and nest parasite (all nesting behaviors recorded as present or absent); and (5) foraging behavior: aerial, aquatic, semiaquatic, bark, foliage, ground, and soaring (foraging traits recorded as present/absent). We obtained species trait information from The Cornell Lab of Ornithology “All About Birds” and the Audubon “Guide To North American Birds” websites (<https://www.allaboutbirds.org> and <https://www.audubon.org/bird-guide>, respectively).

We classified bird species into trait groups using a hierarchical clustering approach. We used the `hclust` function in the R stats package, using the `ward.D2` linkage method to implement Ward’s clustering criterion, which generates groups with a more even distribution of members (Murtagh and Legendre 2014). We log-transformed continuous variables (maximum body length, maximum body size, and clutch size) prior to the clustering analysis. The resultant clustering dendrogram suggested that between three and four groups produced optimal clusters. We chose four clusters because it produced four groups with clear interpretations based on body size (small vs. large birds) and breeding status (those that breed in the region and those that do not). Mean trait values and number of species in each cluster are provided in Table 2, and trait values and groupings for each species are provided in Data S1. As above, we conducted a series of analyses investigating the long-term changes within and among groups. We used GLMs with land use and time as two crossed fixed effects with the abundance and species richness of each group for each survey as the response variables. Lastly, we used the species contribution to beta-diversity metric as a response variable in a GLM with trait group and time as crossed fixed effects

to compare how taxa in each trait group contributed to total beta diversity, and whether these contributions changed over time.

RESULTS

Effects of land use and time on bird communities

We observed no effect of time on gamma diversity for winter bird communities ($F_{1,13} = 3.15$, $P = 0.099$), but we did observe a significant decrease in gamma diversity for spring bird communities ($F_{1,13} = 5.98$, $P = 0.030$, $R^2 = 0.32$, Fig. 2). Total beta diversity increased over time during winter ($F_{1,13} = 6.48$, $P = 0.025$, $R^2 = 0.33$) and spring ($F_{1,13} = 8.80$, $P = 0.011$, $R^2 = 0.40$) seasons (Fig. 2). We found significant time-by-land use interactions for LCBD in both winter and spring bird communities (Table 3). The interactions were similar for both winter and spring bird communities, where the LCBDs of urban riparian bird communities strongly decreased over time, LCBDs of desert communities showed little change, and agriculture, urban, and desert riparian increased over time (Fig. 3). In both seasons, urban riparian bird communities had the highest LCBDs at the beginning of the time series. However, by the end of the time series they were similar in magnitude to desert riparian and agricultural communities in the winter, while in the spring desert riparian communities had increased to have the highest LCBDs by the end of the study.

We found significant land use-by-time interactions for species richness of bird communities in both winter and spring (Table 3). Species richness of desert riparian bird communities declined in both seasons, while richness of urban riparian communities declined in the spring (Fig. 3). Conversely, richness of urban communities increased over time in both seasons, and richness of agricultural communities increased in the winter. For Pielou’s evenness, we observed significant effects of time and land, but no interaction, in the winter. In the spring, however, we did observe a significant land use-by-time interaction on evenness (Table 3). In all seasons, Pielou’s evenness of bird communities largely declined over time, while desert, desert riparian, and urban riparian bird communities had the highest evenness overall. In the spring, however, evenness of urban communities remained

Table 2. Number of species and mean trait values for each of the four trait groups based on clustering analysis.

Group	Species	Body size		Range		Life history		Diet		Foraging	
Group 1 (small breeder)	86	ML	19.8	NN	0.06	MC	5.72	Frug	0.44	AE	0.23
		MW	57.9	BR	1.00	TR	0.44	Gran	0.49	AQ	0.00
				YR	0.70	SH	0.41	Plan	0.06	SA	0.00
				MI	0.00	CV	0.21	Inse	0.91	BK	0.07
				SR	0.30	FL	0.01	Nect	0.12	FG	0.22
				WR	0.00	GR	0.15	PrTr	0.07	GR	0.44
						BU	0.02	PrAq	0.00	SO	0.01
						CL	0.08	Carr	0.01		
						NP	0.02				
	Group 2 (large nonbreeder)	46	ML	52.9	NN	0.00	MC	0.00	Frug	0.11	AE
MW			1165	BR	0.00	TR	0.00	Gran	0.24	AQ	0.43
				YR	0.00	SH	0.00	Plan	0.22	SA	0.30
				MI	0.41	CV	0.00	Inse	0.67	BK	0.00
				SR	0.00	FL	0.00	Nect	0.02	FG	0.00
				WR	0.61	GR	0.00	PrTr	0.22	GR	0.09
						BU	0.00	PrAq	0.35	SO	0.04
						CL	0.00	Carr	0.02		
						NP	0.00				
Group 3 (large breeder)		30	ML	63.5	NN	0.10	MC	7.23	Frug	0.13	AE
	MW		1493	BR	1.00	TR	0.53	Gran	0.23	AQ	0.33
				YR	0.83	SH	0.13	Plan	0.23	SA	0.17
				MI	0.00	CV	0.07	Inse	0.47	BK	0.00
				SR	0.17	FL	0.13	Nect	0.00	FG	0.00
				WR	0.00	GR	0.17	PrTr	0.53	GR	0.20
						BU	0.00	PrAq	0.53	SO	0.23
						CL	0.17	Carr	0.20		
						NP	0.00				
	Group 4 (small nonbreeder)	57	ML	15.7	NN	0.02	MC	0.00	Frug	0.35	AE
MW			25.2	BR	0.00	TR	0.00	Gran	0.49	AQ	0.00
				YR	0.00	SH	0.00	Plan	0.02	SA	0.02
				MI	0.42	CV	0.00	Inse	0.96	BK	0.00
				SR	0.00	FL	0.00	Nect	0.02	FG	0.35
				WR	0.56	GR	0.00	PrTr	0.00	GR	0.39
						BU	0.00	PrAq	0.02	SO	0.00
						CL	0.00	Carr	0.00		
						NP	0.00				

Notes: Body size traits' abbreviations are ML, maximum length (cm); and MW, maximum weight (g). Range traits' abbreviations are NN, nonnative; BR, onsite breeder; YR, present year-round; MI, migrant only; SR, summer range only; and WR, winter range only. Life-history traits' abbreviations are MC, max clutch size (number of eggs); TR, tree nesting; SH, shrub nesting; CV, cavity nesting; FL, floating nesting; GR, ground nesting; BU, burrow nesting; CL, cliff nesting; and NP, nest parasite. Diet traits' abbreviations are Frug, frugivore; Gran, granivore; Plan, plantivore; Nect, nectivore; Inse, insectivore; PrTr, predator of terrestrial prey; PrAq, predator of aquatic prey; and Carr, carrion feeder. Foraging traits' abbreviations are AE, aerial forager; AQ, aquatic forager; SA, semiaquatic forager; BK, bark forager; FG, foliage gleaner; GR, ground forager; and SO, soaring forager. For all presence/absence traits (all except ML, MW, and MC), a value of 1 indicates trait is present in the 100% of species in the group, and a value of 0 indicates trait is absent in all species in the group.

unchanged over time, while other land uses declined at different rates (Fig. 3). For bird abundance, we found a significant effect of land use and time in the winter. Overall, bird abundance was highest in the urban riparian land use and lowest in the desert, and bird abundance increased over time (Table 3, Fig. 3). We found a

significant land use-by-time interaction in the spring, however. Bird communities in most land uses increased over time, but desert riparian bird communities which marginally decreased in abundance over time (Table 3, Fig. 3).

The abundance of birds in the four different trait groups showed different responses over

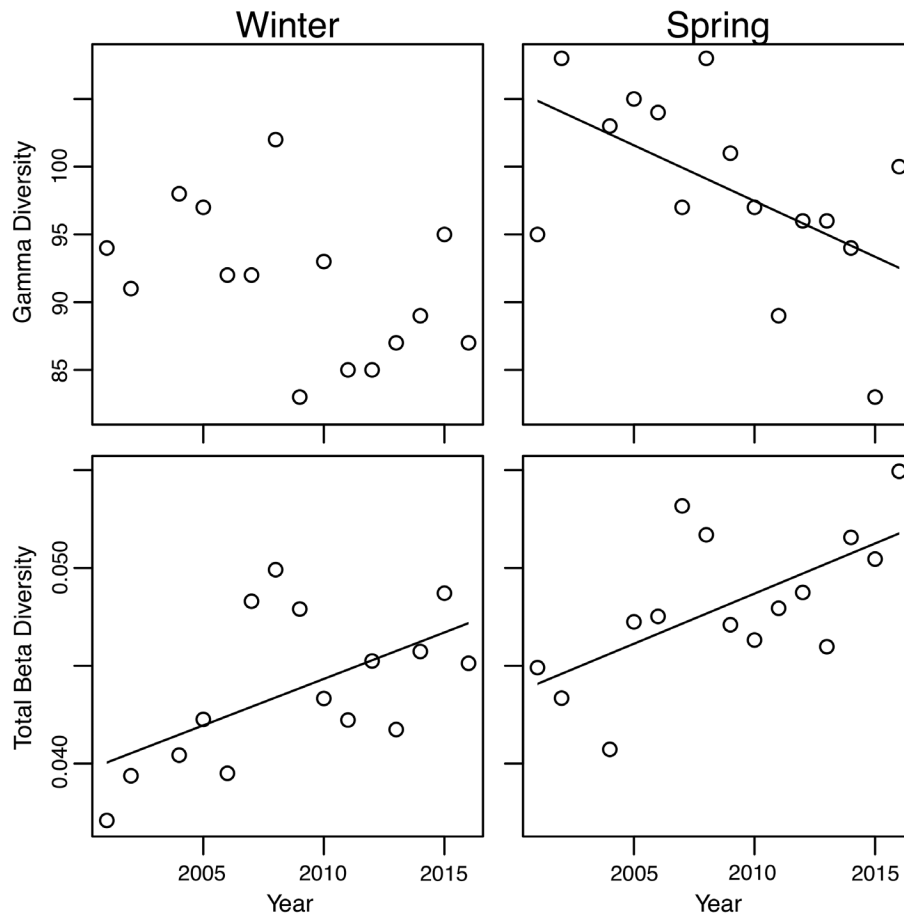


Fig. 2. Summary of landscape and regional bird community response variables over time (2001–2016). Total gamma diversity of winter (left top panel) and spring (right top panel), and total beta diversity of winter (left bottom panel) and spring (right bottom panel).

time (Table 4, Fig. 4). The abundance of birds in trait group 1 (small breeders) differed by land use in the winter, with the greatest abundance in urban areas and the lowest in desert, while abundance in all land uses increased over time. In the winter, however, we observed a significant land use-by-time interaction, where the trait group 1 abundance increased in all land uses but desert riparian areas, which showed little change over time. For abundance of birds in trait groups 2 and 3 (large nonbreeding and large breeding birds, respectively), we observed no change in abundance in over time, but did observe differences between land uses. For both trait groups, abundance was typically greatest in urban riparian and agricultural land uses, and lowest in

desert and desert riparian land uses. Finally, the abundance of birds in trait group 4 (small nonbreeding birds) varied between land uses in both winter and spring, being typically greatest in the urban riparian and desert riparian land uses, and lowest in urban land uses. In the winter, the abundance of birds in trait group 4 increased over time but did not change over time in the spring.

The richness of birds in the four trait groups showed two types of responses over time, either no effect of time but differences in land use, or a significant land use-by-time interaction (Table 5, Fig. 5). Species richness of birds in trait group 1 (small breeders) and in trait group 4 (small nonbreeders) showed significant land use-by-time

Table 3. Summary of GLM results using community metrics measured at each site (Local contributions to beta diversity [LCBD], species richness, species evenness, abundance) as response variables, with land use as a fixed categorical variable crossed with year as a fixed continuous variable.

Factor	Winter			Spring		
	df	F	P	df	F	P
LCBD (0.26, 0.39)						
Year	1, 635	0.00	1.000	1, 635	0.00	1.000
Land use	4, 635	55.35	<0.001	4, 635	101.74	<0.001
Year × land use	4, 635	3.06	0.016	4, 635	4.86	<0.001
Richness (0.38, 0.50)						
Year	1, 635	4.59	0.033	1, 635	1.25	0.263
Land use	4, 635	97.75	<0.001	4, 635	155.75	<0.001
Year × land use	4, 635	270	0.030	4, 635	5.64	0.002
Evenness (0.26, 0.34)						
Year	1, 635	31.32	<0.001	1, 635	9.35	0.002
Land use	4, 635	46.11	<0.001	4, 635	77.44	<0.001
Year × land use	4, 635	2.12	0.077	4, 635	2.88	0.022
Abundance (0.39, 0.44)						
Year	1, 635	22.67	<0.001	1, 635	50.41	<0.001
Land use	4, 635	99.44	<0.001	4, 635	110.60	<0.001
Year × land use	4, 635	1.42	0.224	4, 635	4.78	<0.001

Note: Adjusted- R^2 values are shown for each model, provided in parentheses after each variable (winter, spring).

interactions in both seasons. For trait group 1, richness increased in urban riparian and urban areas, while decreasing in desert riparian areas, in both seasons. For trait group 4, richness decreased in urban riparian and desert riparian areas, and slightly increased in desert and urban areas in the winter and in desert areas only in the spring. The richness of birds in trait group 2 (large nonbreeders) showed no effect of time but differed by land use, being greatest in urban riparian and lowest in desert land uses. For trait group 3 (large breeders), richness showed differences in land use in winter, again being greatest in urban riparian and lowest in desert land uses, and no effect of time. However, in the spring we observed a significant land use-by-time interaction, where we observed a steep decline in urban riparian areas and marginal change over time in other land uses.

Species contributions to beta diversity varied by trait group in both winter ($F_{3, 3277} = 105.07$, $P < 0.001$) and spring ($F_{3, 3277} = 162.31$, $P < 0.001$). However, there was no effect of time, and the time-by-guild interaction was also not significant. In both seasons, species in the trait group 1 (small breeders) had the greatest contributions to beta diversity, whereas species in the trait groups 2 (large nonbreeders) and 4 (small nonbreeders) had the lowest contributions (Fig. 6).

DISCUSSION

The most striking result of our study was that long-term effects of land-use change on bird biodiversity were dependent upon the spatial scale considered. At the largest spatial scale, we observed declines in regional-scale gamma diversity during the spring season, a time marked by the presence of spring migrants and summer breeders. This observation is concurrent with our predictions given other studies that have shown bird community declines in the desert southwest (Iknayan and Beissinger 2018) and other parts of the world (Spooner et al. 2018). However, we observed increases in landscape-scale beta diversity during both winter and spring seasons, meaning that bird communities are exhibiting greater differentiation among sites over time. This effect of increasing beta diversity over time is counter to our predictions given results of previous work showing that urbanization has homogenizing effects, making communities more similar to each other (Groffman et al. 2014, Murthy et al. 2016). However, a study with plants in Baltimore, Maryland, suggests that beta diversity could increase in highly human-managed land uses such as residential areas, relative to unmanaged land uses such as vacant lots (Swan et al. 2017). Although birds and plants

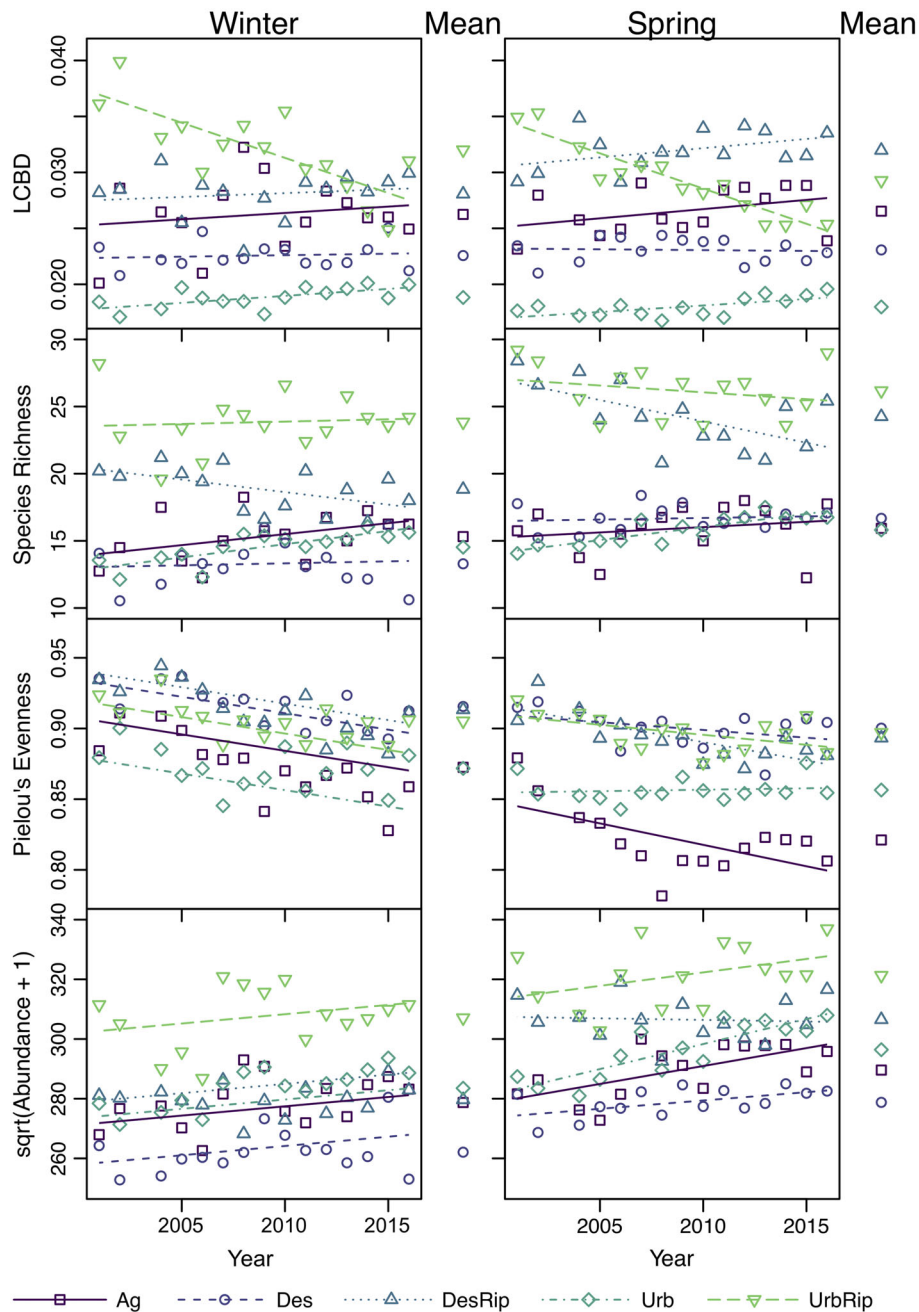


Fig. 3. Summary of local-scale bird community response variables over time (2001–2016). Top row: local contributions to beta diversity (LCBD), second row from top: species richness, third row from top: Pielou's evenness, and bottom row: abundance (square-root-transformed). Left column is winter season, and right column is spring season. Each land use is a different color, point shape, and line type (see legend). Abbreviations are Ag, agriculture; Des, desert; DesRip, desert riparian; Urb, urban; and UrbRip, urban riparian. Data in each graph are means of each land use in each year. To the right of each graph, the floating points represent the grand land-use mean across all years.

Table 4. Summary of GLM results using abundance of a given trait group (group 1, small breeder; group 2, large nonbreeder; group 3, large breeder; and group 4, small nonbreeder) as response variables.

Factor	Winter			Spring		
	df	F	P	df	F	P
Group 1 (0.36, 0.44)						
Year	1, 635	43.86	<0.001	1, 635	123.35	<0.001
Land use	4, 635	82.01	<0.001	4, 635	91.22	<0.001
Year × land use	4, 635	0.468	0.760	4, 635	5.03	<0.001
Group 2 (0.37, 0.35)						
Year	1, 635	1.02	0.313	1, 635	0.00	0.997
Land use	4, 635	95.47	<0.001	4, 635	86.49	<0.001
Year × land use	4, 635	0.283	0.889	4, 635	1.530	0.192
Group 3 (0.47, 0.52)						
Year	1, 635	0.873	0.351	1, 635	1.18	0.28
Land use	4, 635	142.7	<0.001	4, 635	177.93	<0.001
Year × land use	4, 635	2.16	0.072	4, 635	2.14	0.074
Group 4 (0.31, 0.37)						
Year	1, 635	5.54	0.019	1, 635	0.259	0.611
Land use	4, 635	70.92	<0.001	4, 635	97.79	<0.001
Year × land use	4, 635	1.26	0.283	4, 635	0.747	0.560

Notes: Land use is a fixed categorical variable crossed with year as a fixed continuous variable. Adjusted- R^2 values are shown for each model, provided in parentheses after each variable (winter, spring).

differ greatly in the mechanisms by which human activity affects species turnover, a study of birds in Paris found patterns somewhat consistent with the predictions from the Baltimore study (Husté and Boulinier 2007). There were greater rates of colonization in more urban sites in Paris and by sedentary species than by migratory ones (Husté and Boulinier 2007). The increase in beta diversity we observed could also be explained by increasing rates of local extinction and colonization of species over time in a fragmented landscape, leading to increasing rates of turnover among sites.

Local contributions to beta diversity by a given site over time were greatly dependent upon land use. At the beginning of the time series, urban riparian sites contributed the most to beta diversity in both seasons. However, by the end of our dataset urban riparian site contributions had declined to about the same level as agricultural and desert riparian sites. Conversely, contributions of agriculture and desert riparian land uses to beta diversity increased throughout the long-term study. Urban site contributions to beta diversity were low overall but increased slightly over time, whereas contributions of desert sites remained the same. These changes are consistent with observations from previous studies in Phoenix that the bird species composition of urban

riparian sites becoming more similar to that of upland and urban sites (Banville et al. 2017).

At the local spatial scale, we found that long-term changes in bird diversity varied by land use and by biodiversity metric. For species richness, we found interaction between time and land use in both seasons. The more rapid declines in riparian bird communities were consistent with our expectations, as this trend has been found previously in urban riparian areas in this region (Banville et al. 2017). However, we did not expect to see increases in richness over time in urban and agricultural land uses. Overall species richness was greatest in the two riparian land uses in both seasons, with the urban riparian sites showing more species than the desert riparian sites. Because the two riparian land uses experienced species losses, it is likely that declines in these areas specifically may be driving the decline in gamma diversity we observed at the regional, spatial scale. Additionally, because the urban riparian sites also had the highest LCBD, which also declined over time, bird communities at these sites may be an area of high conservation value to their combined high richness and high uniqueness (Brand et al. 2011, Merritt and Bateman 2012, Banville et al. 2017). Nevertheless, we found declines in species evenness across all land uses in both seasons. In the winter, the declines

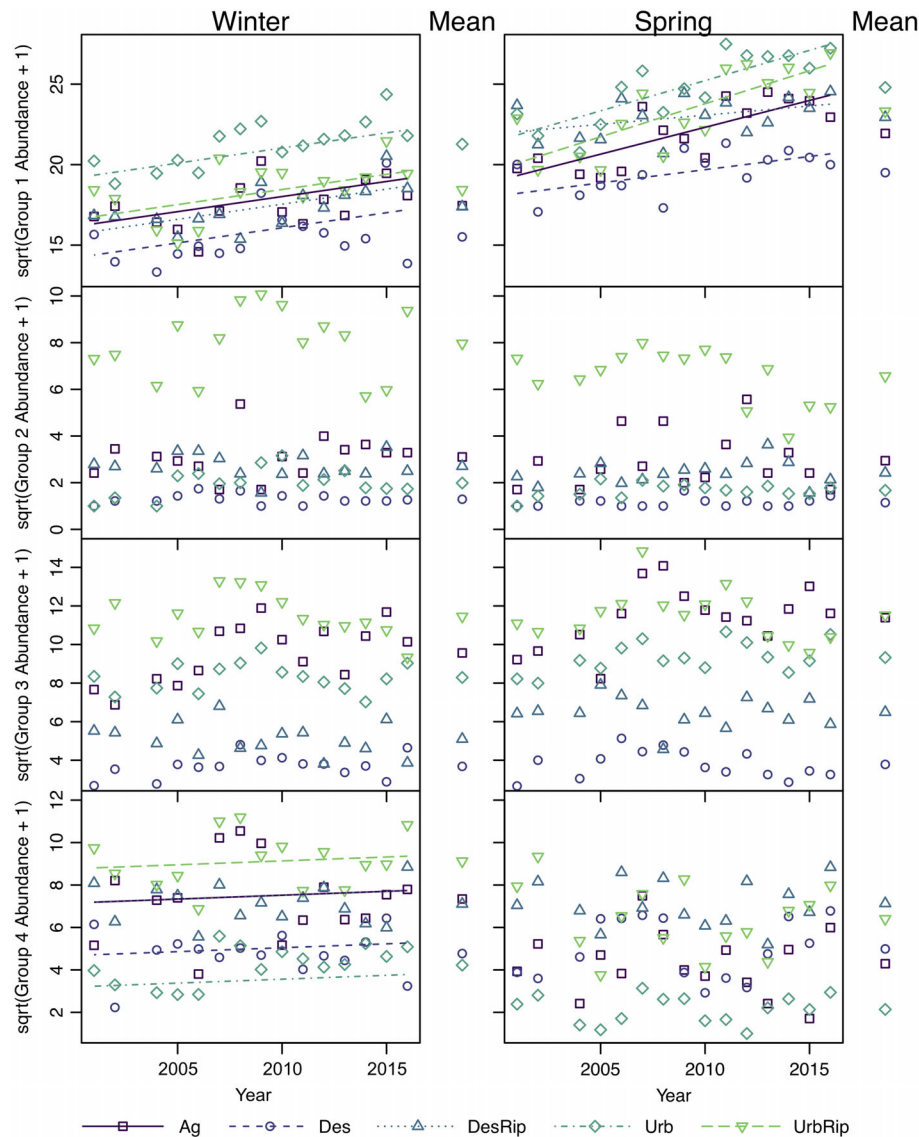


Fig. 4. Summary of trait group abundance over time (2001–2016). Top row: trait group 1 abundance (small breeder), second row: trait group 2 abundance (large nonbreeder), third row: trait group 3 abundance (large breeder), and bottom row: trait group 4 abundance (small nonbreeder). Left column is winter season, and right column is spring season. Each land use is a different color, point shape, and line type (see legend). Abbreviations are Ag, agriculture; Des, desert; DesRip, desert riparian; Urb, urban; and UrbRip, urban riparian. Data in each graph are means of each land use in each year. To the right of each graph, the floating points represent the grand land-use mean across all years.

were consistent among all land uses, while in the spring the declines were more rapid for some land uses (agriculture, desert riparian) than others (urban). This means that the distribution of species abundances became more skewed

toward common species, in both the land uses that lost species and also in those that gained species.

Different temporal responses of species in different trait groups seem to be responsible for

Table 5. Summary of GLM results using species richness of a given trait group (group 1, small breeder; group 2, large nonbreeder; group 3, large breeder; and group 4, small nonbreeder) as response variables.

Factor	Winter			Spring		
	df	F	P	df	F	P
Group 1 (0.11, 0.29)						
Year	1, 635	9.48	<0.001	1, 635	8.70	0.003
Land use	4, 635	16.34	<0.001	4, 635	57.47	<0.001
Year × land use	4, 635	2.55	0.038	4, 635	6.88	<0.001
Group 2 (0.33, 0.31)						
Year	1, 635	0.45	0.501	1, 635	0.01	0.949
Land use	4, 635	81.03	<0.001	4, 635	73.19	<0.001
Year × land use	4, 635	0.16	0.957	4, 635	0.685	0.603
Group 3 (0.30, 0.23)						
Year	1, 635	0.54	0.462	1, 635	4.43	0.036
Land use	4, 635	70.69	<0.001	4, 635	47.04	<0.001
Year × land use	4, 635	1.77	0.134	4, 635	2.47	0.044
Group 4 (0.33, 0.41)						
Year	1, 635	0.00	0.976	1, 635	3.26	0.071
Land use	4, 635	76.35	<0.001	4, 635	109.49	<0.001
Year × land use	4, 635	4.98	<0.001	4, 635	3.89	0.004

Notes: Land use is a fixed categorical variable crossed with year as a fixed continuous variable. Adjusted- R^2 values are shown for each model, provided in parentheses after each variable (winter, spring).

producing these changes at the community level. Of the four different trait groups, the abundance and richness of birds in trait group 1 (small breeding species) and group 4 (small nonbreeding species) changed in ways that most strongly mirror the changes observed at the community level. Birds in trait group 1 increased in abundance in both seasons, though in the spring this increase was greater in some land uses than others. Birds in trait group 4 increased in abundance in the winter, but not the spring. Given that birds in trait groups 2 and 3 (large breeding and large nonbreeding species), and these changes are strikingly similar to the changes in abundance at the community level, species in this trait group are likely driving changes in community-level abundance. Moreover, the richness of birds in trait groups 1 and 4 changed over time in ways that echo the changes we observed at the community level. We observed declines in community species richness in desert riparian land uses in both seasons, much like the declines in richness of birds in trait groups 1 and 4 that we observed. Similarly, we observed increases in community species richness in urban areas over time, much like the increases we observed in trait group 1 and 4 richness. However, birds in these trait groups did not always show consistent

responses, birds in trait group 1 increased in richness over time in urban riparian zones in both seasons, while those in group 4 declined. Lastly, birds in trait group 1 had the greatest species contributions to beta diversity, so the changes in the abundance and richness of these species are likely driving the community-level increase in total beta diversity that we observed as well. Birds in trait groups 2 and 3 showed little change overtime, with the exception of changes in trait group 3 (large breeder) richness that differed by land use in the spring. Here, richness declined strongly in urban riparian areas, while changes in other land uses were marginal.

There are a number of possible explanations for how different species trait combinations could produce different responses to land-use change in birds. One study investigating 58 urban cities across the globe found that urbanization selects for birds of certain body sizes, birds in urban communities tended to be smaller have more narrow distribution of body sizes (Sorte et al. 2018). Indeed, we found that smaller birds (trait groups 1 and 4) increased in abundance in urban areas over our study. Land-use change also alters resource availability across the landscape, and these changes could favor certain trait combinations. Previous studies showed increases

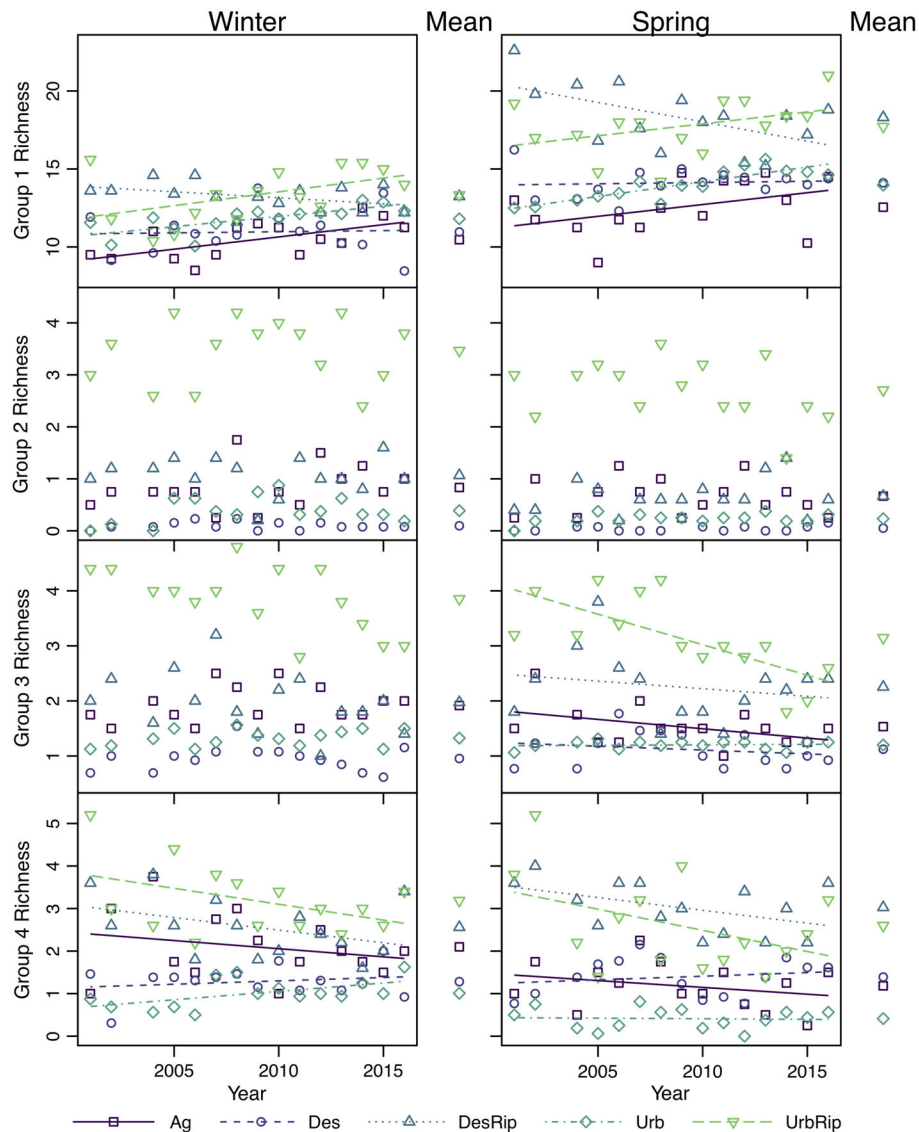


Fig. 5. Summary of trait group species richness over time (2001–2016). Top row: trait group 1 richness (small breeder), second row: trait group 2 richness (large nonbreeder), third row: trait group 3 richness (large breeder), and bottom row: trait group 4 richness (small nonbreeder). Left column is winter season, and right column is spring season. Each land use is a different color, point shape, and line type (see legend). Abbreviations are Ag, agriculture; Des, desert; DesRip, desert riparian; Urb, urban; and UrbRip, urban riparian. Data in each graph are means of each land use in each year. To the right of each graph, the floating points represent the grand land-use mean across all years.

in the abundance of arthropods in urban areas in this region that are prey for insectivorous birds (Bang and Faeth 2011). The increases are attributed to increased water availability for plants (Bang et al. 2012), as well as the increased palatability of the plant taxa used in farming and in the

landscaping of urban areas relative to the native plant taxa in deserts, which have greater defenses against herbivores (Hope et al. 2003). Seed-eating and nectar-feeding birds also benefit from bird feeders, which are common residential areas in the region (Lerman and Warren 2011,

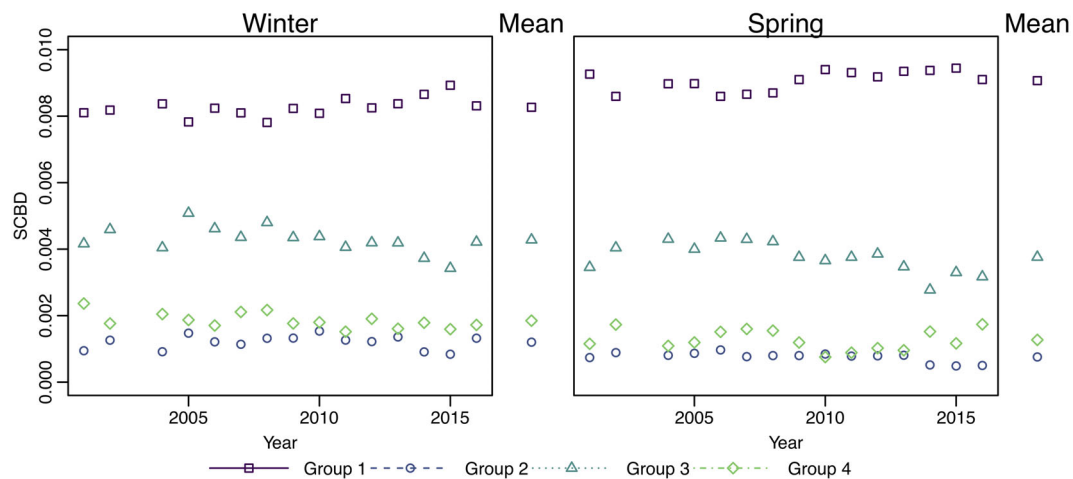


Fig. 6. Species contributions to beta diversity of each trait group over time (2001–2016): trait groups 1 (small breeder), 2 (large nonbreeder), 3 (large breeder), and 4 (small nonbreeder). Data in each graph are means of each trait group in each year. To the right of each graph, the floating points represent the grand trait group mean across all years.

Lepczyk et al. 2012). Accordingly, birds that are insectivores, granivores, and nectivores should benefit most in an urban landscape. Birds in trait groups 1 and 4 were likely driving the community-level increases in abundance and richness in urban zones, and these birds were also highly insectivorous and granivorous, and birds in trait group 1 contained the greatest number of nectivorous taxa.

Climatic effects from urbanization relative to the surrounding desert may also be an important factor in the observed community changes. Some of the hottest conditions found anywhere on the Earth occur in urban areas in the Sonoran Desert of North America. Cities and their built infrastructure can retain and radiate heat, causing warming to occur and elevate nighttime temperatures in the surrounding urban landscape greater than nonurban environments (Chow et al. 2011). However, some urban land uses can decrease high daytime temperatures if vegetation is present due to increased evapotranspiration, particularly in suburban areas (Jenerette et al. 2016). Declines in southwestern U.S. desert bird communities and in other areas across the globe have been attributed to the increased high temperatures resulting from climate change causing heat stress in birds (Iknaayan and Beissinger 2018, Spooner et al. 2018).

So, the increases in abundance and richness in urban areas could also be due to highly vegetated suburban habitats providing a refuge from high temperatures in desert habitats associated with climate change.

Finally, we know that bird species themselves are changing in response to anthropogenic change. In a study that comparing bird distributions over a 100-yr period, Ward et al. (2018) found that habitat use by many bird species changed over time. Species that increased in site occupancy did so by increasing their use of urban habitats, whereas species that declined did not. There are also numerous examples of bird species adapting in response to anthropogenic environments. Blackbird (*Turdus merula*) songs differ between urban and rural populations, as urban birds sing higher-pitched songs to avoid masking by ambient white noise that occurs primarily at lower frequencies (Nemeth and Brumm 2009, Mendes et al. 2011). Indeed, an extensive meta-analysis recently showed that phenotypic changes in plants and animals in urban environments were much greater than those in natural and nonurban anthropogenic habitats (Alberti et al. 2017). Thus, some bird species can adapt to become urban birds over time, so the changes we observed over our 16-yr study period may reflect this process taking place.

CONCLUSION

Biodiversity changes over time were complex and dependent on the contexts of spatial scale and land use. At the regional scale, we observed losses in gamma diversity in the spring and important season for bird migrations. At the landscape scale, total beta diversity increased over time in both seasons. The local contributions of different land-use types to beta diversity changed over time. Urban riparian bird communities had the greatest contributions to beta diversity at the beginning of the time series but declined over time. Meanwhile, desert riparian bird communities increased over time, contributing the most toward beta diversity in the spring by the end of the time series. At the local scale, we mostly observed declines in alpha diversity. All land uses experienced declines in evenness over time during both winter and spring. However, we observed increases in species richness in the winter in all land uses. In the spring, we observed declines in desert and urban riparian land uses in the spring and increases in diversity in urban areas. When we analyzed changes in groups of species that shared certain traits, we found that small breeding and small nonbreeding species were changing in different ways and together changed more than large breeding and large nonbreeding species. Taken together, our results suggest that there are winners and losers when considering bird species responses to land-use change, which can be predicted at least in part by species traits, and that these wins and losses cumulatively determine changes at the community, metacommunity, and regional levels.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2952/full>

Data S1. A datafile containing site information, the CAP LTER site code, latitude and longitude, and land-use type and a datafile containing the four-letter species code, common name, genus, species, and trait grouping, and trait values of all 219 bird taxa observed during this study.