Disentangling an avian assemblages' evolutionary and functional history in a Chihuahuan desert city

Israel Moreno-Contreras [1,2] · Héctor Gómez de Silva [3] · Violeta Andrade-González [2] · Cuauhcihuatl Vital-García [4] · Marco F. Ortiz-Ramírez [1,2]

Abstract

Urban green spaces have been shown to be important hotspots of biodiversity in cities of temperate and humid/semihumid tropical ecoregions. Nonetheless, whether this pattern applies to urban ecosystems of desert environments has been rarely studied. Temperature, precipitation, vegetation complexity, human density, and presence of invasive species could act as urban filters limiting the incidence of desert-adapted species into cities. Such effects could be reshaping biotic communities, favoring habitat generalist species in human-dominated environments. In this study, we examined the phylogenetic and functional structure of avian assemblages in a Chihuahuan desert city and its surroundings to infer the processes underlying community assembly. We used phylogenetic comparative methods to test the hypothesis whether there is an underlying pattern determining which desert-adapted species penetrate or tolerate a novel urban ecosystem. We also performed a regression approach to determine which environmental and anthropogenic variables may be associated with these metrics. We found that urban green spaces present more evolutionary and functional diversity (based on the proportion of total tree branch length) than agricultural fields and desert scrub, although not statistically significant. On the other hand, based on the mean branch length distance among sample taxa, we observed clustered communities suggesting environmental filtering. Most continuous functional traits presented a low and significant phylogenetic signal, but nearly all binary traits were conserved across phylogeny. Phylogenetic predisposition to be a habitat generalist is present in the surveyed avian assemblages. Our regression analysis indicates that invasive bird species richness was negatively correlated with net relatedness index (NRI) and functional net relatedness index (FNRI), while functional diversity metrics were influenced by temperature and precipitation.

Keywords Desert · Functional diversity · Mexico · Niche conservationism · Phylogenetic diversity · Urban ecology

✉ Israel Moreno-Contreras
   israel.moreno.contreras@gmail.com

1   Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Coyoacán, Ciudad de México, México

2   Museo de Zoología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, A.P. 70-399, 04510 Ciudad de México, México

3   Ciudad de México, México

4   Departamento de Ciencias Veterinarias, Instituto de Ciencias Biomédicas, Universidad Autónoma de Ciudad Juárez, Anillo Envolvente del Pronaf y Estocolmo s/n, C.P. 32300, Ciudad Juárez, Chihuahua, México

Introduction

Urbanization is considered one of the main threats to biodiversity (Gómez-Baggethun and Barton 2013; Schwarz et al. 2017). The uncontrolled growth of the human population, inadequate management of urban growth, and land use changes have contributed to local extinctions of species (Kowarik 2011; Aronson et al. 2016). Urbanization affects the assembly of species into urban communities (McKinney 2006). Urban landscapes tend to be fragmented in a hierarchical manner due to social, economic and cultural aspects of a city, which consequently affects animal habitat selection (Walker and Shochat 2009). Such habitat selection creates distinct differences in phylogenetic diversity between urban and natural environments (McKinney 2006).

One of the theoretical models that attempts to explain community dynamics across phylogeny is the niche-based perspective. The niche-assembly theory asserts competitive

interactions and environmental filtering as two important deterministic mechanisms responsible for structuring and maintaining ecological communities (Webb et al. 2002). Competitive exclusion (limiting similarity) occurs when organisms of the same, or different, species utilize a common resource that is of limited supply (Emerson and Gillespie 2008). On the other hand, environmental filtering has been defined as the effect of abiotic conditions selecting those species capable of carrying out their life cycles in a given environment (Webb et al. 2002).

The environmental filtering model allows determining if communities of species are more similar (clustered) or more dissimilar (overdispersed) to one another than expected by chance (Webb et al. 2002; Emerson and Gillespie 2008). Empirical studies have supported the premise that ecological communities in urban environments are structured mostly by phylogenetic and functional clustering (Hagen et al. 2017; Ibáñez-Álamo et al. 2017; Sol et al. 2017). Such trends have been associated with environmental harshness or stressors (e.g. temperature and precipitation, incidence of invasive species), favoring evolutionary lineages or functional traits (e.g. diet types, body mass, foraging technique, seasonality) that tolerate urbanization (McKinney 2006; Aronson et al. 2016; Cadotte and Tucker 2017) underlining the importance of quantifying phylogenetic diversity (PD) and functional diversity (FD) (see Swenson 2011). Therefore, studying patterns in functional and phylogenetic diversity may contribute to understanding ecological and evolutionary processes operating to shape specific species assemblages (Sol et al. 2014; Silva et al. 2016). Furthermore, it is important to determine how functional traits change phylogenetically to arrive at a correct interpretation of clustered or overdispersed communities (Blomberg et al. 2003; Kraft et al. 2007). For example, most urban ecology studies focusing on inferring ecological processes that structure communities have been performed in temperate and humid/semihumid tropical ecoregions (MacGregor-Fors et al. 2017), but how ecological communities are phylogenetically and functionally structured in cities in desert environments remains understudied.

The avian assemblages associated with the Chihuahuan desert ecoregion are an ideal study system to inferring ecological processes that structure communities due urbanization effect. The Chihuahuan desert is considered one of the most biologically diverse arid regions in the world (Brown 1994) and has been experiencing rapid urbanization, with urban areas having been historically established as strategic outposts for geopolitical and security considerations (Portnov and Paz 2008). Desert avian assemblages in North America are evolutionarily and functionally diverse (Hubbard 1974; Brown 1994), easy to sample and to identify (Ralph et al. 1993), and are particularly suitable to analyze biodiversity patterns between urban and natural habitats because they are good ecological indicators (e.g. Hagen et al. 2017; Ibáñez-Álamo

et al. 2017; Sol et al. 2014; Sol et al. 2017; La Sorte et al. 2018). Birds have a well-studied phylogeny and comprehensive information available on their biological characteristics (e.g. Dunning 2008; Jetz et al. 2012; del Hoyo et al. 2017), which is essential when working with phylo-functional measurements.

In this study, we examined the phylogenetic and functional structure of avian assemblages in a Chihuahuan desert city and its surroundings to infer the processes underlying community assembly (Fig. 1). We hypothesized that metrics related to species richness (standardized effect size of PD and FD) should increase in urban habitats (i.e. urban green spaces), due to urban green spaces's tendency to have higher levels of habitat heterogeneity than the habitats that surround the urban landscape (Chace and Walsh 2006; Nielsen et al. 2014). Based on previous research, we hypothesize the presence of non-random phylogenetic and functional communities in urban habitats. The restructuring of biotic communities in urban areas is strongly associated with the loss of species with limited tolerance to urban development (Sol et al. 2014) and therefore should be non-random, with urban environments filtering species according to their ecological and life-history traits (Bonier et al. 2007; Evans et al. 2009; Hagen et al. 2017; Sol et al. 2017; La Sorte et al. 2018). We also expect a significant phylogenetic signal (e.g. due to trait conservationism), with urbanization favoring related lineages with similar functional traits (Kraft et al. 2007; Ndiribe et al. 2013; Sol et al. 2014). We hypothesize that the temperature and precipitation are positively relate to phylogenetic and functional diversity metrics, due to cities are warmer than surrounding areas ("urban island heat effect") and may have higher local rainfall (e.g. urban green spaces) than their surroundings (e.g. desert scrub), thus affecting avian community assembly (Aronson et al. 2016). On the other hand, invasive bird species richness and human footprint are negatively relate to phylogenetic and functional diversity (Aronson et al. 2016). Although Ciudad Juárez was previously established as an urban settlement on desert scrub and nowadays it is only currently surrounded by it, we expect a significant presence of habitat generalist species across the phylogeny of avian assemblages in our study area due to urbanization. Disentangling how urbanization could affect avian assemblages will help to improve urban planning and conservation decisions.

Methods

Study area

Ciudad Juárez is a city located in the northern region of the Mexican state of Chihuahua (31 ° 44 'N, 106 ° 29' W; Fig. 1) and has an altitude of 1140 m above sea level. It borders on the north with El Paso City (Texas, USA) and Las Cruces City
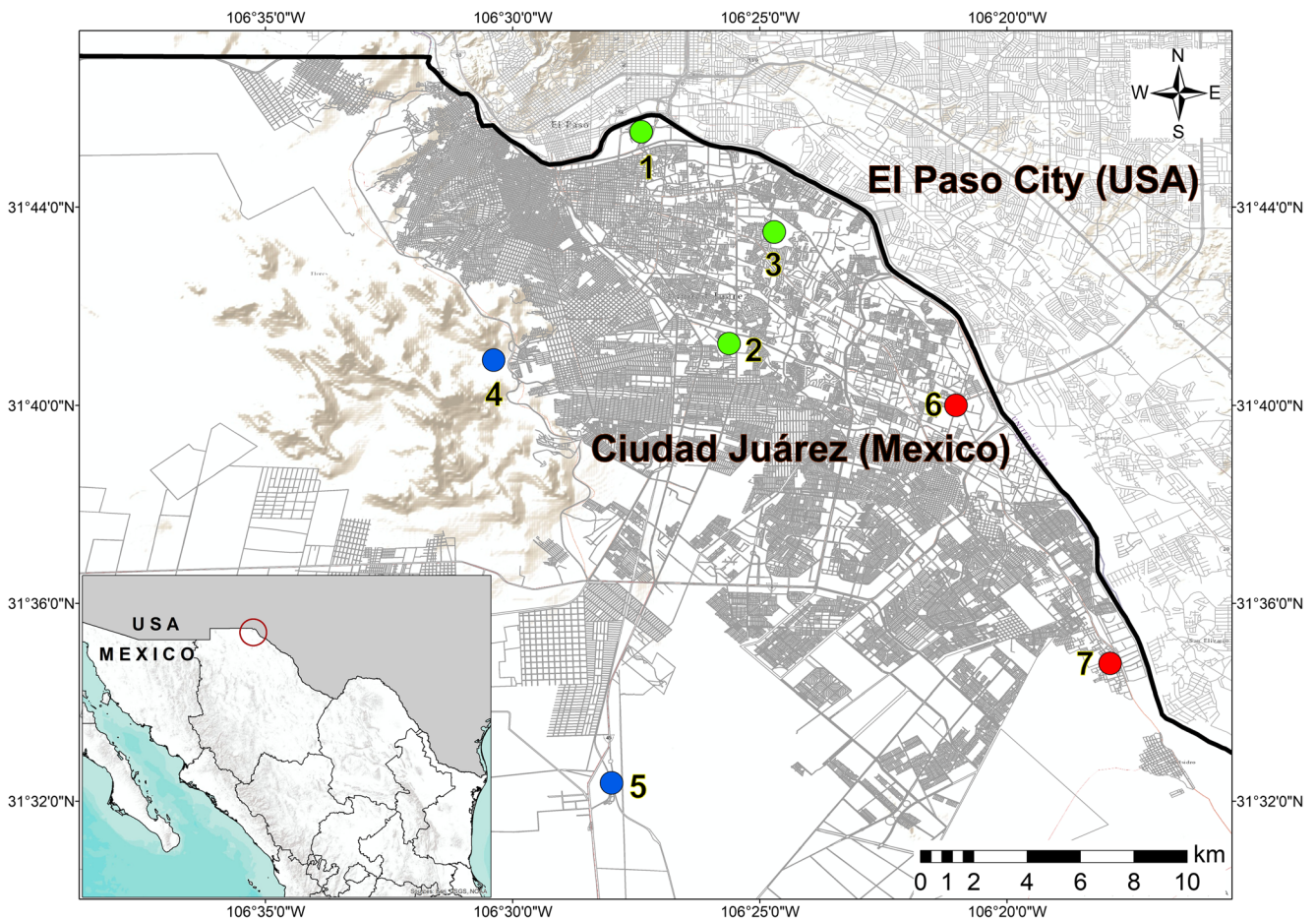
Fig. 1 Sites of bird sampling in Ciudad Juárez, Chihuahua, Mexico. 1. El Chamizal; 2. Parque Central; 3. Club Campestre; 4, Trepachanga; 5. Puerta Juárez; 6. Zaragoza; 7. Loma Blanca. Green dots = urban green spaces, blue dots = desert scrub, red dots = agricultural fields. See Table 1

(New Mexico, USA) representing the international limit with the United States from America (INEGI 2016). In 2015, Ciudad Juárez had nearly 1.4 million residents and a population density of 3919.26 residents/km^2 (INEGI 2016; IMIP 2016). Ciudad Juárez is the fifth largest city in Mexico and encompasses an area of 352.81 km^2. Prior to 2005, Ciudad Juárez experienced decades of rapid population growth due to economic opportunities in the USA-Mexico border region (IMIP 2016).

Due to its location in the Chihuahuan desert ecoregion, Ciudad Juárez has a cold desert climate *BWk(x')* according to García (2004). The average annual temperature is below 18 °C, with summer rainfall and with rain very scarce in winter. The climate of the region is characterized by an abundance of sunny days throughout the year with high temperatures in summer (sometimes exceeding 40 °C), and cold during the winter (temperature often decreases several degrees below zero). The annual rainfall for Ciudad Juárez varies from 200 mm to 300 mm.

We sampled three main habitat types present in Ciudad Juárez: urban green spaces (parks, golf courses), agricultural fields, and desert scrub. The altitudinal range of our sampling points was 1120 to 1290 m above sea level. Typical plants of the desert scrub are creosote bush (*Larrea tridentata*), ocotillo (*Fouquieria splendens*), tarbush (*Flourensia cernua*), viscid acacia (*Acacia neovernicosa*), honey mesquite (*Prosopis glandulosa*), lechugilla (*Agave lechugilla*), yucca (*Yucca* spp.), and joint-pine (*Ephedra* spp.). Agricultural fields generally include Mexican cotton (*Gossypium hirsutum*) or alfalfa (*Medicago sativa*) with some scattered shrubs and trees bordering irrigation channels. The dominant trees in the urban green spaces include Afghan pine (*Pinus eldarica*), Arizona cypress (*Cupressus arizonica*), willows (*Salix* spp.), ash (*Fraxinus* spp.), white mulberry (*Morus alba*), Mexican fan palm (*Washingtonia robusta*), chinaberry tree (*Melia azedarach*), elms (*Ulmus* spp.), and cottonwoods (*Populus* spp.). In all urban green spaces sampled there are relatively medium-size area water bodies (*mean* = 14,940 m^2, *SD* = 11,104.96).

Fieldwork

We surveyed birds in seven points across Ciudad Juárez between July 2012 and August 2015. The surveys were carried

out in three urban green spaces, two agricultural fields, and two desert scrub points (Table 1). We delineated the Ciudad Juárez area with a buffer of 4 km (representing the 'urban fringe') in ArcGIS 10.3 (ESRI, Redlands, California). To ensure that all the species potentially interact, thereby following the definition of ecological community of Wiens (1989), each sampling point was delimited by a circle of 500 m radius using ArcGIS 10.3.

The surveyor employed the area-search method (Ralph et al. 1993) to observe bird species, avoiding rainy and windy conditions. Observations began before sunrise (from 06:00 to 11:00), with occasional nocturnal observations from 17:00 to 19:30 (nocturnal observations were conducted at all sites), thereby surveying diurnal (e.g. aquatic birds, raptors, passerines, among others) and nocturnal avian assemblages (e.g. nightjars and owls). Each study area was surveyed during 74 days (two days every month). All sites were observed throughout the same time of day, and for an equal duration. The method consisted of ten 20-min counts in which the observer moved around within circle of 500 m radius (Ralph et al. 1993). This survey method allowed us to find rare or secretive bird species. Birds were identified by sight and sound with the aid of 10x binoculars and field guides (e.g. Howell and Webb 1995). Species-level taxonomy followed was the most recent supplement of the American Ornithological Society (Chesser et al. 2017).

Phylogenetic analysis

In exploratory analysis, we found that some species of this study were not analyzed in the phylogenetic tree provided by Bird Tree (Jetz et al. 2012). Thus, we performed a new phylogenetic analysis using DNA sequences previously published. We retrieved appropriate DNA sequences from four mitochondrial markers (cytochrome b – *cytb*, cytochrome oxidase I – *COI*, NADH dehydrogenase subunit 2 and 3 – *ND2*, *ND3*), and four nuclear genes (recombination-activating protein gen 1 – *RAG1*, β-Fibrinogen Intron 5 and 7 – *FGB5*, *FGB7*, and myoglobin Intron 2 – *MYO2*) of almost all bird

species recorded in this study and for which samples were available (GenBank accession numbers in Supporting Information Table S1). Two palaeognathous birds were selected as outgroup species (*Struthio camelus* and *Tinamus major*) based on their basal relationships regard to 'Neognathae' clade. See details about phylogenetic reconstruction in Appendix A.

Phylogenetic and functional diversity

We converted the final ML tree into an ultrametric tree using the nonparametric rate smoothing algorithm (*chronos* function) implemented in the package 'ape' (Popescu et al. 2012) for R (R Development Core Team 2017). We employed this ultrametric tree to quantify the phylo-diversity metrics, and to evaluate the phylogenetic signal of the trait data set. We quantified the phylogenetic structure of each avian assemblage using three indices: the standardized effect size of Faith's phylogenetic diversity (ses PD), the net relatedness index (hereafter NRI) and the nearest taxon index (hereafter NTI). In general, NRI is considered more sensitive to tree-wide patterns of phylogenetic clustering and overdispersion, while NTI is more sensitive to patterns of overdispersion and clustering closer to the tips of the phylogenetic tree (Kembel et al. 2010). NRI and NTI are defined as the measure of standardized effect size of mean pairwise distance (MPD) and mean nearest taxon distance (MNTD), respectively. These indices describe the difference in phylogenetic distance (i.e., MPD or MNTD) between observed and null communities generated with randomization methods divided by the standard deviation of phylogenetic distance in the null communities (Webb et al. 2002). Random communities were generated with the 'taxa labels' algorithm, shuffling taxa labels across tips of phylogenetic and functional trees or distance matrix with each running 999 times. Because standardized effect sizes (hereafter "ses") are scaled in units of standard deviation, values of NRI or NTI > 1.96 indicate statistically significant phylogenetic clustering while values < −1.96 indicate statistically significant phylogenetic overdispersion (Webb et al. 2002).

To characterize functional diversity (FD), we followed a dendrogram-based approach (Podani and Schmera 2006), and focused on traits associated with body mass and diet types to reflect resource use, behavioral traits during feeding to reflect how species acquire resources from their environment (Petchey and Gaston 2006), seasonality and irruptive migration to reflect the temporal replacement of avian assemblages in urban environments of the Chihuahuan desert, and acoustic traits (as a proxy of acoustic window, Wilkins et al. 2013; Job et al. 2016; but see Moiron et al. 2015). The overall trait data set consisted of four continuous trait types (body mass, song duration, mean frequency of song, and song entropy), three categorical trait types (foraging technique, social or solitary foraging, seasonality), and four main binary traits (diet types,

Table 1 List of bird surveyed sites and their habitat type of Ciudad Juárez, Chihuahua, Mexico

Sampling point	Geographic coordinates	Habitat type
El Chamizal	31° 45′ N, 106° 27′ W	Urban green spaces
Club Campestre	31° 43′ N, 106° 24′ W	Urban green spaces
Parque Central	31° 41′ N, 106° 25′ W	Urban green spaces
Puerta Juárez	31° 32′ N, 106° 28′ W	Desert scrub
Trepachanga	31° 40′ N, 106° 30′ W	Desert scrub
Zaragoza	31° 40′ N, 106° 20′ W	Agricultural fields
Loma Blanca	31° 35′ N, 106° 18′ W	Agricultural fields

foraging stratum, circadian activity, irruptive migrant). We compiled trait data on diet types from Handbook of the Birds of the World Alive database (HBWA, del Hoyo et al. 2017) following the terminology proposed by Lopes et al. (2016). Foraging-related traits (foraging techniques, stratum, social system, and circadian activity) were extracted from Ehrlich et al. (1988) and The Birds of North America online database (BNA, Rodewald 2017) supplemented with observations during our field work. Mean values of body mass data were obtained from Dunning (2008). Data on seasonality and irruptive migrant status was gathered from our fieldwork.

In order to analyze if bird vocalizations as functional traits are related to avian assemblages, we measured three spectrogram acoustic parameters (song duration, mean frequency of song and song entropy) that have been related with a better sound transmission depending on the habitat type such like open areas, dense forest or urban areas (Bermudez-Cuamatzin et al. 2011; Job et al. 2016). Recordings (songs and calls) were obtained by two sources: a) requested from Macaulay Library (https://www.macaulaylibrary.org/), and b) downloaded directly from Xeno-canto (www.xeno-canto.org) using the function *querxc* implemented in the 'warbleR' package (Araya-Salas and Smith-Vidaurre 2017) for R. We selected the better-quality recordings (those with low noise levels and better signal ratio) for our analyses. See details in *Phylogenetic and functional diversity* section in Appendix A.

We measured functional diversity using three metrics related to species presence/absence. As we included mixed categorical/binary and continuous trait variables, we performed the following steps to obtain a subset of the PCoA (Principal co-ordinates analysis) axes as the new 'traits' for use in computing the functional diversity indices. Our codified continuous traits were standardized to vary from zero to one and thus match the range of values of the binary traits. Trait matrix was converted into Gower dissimilarity matrix with the *gowdis* function implemented in the 'FD' R package (Laliberté et al. 2014). This dissimilarity matrix was transformed into a functional dendrogram using the *hclust* function with UPGMA cluster algorithm in R. Finally, the functional tree was exported as a 'phylo' object to quantify the functional metrics. The functional structure was measured using the analog metrics (ses FD, FNRI, FNTI), following the same procedure to generate phylogenetic null communities. We also tested for significant differences among habitat types for each metric with a Kruskal–Wallis test in R. If the statistical cutoff value $p <= 0.05$, we reject the null hypothesis that there are no differences among habitat types.

Phylogenetic trait conservatism

To assess the extent to which phylogenetic relatedness between species reflects ecological similarity (i.e. phylogenetic conservatism), we used Blomberg's K-statistic (Blomberg et al. 2003) to quantify the tree-wide phylogenetic signal in continuous traits in R package 'phytools' (*phylosig* function, Revell 2012). K values close to zero indicate less phylogenetic signal than expected from a Brownian motion model of trait evolution (Blomberg et al. 2003), thus implying that closely related species are functionally distinct. For binary traits, we calculated phylogenetic signal with the *phylo.d* function of the 'caper' R package (Orme et al. 2013). This metric compares the observed sister-clade differences in the study trait against those expected for a random phylogenetic pattern (Fritz and Purvis 2010). To calculate the strength of the phylogenetic signal in binary traits we followed Fritz and Purvis (2010), thus if $D < 0$ the trait is considered to have a strong phylogenetic signal, as expected under Brownian motion, and if $D > 0$ it is considered to have less phylogenetic signal. In the case of categorical traits, we tested for phylogenetic signal with the 'fixed tree, character randomly reshuffled model' proposed by Maddison and Slatkin (1991) implemented in R as the *phylo.signal.disc* function developed by E.L. Rezende (Universidad Andrés Bello, Santiago, Chile). See details about how was assessed the significance of the phylogenetic signal of functional traits in Appendix A.

Phylogenetic comparative methods

For ancestral character estimation, we used the threshold model from evolutionary quantitative genetics (Revell 2014). We coded the species' habitat use (desert scrub specialist, agricultural fields specialist, urban green spaces specialist, and habitat generalist) as categorical traits (i.e. as ancestral states) ordered by increasing tolerance to urbanization. In this study, we considered the species according to our fieldwork as 'specialist' when its occurrence was recorded only in one habitat; and 'generalist' when its occurrence was documented in all habitat types. We codified equal probability for those species where its presence was observed in two habitat types. We used the function *ancThresh* in the R package 'phytools' (Revell 2012) to estimate the species' habitat use (as a proxy of urban tolerance) in avian assemblages using Bayesian Markov chain Monte Carlo (MCMC) as proposed by Revell (2014). We simulated ancestral states using a Brownian Motion model for 10,000,000 generations sampling every 100 generations and rejecting the first 2,000,000 generations as burn-in. This method estimates both ancestral character states and tips, allowing us to draw conclusions about species with ambiguous character states. Under threshold model, the evolving discrete traits are considered to have a continuous underlying liability. When the value of liability exceeded the threshold value, the discretely valued state of the observable character trait changed (Revell 2014). We used these mean values to map them throughout the phylogeny with the *contMap* function of the 'phytools' R package (Revell 2012). See details in Appendix A.

Predictor variables for urbanization effect

A set of environmental and anthropogenic predictor variables were selected for model construction based on their suitability for hypothesis testing and their influence on phylogenetic and functional metrics in urban environments (Aronson et al. 2016). These variables are related to current climate (annual mean temperature and annual precipitation), habitat heterogeneity (vegetation complexity), elevation, and anthropogenic (human footprint and invasive bird species richness). Geoprocessing of data was performed in ArcGIS 10.3 (ESRI, Redland, USA).

To summarize climate, we downloaded two bioclimatic variables from Chelsa Climate project (Karger et al. 2017): annual mean temperature (TEMP) and annual precipitation (PREC). To obtain the vegetation complexity (VEGE) raster, as a proxy of habitat heterogeneity, thus we gathered four land-cover variables (mixed trees, shrubs, herbaceous vegetation, and cultivated and managed vegetation) from Global 1-km Consensus Land Cover project available at http://www.earthenv.org/landcover (Tuanmu and Jetz 2014). These rasters have land-cover information in an approximately continuous scale. Then we performed a principal component analysis (PCA) of the four land-cover variables. The PCA analysis was carried out using SDMtoolbox v.1.1.c (Brown 2014). The raster layer represents the sum of all vegetation components within urban settlements, ranging from large native vegetation patches or remnants to isolated street trees. We did the raster to avoid possible overfitting in spatial regression models due to a small sample size. Elevation (ELEV) raster was downloaded from the Hydro1k project (https://lta.cr.usgs.gov/HYDRO1K). The human footprint (HUMF) of the Last of the Wild Project was downloaded from http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-ighp (version 2). The invasive bird species richness shapefile (INSR hereafter) was based on the vector range maps from Howell and Webb (1995), minimum convex polygons delimited by our buffer observation sites, and unpublished bird observations.

All layers have 30 arc-second resolutions (1 km^2) and were re-projected at WGS 1984 UTM Zone 13 N. We extracted spatial values with a bilinear interpolation in the sampling point locations in a geographic information system (ArcGIS 10.3) to obtain raw data. All predictor variables were scaled to a mean of zero and variance of 1 (z-standardization) before the analysis to make model coefficients comparable. The TEMP, VEGE, ELEV, HUMF, and INSR variables were log-transformed, while the PREC was square-root-transformed.

Regression analysis

We performed spatial correlations of the overall standardized and transformed predictor variables above mentioned. Only those predictor variables with non-collinearity (Pearson's correlation, r < 0.7; Dormann et al. 2013) were analyzed in the multiple regressions. Inherently, some environmental processes that drive species richness show spatial autocorrelation (Kissling and Carl 2008). To account for spatial autocorrelation, we used Dutilleul's modified *t-test*, provided in the 'SpatialPack' R package (Osorio and Vallejos 2014). This resulted in five predictor variables for the analyses, excluding elevation (ELEV).

Starting with a full model that fitted all uncorrelated predictors for each metric, we created every possible two-variable model (due to the small sample size) by employing the *dredge* function of the 'MuMIn' R library (Barton 2018). We then compared support for these competing models using Akaike Information Criterion corrected (AICc). We selected the best combined two-variable models having the lowest AICc value (Burnham and Anderson 2002). The selected models were considered the most parsimonious and ecologically meaningful to test each multiple regression model (see set of top models in Supporting Information Table S3). To explain the phylogenetic and functional metrics captured for each sampling point, models were analyzed using spatial autoregressive (SAR) modelling to account for spatial autocorrelation in our data set. To account for spatial autocorrelation across our study area, we used the *errorsarlm* function of the R package 'spdep' (Bivand and Piras 2015). Details about how we selected the minimum distance, the neighborhood contiguity and spatial weight matrix are in Appendix A.

Results

Phylogenetic and functional diversity

A total of 217 bird species were observed on seven sampling points across Ciudad Juárez (Supporting Information Table S2). Of these species, 164 bird species were terrestrial in our study area. We recorded the highest levels of species richness in the urban green spaces (*mean* = 109 species, *SD* = 31.94), followed by those of agricultural fields (*mean* = 80 species, *SD* = 38.18) and desert scrub (*mean* = 71 species, *SD* = 4.24). The sampling point with the highest bird richness was Club Campestre (133 species) and the locality with lowest richness was Zaragoza (53 species).

Although urban green spaces have more phylogenetic and functional diversity than agricultural fields and desert scrub, we found no statistically significant differences among the three types of habitat in ses phylogenetic diversity (H = 3.75, p = 0.15) or ses functional diversity, although both metrics indicate clustered communities (H = 3.75, p = 0.15; metrics based on the proportion of total tree branch length; Fig. 2). For metrics based on mean branch length among sample taxa, we found in broad sense clustered communities, urban green spaces being slightly overdispersed (Fig. 2). We also found no statistically significant differences in net relatedness index
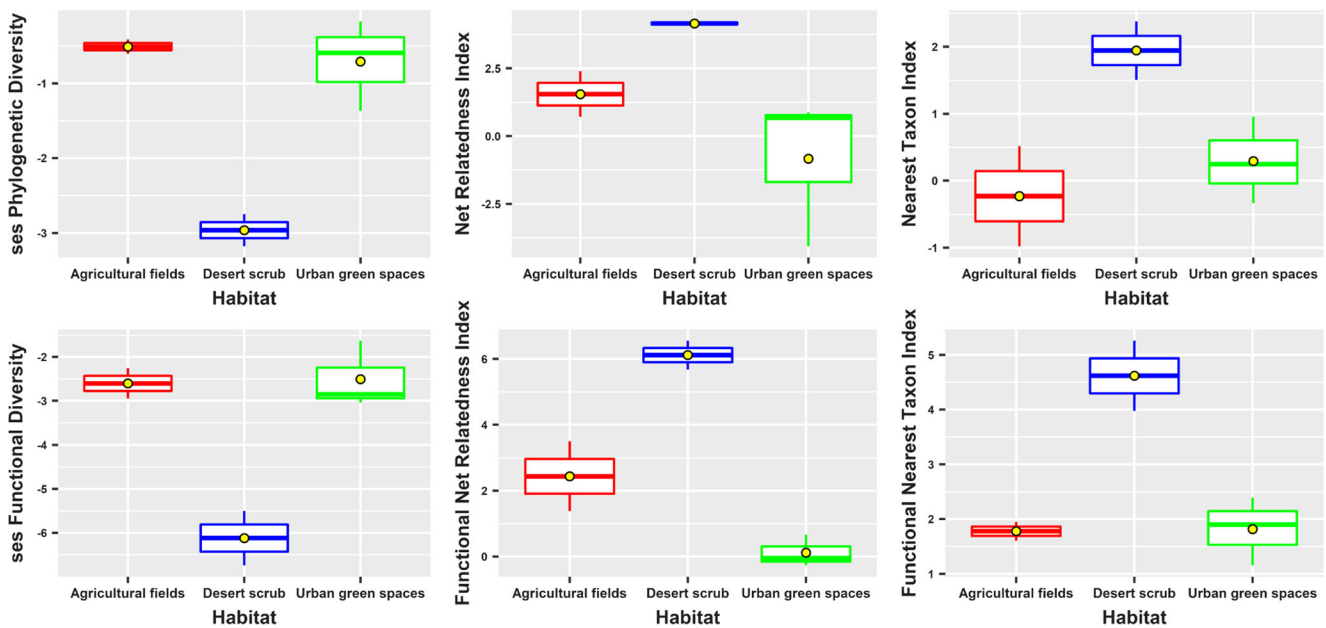
Fig. 2 Comparison of phylogenetic and functional metrics of bird assemblages among habitats. y-axis represents the estimated variable; boxplots shows the interquartile values; yellow dots represent the mean values and colored horizontal bars the median (bar in the middle of rectangles), maximum and minimum values (vertical lines)

(H = 4.46, p = 0.10), nearest taxon index (H = 3.92, p = 0.14), functional net relatedness index (H = 5.35, p = 0.06), or functional nearest taxon index (H = 3.75, p = 0.15).

Phylogenetic trait conservatism

All continuous traits presented a low and significant phylogenetic signal for the surveyed avian assemblages (Table 2). The most phylogenetically conserved trait with $K = 0.35$ ($P = 0.001$) was mean frequency of song, while the smallest K was also for an acoustic trait, song entropy with $K = 0.12$ ($P = 0.002$). Among the 20 discrete binary characters examined, one character showed weak phylogenetic signal ($D > 0$), the crepuscular activity, with $D = 0.3666$ (Table 2). The scavenger category was the only binary trait that had statistical significance ($D = -0.3355$). The most phylogenetically conserved binary characters were orderly: the presence/absence of diurnal activity pattern with $D = -1.0266$, followed by foraging stratum in the air with $D = -0.6496$, and the presence/absence of worms as diet with $D = -0.4794$ (Table 2). For the categorical traits, all characters showed phylogenetic signal. For example, the seasonality with four state characters suggested 102 evolutionary transitions (randomized median = 110, $P = 0.024$, Table 2).

Phylogenetic comparative methods

The ESS of the ancestral state reconstruction under the threshold model was 104.44, while the Highest Posterior Density (HPD) intervals were between −123.42 (lower) and −21.57 (upper). After excluding 20% as burn-in, ancestral state reconstruction performed under the threshold model indicated that liability threshold for desert scrub was zero, followed by agricultural fields (0.82), urban green spaces (1.27), and habitat generalist (infinite value). See Fig. 3 for details.

Regarding the visualization of the liability mapping, our results indicate that liability in the recorded species have been non-randomly distributed through the phylogeny (Fig. 4). For example, 21 species belonging to nine bird families have a phylogenetic predisposition to be found only in desert environments (mean = −0.18, SD = 0.13); being present in Odontophoridae (*Callipepla squamata*), Caprimulgidae (*Phalaenoptilus nuttallii* and *Chordeiles minor*), among others (see Fig. 4). The Columbidae family (doves and pigeons) was the clade with highest liability (mean = 2.69, SD = 0.01), being habitat generalists in our study area. The second clade with highest liability was Cathartidae, represented by *Cathartes aura* with a liability of 1.83. The Accipitridae clade (excluding 'Falconidae' raptors) had a moderate liability (mean = 1.04, SD = 0.33), although one raptor species (*Elanus leucurus*) recorded only in agricultural fields had a low liability with 0.52. One family practically omnipresent in urban green spaces, Picidae (woodpeckers), had a relatively high liability (mean = 1.29, SD = 0.29). Finally, the most diverse clade of living birds, Passeriformes (passerines), presented a moderate liability threshold (mean = 0.87, SD = 0.45).

Regression analysis

The ses phylogenetic diversity model included temperature (TEMP) and human footprint (HUMF) as positive predictors explaining 90% of the variance ($R^2 = 0.90$) (Table 3). Invasive

Table 2 Phylogenetic signal test for every trait used with its respective significance value

Variable type	Continuous		Binary		Categorical	
Traits	K	p	D	p*	ETO**	p
Body mass	0.2714	0.001				
Song duration	0.1684	0.015				
Mean frequency of song	0.3544	0.001				
Song entropy	0.1222	0.001				
Scavenger			−0.3355	0.001		
Vertebrates			−0.5019	0.915		
Insects			−0.1986	0.765		
Worms			−0.4794	0.897		
Crustaceans			−0.1857	0.753		
Mollusks			−0.3074	0.866		
Fish			−0.1814	0.733		
Seeds			−0.2152	0.847		
Fruits			−0.0721	0.633		
Plants			−0.1810	0.750		
Nectar			−0.8680	0.908		
Sap			−0.4527	0.726		
Foraging stratum terrestrial/aquatic			−0.4266	0.969		
Foraging stratum between 1 and 2 m			−0.0924	0.656		
Foraging stratum above 2 m			−0.0424	0.582		
Foraging stratum in the air			−0.6496	0.944		
Diurnal			−1.0266	0.986		
Crepuscular			0.3666	0.254		
Nocturnal			−0.0155	0.561		
Irruptive			−0.1844	0.652		
Foraging technique					104	0
Social foraging					77	0
Seasonality					102	0.024

*$p = p$ value under a Brownian evolution threshold model

**ETO = Evolutionary Transitions Observed

bird species richness (INSR) was a negative predictor for net relatedness index. The vegetation complexity variable had moderate importance in the capture of nearest taxon index, although negatively affected by human footprint (HUMF) (Table 3). In the case of ses functional diversity, the temperature variable was a positive predictor, while that vegetation complexity was a negative predictor. In general, temperature and precipitation were negative predictors for functional net relatedness index (FNRI) and functional nearest taxon index (FNTI).

Discussion

Phylogenetic and functional diversity

Regarding to our first hypothesis, we do not find statistical differences that ses phylogenetic diversity and ses functional diversity was higher in human-made environments (e.g. urban green spaces and agricultural fields) than desert scrub habitats. Although we did not find statistical support, such observed pattern is probably a reflection of greater habitat diversity and microhabitat heterogeneity in the urban green spaces facilitating the occurrence of species with a greater range of functional traits and evolutionary tendencies (McKinney 2008; Nielsen et al. 2014; Hagen et al. 2017) than more specialized species that occur within a single natural habitat proper of the regional species pool (Aronson et al. 2016). Recent global-scale studies mention that urbanization decreases the evolutionary history (Sol et al. 2014; Ibáñez-Álamo et al. 2017; Sol et al. 2017) and increase functional diversity of avian assemblages (Hagen et al. 2017). Nonetheless, La Sorte et al. (2018) using breeding bird range maps and presence-absence bird data of the largest sample size for global comparisons ($n = 58$ cities), concluded that urbanization is associated with an overall decrease and constriction in the evolutionary and functional diversity of breeding avian assemblages.
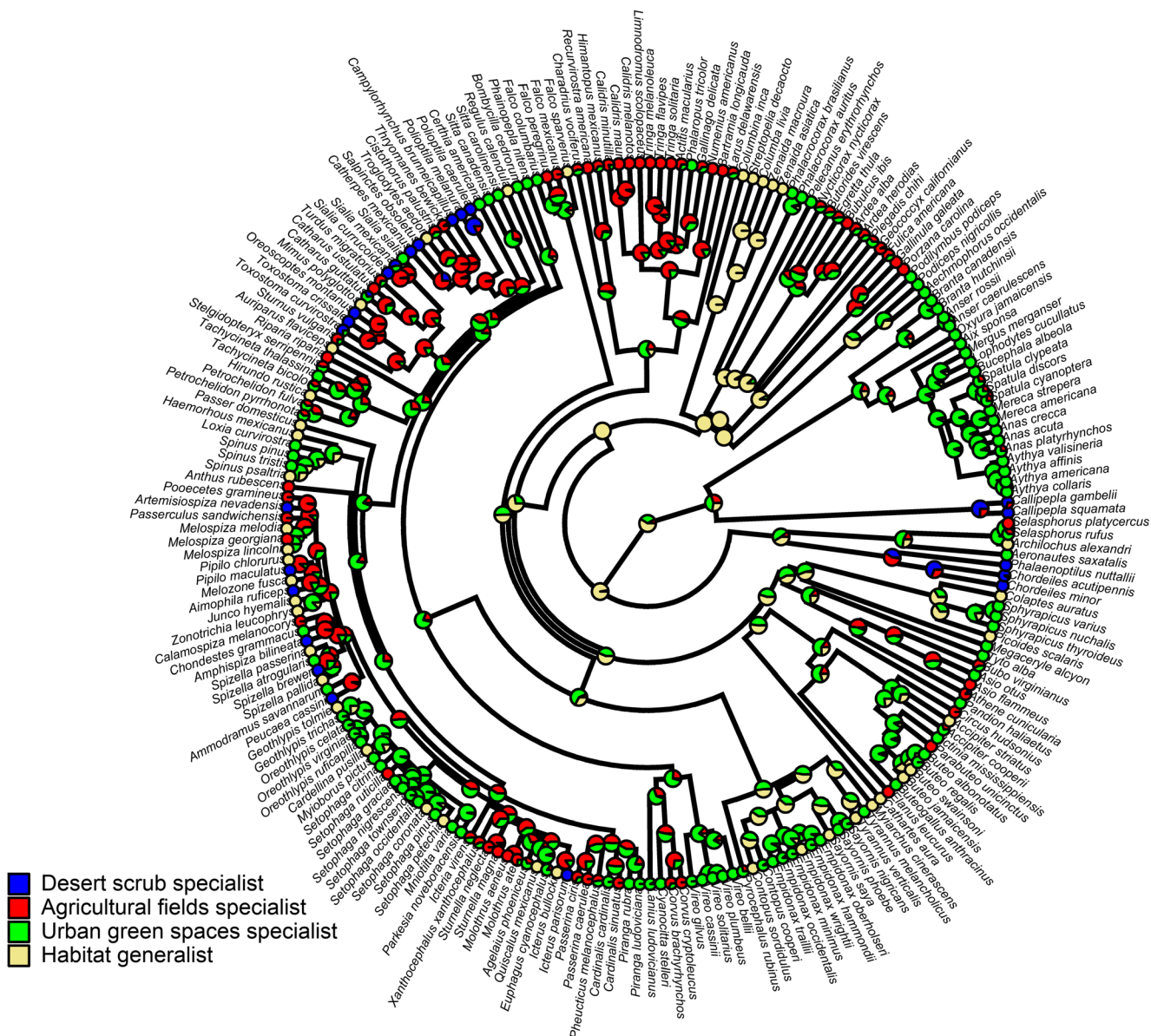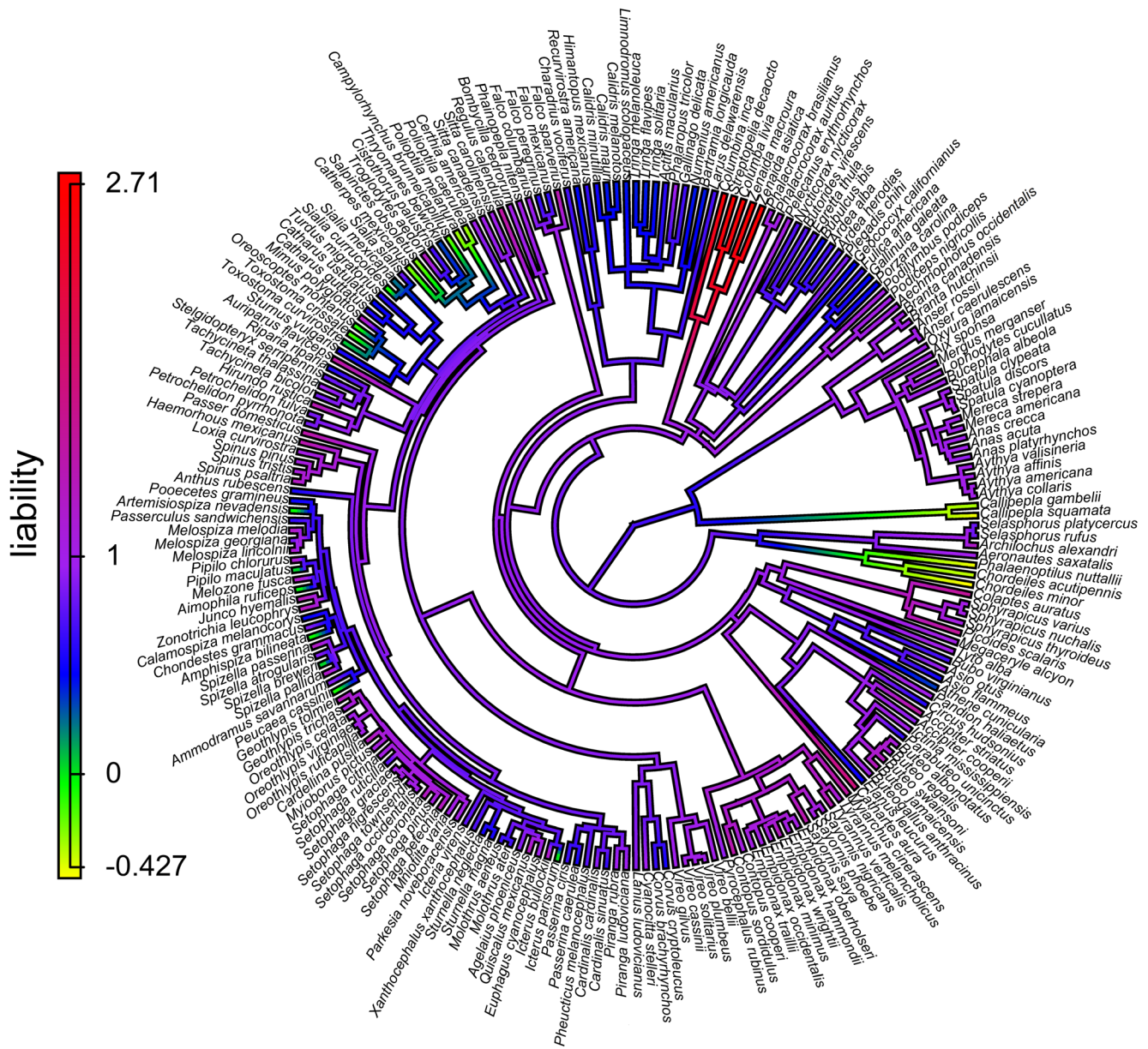
Fig. 3 Ancestral state reconstruction for "urban occurrence" in bird species of our study area under the threshold model. Different colors in the pie charts of the internal nodes depict the posterior probability of belonging to each of the four states. Tip states represent estimated values

The observed pattern of high phylogenetic and functional diversity in urban habitats coincides in part with the presence of irruptive bird species (e.g. *Cyanocitta stelleri*, *Sitta canadensis*) during our fieldwork. These species perform altitudinal migrations approximately every five years, being present in greening areas in El Paso-Juárez region (Lockwood and Freeman 2014), but mostly absent in desert scrub habitats and agricultural fields. Most of the irruptive species in this study are diurnal winter visitors, small to medium-sized birds (mean = 37.96 g, min = 9.80, max = 128, SD = 37.54), foliage gleaners, insectivores, granivores, frugivores, and with a social foraging in bonded or aggregation. Besides, a high evolutionary history in urban habitats is the obvious presence of geese and ducks (Anseriformes). Species of desert habitats must cope with several

environmental harshness occasioned by spatial arrangement, microclimate heterogeneity and water availability of urban green spaces and agricultural fields, contrasting with extreme climates of the surrounding desert (Green and Baker 2003; Walker and Shochat 2009; Kowarik 2011; Gómez-Baggethun and Barton 2013; Nielsen et al. 2014). Therefore, this finding emphasizes the importance of urban green spaces for 'bird diversity hotspots' in the Chihuahuan desert.

Nonrandom distributions of avian assemblages' evolutionary and functional history

Regarding metrics based on mean branch lengths between taxa, we found mainly clustered communities in urban

Fig. 4 Ancestral state reconstruction for mean values of liability in bird species of our study area. Different colors in the scale bar depict the continuous mean values of liability from our analysis conducted under the threshold model

habitats, as expected since urbanization tends to favor a small number of lineages with similar or redundant functional traits given by phylogenetic relatedness (Webb et al. 2002; Ndiribe et al. 2013; Sol et al. 2014; Ibáñez-Álamo et al. 2017; La Sorte et al. 2018). For the avifauna, it is generally assumed that urbanization is associated with the presence of seed eaters (generally passerine birds), ground foraging insectivores, water dependent, and crevice nesting species (Chace and Walsh 2006; Evans et al. 2011; Sol et al. 2014), thus contributing with this pattern of non-random communities observed in our study (Bonier et al. 2007; Silva et al. 2016; Hagen et al. 2017; La Sorte et al. 2018). Nonetheless, Lepczyk et al. (2008) found that natural-

history traits poorly predicted whether a bird species was positively or negatively correlated with human influence, although foraging type had a negative response to human influence.

We found non-random communities in agricultural fields because these areas mainly support shorebird species (Charadriiformes) with similar functional traits within this taxonomic group. Functional traits such as relatively-large size ($mean = 184.21$ g, $min = 23.80$, $max = 642$, $SD = 181.40$), commonly present diets consisting of invertebrates (insects, worms, crustaceans, molluscs), grains and herbs, many of them are probers or ground gleaners with a social foraging in aggregations, this characteristic

Table 3 Best selected models explaining the captured variance in spatial regressions (SAR err). Low AICc values indicate a better model. Significance level: $*p < 0.05$

Model	Variables	Coefficients ± SE	R^2	AICc	Akaike weights
ses PD	TEMP	$1.13 \pm 0.13*$	0.90	75.11	1.557e-09
	HUMF	$0.27 \pm 0.10*$			
	INTE	$-1.26 \pm 0.06*$			
NRI	PREC	$1.52 \pm 0.32*$	0.92	85.18	1.499e-09
	INSR	$-1.66 \pm 0.41*$			
	INTE	$1.23 \pm 0.11*$			
NTI	VEGE	$1.04 \pm 0.26*$	0.64	83.14	2.411e-11
	HUMF	$-0.51 \pm 0.22*$			
	INTE	$0.66 \pm 0.11*$			
ses FD	TEMP	$1.63 \pm 0.21*$	0.95	75.61	1.569e-09
	VEGE	-0.32 ± 0.22			
	INTE	$-3.59 \pm 0.04*$			
FNRI	TEMP	$-1.95 \pm 0.23*$	0.95	81.81	2.088e-08
	INSR	$-1.56 \pm 0.22*$			
	INTE	$2.49 \pm 0.22*$			
FNTI	TEMP	$-2.27 \pm 0.52*$	0.95	72.59	1.725e-09
	PREC	-0.86 ± 0.53			
	INTE	$2.60 \pm 0.07*$			

could determine the presence of these species in agricultural fields. Nonetheless, *Phalaropus tricolor* a surface dipper was found exclusively in urban green areas, suggesting that the foraging technique and foraging stratum possibly influence the occurrence of certain aquatic species to tolerate the urban sprawl. Unexpectedly, the desert scrub habitats were also phylo-functionally clustered communities, suggesting that communities are mostly created by strong filtering interactions (especially if the phenotypes considered are under selection) from the regional species pool (Ndiribe et al. 2013).

Phylogenetic trait conservatism

Contrary to expectations, we found that all continuous traits had a low and significant phylogenetic signal (i.e. closely related species are functionally distinct). A recent study showed that song frequency is not related to urban success (Moiron et al. 2015). However, some variation in song frequency reflects plastic adjustments and the degree of plasticity varies among species (Moiron et al. 2015). Besides it is still possible that some desert species could be recent colonizers (Luther and Baptista 2010; Bermudez-Cuamatzin et al. 2011; Job et al. 2016). Probably behavioral flexibility of some desert bird species (e.g. *Callipepla gambelii*) allows them to exploit novel resource opportunities or have a life-history strategy that

reduces extinction risk in increasing urbanizing environments (Moiron et al. 2015). However, this hypothesis should be tested in order to determine if the frequency of the song changes along the urban landscape of this Chihuahuan desert city.

Most binary traits had a strongly conserved phylogenetic signal ($D < 0$), although only the scavenger trait was significant under a Brownian motion model. While *Cathartes aura* (Cathartidae) is the only obligate terrestrial vertebrate scavenger in our study area, facultative scavenging is phylogenetically (e.g. *Circus hudsonius*, *Corvus cryptoleucus*) and geographically widespread, and may in some cases can be favored over predation in urban environments than surrounding habitats (Inger et al. 2016). The avian assemblages' seasonality status was the only categorical traits that had phylogenetic signal. Apparently, bird communities in our study area that were significantly structured could be due to seasonal movement patterns, local and regional habitat changes, and climatic conditions. The distinct seasonality of rainfall and seasonal variation in the abundance of food resources result in seasonal changes in the species occurrence of bird species (Brown 1994). The distribution of many desert bird species is determined by the composition of the vegetation that forms a major element of their habitats (Brown 1994). It is known that the desert vegetation composition and structure is affected by precipitation patterns which change between wet and dry seasons (Brown 1994).

Phylogenetic predisposition to be present in urban environments

We found that urbanization significantly disfavors desert species with medium body mass (*mean* = 37.60 g, *min* = 5.2, *max* = 177, *SD* = 40.29), a song duration of 1.69 (*min* = 5.2, *max* = 177, *SD* = 3.46), mean frequency of song of 4.51 (*min* = 2.05, *max* = 9.15, *SD* = 2.12), and song entropy of 0.73 (*min* = 0.61, *max* = 0.81, *SD* = 0.068), and that are principally diurnal residents, being ground or foliage gleaners mainly in pairs or aggregations (see Table 2). The ability to be habitat generalist is present in the surveyed avian assemblages (Fig. 3). In other words, prior to human colonization and subsequent urban growth in desert habitats of northern Mexico (e.g. Ciudad Juárez), bird species were predisposed phylogenetically to tolerate habitat perturbation such as anthropogenic habitat modifications (Fig. 3). Only a few desert-adapted species remain habitat specialists (Fig. 3). This is not surprising given habitat specialist species may be replaced by habitat generalists during urbanization process (Chace and Walsh 2006; Lepczyk et al. 2017).

Probably active colonizers of new habitats, mainly generalist and adaptable species (perhaps migrant species) would likely be most successful when urbanization favors traits allowing them to colonize new niches and new habitats (e.g. urban green spaces). Such pattern is reflected in the ancestral

reconstruction state of liability, where there is a notable presence of habitat generalists across the phylogeny (Fig. 3 and 4). Closely related species tend to respond to urbanization in a similar way (Bonier et al. 2007; Sol et al. 2014), possibly because they share features that affect their tolerance to urbanization as observed in some avian families (e.g. Columbidae, Accipitridae, Picidae). This coincides with the phylogenetic similarity of the functional traits of these avian assemblages (see Table 2). For example, a recent study demonstrated that in areas with urbanization their fauna was associated with presence of fewer small and especially large bodied species, fewer narrowly and especially wide distributed species, and with an increased prevalence of granivorous species (La Sorte et al. 2018). Moreover, bird species which nest or forage on or close to the ground are adversely impacted by urbanization due to increased nest predation (Sims et al. 2008; Evans et al. 2011). For instance, *Salpinctes obsoletus* and *Catherpes mexicanus*, have niches associated with rocky areas present in desert scrubs and both nesting on or close to the ground (del Hoyo et al. 2017), thus, urbanization is probably limiting the occurrence and nesting of these rock-loving bird species in urban green spaces of Ciudad Juárez and perhaps in other Chihuahuan desert cities.

Environmental variables influencing phylogenetic and functional diversity

Our regression analysis indicates that NTI is positively correlated with vegetation complexity while human footprint (HUMF) was negatively correlated with this phylogenetic metric. Walker and Shochat (2009) suggests that the urban ecosystem does not necessarily serve as a rigid ecological barrier for native species of birds. For example, urban green spaces surveyed presented desert native vegetation, allowing the occurrence of many desert bird species. This is not surprising since humans have reconfigured desert landscapes historically for agricultural activities and urbanization, causing dramatic changes to native bird communities (Portnov and Paz 2008). Pautasso (2007) and Lepczyk et al. (2008) have showed that human population density is negatively correlated with species richness in studies done at fine spatial scales. A likely cause of this scaling relationship is that, at small (local) spatial scales, increasing human population size (e.g. in highly populated urban core areas) tends to eliminate phylogenetically related species via extreme human disturbances in the local vicinity (McKinney 2008).

We found a negative effect of invasive bird species richness (INSR) on NRI and FNRI (Table 3). In our study area, invasive bird species such as *Columba livia*, *Streptopelia decaocto* and *Passer domesticus* are practically omnipresent and abundant in all habitats, although *Sturnus vulgaris* is locally abundant in urban habitats. Possibly, the presence of native bird species with similar functional traits like those presented by

invasive bird species may determine the incidence of native species of the regional species pool, which subsequently lead to a functional similarity of these avian assemblages (McKinney 2006; Olden et al. 2011). Thus, the role of invasive species in defining patterns of urban bird diversity may be more significant than our findings suggest, along with the encouraged need to acquire and incorporate abundance information into future studies as suggested by La Sorte et al. (2018).

On the other hand, all functional diversity indices are influenced by temperature, precipitation, and vegetation complexity, which are considered as important environmental filters as emphasized for avian assemblages in desert cities (Aronson et al. 2016). Cities are well known to be urban heat islands affecting species distributions and biotic interactions (Aronson et al. 2016). One consequence may be environmental filtering due to overheating occasioned by urbanization (i.e. human health and comfort, energy use, air pollution, water use) may be enhanced, limiting the occurrence of high trait diversity and resulting in highly functional similar communities.

Final remarks

In conclusion, urban green spaces constitute important refuges for wildlife in urbanized environments where scenarios of urban growth are expected (e.g. Ciudad Juárez). Urban green spaces present more evolutionary and functional diversity than agricultural fields and desert scrub, but not in any significant manner. The avian assemblages associated to urban habitats were mainly clustered. All continuous traits had a low and significant phylogenetic signal. Most binary functional traits presented a strong phylogenetic signal, but only a binary trait did differ significantly from the Brownian model ($P < 0.05$). We found a negative effect of invasive bird species richness (INSR) on NRI and FNRI. Only a few desert-adapted species remain habitat specialists. Furthermore, these urban green spaces can help to create less dense urban settlements, such that an intermediate level of urbanization should have less negative impact on overall biodiversity (Chace and Walsh 2006; Nielsen et al. 2014; Lepczyk et al. 2017). It is important to note that no global-scale study (e.g. Hagen et al. 2017; Ibáñez-Álamo et al. 2017; La Sorte et al. 2018) has included a 'Chihuahuan desert city', thus our study fills this knowledge gap for a better understanding on avian urban ecology in Latin America (MacGregor-Fors et al. 2017). Managers and urban planners should be into account evolutionary and functional history of biodiversity for a better urban growth in cities with surrounding desert habitats. The methods implemented in this study can be easily applicable in other biological groups when its phylogeny and natural history are well studied.

References

Araya-Salas M, Smith-Vidaurre G (2017) warbleR: an r package to streamline analysis of animal acoustic signals. Methods Ecol Evol 8(2):184–191. https://doi.org/10.1111/2041-210X.12624

Aronson MFJ, Nilon CH, Lepczyk CA, Parker TS, Warren PS, Cilliers SS, Goddard MA, Hahs AK, Herzog C, Katti M, La Sorte FA, Williams NSG, Zipperer W (2016) Hierarchical filters determine community assembly of urban species pools. Ecology 97(11):2952–2963. https://doi.org/10.1002/ecy.1535

Barton K (2018). MuMIn: Multi-Model Inference. R package version 1.40.4. https://CRAN.R-project.org/package=MuMIn. Accessed 21 June 2018

Bermudez-Cuamatzin E, Rios-Chelen AA, Gil D, Garcia CM (2011) Experimental evidence for real-time song frequency shift in response to urban noise in a passerine bird. Biol Lett 7(1):36–38. https://doi.org/10.1098/rsbl.2010.0437

Bivand R, Piras G (2015) Comparing implementations of estimation methods for spatial econometrics. J Stat Softw 63(18):1–36. https://doi.org/10.18637/jss.v063.i18

Blomberg SP, Garland T Jr, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57(4):717–745. https://doi.org/10.1554/0014-3820(2003)057[0717:TFPSIC]2.0.CO;2

Bonier F, Martin PR, Wingfield JC (2007) Urban birds have broader environmental tolerance. Biol Lett 3(6):670–673. https://doi.org/10.1098/rsbl.2007.0349

Brown DE (1994) Chihuahuan desert scrub. In: Brown DE (ed) Biotic communities: southwestern United States and northwestern Mexico. Utah University Press, Salt Lake City, pp 169–179

Brown JL (2014) SDMtoolbox: a python–based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol Evol 5(7):694–700. https://doi.org/10.1111/2041-210X.12200

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Cadotte MW, Tucker CM (2017) Should environmental filtering be abandoned? Trends Ecol Evol 32(6):429–437. https://doi.org/10.1016/j.tree.2017.03.004

Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plan 74(1):46–49. https://doi.org/10.1016/j.landurbplan.2004.08.007

Chesser RT, Burns KJ, Cicero C, Dunn JL, Kratter AW, Lovette IJ, Rasmussen PC, Remsen JV, Rising JD, Stotz DF, Winker K (2017) Fifty-eighth supplement to the American ornithological Society's check-list of north American birds. Auk 134(3):751–773. https://doi.org/10.1642/AUK-17-72.1

del Hoyo J, Elliott A, Sargatal J, Christie DA, and de Juana E (eds) (2017) Handbook of the birds of the world alive. Lynx Edicions, Barcelona. http://www.hbw.com/. Accessed 21 April 2017

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, García Marquéz JR, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AD, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal

with it and a simulation study evaluating their performance. Ecography 36(1):27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dunning JB Jr (2008) CRC handbook of avian body masses, 2nd edn. CRC Press, Florida

Ehrlich PR, Dobkin DS, Wheye D (1988) The birder's handbook: a field guide to the natural history of north American birds. Simon and Schuster, New York

Emerson BC, Gillespie RG (2008) Phylogenetic analysis of community assembly and structure over space and time. Trends Ecol Evol 23(11):619–630. https://doi.org/10.1016/j.tree.2008.07.005

Evans KL, Chamberlain DE, Hatchwell BJ, Gregory RD, Gaston KJ (2011) What makes an urban bird? Glob Chang Biol 17(1):32–44. https://doi.org/10.1111/j.1365-2486.2010.02247.x

Fritz SA, Purvis A (2010) Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. Conserv Biol 24(4):1042–1051. https://doi.org/10.1111/j.1523-1739.2010.01455.x

García E (2004) Modificaciones al sistema de clasificación climática de Koppen, 5th edn. Instituto de Geografía, UNAM, Mexico City

Gómez-Baggethun E, Barton DN (2013) Classifying and valuing ecosystem services for urban planning. Ecol Econom 86:235–245. https://doi.org/10.1016/j.ecolecon.2012.08.019

Green DM, Baker MG (2003) Urbanization impacts on habitat and bird communities in a Sonoran desert ecosystem. Landsc Urban Plan 63(4):225–239. https://doi.org/10.1016/S0169-2046(02)00195-0

Hagen EO, Hagen O, Ibáñez-Álamo JD, Petchey OL, Evans KL (2017) Impacts of urban areas and their characteristics on avian functional diversity. Front Ecol Evol 5:84. https://doi.org/10.3389/fevo.2017.00084

Howell SNG, Webb S (1995) A guide to the birds of Mexico and northern Central America. Oxford University Press, Oxford

Hubbard JP (1974) Avian evolution in the aridlands of North America. Living Bird 12:155–196

Ibáñez-Álamo JD, Rubio E, Benedetti Y, Morelli F (2017) Global loss of avian evolutionary uniqueness in urban areas. Glob Chang Biol 23(8):2990–2998. https://doi.org/10.1111/gcb.13567

Inger R, Cox DTC, Per E, Norton BA, Gaston KJ (2016) Ecological role of vertebrate scavengers in urban ecosystems in the UK. Ecol Evol 6(19):7015–7023. https://doi.org/10.1002/ece3.2414

Instituto Municipal de Investigación y Planeación (IMIP) (2016) Radiografía socioeconómica del Municipio de Juárez 2015. Instituto Municipal de Investigación y Planeación, Ciudad Juárez

Instituto Nacional de Estadística y Geografía (INEGI). (2016) Panorama sociodemográfico de Chihuahua 2015. Instituto Nacional de Estadística y Geografía, Aguascalientes

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO (2012) The global diversity of birds in space and time. Nature 491(7424):444–448. https://doi.org/10.1038/nature11631

Job JR, Kohler SL, Gill SA (2016) Song adjustments by an open habitat bird to anthropogenic noise, urban structure, and vegetation. Behav Ecol 27(6):1734–1744. https://doi.org/10.1093/beheco/arw105

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth land surface areas. Sci Data 4:170122. https://doi.org/10.1038/sdata.2017.122

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26(11):1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kissling WD, Carl G (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. Glob Ecol Biogeogr 17(1):59–71. https://doi.org/10.1111/j.1466-8238.2007.00334.x

Kowarik I (2011) Novel urban ecosystems, biodiversity, and conservation. Environ Pollut 159(8):1974–1983. https://doi.org/10.1016/j.envpol.2011.02.022

Kraft NJB, Cornwell WK, Webb CO, Ackerly DD (2007) Trait evolution, community assembly, and the phylogenetic structure of ecological communities. Am Nat 170(2):271–283. https://doi.org/10.1086/519400

La Sorte FA, Lepczyk CA, Aronson MFJ, Goddard MA, Hedblom M, Katti M, MacGregor-Fors I, Mörtberg U, Nilon CH, Warren PS, Williams NSG, Yang J (2018) The phylogenetic and functional diversity of regional breeding bird assemblages is reduced and constricted through urbanization. Divers Distrib 24(2):928–938. https://doi.org/10.1111/ddi.12738

Laliberté E, Legendre P, Shipley B (2014) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0–12. https://CRAN.R-project.org/package=FD. Accessed 27 June 2018

Lepczyk CA, Flather CH, Radeloff VC, Pidgeon AM, Hammer RB, Liu K (2008) Human impacts on regional avian diversity and abundance. Conserv Biol 22(2):405–416. https://doi.org/10.1111/j.1523-1739.2008.00881.x

Lepczyk CA, Aronson MFJ, Evans KL, Goddard MA, Lerman SB, Macivor JS (2017) Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. BioScience 67(9):799–807. https://doi.org/10.1093/biosci/bix079

Lockwood MW, Freeman B (2014) The Texas Ornithological Society Handbook of Texas Birds, 2nd edn. Texas A&M University Press, College Station

Lopes EL, Fernandes AM, Medeiros MCI, Marini MA (2016) A classification scheme for avian diet types. J Field Ornithol 87(3):309–322. https://doi.org/10.1111/jofo.12158

Luther D, Baptista L (2010) Urban noise and the cultural evolution of bird songs. Proc Biol Sci 277(1680):469–473. https://doi.org/10.1098/rspb.2009.1571

MacGregor-Fors I, Escobar-Ibáñez J, Rueda-Hernández R (2017) Concluding remarks: current knowledge and future directions. In: MacGregor-Fors I, Escobar-Ibáñez JF (eds) Avian ecology in Latin American cityscapes. Springer, Cham, pp 159–168

Maddison WP, Slatkin M (1991) Null models for the number of evolutionary steps in a character on a phylogenetic tree. Evolution 45(5):1184–1197. https://doi.org/10.1111/j.1558-5646.1991.tb04385.x

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127(3):247–260. https://doi.org/10.1016/j.biocon.2005.09.005

McKinney ML (2008) Effects of urbanization on species richness: a review of plants and animals. Urban Ecosyst 11(2):161–176. https://doi.org/10.1007/s11252-007-0045-4

Moiron M, González-Lagos C, Slabbekoorn H, Sol D (2015) Singing in the city: high song frequencies are no guarantee for urban success in birds. Behav Ecol 26(3):843–850. https://doi.org/10.1093/beheco/arv026

Ndiribe C, Salamin N, Guisan A (2013) Understanding the concepts of community phylogenetics. Evol Ecol Res 15(8):1–16 http://www.evolutionary-ecology.com/abstracts/v15/2856.html. Accessed 15 July 2018

Nielsen AB, van den Bosch M, Maruthaveeran S, van den Bosch CK (2014) Species richness in urban parks and its drivers: a review of empirical evidence. Urban Ecosyst 17(1):305–327. https://doi.org/10.1007/s11252-013-0316-1

Olden JD, Lockwood JL, Parr CL (2011) Biological invasions and the homogenization of faunas and floras. In: Ladle RJ, Whittaker RJ (eds) Conservation biogeography. Wiley-Blackwell, West Sussex, pp 224–243

Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W (2013) Caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2. https://CRAN.R-project.org/package=caper. Accessed 10 November 2017

Osorio F, Vallejos R (2014) SpatialPack: package for analysis of spatial data. R package version 0.2-3. https://CRAN.R-project.org/package=SpatialPack. Accessed 18 March 2017

Pautasso M (2007) Scale-dependence of the correlation between human population presence and vertebrate and plant species richness. Ecol Lett 10(1):16–24. https://doi.org/10.1111/j.1461-0248.2006.00993.x

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecol Lett 9(6):741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Podani J, Schmera D (2006) On dendrogram-based measures of functional diversity. Oikos 115(1):179–185. https://doi.org/10.1111/j.2006.0030-1299.15048.x

Popescu AA, Huber KT, Paradis E (2012) Ape 3.0: new tools for distance based phylogenetics and evolutionary analysis in R. Bioinformatics 28(11):1536–1537. https://doi.org/10.1093/bioinformatics/bts184

Portnov BA, Paz S (2008) Climate change and urbanization in arid regions. Ann Arid Zone 47(3–4):1–15

R Development Core Team (2017) R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing. http://www.R-project.org. Accessed 10 March 2017

Ralph CJ, Geupel GR, Pyle P, Martin TE, Desante DF (1993) Handbook of field methods for monitoring landbirds. General technical report PSW-GTR-144. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany

Revell LJ (2012) Phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol Evol 3(2):217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Revell LJ (2014) Ancestral character estimation under the threshold model from quantitative genetics. Evolution 68(3):743–759. https://doi.org/10.1111/evo.12300

Rodewald P (ed) (2017) The birds of North America. Cornell Lab of Ornithology, Ithaca https://birdsna.org. Accessed 25 March 2017

Schwarz N, Moretti N, Bugalho MN, Davies ZG, Haase D, Hack J, Hof A, Melero Y, Pett TJ, Knapp S (2017) Understanding biodiversity-ecosystem service relationships in urban areas: a comprehensive literature review. Ecosyst Serv 27:161–171. https://doi.org/10.1016/j.ecoser.2017.08.014

Silva PC, Sepúlveda RD, Barbosa O (2016) Nonrandom filtering effect on birds: species and guilds response to urbanization. Ecol Evol 6(11):3711–3720. https://doi.org/10.1002/ece3.2144

Sims V, Evans KL, Newson SE, Tratalos JA, Gaston KJ (2008) Avian assemblage structure and domestic cat densities in urban environments. Divers Distrib 14(2):387–399. https://doi.org/10.1111/j.1472-4642.2007.00444.x

Sol D, González-Lagos C, Moreira D, Maspons J, Lapiedra O (2014) Urbanization tolerance and the loss of avian diversity. Ecol Lett 17(8):942–950. https://doi.org/10.1111/ele.12297

Sol D, Bartomeus I, González-Lagos C, Pavoine S (2017) Urbanisation and the loss of phylogenetic diversity in birds. Ecol Lett 20(6):721–729. https://doi.org/10.1111/ele.12769

Swenson NG (2011) The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. Am J Bot 98(3):472–480. https://doi.org/10.3732/ajb.1000289

Tuanmu MN, Jetz W (2014) A global 1-km consensus land-cover product for biodiversity and ecosystem modeling. Glob Ecol Biogeogr 23(9):1031–1045. https://doi.org/10.1111/geb.12182

Walker JS, Shochat E (2009) Scalar effects of vegetation on bird communities in an urbanizing desert ecosystem. Urban Ecosyst 13(2):155–167. https://doi.org/10.1007/s11252-009-0112-0

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and community ecology. Annu Rev Ecol Syst 33(1):475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Wiens JA (1989) The ecology of bird assemblages. In: Foundations and patterns, vol 1. Cambridge University Press, Cambridge

Wilkins MR, Seddon N, Safran RJ (2013) Evolutionary divergence in acoustic signals: causes and consequences. Trends Ecol Evol 28(3):156–166. https://doi.org/10.1016/j.tree.2012.10.002