

Title

Urbanization Differentially Affects the Distributions of Two Sympatric Congeners with Similar Ecological Niches

Running Title

Comparison of *Cardinalis* Urban Distributions

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Conflict of Interest

We have no conflicts of interest.

Abstract

Urbanization has altered organisms and ecosystems around the world and will continue to do so into the foreseeable future. Although avian responses to urbanization at the community level have been well characterized, we lack species-level studies examining differences in spatial distributions in response to urbanization. We tested for differences in spatial distributions of two congeneric passerine bird species across an urban ecosystem: northern cardinals (*Cardinalis cardinalis*) and pyrrhuloxia (*Cardinalis sinuatus*), two closely related songbird species that overlap in distribution. We developed and deployed a new method for testing differences in spatial distributions between species using MaxENT, eBird, and structured bird-survey data across two regions: the state of Arizona and across the Tucson metropolitan area. We then investigated potential urban-environmental factors that may similarly or differentially influence spatial distribution of (a) northern cardinal populations in two urban centers in the state (Tucson and Phoenix) and (b) both species in and around Tucson. We found that northern cardinals occur both further north in the state of Arizona and further into the city of Tucson than pyrrhuloxia. We also found that pyrrhuloxia are excluded from urban areas by habitat availability, but that they are positively associated with human development in the areas that they do reside. High-intensity

47 urbanization has limited urban northern cardinal distributions, and their affinity for areas near
48 open water may have facilitated their northward expansion across the state. Species distributions
49 in response to habitat urbanization differ between even closely related species with very similar
50 niches. Further research into the morphological, physiological, behavioral, and evolutionary
51 differences between pyrrhuloxia and northern cardinals in Arizona may reveal the mechanisms
52 that facilitate urban adaptation, expansion, or avoidance of some species but not of others.

53

54 **Key Words (6-10, arranged alphabetically)**

55 Avian, comparative, ecology, MaxENT, niche, spatial, urbanization

Main Text

Introduction

Human activities have rapidly changed natural landscapes throughout the globe over the last two centuries, and these changes continue to exert extreme pressures on free-ranging organisms (Allan et al. 2017, Elhacham et al. 2020, Gerten et al. 2019, Pörtner et al. 2023, Rosenberg et al. 2019, Seto et al. 2012, Watson et al. 2018). Cities contain novel resource distributions, temperature gradients, and ecological communities alongside unique anthropogenic disturbances that are driven by socioeconomic factors like wealth inequities (Chamberlain et al. 2019, Chen et al. 2021, Jenerette 2011, Kinzig et al. 2005, Schell et al. 2020, Sepp et al. 2017, Seress and Liker 2015). Not all species respond similarly to these changes, with some expanding (Clark 2017), contracting (Muñoz et al. 2021), or shifting their ranges (Arnold et al. 2021, Żmihorski et al. 2020) in response to human development.

Urbanization is broadly associated with declines in species richness (Afrifa et al. 2022, Chen et al. 2023, Haight et al. 2023, Hensley et al. 2019, Knapp et al. 2021, Lerman et al. 2021, Sol et al. 2020, Vasquez et al. 2022, Warren et al. 2019), but we lack an understanding of the more fine-scale, species-specific mechanisms underlying these patterns. The majority of comparative work into the effects of urbanization on species distributions is focused largely on comparisons of generalist versus specialist species (Abilhoa et al. 2017, Callaghan et al. 2019 and 2020, Devictor et al. 2007, Luck et al. 2010) or native versus introduced species (Humphrey et al. 2023, Lerman et al. 2020, Mills et al. 1989, Tsang et al. 2019). Comparative genetic, morphological, and behavioral studies have revealed that urbanization can have quite different effects on even closely related species, and those differences can illuminate some of the mechanisms underlying species responses to urbanization (Fusco et al. 2021), e.g. differences in

migration and dispersal rate (Markowski et al. 2021), body size (McNew et al. 2017), and feeding preferences (De León et al. 2018). To our knowledge, no study to date has compared spatial and habitat distributions between species with shared niches and evolutionary histories to test for differences in their responses to urbanization.

Species-distribution models can be constructed by using occurrence data of the species and spatial data of relevant environmental variables across the region of interest (Sillero et al. 2021). The probable spatial distribution of the species based on the association between occurrence and the environmental variables is called either a spatial distribution model (SDM) or an environmental niche model (ENM; see Peterson & Soberón 2012 for a terminology discussion). Contemporary methods for constructing these models include generalized additive models, maximum entropy models, random forest models, regularized regression models, and others, but MaxENT (a maximum entropy modeling approach, Phillips et al. 2004, 2006) is both widely used and among the top-performing spatial-distribution modeling approaches (Valavi et al. 2022). Although MaxENT has often been used to model species ranges under various human activities such as climate change (Nameer 2020), it has only rarely been applied to urban areas (but see Davis et al. 2012, Ito et al. 2020, Préau et al. 2018, Sallam et al. 2017, and Wiese et al. 2019), and never with a specific focus on differences in species distributions across urban areas. Similarly, MaxENT has not commonly been employed to compare species distributions (Espinosa et al. 2018) and has never been used within a hypothesis-testing framework to identify regions where species differ in their predicted occupancies. The software ENMTools implements tests to determine if two species have identical distributions or if they have more similar distributions than would be expected by chance (Warren et al. 2010 and 2021), but no test exists to determine areas of significant difference between species.

Study system

Northern cardinals (*Cardinalis cardinalis*) and pyrrhuloxia (*Cardinalis sinuatus*) are two songbird species (Order Passeriformes: Family Cardinalidae) that are similarly distributed throughout much of the Sonoran Desert in the USA and Mexico and were estimated to have diverged around 6 million years ago (Provost et al. 2018, Barker et al. 2015, Hooper and Price 2017, Jetz et al. 2012, Kaiya Provost pers. comm). The southwestern northern cardinal subspecies (*C. c. igneus*) is a distinct population that is thought to have diverged from the nominate subspecies ~2.4 million years ago (Smith et al. 2011). However, there is not perfect geographic overlap between the two *Cardinalis* species. The range of *C. c. igneus* extends further north than that of *C. sinuatus*, and while both species are observed around the Tucson metropolitan area (pers. obs.), only northern cardinals are commonly seen around the Phoenix metropolitan area, although both are much more sparsely distributed than the eastern USA population of northern cardinals (Halkin et al. 2021). The northern expansion of the eastern U.S. population of northern cardinals, *C. c. cardinalis*, is believed to have only occurred after European colonization as a result of human-driven land-use changes (Halkin et al. 2021). The historic range of northern cardinals in the Sonoran Desert region was possibly much more similar to that of pyrrhuloxia, with water and land use changes driving the northern expansion of this subspecies as well.

In this study, we combined community-science data (eBird; Fuller 2020, Sullivan et al. 2009) and structured survey data (Tucson Bird Count: Turner 2003; Central Arizona Phoenix Long Term Ecological Research Station Bird Survey, Warren et al. 2023) to compare the distributions of northern cardinals and pyrrhuloxia across two regions: the state of Arizona and

across the Tucson metropolitan area. We also investigated the extent to which various biotic, bioclimatic, and socioeconomic environmental factors predicted distributions of both species in Tucson, and in northern cardinals between two cities in Arizona (Tucson and Phoenix). We outline the specific hypotheses and predictions tested in this study in Table 1. To our knowledge, this is the first comparative study of spatial distributions of congeneric species across an urban landscape, and our methods can provide a foundation for future investigations into the mechanisms underlying species responses to human disturbances.

Table 1: Hypotheses and predictions.

<i>Test #</i>	<i>Description</i>
<i>H10.</i>	The two species do not differ in their distributions across an urban environment.
<i>H1A.</i>	Given the pattern that generalist species with broader ecological niches tend to persist in cities better than their specialist counterparts (Warren et al. 2019), we predict that the species that has a broader statewide range (northern cardinals) will also have a broader range in the urban environment compared to their congener (pyrrhuloxia).
<i>H20.</i>	The same environmental variables will predict the distributions of a given species in the Tucson area and across the state of Arizona.
<i>H2A.</i>	Given general, observed/reported differences in the ranges and densities of these birds in urban versus rural environments in Tucson, the environmental variables that predict the distributions of the two species in an urban environment will be different from those across the broader range.

H30. The environmental variables that predict the distributions of northern cardinals will not differ between cities (i.e. Phoenix v. Tucson).

H3A. Given the differences in size, history, growth rates, and human population densities of Phoenix and Tucson, the environmental variables that predict the distributions of northern cardinals will differ between two cities.

Methods

Species Occurrence Data

To determine presence of both bird species across Arizona, we used observational data from the Tucson Bird Count (TBC; 2001-2020, Turner 2003), the Central Arizona Phoenix Long Term Ecological Research Station Bird Survey (CAP LTER; 2000-2020, Warren et al. 2023) and eBird (2017-2021, Sullivan et al. 2009). We used all years available from TBC, and we filtered eBird data to keep only 5 years of data because eBird has increased in popularity over time, and some of the datasets from earlier years may have been more biased by cultural differences in accessibility of eBird (Grade et al. 2022, Perkins 2020). We filtered all datasets to retain observations only during the breeding season, which we conservatively approximated in both species to be April and May (Halkin et al. 2021, Tweit and Thompson 2020, pers. obs.; statewide northern cardinal N = 9488, pyrrhuloxia N = 4139; Tucson northern cardinal N = 1991, pyrrhuloxia N = 1218; Phoenix northern cardinal N = 1119). For maxent analyses, we also filtered to keep only one observation per raster cell (1 km²) of each species (Johnston et al. 2021;

statewide northern cardinal N = 1338, pyrrhuloxia N = 751; Tucson northern cardinal N = 381, pyrrhuloxia N = 335; Phoenix northern cardinal N = 199).

Environmental Data:

As predictors of species distributions, we used the following environmental variables: elevation (United States Geological Survey National Land Cover Database (USGS NLCD) Digital Elevation Model; USGS 2020), 19 bioclimatic variables (WorldClim database, Table S1.1, Fick and Hijmans 2017), tree cover (2016 USGS NLCD Tree Canopy Cover file, Homer et al. 2020; the 2019 USGS NLCD Tree Canopy Cover file is not yet available at the time of these analyses, as of May 10, 2023), percent developed imperviousness (2019 NLCD Percent Developed Imperviousness (CONUS) file, Dewitz and U.S. Geological Survey, 2021), land-cover variables (2019 USGS NLCD, Table S1.2, Dewitz and U.S. Geological Survey, 2021), and Median Household Income by census tract (U.S. Census Bureau 2020). These variables are commonly used in MaxENT models of avian distributions (i.e. Jenkins and Ha 2022).

We prepared and analyzed our data in R Statistical Software (v4.1.0; R Core Team 2021) using the packages ‘dismo’ (Hijmans et al. 2011), ‘raster’ (Hijmans and Van Etten 2012), ‘rgdal’ (Bivand et al. 2015), ‘rgeos’ (Bivand et al. 2017), ‘ENMTools’ (Warren et al. 2010 and 2021), ‘fnn’ (Beygelzimer et al. 2015), and ‘leaflet’ (Graul and Graul 2016).

We split the NLCD file into separate tiff files, each representing 1 of the 20 variables in the NLCD file, excluding the 4 that exclusively pertain to Alaska, 1 that is irrelevant to the low desert (perennial ice/snow), and all 4 variables relating to urban development (Developed, Open Space; Developed, Low Intensity; Developed, Medium Intensity; and Developed, High Intensity). We excluded the urban-development variables because they are categorical

representations of the percent of impervious surfaces in an area, which would be redundant with and less informative than the NLCD Percent Developed Impervious file. The cells in each of the files generated from the NLCD land-cover file represented either the presence of that variable with a 0 value, or the distance from that cell to the nearest cell containing that variable in meters. These represented distance to open water, barren land, deciduous forest, evergreen forest, mixed forest, shrub/scrub, grassland/herbaceous, pasture/hay, cultivated crops, woody wetlands, and emergent herbaceous wetlands.

We reduced the bioclimatic files to raster files representing their second and third principal components across the Arizona region because the original files were highly correlated with each other (Tables S1.3, S1.4, and S1.5). We excluded the first principal component because it was nearly perfectly correlated with the elevation file, and likely just represented variation in climate due to elevation. None of our final files had a final Pearson's correlation coefficient above 0.8 across the state of Arizona or the Tucson and Phoenix regions (Tables S1.6, S1.7, and S1.8).

Prior to analysis, each tiff file was reprojected to the World Geodetic System 84 (WGS 84) coordinate reference system, cropped to the boundaries of the state of Arizona, and resampled across the lowest resolution file, which were the bioclim variables with a 30-arc-second resolution ($\sim 1 \text{ km}^2$). We converted each file to an ASCII file, which is required for input into MaxENT. We then cropped these ASCII files for an analysis across the city of Tucson using the extent of a minimum longitude of -111.183682, a max of -110.720903, a minimum latitude of 32.034553, and a maximum latitude of 32.554540, and across the city of Phoenix using the extent of a minimum longitude of -112.584727, a max of -111.425540, a minimum latitude of 33.089419, and a maximum latitude of 33.885028. These were selected by determining the

boundaries of the urban area from the US Census urban-area spatial file (U.S. Census Bureau 2020).

Analyses:

For the MaxENT analysis of each species across the entire state of Arizona, we randomly selected 10,000 points across the region for use as the background environmental conditions and randomly selected 50% of the observations for training data and used the remaining for model testing (Feng et al. 2017). Our analyses across Tucson and Phoenix used the same methods but only used 2,500 background points. All MaxENT models used the default modeling settings. We replicated these methods using subsets of observational data across the state using only eBird data, across Tucson using only eBird or only TBC data, and across Phoenix using only eBird or only CAP LTER data and we found similar results (data not shown). We only present the model that used the entire available data for observations. This produced our empirical models representing the distributions of northern cardinals and pyrrhuloxia across the state of Arizona and across the city of Tucson, and the distribution of northern cardinals across the city of Phoenix.

We applied three tests of niche similarity, which test the null hypothesis that the two species distributions are randomly sampled from the same distribution of environmental variables and are effectively the same (Graham et al. 2004). We report these as *D*, *I*, and a rank correlation test, which test for significant differences in range of the species, and as *D env*, *I env*, and *rank correlation env*, which test for significant differences in the environmental niche of the species (Warren et al. 2008). These three test statistics have been shown to produce similar

results, but we present the results of all three for consistency and comparability across the literature.

To test where the two species differed in their distributions across the city of Tucson, we removed the species designations associated with each observation in the dataset of raw observations. Then, we randomly assigned each of the observations to one of the two species, keeping the number of total observations for each species equal to the true number of observations of that species. We then ran the MaxENT model using the same parameters as we did for our empirical analysis, and then subtracted the pseudoreplicate model for the spatial distribution of the probability of occurrence of pyrrhuloxia from the pseudoreplicate model for the spatial distribution of the probability of occurrence of northern cardinals. We repeated this process 1,000 times with different random permutations of the data to generate a null distribution of the differences between the distributions of the two species given the number of observations of each species. Finally, we subtracted the empirical model of the distribution of pyrrhuloxia from the empirical model of the distribution of northern cardinals and compared this file to the 1,000 null files. We used a significance level of 0.05, so we considered any cell in the empirical difference file to be significant if it demonstrated an absolute difference between the probabilities of the two species that is greater than 950 of the null models. Every nonsignificant cell was converted to 0, which appears as regions of no difference in the figure. We repeated this process using models across the state of Arizona to identify regions across the state where the two species differ. We visualized the spatial distribution of the significant differences in probability of occurrences of the two species in QGIS (QGIS 2023) and added major interstates to the map for visual reference (U.S. Census Bureau 2021).

We also compared permutation-importance values of the empirical MaxENT models. We used an arbitrary cutoff of a minimum of 5% to determine which variables contributed to the model, and then compared between species and regions to identify factors that differ in determining the distributions of the species.

Finally, to test for differences in the environmental variables associated with the distribution of each species, we extracted values from the raster files of each environmental variable for each observation of either species. We then ran t-tests on each environmental variable to compare for differences between species across the entire state of Arizona and across the Tucson region.

Results

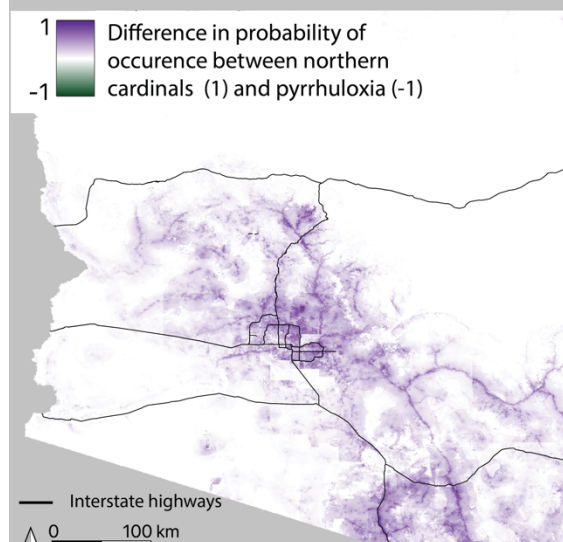
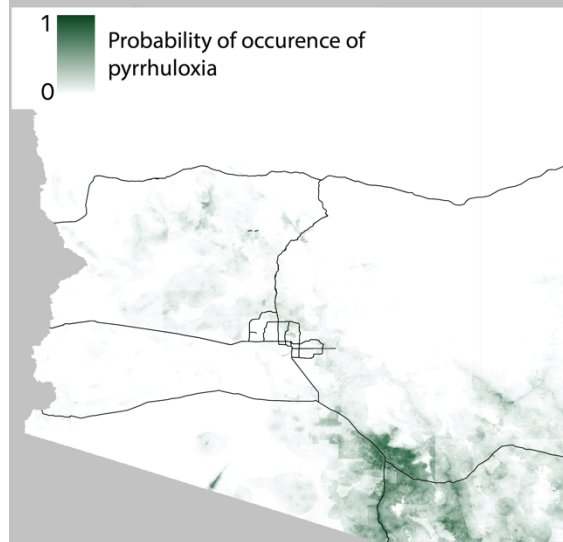
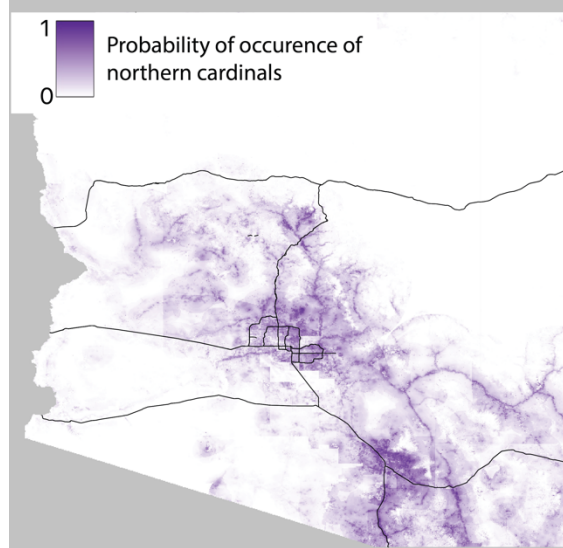
Distributions of pyrrhuloxia and northern cardinals were significantly different across both Tucson and across the state of Arizona in all test statistics except for rank correlation of the Tucson model, which was nearly significant (p -value = 0.05; Table S1.9). Northern cardinals had a higher probability of occurrence in the city of Tucson than pyrrhuloxia and had a higher probability of occurrence than pyrrhuloxia in the regions north of Tucson in the statewide analysis (Fig. 1). However, the environmental niches were not significantly different between the two species in any of the test statistics, although several were nearly significant (Table S1.9).

Figure 1: Predicted probabilities of occurrence of *Cardinalis* species across Tucson and across Arizona

MaxENT models of the predicted probability of occurrence of northern cardinals in purple (top) and pyrrhuloxia in green (center), and the regions of significant difference between the two

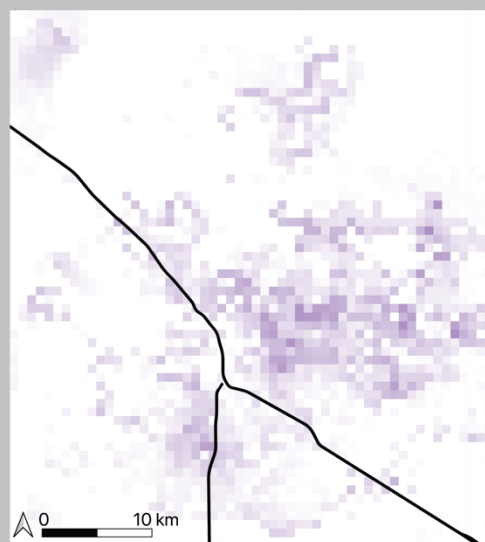
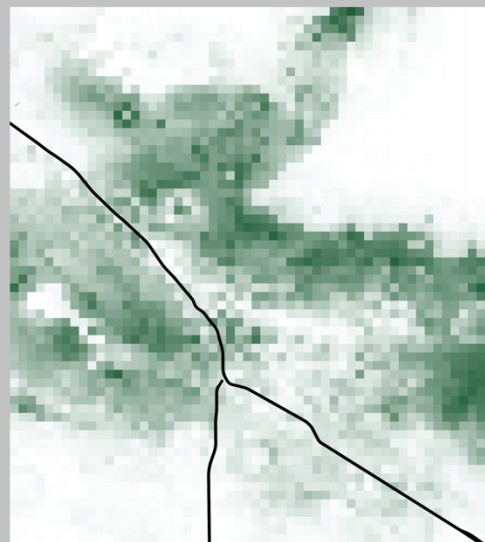
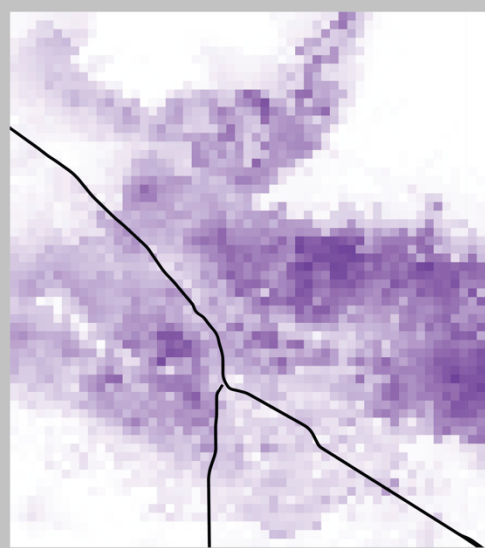
263 (bottom). Models across the Arizona region are on the left column and models across the Tucson
264 region are on the right column. Interstates and major highways are displayed as a spatial
265 reference. Each pixel represents a square kilometer.

Arizona



— Interstate highways
0 100 km

Tucson



0 10 km

Differences between species across Tucson

Five environmental variables contributed to the models both species' distributions across the city of Tucson (Table 2). These were the second and third principal components of the climate variables (northern cardinals: 19.8%, 18%; pyrrhuloxia: 20.1%, 7.3% respectively), elevation (northern cardinals: 5.1%, pyrrhuloxia: 8.7%), distance to evergreen forests (NLCD 42; northern cardinals: 20.9%, pyrrhuloxia: 16.1%), and distance to cultivated crops (NLCD 82; northern cardinals: 7.7%, pyrrhuloxia: 5.9%). None contributed only to the model of northern cardinals, and four contributed only to the model of pyrrhuloxia. They were surface imperviousness (8.3%), distance to barren land (NLCD 31, 7.2%), distance to deciduous forest (NLCD 41, 5.6%), and distance to grassland/herbaceous (NLCD 71, 5.2%).

Table 2: Permutation Importance of Environmental Variables in MaxENT Models

Variables representing the permutation-importance scores for northern cardinals and pyrrhuloxia from each empirical MaxENT model are shown. All units are percentages. Any variable with a permutation-importance score above 5% is considered to have significantly contributed to the model, and significant values are bolded.

	<u>Tucson</u>		<u>Arizona</u>		<u>Phoenix</u>
Variable	Northern Cardinal Permutation importance	Pyrrhuloxia Permutation importance	Northern Cardinal Permutation importance	Pyrrhuloxia Permutation importance	Northern Cardinal Permutation importance
<u>ClimPC2</u>	19.8	20.1	1.3	0.3	1.6
<u>ClimPC3</u>	18	7.3	5.9	35.7	2.6
<u>Elev</u>	5.1	8.7	3.8	0.7	0.5
<u>imperviousness</u>	4.3	8.3	27.6	21.8	23.4
<u>MedianHouseholdIncome</u>	2.7	1.2	4	1.6	4.2
<u>canopy</u>	0.6	0	9.4	5.6	1.1
<u>NLCD 11: Open Water</u>	3.2	4.6	10.3	7.3	15.8

NLCD 31: Barren Land	2.8	7.2	2.2	1.5	2.8
NLCD 41: Deciduous Forest	2.4	5.6	2.7	2.3	5.1
NLCD 42: Evergreen Forest	20.9	16.1	2.6	0.8	11.6
NLCD 52: Shrub/Scrub	2.4	2.5	0	0	4.3
NLCD 71: Grassland/Herbaceous	4.8	5.2	0.8	1.1	11.2
NLCD 81: Pasture/Hay	1.7	2.4	1.1	0.6	2.5
NLCD 82: Cultivated Crops	7.7	5.9	22.4	18.9	10.2
NLCD 90: Woody Wetlands	3.4	5	5.9	1.6	3.1

Across Tucson, northern cardinals were more likely to be observed at areas of greater percent impervious surface and greater percent canopy cover compared to pyrrhuloxia (Table 3). Northern cardinals were also closer to open water, barren land, deciduous forest, evergreen forest, and woody wetlands (NLCD 11, 31, 41, 42, 90), and further from shrub/scrub (NLCD 52) compared to pyrrhuloxia (Table 3).

However, in the response curves of the MaxENT model for Tucson (Fig. S1.1), which depict relationship between each variable in the model and probability of presence of the species, the distribution of pyrrhuloxia was positively related to percent surface imperviousness, whereas the relationship between northern cardinal distribution and impervious surface area increased until 80% imperviousness, then steeply declined. Northern cardinals showed an affinity for proximity to open water, while pyrrhuloxia showed no relationship. Northern cardinals showed a negative relationship with barren land, and pyrrhuloxia showed a positive relationship with it. Northern cardinals showed an affinity for deciduous and evergreen forests, while pyrrhuloxia showed a negative relationship with the former but a positive relationship with the latter. Both species showed complex relationships with woody wetlands.

Table 3: Comparison of Environmental Variable Means for Northern Cardinal vs. Pyrrhuloxia Across Tucson

Means, standard deviations, and results of the t-test for the difference in means between the species are shown for each variable. Elevation is in meters. All units for NLCD files are in meters. Climate temperatures are in Celsius and precipitation values are in millimeters. A p-value of < 0.05 is considered significant, and rows with significant p-values are bolded.

<u>Environmental variable</u>	<u>Northern cardinal mean</u>	<u>Northern cardinal SD</u>	<u>Pyrrhuloxia mean</u>	<u>Pyrrhuloxia SD</u>	<u>T</u>	<u>DF</u>	<u>P</u>
Canopy	0.69	3.47	0.16	1.01	3.55	727	< 0.01
Elevation	826.54	84.23	831.11	81.04	-0.89	1004	0.37
Imperviousness	22.77	25.81	18.72	23.40	-205.85	529	< 0.01
Median Household Income	\$79665.67	\$21707.97	\$80802.45	\$21663.16	-0.85	987	0.40
NLCD 11: Open Water	2585.76	1664.41	2875.35	1767.62	-2.71	954	0.01
NLCD 31: Barren Land	1197.14	997.49	1337.19	1232.12	-1.99	866	0.05
NLCD 41: Deciduous Forest	8782.49	7450.85	10951.92	8083.57	-4.48	942	< 0.01
NLCD 42: Evergreen Forest	6572.56	5870.97	7660.52	6903.74	-2.71	895	0.01
NLCD 52: Shrub/Scrub	87.33	204.22	44.96	118.38	4.24	991	< 0.01
NLCD 71: Grassland/Herbaceous	2731.93	1590.36	2720.45	1634.67	0.12	972	0.91
NLCD 81: Pasture/Hay	12400.45	5715.35	13066.78	5646.68	-1.89	992	0.06
NLCD 82: Cultivated Crops	7445.95	3992.82	7650.06	3902.69	-0.84	997	0.40
NLCD 90: Woody Wetlands	4358.03	2616.70	4673.02	2538.61	-1.97	1000	0.05
Clim 1: Annual Mean Temperature	20.14	0.55	20.10	0.52	1.32	1017	0.19
Clim 2: Mean Diurnal Range	15.35	0.59	15.30	0.63	1.41	953	0.16
Clim 3: Isothermality	45.61	0.83	45.51	0.91	1.81	937	0.07
Clim 4: Temperature Seasonality	733.62	12.47	732.98	11.78	0.85	1011	0.40
Clim 5: Max Temp of Warmest Month	37.30	0.80	37.24	0.76	1.34	1008	0.18
Clim 6: Min Temp of Coldest Month	3.65	0.42	3.63	0.43	0.64	966	0.52
Clim 7: Temperature Annual	33.65	0.82	33.61	0.84	0.93	974	0.35

Range							
Clim 8: Mean Temp of Wettest Quarter	28.68	0.66	28.62	0.61	1.53	1022	0.13
Clim 9: Mean Temp of Driest Quarter	23.43	0.65	23.39	0.60	1.22	1020	0.22
Clim 10: Mean Temp of Warmest Quarter	29.22	0.68	29.15	0.61	1.72	1027	0.09
Clim 11: Mean Temp of Coldest Quarter	11.50	0.46	11.44	0.43	2.01	1011	0.05
Clim 12: Annual Precipitation	338.88	31.53	340.41	29.86	-0.80	1010	0.42
Clim 13: Precipitation of Wettest Month	60.74	4.71	60.95	4.40	-0.73	1016	0.47
Clim 14: Precipitation of Driest Month	5.59	0.64	5.59	0.61	-0.17	1008	0.87
Clim 15: Precipitation Seasonality	60.66	3.15	60.49	3.23	0.90	973	0.37
Clim 16: Precipitation of Wettest Quarter	154.39	12.75	154.68	12.05	-0.38	1011	0.71
Clim 17: Precipitation of Driest Quarter	21.60	2.21	21.61	2.09	-0.04	1011	0.97
Clim 18: Precipitation of Warmest Quarter	125.57	10.69	125.57	10.17	0.00	1009	1.00
Clim 19: Precipitation of Coldest Quarter	85.65	10.42	86.59	10.09	-1.48	1001	0.14

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310 Differences between species across Arizona

311 In species-distribution models across the state of Arizona, five variables contributed to
312 the models of both species (Table 2): the second principal component of the climate variables
313 (northern cardinals: 5.9%, pyrrhuloxia: 35.7%), elevation (northern cardinals: 27.6%,
314 pyrrhuloxia: 21.8%), median household income (northern cardinals: 9.4%, pyrrhuloxia: 5.6%),
315 NLCD 11 (distance to open water; northern cardinals: 10.3%, pyrrhuloxia: 7.3%), and NLCD 82
316 (distance to cultivated crops; northern cardinals: 22.4%, pyrrhuloxia: 18.9%). For the model of
317 northern cardinals, NLCD 90 (distance to woody wetlands) also contributed (5.9%). No variables
318 were significant only for the model of pyrrhuloxia.

Across the state of Arizona, northern cardinals were more likely to be observed at sites of significantly greater surface imperviousness and at lower elevation compared to pyrrhuloxia (Table 4). Northern cardinals were also closer to pasture/hay and woody wetlands, but further from deciduous forest, evergreen forest, shrub/scrub, and cultivated crops, compared to pyrrhuloxia (Table 4).

In response curves output by the MaxENT model for Arizona, the two species followed very similar trends for all variables except for the third principal component of the climate variables, for which northern cardinals had a positive relationship and pyrrhuloxia had a complicated but negatively trending relationship (Fig. S1.2).

For climate variables across Arizona (Table 4), compared to pyrrhuloxia, northern cardinals were found at higher Mean Diurnal Range (Clim 2), Temperature Seasonality (Clim 4), Max Temperature of Warmest Month (Clim 5), Temperature Annual Range (Clim 7), Mean Temperature of Warmest Quarter (Clim 10), Precipitation of Driest Quarter (Clim 17), and Precipitation of Coldest Quarter (Clim 19) (Clim 2, 4, 5, 7, 10, 17, 19). Northern cardinals were found at lower Isothermality (Clim 3), Mean Temperature of Wettest Quarter (Clim 8), Precipitation of Wettest Month (Clim 13), Precipitation Seasonality (Clim 15), and Precipitation of Warmest Quarter (Clim 18).

Table 4: Comparison of Environmental Variable Means for Northern Cardinal vs. Pyrrhuloxia Across Arizona

Means, standard deviations, and results of the t-test for the difference in means between the species are shown for each variable. Elevation is in meters. All units for NLDC files are in

341 meters. Climate temperatures are in Celsius and precipitation values are in millimeters. A p-
 342 value of < 0.05 is considered significant, and rows with significant p-values are bolded.

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<u>Environmental variable</u>	<u>Northern cardinal mean</u>	<u>Northern cardinal SD</u>	<u>Pyrrhuloxia mean</u>	<u>Pyrrhuloxia SD</u>	<u>T</u>	<u>DF</u>	<u>P</u>
Canopy	1.10	4.15	0.79	3.95	1.95	2129	0.05
Elevation	934.16	294.09	1008.02	278.77	-6.69	2135	< 0.01
Imperviousness	14.55	22.91	11.66	20.56	3.48	2239	< 0.01
Median Household Income	\$68947.52	\$27263.93	\$69803.92	\$23140.01	-0.90	2346	0.37
NLCD 11: Open Water	2943.13	2896.10	3071.06	2527.69	-1.24	2293	0.22
NLCD 31: Barren Land	3205.36	3753.89	2961.45	3584.97	1.72	2121	0.09
NLCD 41: Deciduous Forest	18475.40	22291.06	10610.19	13780.84	11.94	2858	< 0.01
NLCD 42: Evergreen Forest	7527.39	9341.36	6468.55	7794.03	3.26	2379	0.01
NLCD 52: Shrub/Scrub	67.72	153.58	39.46	94.87	6.15	2859	< 0.01
NLCD 71: Grassland/Herbaceous	1792.84	1642.24	1836.66	1859.83	-0.63	1830	0.53
NLCD 81: Pasture/Hay	10850.86	8794.86	12422.67	8553.75	-4.69	2087	< 0.01
NLCD 82: Cultivated Crops	8392.41	7861.74	7942.76	6408.66	1.67	2424	0.01
NLCD 90: Woody Wetlands	3231.30	3261.02	4470.37	3716.73	-8.94	1820	< 0.01
Clim 1: Annual Mean Temperature	18.91	1.99	18.82	1.77	1.37	2259	0.17
Clim 2: Mean Diurnal Range	16.40	1.30	16.24	1.37	3.02	1950	< 0.01
Clim 3: Isothermality	46.83	2.65	47.36	2.46	-5.40	2177	< 0.01
Clim 4: Temperature Seasonality	733.63	46.77	714.27	34.30	12.78	2619	< 0.01
Clim 5: Max Temp of Warmest Month	37.04	2.21	36.34	1.86	9.05	2360	< 0.01
Clim 6: Min Temp of Coldest Month	2.03	2.05	2.09	1.93	-0.79	2144	0.43
Clim 7: Temperature Annual Range	35.01	1.87	34.25	1.51	11.92	2438	< 0.01
Clim 8: Mean Temp of Wettest Quarter	24.63	6.01	26.87	2.64	-14.05	2881	< 0.01
Clim 9: Mean Temp of	21.10	2.17	22.03	1.85	-0.40	2334	0.69

Driest Quarter							
Clim 10: Mean Temp of Warmest Quarter	28.03	2.27	27.66	2.07	4.46	2206	< 0.01
Clim 11: Mean Temp of Coldest Quarter	10.28	1.85	10.36	1.56	-1.33	2353	0.19
Clim 12: Annual Precipitation	376.10	76.07	373.24	64.39	1.07	2352	0.29
Clim 13: Precipitation of Wettest Month	69.06	23.27	76.20	21.63	-8.28	2172	< 0.01
Clim 14: Precipitation of Driest Month	5.44	1.47	5.45	0.90	-0.15	2861	0.88
Clim 15: Precipitation Seasonality	61.57	14.34	68.91	11.42	-15.13	2468	< 0.01
Clim 16: Precipitation of Wettest Quarter	169.27	49.80	185.04	44.74	-8.73	2236	< 0.01
Clim 17: Precipitation of Driest Quarter	25.57	8.43	23.43	4.21	9.17	2940	< 0.01
Clim 18: Precipitation of Warmest Quarter	137.06	46.55	153.33	40.70	-9.79	2289	< 0.01
Clim 19: Precipitation of Coldest Quarter	96.64	22.85	88.31	15.50	11.70	2744	< 0.01

Differences between northern cardinals in Tucson versus Phoenix

In comparisons of the models of northern cardinal distributions between the cities of Tucson and Phoenix (Table 2, Figs. 1, S1.3), two environmental variables – distance to evergreen forests (20.9% and 11.6% respectively) and to cultivated crops (7.7% and 10.2% respectively) – contributed to the models across both cities. Four additional environmental variables contributed to the Phoenix model of northern cardinals but not to the Tucson model: surface imperviousness (23.4%), distance from open water (NLCD 11, 15.8%), from deciduous forest (NLCD 41, 5.1%), and from grassland/herbaceous (NLCD 71, 11.2%). Three variables only contributed to the models in Tucson: climate PC2 (19.8%), climate PC3 (18%), and elevation (5.1%).

In response curves output by the MaxENT model for each city, the distribution of northern cardinals differed in many variables between Tucson and Phoenix, but had similar

response curves for percent surface imperviousness, and distances to barren land, deciduous forest, and evergreen forest (Fig. S1.3).

Thirty of the thirty-two environmental variables associated with the distribution of northern cardinals differed significantly between the cities of Tucson and Phoenix (Table S1.10); the only ones that did not differ were surface imperviousness and distance from shrub/scrub (NLCD 52).

Discussion

We demonstrated that two closely related cardinal species do not have significantly different environmental niches, but that they differ in their probability of occurrence in both the highly urbanized center of Tucson and across the recently developed northern extent of Arizona. Northern cardinals have a broader range of occurrence than pyrrhuloxia in both regions. However, we also present evidence that pyrrhuloxia may be excluded from the urban center due to other environmental variables besides urbanization alone. Our findings further demonstrate that urbanization has similar effects on the same species in different cities (northern cardinals in both Tucson and Phoenix) but has different effects on even closely related species in the same city (pyrrhuloxia and northern cardinals in Tucson), and that fine-scale species differences underlie the ability of a species to persist in urban areas. Our work emphasizes the need for species-specific studies to inform urban planning, specifically suggesting that urban residents and planners can reduce the negative impacts of human development on cardinal species by integrating a mixture of native canopy cover, shrub/scrub, and open ecosystems into the urban landscape. We also demonstrate that the impacts of human land-use extend beyond urbanization.

Are responses to urbanization similar between closely related species?

We found that effects of urbanization were similar within a species in different cities, but not between closely related species within the same city. Though neither species were present in the highest regions of surface imperviousness, northern cardinals were more likely to be observed in Tucson in areas with more impervious surface than were pyrrhuloxia. Interestingly pyrrhuloxia had a positive relationship with percent surface imperviousness in the MaxENT model response curves from Tucson. Pyrrhuloxia also seem to be choosier in their habitat selection, since more variables are important in explaining the likelihood of presence of pyrrhuloxia in the Tucson area compared to northern cardinals. This suggests that pyrrhuloxia may be excluded from the city of Tucson by other environmental factors besides surface imperviousness, such as natural habitat availability (e.g. shrub/scrub and open habitat, Gould 1960), but that they may have an affinity for human development that occurs within their fundamental niche. Other studies of avian community structure have found differences in urban occupancies of closely related species (e.g. Davis et al. 2012, Leveau et al. 2017), which suggests that species level differences may underlie urban community structures in many contexts. Our results emphasize that the effects of human development differ between even closely related species, with mid-to-high intensity urbanization having a greater impact on northern cardinals and low-intensity human development and resource management along the suburban outskirts shaping the distribution of pyrrhuloxia, but with both species being largely impacted by habitat availability. Much of our understanding of avian responses to urbanization comes from only a few species (Fidino and Magel 2017), and our findings here demonstrate the need for species specific investigations to uncover the factors underlying species responses to urbanization. Further studies into the morphological, physiological, and genetic mechanisms that allow

northern cardinals to persist in regions of higher urbanization than pyrrhuloxia will provide important clarity into the stressors affecting these species in Tucson.

Are responses to urbanization similar between the same species (northern cardinals) in different cities?

Despite differences in every other climate and land-use variable aside from canopy cover and distance from shrub/scrub, northern cardinals demonstrated a consistent response to urbanization in both Phoenix and Tucson. The consistency of the relationship between this species with canopy and shrub/scrub variables highlights the importance of these aspects of their environment to their persistence. These findings align with previous fieldwork that found northern cardinals require both open habitat and dense foliage within their nesting territories (Gould 1960). However, comparative studies of urban assemblages between cities in the southwestern U.S. found that overall avian communities differ between urban sites in cities (Hensley et al. 2019). Differences in percent impervious surface between cities may explain this seeming contradiction, since despite maintaining a similar association with urbanization between sites, the model of northern cardinal distribution found more regions that excluded northern cardinals in the urban center of Phoenix than the Tucson model found (Figures 1, S4). Our findings show that this species retains specific habitat needs across climate conditions that could be addressed with land use management plans along mid-to-high intensity urban areas that create interconnected patches of open space with dense foliage throughout the urban landscape. Several studies have found parallel responses in genetic variation to urbanization across multiple cities within the same species (Mueller et al. 2013, Mueller et al. 2020, Salmón et al. 2021, Winchell et al. 2023), and we show that spatial distributions are also consistently affected by urbanization.

What drives differences in species responses to urbanization?

We found differences between these species in their associations with land-cover variables in the city, and these differences affected the responses of these species to urbanization. Northern cardinals were found closer to open water and at higher levels of both impervious surface and canopy cover. The distribution of open water in the state of Arizona is heavily engineered, especially in urban areas, with irrigation systems, dams, and man-made lakes creating a novel pattern of water availability for the native wildlife (Colby and Jacobs 2007), and city planning in the desert creates novel matrixes of canopy coverage, with some sparse regions and some very dense regions (Nelson et al. 2021). This suggests that underlying differences in preferences for canopy density may allow northern cardinals to persist in the city, but not pyrrhuloxia, who demonstrate a greater affinity for shrub/scrub than northern cardinals (Gould 1960). Our work here expands upon previous findings in Phoenix that show effects of landscaping on avian communities (Warren et al. 2019), and we demonstrate the role of species differences in shaping urban wildlife communities. Urban planning and landscaping that better integrate native shrub/scrub ecologies into the city may help reduce the exclusionary effects of urbanization on pyrrhuloxia. Our findings echo those from other systems that have found effects of various urban planning strategies on avian community structure (Benitez et al. 2021), but we emphasize the importance of understanding species specific associations with ecological variables within each urban area.

Our findings also illuminate climatic differences in ecological niches that might allow for differences in statewide distributions of these two species. Twelve climate variables differed between the species across the state of Arizona. Northern cardinals were found in areas with

higher fluctuations in temperature at the daily, seasonal, and annual scales and with greater precipitation in the driest and coldest parts of the year. In contrast, pyrrhuloxia were found in areas with more precipitation in the wettest month and warmest quarter, which is the summer monsoon season. Pyrrhuloxia are also found in areas with higher mean temperatures during the wettest quarter, but northern cardinals were found in areas with higher mean temperature of the warmest quarter and maximum temperature of the warmest month. Although climate played an important role in shaping northern cardinal and pyrrhuloxia distributions at both citywide and statewide models, no climate variables differed significantly between observations of the two species across the city of Tucson. The overall combination of climatic factors may therefore be more deterministic for the occupancy of an area by either one of these species and could be highly influenced by the climates of regions they historically occupied. For instance, evidence from several desert species show the effects of Pleistocene environmental processes on contemporary patterns of genetic variation (Provost et al. 2022), and our methods in this study did not integrate historical climate data associated with these species. It is also possible that the two species depend on plants that are sensitive to different climatic phenologies, although no differential ecological specializations have yet been identified. Plant communities in Arizona are rapidly changing in response to climate change (Brusca et al. 2013) and if *Cardinalis* species show differences in associations with particular plants, this could explain differences in species responses both in urban areas and across the state.

Human impacts beyond urbanization

Only one land-use variable influenced the models of both species in all analyses: proximity to cultivated crops. This suggests that human land use beyond just city development

plays a large role in shaping contemporary species distributions. Many studies of the effects of urbanization on avian wildlife compare populations along an urban to rural gradient, but our findings contribute to a growing body of evidence that suggest that rural land use changes may affect species alongside urbanization (e.g. Kumar and Kaur Kler 2021, Lazarina et al. 2020). Much of the research on cropland has focused on its effects on grassland species, which are often declining due to habitat loss (Pool et al. 2014, Scholtz et al. 2017). However, much like urbanization, croplands also facilitates range expansion of some species, with evidence of species differences within families (Veech et al. 2010), and further research into the complex effects of anthropogenic land use changes on avian community dynamics is needed at multiple scales beyond urbanization.

In the model of the entire Arizona region, three additional variables associated with human-influenced land use changes affected the distribution of both species: surface imperviousness, canopy cover, and proximity to open water. Proximity to open water also significantly contributed to the model of northern cardinal distribution across Phoenix, but not across Tucson, which further supports the notion that open water, and therefore the human engineering of it, is increasingly important for northern cardinals along the northern extent of their range in the state of Arizona. This aligns with evidence that riverways have historically been important for the ranges of northern cardinals (Smith et al. 2011). And the distribution of cultivated crops shapes much of the open space in areas along the outskirts of human development and within the habitats of these species. However, these variables also affected pyrrhuloxia distributions across Arizona, and observation locations of the two species only differed significantly from each other in their means of distance to cultivated crops, with pyrrhuloxia found closer to croplands than northern cardinals. This suggests that land-use change

resulting from human activities underlies contemporary distributions of both species, leaving open questions about how and why northern cardinals have experienced a northward range expansion but not pyrrhuloxia. We did not differentiate between types of cropland, and crop diversity affects avian diversity in agricultural regions (Katuwal et al. 2022, Marcacci et al. 2021). Cropland management strategies could be differentially affecting these species. The difference in the response curves of the species to the climate variables, and only to climate variables, across the state of Arizona suggests that differences in the fundamental climate niches of the two species may have permitted northern cardinals but not pyrrhuloxia to expand their range in response to human development.

Summary

In conclusion, we demonstrate a novel method using permutations of species observations and MaxENT models to test for differences in the spatial distributions of species with similar niches. We found significant differences in urban occupancy between two congeneric species that share very similar ecological niches, and we also identify several anthropogenic and ecological variables associated with these distributional differences. The finding that environmental predictors of urban occupancy differ between northern cardinals and pyrrhuloxia in Arizona suggests that species differences in nesting and territory habitats have permitted northern cardinals to better adapt to areas of high human disturbance compared to pyrrhuloxia and highlights fertile ground for future comparative urban research. Our work emphasizes the importance of comparative studies in urban ecology as a method of understanding mechanisms underlying differences in species responses to human disturbances.

518 **Conflict of Interest**

519 The authors declare no conflicts of interest.

520

521 **Data Availability**

522 All data are made available on Dryad at (link to come). The scripts used to run these analyses are
523 available on github at: https://github.com/dannyjackson/Spatial_Github

524

525 **Biosketches**

526 Danny Jackson researches the effects of urbanization on the spatial ecology, morphology,
527 physiology, and genetic variation of native species. This work represents a component of their
528 dissertation research at Arizona State University.

529

530 Kevin McGraw studies urban impacts on phenotypic variation – including coloration, disease,
531 and behavior – in birds.

532

533 **Author Contributions**

534 Danny Jackson led the development and implementation of this project and wrote the paper.

535 Kevin McGraw edited the paper and provided valuable feedback and advice throughout the
536 design and execution of the research.

537

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