

# The role of climate change and niche shifts in divergent range dynamics of a sister-species pair

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## Abstract

Species ranges are set by limitations in factors including climate tolerances, habitat use, and dispersal abilities. Understanding the factors governing species range dynamics remains a challenge that is ever more important in our rapidly changing world. Species ranges can shift if environmental changes affect available habitat, or if the niche or habitat connectivity of a species changes. We tested how changes in habitat availability, niche, or habitat connectivity could contribute to divergent range dynamics in a sister-species pair. The highly behaviorally flexible great-tailed grackle (*Quiscalus mexicanus*) has expanded its range northward from Texas to Nebraska in the past 40 years, while its closest relative, the boat-tailed grackle (*Quiscalus major*), has remained tied to the coasts of the Atlantic Ocean and the Gulf of Mexico. We created species distribution and connectivity models trained on citizen science data from 1970-1979 and 2010-2019 to determine how the availability of habitat, the types of habitat occupied, and range-wide connectivity have changed for both species. We found that the two species occupy distinct habitats and that the great-tailed grackle has shifted to occupy a larger breadth of urban, arid environments farther from natural water sources. Meanwhile, the boat-tailed grackle has remained limited to warm, wet, coastal environments. We found no evidence that changes in habitat connectivity affected the ranges of either species. Overall, our results suggest that the great-tailed grackle has shifted its realized niche as part of its rapid range expansion, while the range dynamics of the boat-tailed grackle may be shaped more by climate change. The expansion in habitats occupied by the great-tailed grackle is consistent with observations that species with high behavioral flexibility can rapidly expand their geographic range by using human-altered habitat. This investigation identifies how opposite responses to anthropogenic change could drive divergent range dynamics, elucidating the factors that have and will continue to shape species ranges.

## Introduction

Species ranges determine the patterns of biodiversity across the world, shaping the environments different species encounter and the other species they can interact with (Gaston, 1996; 2003; Holt, 2003). We are still determining how abiotic and biotic factors limit species ranges (Buckley et al., 2018; Sirén & Morelli, 2020; Paquette & Hargreaves, 2021) and to what degree a species is able to expand to new habitats (Holt, 2003; Ralston et al., 2016). Within the limits that determine species ranges, many animal species today are experiencing massive declines due to loss of habitat (IUCN 2021). These declines have been linked to limitations in the ability of many species to change their realized niche, the range of habitats that these species occupy, despite movement to new geographic areas or environmental change (Holt & Gains, 1992; Wiens et al., 2010; Liu et al., 2020). The realized niche of a species is the result of environmental limitations

39 due to physiology and behavior, geographic limitations due to dispersal, and ecological limitations due to  
40 interspecific interactions. Together, these three limitations determine species ranges (Soberón et al., 2009).  
41 However, some species can change their realized niche through occupying novel environmental conditions, a  
42 process referred to as a niche shift (Guisan et al., 2014; Broennimann et al., 2007; Hill et al., 2017; Sherpa  
43 et al., 2019), potentially allowing them to expand their ranges while other species cannot (Holt & Gains,  
44 1992; Holt, 2003; Wiens et al., 2010). The factors that allow some species to shift their niche have remained  
45 difficult to identify (Wiens et al., 2010).

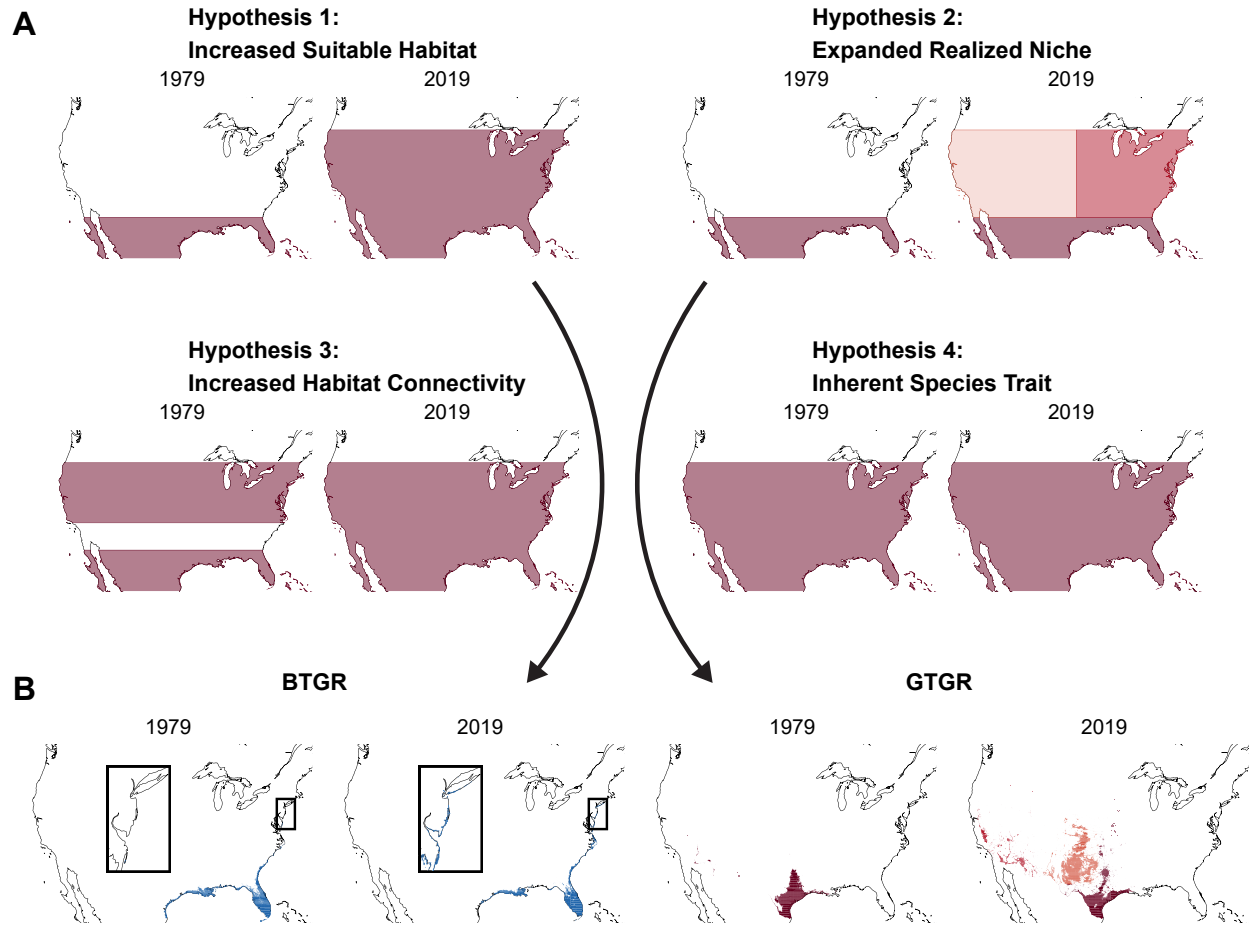
46 A species expanding into new areas is assumed to have overcome some of the trade-offs or limitations that  
47 shape a species' realized niche. Niche shifts can occur via physiological or behavioral changes, as well as  
48 interactions between these factors (Wiens et al. 2010). Physiological changes reflect evolutionary changes in  
49 the phenotypes of individuals, such as changes in body size or metabolic processes, through which individuals  
50 of a species can occupy different niches (Buckley et al., 2018). Such physiological changes often occur over  
51 longer time spans (Swanson & Garland, 2009), suggesting that fast expansions into new niches are presumably  
52 facilitated by already existing plasticity in physiological tolerances. One potential cause of niche shifts over  
53 shorter time spans is behavioral flexibility, the ability to change behavior when circumstances change (see  
54 Mikhalevich et al., 2017 for theoretical background on our flexibility definition) (Chow et al., 2016; Griffin  
55 & Guez, 2014; e.g., Lefebvre et al., 1997; Sol et al., 2002; 2005; 2007; Sol & Lefebvre, 2000). This idea  
56 predicts that flexibility, exploration, and innovation facilitate the expansion of individuals into completely  
57 new areas and that the role of these characteristics diminishes after a certain number of generations (Wright  
58 et al., 2010). Experimental studies have shown that latent abilities are primarily expressed in a time of need  
59 (Auersperg et al., 2012; Bird & Emery, 2009; Laumer et al., 2018; Manrique & Call, 2011; e.g., Taylor et  
60 al., 2007). Therefore, we do not expect the founding individuals who initially dispersed out of their original  
61 range to have unique behavioral characteristics that are passed on to their offspring. Instead, the actual  
62 act of continuing a range expansion likely relies on flexibility, exploration, innovation, and persistence, and  
63 thus these behaviors should therefore be expressed more on the edge of the expansion range where there  
64 have not been many generations to accumulate relevant knowledge about the environment. There is also  
65 evidence that some species can behaviorally shift their niche in response to anthropogenic climate change or  
66 can expand their range by using human altered environments (Wong & Candolin, 2015; Wolff et al., 2020).  
67 Human-modified environments are increasing (Goldewijk, 2001; e.g., Liu et al., 2020; Wu et al., 2011), and  
68 species associated with these habitats show differences in their behavior (Chejanovski et al., 2017; e.g., Ciani,  
69 1986; Federspiel et al., 2017).

70 However, range dynamics are also influenced by factors beyond changes in the realized niche: environmental  
71 change leading to a recent increase in the amount of available habitat representing the current niche can facil-  
72 itate a geographic range expansion (Hanski & Gilpin, 1991; Wiens, 1997), and change in habitat connectivity  
73 can alter species range limits (Holt, 2003; Platts et al., 2019). A species may not need to be behaviorally  
74 flexible to move into new areas if it can continue to use the same habitats within its expanded range. For  
75 example, a species may expand its range because changes in climate have caused more geographic areas to  
76 fall within its niche or if previously isolated habitat patches become connected. Thus, it is important to  
77 identify how changes in the availability of habitats, the usage of different habitats, and habitat connectivity  
78 contribute to range shifts to understand whether niche shifts are truly happening and to identify potential  
79 causes of range shifts.

80 Here we investigated the drivers of different range dynamics in two closely related grackle species, the  
81 great-tailed grackle (*Quiscalus mexicanus*) and boat-tailed grackle (*Quiscalus major*). These species offer  
82 an opportunity for simultaneous investigation of the roles of behavior and increased habitat availability in  
83 a rapidly increasing geographic range expansion. The great-tailed grackle has rapidly expanded its range  
84 northward over the course of the 20th century (Post et al., 1996; Wehtje, 2003), moving its northern range  
85 edge from Southern Texas to Nebraska (Fig 1B). In contrast, the boat-tailed grackle range has remained  
86 largely the same, with only minor changes to the northern edge of its range (Wehtje, 2003), despite both  
87 species having similar foraging habits and successfully using human-altered environments (Selander & Giller,  
88 1961; Post et al., 1996; Johnson & Peer, 2020). Detailed reports on the breeding ecology of these two species  
89 indicate that range expansion in the boat-tailed grackle but not the great-tailed grackle may be constrained  
90 by the availability of suitable nesting sites (Selander & Giller, 1961; Wehtje, 2003). Boat-tailed grackles  
91 may be limited by the need for coastal marshes or isolated groves near water for nesting sites (Post et al.,

92 1996), while great-tailed grackles can nest in agricultural lands, marshes, and urban areas with vegetation  
93 and surface water (Johnson & Peer, 2020). Great-tailed grackles inhabit a wide variety of habitats (but  
94 not forests) at a variety of elevations (0-2134m), while remaining near water bodies. Boat-tailed grackles  
95 exist mainly in coastal areas (Selander & Giller, 1961). There is also evidence that great-tailed grackles  
96 have preferred different habitats over time and across their range. Ornithologists have recorded great-tailed  
97 grackles breeding primarily in natural and human-made wetlands, while those within the recently expanded  
98 range readily breed in urban parks (Wehtje, 2003). However, this apparent difference in niche has yet to be  
99 rigorously quantified.

100 The range expansion in the great-tailed grackle and range stability in the boat-tailed grackle could be  
101 due to differences in realized niche change between these two closely related species. We characterized  
102 the historic (1970-1979) and current (2010-2019) realized niches of the great-tailed grackle and the boat-  
103 tailed grackle using species distribution models (SDMs) to test three hypotheses on the causes of range  
104 expansion in the great-tailed grackle and range stability in the boat-tailed grackle (Fig 1A). **Hypothesis 1:**  
105 **change in habitat availability:** The great-tailed grackle and the boat-tailed grackle use different habitats,  
106 and the suitable habitat of the great-tailed grackle, but not that of the boat-tailed grackle, has increased  
107 northward over the past few decades. We define habitat suitability in this paper as the predicted habitat  
108 suitability for occupancy by the focal species, habitat that is within the limits of tolerability of the climate  
109 and environmental factors as determined by the areas occupied by individuals of the species at a given time.  
110 Support for this hypothesis would indicate that the availability of habitat due to environmental change,  
111 not inherent species differences, explains why the great-tailed grackle has rapidly expanded its range while  
112 the boat-tailed grackle has not. **Hypothesis 2: change in realized niche:** Over the past few decades,  
113 the great-tailed grackle has expanded its realized niche, whereas the boat-tailed grackle continues to use  
114 the same limited habitat types. In other words, a niche shift, possibly due to changes in behavioral traits,  
115 facilitated the geographic range expansion of the great-tailed grackle. **Hypothesis 3: changes in habitat**  
116 **connectivity:** Species distribution models generally do not account for additional factors such as dispersal  
117 limitations due to landscape heterogeneity when estimating suitable habitat. Therefore, we conducted a  
118 separate analysis to examine possible changes in connected habitat due to environmental change. Support  
119 for this hypothesis would indicate that environmental change has facilitated the range expansion of the  
120 great-tailed grackle. **Hypothesis 4: inherent species trait(s):** Other species traits, such as demographic  
121 dynamics or dispersal physiology, limited the historic species range, resulting in no apparent environmental  
122 difference between the newly occupied and historically occupied ranges. Given this hypothesis, there are  
123 no changes in habitat availability, but both species have suitable but unoccupied habitat available to them.  
124 Only the great-tailed grackle is able to occupy additional habitat due to changes in the other traits or  
125 conditions that previously limited the species range. This hypothesis would support the hypothesis that the  
126 original behavior of the great-tailed grackle was already well adapted to facilitate a range expansion while  
127 the behavior of the boat-tailed grackle restricts it to its current range.

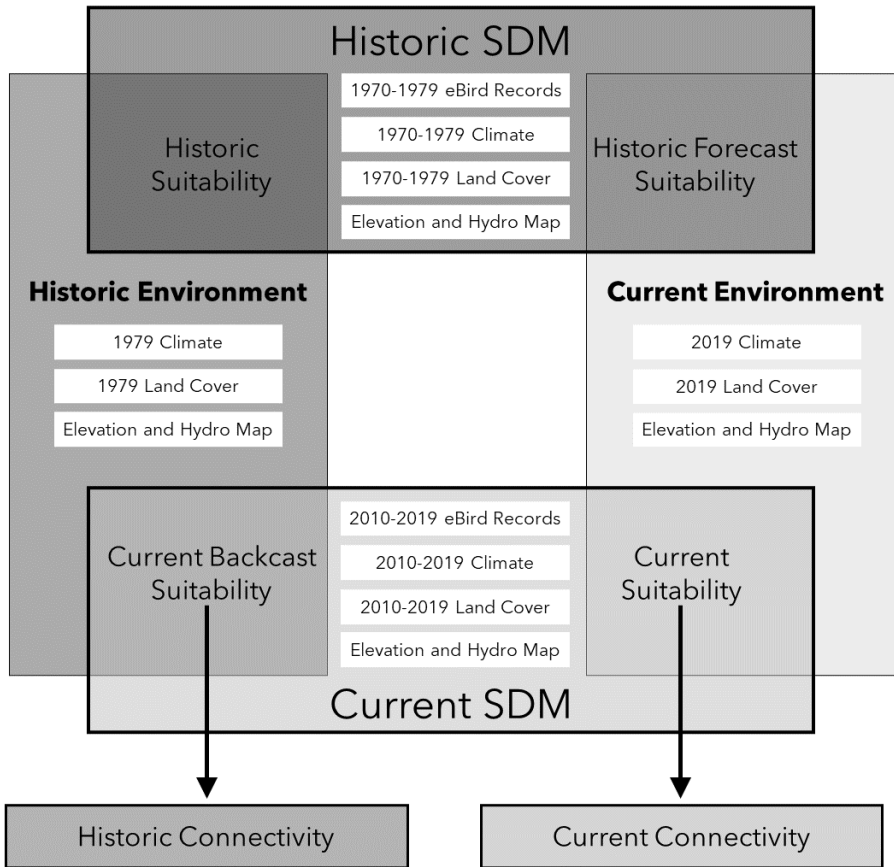


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129 **Figure 1.** Comparison between the predicted patterns depending on the forces that facilitated range expansion and habitat  
 130 suitability predicted by the species distribution models (SDMs) for the great-tailed grackle (GTGR) and boat-tailed grackle  
 131 (BTGR). (A) The pairs of plots display the predictions for the historic and current models if increased suitable habitat  
 132 (Hypothesis 1), expanded realized niche (Hypothesis 2), increased habitat connectivity (Hypothesis 3), or other inherent species  
 133 trait(s) (Hypothesis 4) drove range expansion. (B) The suitable habitat predictions for the historic and current models based on  
 134 environmental data from 1979 and 2019. We used the maximum-sensitivity-specificity thresholds for each model (great-tailed  
 135 grackle current: 0.4440, boat-tailed grackle current: 0.4780, great-tailed grackle historic: 0.4635, boat-tailed grackle historic:  
 136 0.3935) to assign habitat as suitable. The different colors in the great-tailed grackle map indicate that some environmental  
 137 conditions within its 2019 expanded range were not found in its 1979 range. The arrows connect the species ranges to the most  
 138 supported predicted range dynamics.

139 We used ecological niche modeling to examine temporal habitat changes over these past four decades using  
 140 observation data for both grackle species from existing citizen science databases. We determined the change  
 141 in habitat availability using predictions produced by both our current and historic models for each species  
 142 based on environmental data from 1979 and 2019 (Fig 2, Analysis 1). We also tested the ability of our current  
 143 and historic models to predict species presence and absence using data from the opposite time period to  
 144 validate the predicted changes in suitable habitat (Torres et al., 2015; Regos et al., 2018; Yates et al., 2018)  
 145 (Analysis 1). Together, the components of Analysis 1 address our Hypothesis 1 that environmental change  
 146 could have led to the range dynamics seen in both species. Then, we compared how the importance and  
 147 effect of environmental predictors (Analysis 2) and occupied environments changed between our current and  
 148 historic models (Analysis 3). Analyses 2 and 3 both address our Hypothesis 2, that changes in the types  
 149 of habitat occupied could have led to the observed range dynamics. Finally, we used a circuit theory-based  
 150 connectivity model to test for changes in habitat connectivity between 1979 and 2019 (Analysis 4), which

151 addresses our Hypothesis 3, that changes in habitat connectivity caused by environmental change could have  
 152 led to the observed range dynamics. In combination, our analyses allowed us to investigate whether the range  
 153 of the great-tailed grackle, but not the boat-tailed grackle, might have increased due to an increase in habitat  
 154 availability, expansion of the realized niche of the great-tailed grackle, or changes in habitat connectivity.



155  
 156 **Figure 2.** Overview of modeling approach and steps. The white boxes list the data used to generate the species distribution  
 157 models (SDMs) and environments used for predicting habitat suitability. The overlap between shaded boxes indicates that a  
 158 habitat suitability prediction was created using the overlapping species distribution model and environmental predictors. The  
 159 arrows indicate the habitat suitability predictions used to create the connectivity models (see Methods for a detailed description  
 160 of data sources and steps).

## 161 Methods

162 This article is the first of three articles that will be produced from a preregistration (<http://corinalogan.com/Preregistrations/gxpopbehaviorhabitat.html>) that passed pre-study peer review at Peer Community in  
 163 Ecology in 2020. The hypotheses, predictions, and methods in this manuscript come from the preregistration,  
 164 and we detail all changes to the methods below.

### 166 Preregistered Analysis Plan

167 *Response Variable:* Presence/absence of great-tailed grackles and boat-tailed grackles

### 168 Explanatory Variables

- 169 1. **Land cover** (e.g., forest, urban, arable land, pastureland, wetlands, marine coastal, grassland, man-  
 170 grove) - we chose these land cover types because they represent the habitat types in which both species

171 exist, as well as habitat types (e.g., forest) they are not expected to exist in (Selander & Giller, 1961). If  
172 the suitable and unsuitable habitat of the great-tailed grackle agrees with these expectations, it is pos-  
173 sible that large forested areas are barriers for the range expansion of one or both species. We planned to  
174 download global land cover type data from MODIS (16 terrestrial habitat types) and/or the IUCN habi-  
175 tat classification (47 terrestrial habitat types). The IUCN has assigned habitat classifications for the  
176 great-tailed grackle (<https://www.iucnredlist.org/species/22724308/132174807#habitat-ecology>) and  
177 the boat-tailed grackle (<https://www.iucnredlist.org/species/22724311/94859792#habitat-ecology>);  
178 however, these classifications appear to be out of date, and we updated them for the purposes of this  
179 project.

180 • **Further details:** We limited our study extent to the contiguous United States, which should  
181 not affect our investigation of distribution changes because the entire range of the boat-tailed  
182 grackle and the northern expanding edge of the great-tailed grackle range are both within the  
183 contiguous United States. We verified this assumption by comparing species distribution models  
184 using 2010-2019 observations and MODIS land cover data with and without the limited spatial  
185 extent. Restricting the training data to the contiguous United States caused no drop in the AUC  
186 when predicting habitat suitability within the US relative to the unrestricted model.

187 • **Deviations from the preregistered plan:** We used the National Land Cover Database (NLCD)  
188 and historical land cover modeling data from Sohl et al., 2016 instead of MODIS for our land  
189 cover dataset because the former datasets have a greater temporal range. MODIS data exists for a  
190 continuous period of 2001-present, and could only be extended to 1993 using compatible data from  
191 the Global Land Cover Characterization (GLCC) land cover dataset. Using MODIS data would  
192 require limiting the temporal range of our study to 1993-present, yet the most rapid period of the  
193 great-tailed grackle expansion occurred from 1967-1977 (Wehtje, 2003). We initially proposed to  
194 use data from 1968-1970 for our historical model, and data from 2018 for our present-day model.  
195 Instead, we used land cover projections from Sohl et al., 2016 for our historical land cover data  
196 (1970-1979) and the NLCD (2011, 2013, 2016; and 2019) for our modern land cover data, which  
197 allowed us to model species distributions closer to our proposed temporal range. Both datasets  
198 use a modified version of the Anderson Land Classification System (Hardy & Anderson, 1973),  
199 share the same geographic extent, and are high resolution (250m and 30m, respectively). The  
200 land cover classification system includes classes for forests, urban areas, pasture and crop lands,  
201 wetlands, and grasslands.

202 2. **Elevation** - Selander & Giller (1961) notes the elevation range for the great-tailed grackle (0-2134m),  
203 but not the boat-tailed grackle, therefore establishing that the current elevation ranges for both species  
204 may allow us to determine whether and which mountain ranges present range expansion challenges. We  
205 obtained elevation data from the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010;  
206 Danielson & Gesch, 2011) available through USGS.

207 3. **Climate** (e.g., daily/annual temperature range) - the great-tailed grackle was originally from the  
208 tropics (Wehtje, 2003), which generally have a narrow daily and annual climate range, and now exists in  
209 temperate regions, which have much larger climate ranges. Accordingly, the daily/annual temperature  
210 range could allow us to determine the role of potential climatic limits in explaining ranges and range  
211 changes for both species. If there are limits, climate conditions could inform the difference between the  
212 range expansion rates of the two species. We considered the 19 bioclimatic variables from WorldClim.

213 • **Further details:** We converted monthly climate data for each time period from WorldClim  
214 (Fick & Hijmans, 2017) into the set of 19 climate variables included in the BioClim dataset  
215 using the *biovars* function from the *dismo* package in R (Hijmans et al., 2017). We tested the  
216 19 BioClim variables across the ranges of both species for collinearity using the *vifcor* function  
217 from the *usdm* package in R (Naimi et al., 2014) with a correlation threshold of 0.7. For highly  
218 correlated variables, we excluded the variable with the greater variable inflation factor. Our final  
219 dataset included 7 climate variables: mean diurnal temperature range, maximum temperature of  
220 the warmest month, mean temperature of the wettest quarter, precipitation of the wettest month,  
221 precipitation of the driest month, and precipitation of the coldest quarter.

222 4. **Presence/absence of water in the cell for each point** - both species are considered to be highly  
223 associated with water (e.g., Selander & Giller, 1961), therefore we identified how far from water each  
224 species can exist to determine whether it is a limiting factor in the range expansion of one or both  
225 species. We had planned to use data from USGS National Hydrography.

226 • **Further details:** We separated the coastlines and bodies of freshwater due to the associations  
227 the boat-tailed grackle has with salt water (Post et al., 1996) and the great-tailed grackle has  
228 with freshwater (Selander & Giller, 1961).

229 • **Deviations from the preregistered plan:** We used the river, lake, and coastline shapefiles  
230 from the Natural Earth database (<http://www.naturalearthdata.com/>) as the basis for water  
231 bodies instead of the USGS National Hydrography database. The USGS National Hydrography  
232 database does not differentiate between minor and major bodies of water, resulting in near-  
233 complete coverage of the contiguous US map with bodies of water. The Natural Earth database  
234 incorporates data on rivers and lakes from the North American Environmental Atlas at a 1:10  
235 million scale. The lower resolution data allowed for the computation of distances between the  
236 more than 1 million sample points and all water bodies. Natural Earth shapefiles have also been  
237 used in other SDMs to calculate distances to water bodies (Mi et al., 2017).

238 5. **Connectivity:** We planned to use connectivity as the distance between points on the northern edge  
239 of the range to the nearest uninhabited suitable habitat patch to the north in 1970 compared with  
240 the same patches in ~2018. We identified the northern edge of the distribution based on reports  
241 on eBird.org from 1968-1970, which resulted in recordings of great-tailed grackles in 48 patches and  
242 recordings of boat-tailed grackles in 30 patches. For these patches, we calculated the connectivity (the  
243 least cost path) to the nearest uninhabited suitable habitat patch in 1970 and again in ~2018. Given  
244 that great-tailed grackles are not found in forests or beyond certain elevations (Selander & Giller,  
245 1961), large forests and high elevation geographic features could block or slow the expansion of one or  
246 both species into these areas and their surroundings. For each point, we planned to calculate the least  
247 cost path between it and the nearest location with grackle presence using the `leastcostpath` R package  
248 (Lewis, 2022). This approach would allow us to determine the costs involved in a grackle's decision to  
249 fly around or over a mountain range/forest. We would define the forest and mountain ranges from the  
250 land cover and/or elevation maps.

251 • **Deviations from the preregistered plan:** We did not include connectivity as an explanatory  
252 variable within our SDMs because we used a method for calculating connectivity that was de-  
253 pendent on the output of our SDMs. We quantified changes in connectivity using `Circuitscape`  
254 version 4.0.5 (Anatharaman et al., 2020), a method that uses electrical circuit theory, treating  
255 a landscape as an electrical circuit with different landscape features offering different levels of  
256 resistance. We created our resistance surfaces using the results of our SDMs, which is a common  
257 practice when experimental data on species movement through a landscape is not available (Beier  
258 et al., 2011; Justen et al., 2021; de Sousa Miranda et al., 2021). See the Analysis 4 section below  
259 for more details on our connectivity models.

## 260 Species Distribution Models

261 One model, including all explanatory variables, was run for the great-tailed grackle and a separate model  
262 was run for the boat-tailed grackle. We planned to use the program `MaxEnt` (Phillips et al., 2008) to create  
263 the species distribution models. `MaxEnt` is a maximum entropy based software that compares environments  
264 between species presence and a set of background points to estimate habitat suitability (Phillips et al., 2008).  
265 For the explanatory variables, `MaxEnt` produces a continuous prediction of habitat suitability for each grid  
266 cell (0 is least suitable and 1 is most suitable). We planned to use `MaxEnt` followed by jackknifing procedures  
267 to evaluate the relative contribution/importance of different environmental variables to the probability of  
268 species occurrence. We planned to optimize the model by trying different regularization coefficient values,  
269 which controls how much additional terms are penalized (`MaxEnt`'s way of protecting against overfitting),  
270 and choosing the value that maximizes model fit. Most `MaxEnt` papers use cross-validation and the area  
271 under the curve (AUC) to evaluate model performance, and we planned to do the same.

272 For all models we fit, we selected one presence and one absence from a 2.5 km hexagonal grid per week  
273 to geographically subsample the data and reduce imbalance in observation effort. We then separated the  
274 subsampled checklists into a set to train our model (80% of checklists) and a set for model validation (20%  
275 of checklists). We used a balanced random forest approach, in which absence points are selected at an  
276 equal frequency as presence points, thus addressing the imbalance in the ratio of presence and absence  
277 points (Strimas-Mackey et al., 2020). Random forests are machine learning algorithms that generate a large  
278 number of classification trees based on different subsets of the given data (Evans et al., 2011). Once all trees  
279 are generated, the average result is taken and used as the final classification method, which determines which  
280 environmental factors differentiate species presences from species absences. We accounted for stochasticity  
281 in the geographic subsampling, dataset separation, and balanced random forest processes by repeating model  
282 creation 10 times independently for each time period and species. We used the ranger package in R to create  
283 each model (Wright & Ziegler, 2017).

284 We predicted habitat suitability across the contiguous United States using environmental data from 1979  
285 and 2019. We produced three types of predictions (contemporary predictions, forecasts, and backcasts)  
286 depending on whether the time period of the SDM matched the time period of the environmental data (Fig  
287 2). When the time periods matched, we produced contemporary predictions (e.g., predictions using the  
288 historic great-tailed grackle model with the 1979 environmental data). The predictions we made using the  
289 historic models and the 2019 environmental data were forecast predictions, and the predictions we made  
290 using the current model and the 1979 environmental data were backcast predictions. To standardize the  
291 predicted suitabilities, we set all effort covariates to the same values within the models of each species. We  
292 set the day of the year to April 1st, the observation time to maximize the encounter rate for each species (5  
293 AM for the boat-tailed grackle and 6 AM for the great-tailed grackle, based on most common observation  
294 times), observation duration to one hour, distance traveled to one km, and the number of observers to one.  
295 We present the average habitat suitability predicted by the 10 replicates of each model.

296 • **Deviations from the preregistered plan:** We used a random forest model to estimate habitat  
297 suitability in place of Maxent due to the advantages offered by using presence-absence data instead  
298 of presence-background data. Presence-background data can only determine the habitat suitability  
299 of points relative to the background environment (Guillera-Arroita et al., 2014), thus the results of  
300 presence-background models such as Maxent cannot be compared between different environments due  
301 to the difference in backgrounds. This limitation of presence-background models makes them a poor fit  
302 for comparing range shifts over long periods of time (Sofaer et al., 2018). In contrast, presence-absence  
303 data allows relative likelihood to be proportional to the probability of occurrence so long as the sampling  
304 process is included within the model through effort covariates (Guillera-Arroita et al., 2015). Random  
305 forest models incorporate absence points and are similarly robust to limited sample sizes and against  
306 overfitting as are Maxent models (Elith & Graham, 2009; Evans et al., 2011; Mi et al 2017; Norberg  
307 et al., 2019). Random forest models have also been used to fit species distribution models based on  
308 citizen science data (Robinson et al., 2020), including in the best practices for eBird data (Strimas-  
309 Mackey et al., 2016). Johnston et al. (2021) directly compared Maxent and random forest models  
310 using eBird data and found that the random forest model that included effort covariates performed  
311 the best in terms of the AUC and Cohen’s Kappa. Cohen’s Kappa is a chance-corrected measurement  
312 of agreement between groups made by a classification system and a set of samples classified into real  
313 values (Titus et al., 1984). We fit species distribution models based on the 2010-2019 data for the  
314 great-tailed grackle and the boat-tailed grackle using both random forest and Maxent and found that  
315 the random forest model outperformed the Maxent model based on AUC and kappa for both species.  
316 The data preparation methods have remained the same, and the models still output a continuous  
317 habitat suitability metric between 0 and 1 for each grid cell.

## 318 Analysis instructions

- 319 1. Download and preprocess eBird data. Conduct spatial filtering to account for sampling bias
- 320 2. Clean the species occurrence data: remove any uncertain records or geographic outliers



- 321 3. Import climactic variables from WorldClim and landscape data from MODIS and crop to region of  
322 interest
- 323 4. Match environmental data to grackle occurrence records
- 324 5. Fit models with maxent to get predicted distributions and estimate importance/contribution of each  
325 environmental variable

326 We referred to Strimas-Mackey et al., (2020) best practices for using eBird data when extracting data on  
327 grackle presence in a region from eBird.org. We planned to gather environmental data from databases,  
328 including a database that maps global urban change from 1985-2015 to a high (30 m) resolution (Liu et al.,  
329 2020). We used a variety of R packages, including auk (Strimas-Mackey et al., 2018), dismo (Hijmans et  
330 al., 2017), raster (Hijmans, 2020), maptools (Bivand & Lewin-Koh, 2019), tidyverse (Wickham et al., 2019),  
331 rgdal (Bivand et al., 2019), rJava (Urbanek, 2020), and elevatr (Hollister & Tarak Shah, 2017).

332 We used the R package auk (Strimas-Mackey et al., 2018) to download and process occurrence records for  
333 both the great-tailed grackle and the boat-tailed grackle from the citizen science project eBird (Sullivan  
334 et al., 2014), matching our preregistered analysis plan. We included only complete checklists to allow us  
335 to infer non-detections (Johnston et al., 2021). We filtered the selected checklists to only include those  
336 less than 5 hours long, less than 5 km in length, and with fewer than 10 observers, in accordance with  
337 recommendations from Strimas-Mackey et al. (2020). We also excluded presence points outside the current  
338 known range for either species (Johnson & Peer, 2020; Post et al., 1996). We kept all checklists within  
339 600 km of the remaining presence points to restrict our datasets to areas near the species ranges while  
340 including a wide area of environmental conditions. We also included information on the year of observation,  
341 day of the year, time of observation, distance traveled, observation duration, and number of observers as  
342 effort covariates for use in our SDMs. In total, we included 8,163 historic and 8,606,111 current great-tailed  
343 grackle checklists (with 502 and 519,082 great-tailed grackle observations, respectively) and 6,940 historic  
344 and 7,211,101 current boat-tailed grackle checklists (with 467 and 304,028 boat-tailed grackle observations,  
345 respectively). All species observation locations can be found in Supplementary Figure S1.

- 346 • **Deviations from preregistered plan:** For our historic models, we used checklists from 1970-1979,  
347 and for the current models we used checklists from 2010-2019 (eBird Basic Dataset, Jan 2021) instead  
348 of 1960 and 2018, respectively. The temporal ranges for our dataset were selected for both sufficient  
349 sample size and overlap with the period of maximum great-tailed grackle range expansion (Wehtje,  
350 2003). To determine the minimum number of samples needed to make our present and historical models  
351 comparable, we created species distribution models using subsamples of the 2010-2019 eBird dataset  
352 with different numbers of positive observations. We found that retaining  $\geq 300$  observations allowed  
353 our models to have a  $\Delta\text{AUC}$  of less than 0.1. Using this limit, we set the temporal range for our  
354 historical model to 1970-1979 because this range had  $> 300$  observations of both species and precedes  
355 the most rapid period of great-tailed grackle range expansion. We also limited our spatial extent to  
356 the contiguous United States to ensure consistent coverage of historic and current environmental data.

357 **Analysis 1: habitat availability:** Has the available habitat for both species increased over time? We fit  
358 species distribution models for both species in 1970 and in 2018 and determined for each variable, the range  
359 in which grackles were present (we define this area as the habitat suitability for each species). We then  
360 planned to take these variables and identify which locations in the Americas fall within the grackle-suitable  
361 ranges in 1970 and in 2018. We would then be able to compare the maps (1970 and 2018) to determine  
362 whether the amount of suitable habitat has increased or decreased. If we would be able to find data for these  
363 variables before 1970 across the Americas, we would additionally run models using the oldest available data  
364 to estimate the range of suitable habitat earlier in the great-tailed grackle range expansion period.

- 365 • **Final analysis:** We used the discrimination ability of our SDMs as metrics for how accurately our  
366 models predict grackle-suitable habitat and whether one model could be used to predict suitable habitat  
367 in both the historic and current time periods for each species. We tested discrimination ability using

368 the 20% of data excluded from the training set of each model. We measured Cohen’s Kappa and  
369 AUC for each model. We also used these metrics to quantify model transferability, the ability of a  
370 model to perform accurately using datasets independent of the training dataset. Model transferability  
371 has been used to measure the consistency of habitat associations over time (Torres et al., 2015; Wu  
372 et al., 2016; Regos et al., 2018). Low transferability would indicate that the backcast or forecast  
373 suitability predictions do not accurately represent the species range and that the relationship between  
374 occurrence probability and environmental predictors has changed. We used the 20% excluded from  
375 the opposite time period (1970-1979 for the current backcast and 2010-2019 for the historic forecast)  
376 model to test the transferability of our models over time. We also compared the geographic extents of  
377 suitable habitat based on the historic and current models for both species to determine whether the  
378 models agree on the range dynamics for their species (Fig 2). We used the sensitivity-specificity-sum-  
379 maximum threshold (Liu et al., 2005) to classify suitable habitat. We applied the suitability threshold  
380 to the contemporary prediction maps and the backcast/forecast prediction maps to generate predicted  
381 suitable habitat ranges in 1979 and 2019. We then mapped changes in habitat suitability classifications  
382 to determine the range dynamics predicted by each model.

- 383 • **Deviations from the preregistered plan:** We predicted habitat suitability in 1979 and 2019 instead  
384 of 1970 and 2018 to line up with the most recent years within our historic and current datasets.

385 **Analysis 2: habitat associations:** Does the range of variables that characterize suitable habitat for the  
386 great-tailed grackle differ from that of the boat-tailed grackle? We fit species distribution models for both  
387 species in 2018 to identify the variables that characterize suitable habitat. We planned to examine the raw  
388 distributions of these variables from known grackle occurrence points or extract information on how the  
389 predicted probability of grackle presence changes across the ranges for each habitat variable. The habitat  
390 variables for each species would be visualized in a figure that shows the ranges of each variable and how  
391 much the ranges of the variables overlap between the two species or not.

- 392 • **Final analysis:** To determine changes in habitat associations over time, we quantified the importance  
393 of each environmental predictor using the Gini index and calculated the partial dependence of each  
394 model to the environmental predictors. The Gini index quantifies the classification information gained  
395 when a predictor was included in our random forests, with more informative predictors receiving greater  
396 values (Strimas-Mackey et al., 2020). We calculated partial dependence by averaging the predicted  
397 habitat suitability across 1000 randomly selected checklists in which one predictor was set to 1 of 25  
398 evenly spaced values across its observed range. We repeated the partial dependence calculation across  
399 all 25 values to create a partial dependence curve for every predictor. To compare partial dependence  
400 across predictors, we subtracted all partial dependence values by the minimum habitat suitability for  
401 each curve to obtain the marginal effect of each predictor.
- 402 • **Deviations from the preregistered plan:** We did not compare the distribution of environmental  
403 values at observation points. Instead, we used predictor importance and the partial dependence of  
404 habitat suitability on each predictor because they are more informative metrics of habitat breadth.  
405 Predictor importance and the partial dependence of habitat suitability on each predictor take into  
406 account differences in sampling effort across geographic areas and predictor covariation. Comparing  
407 the distribution of environmental values at observation points would not have accounted for these  
408 confounding effects and would not take full advantage of the information available through our SDMs.

409 **Analysis 3: habitat occupancy:** Have the habitats occupied by both species changed over time? We  
410 planned to count the number of different land cover categories each species is or was present in during 1970  
411 and 2018. To determine whether land cover influences their distributions, we would calculate how much  
412 area in the Americas is in each land cover category, which would then indicate how much habitat is suitable  
413 (based solely on land cover) for each species.

- 414 • **Final analysis:** We compared the proportion of observations located on each land cover class in  
415 addition to the number of different land cover classes that each species was observed on. Changes in

416 the number of land cover classes either species was observed on would indicate that the species occupies  
417 novel habitat.

418 We also performed a niche overlap test using the *ecospat.niche.similarity.test* function within the R package  
419 *ecospat* (Broennimann et al., 2022). This function compares the environmental space occupied by the ob-  
420 served points for a species across two different time periods to determine if the differences in the environments  
421 that the species are found in across these ranges are significant when compared to a null space generated  
422 by simulations that randomly reassign observations to either time range. We generated the environmental  
423 space using a principal component analysis of the environmental predictors found at species occurrence points  
424 within both the historic and current time periods. We used the two principal components that explained the  
425 largest proportion of variation to create the environmental space because the *ecospat.niche.similarity.test*  
426 function is limited to two dimensions. We binned the first two principal components to create a 100x100  
427 grid of environmental predictor values, and we used 100 simulations to create our null expectations. Our  
428 two ranges were the historic and current datasets, and we ran the niche overlap test independently for each  
429 species. We quantified the niche overlap using Warren’s I (Warren et al., 2008, Broennimann et al., 2012),  
430 a commonly used metric of niche overlap that is calculated using the difference in the occupancy rate of  
431 grid cells within the environmental space (frequency of occurrences within each grid cell normalized by the  
432 frequency of observations). Lower values of Warren’s I indicate greater differences in the environmental  
433 space occupied by the species than expected by chance if the habitat usage for the species is the same across  
434 both time ranges. We used Warren’s I instead of the more common Schoener’s D statistic, which Warren’s  
435 I is modified from, due to disagreements between these statistics in cases where the ranges compared are  
436 drastically different in size (Rödder & Engler, 2011). The historic and current range sizes for the great-tailed  
437 grackle differ greatly and could result in the Schoener’s D statistic underestimating niche overlap within the  
438 simulations that form the null expectation we compare the observed overlap to. We used direct observations  
439 of each species, also known as ordinations, for our niche overlap test instead of the predicted suitability values  
440 from our SDMs because ordination-based tests more accurately quantify niche overlap (Guisan et al., 2014).  
441 The niche overlap test excludes areas of niche space that were not sampled within one of the two ranges to  
442 avoid non-analogous comparisons.

- 443 • **Deviations from the preregistered plan:** We compared species observations from 1970-1979 and  
444 2010-2019 instead of only using observations from 1970 and 2018 to use all available data. We also  
445 performed a niche overlap test to compare the observed differences in the environments of the historic  
446 and current ranges for each species to a null expectation. Significant differences between the observed  
447 habitat occupancy changes and the null expectation indicate that our focal species are occupying  
448 different habitats over time.

449 **Analysis 4: habitat connectivity:** Has habitat connectivity for both species increased over time? If the  
450 connectivity distances are smaller in 2018, this would indicate that habitat connectivity has increased over  
451 time. We planned to calculate the least cost path from the northern edge to the nearest suitable habitat  
452 patch. To compare the distances between 1970 and 2018, and between the two species, we would run two  
453 models where both have the distance as the response variable and a random effect of location to match  
454 the location points over time. The explanatory variable for model 1 would be the year (1970, 2018), and  
455 for model 2 the species (great-tailed grackle, boat-tailed grackle). If we were be able to find data for these  
456 variables before 1970 across the Americas, we would additionally run models using the oldest available data  
457 to estimate the range of connected habitat earlier in their range expansion.

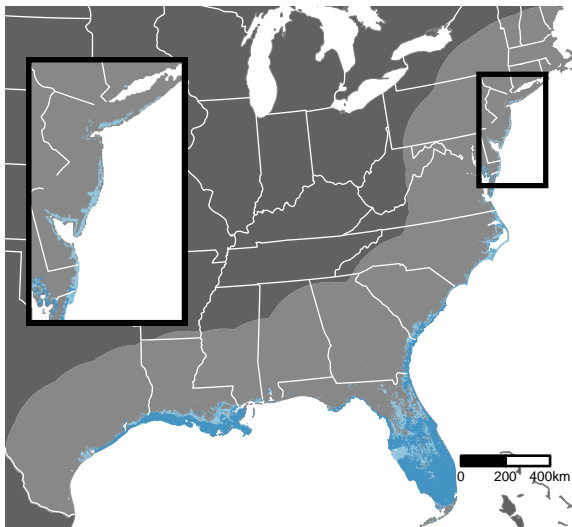
- 458 • **Final analysis:** We used Circuitscape version 4.0.5 (Anatharaman et al., 2020) to determine whether  
459 changes in access to habitat due to connectivity caused by environmental change could explain range  
460 shifts in the boat-tailed grackle or the great-tailed grackle. Circuitscape uses electrical circuit theory,  
461 treating a landscape as an electrical circuit with different landscape features offering different levels of  
462 resistance. We created our resistance surfaces using the results of our current SDMs, which is a common  
463 practice when experimental data on species movement through a landscape is not available (Beier et  
464 al., 2011; Justen et al., 2021; de Sousa Miranda et al., 2021). Because we used the current SDMs

465 to create our resistance surfaces, our models tested whether environmental change has connected or  
466 isolated areas of suitable habitat given the current realized niche of the species. We converted habitat  
467 suitability to resistance using a negative exponential function because this function performs well for  
468 avian species (Trainor et al., 2012). Our final resistance surface had values ranging from 1 to 100,  
469 with 1 as the minimum resistance value. To calculate connectivity across the entire species range,  
470 we used a method that does not require *a priori* selection of habitat patches. This method uses  
471 randomly selected points, called nodes, as the locations where current enters and exits the resistance  
472 surface (Koen et al., 2014). Connectivity is measured as the current that travels through each cell  
473 when moving between these nodes. Current is elevated near the node locations, so we created a buffer  
474 surrounding the ranges for each species and selected random points from the perimeter of this buffer for  
475 our nodes in Circuitscape (Koen et al., 2014). The elevated connectivity values adjacent to the nodes  
476 thus existed outside of the species range, allowing the connectivity values within the species range  
477 to remain constant regardless of the location of the randomly selected nodes. The buffer removed  
478 the correlation between node location and connectivity values within the checklist ranges, resulting  
479 in connectivity values that were only dependent on the resistance map. We used a buffer that was  
480 600 km removed from the edge of the checklist ranges and used 18 randomly selected nodes. We then  
481 simulated current between each node using the pairwise function in Circuitscape and used the summed  
482 accumulated current as our metric of connectivity. We defined regions within the 75th percentile of  
483 the accumulated current values as high connectivity areas because the rank of suitability values, rather  
484 than the magnitude of suitability values, are the most transferable feature of SDMs (Guillera-Arroita  
485 et al., 2015). We chose the 75th percentile as our threshold based on Bonnin et al., (2020).

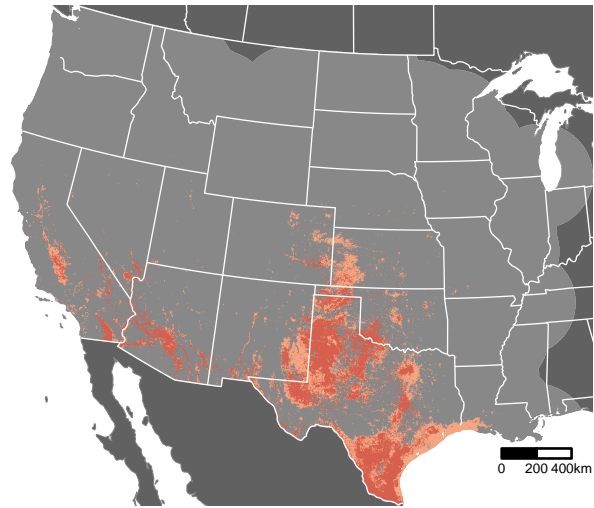
- 486 • **Deviations from the preregistered plan:** We did not calculate the least cost path between habitat  
487 patches because we did not have experimental data on species movement nor did we have a priori suit-  
488 able habitat patches for either species. We used Circuitscape 4.0.5 instead to quantify the accumulated  
489 current as a measure of ease of movement through the landscape.

## Results

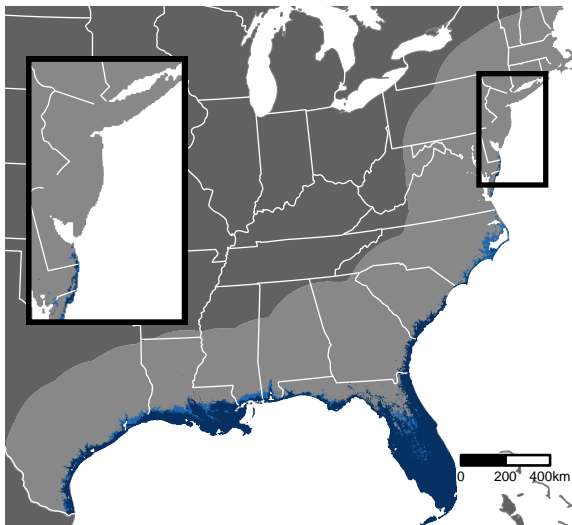
### A. BTGR Current Prediction



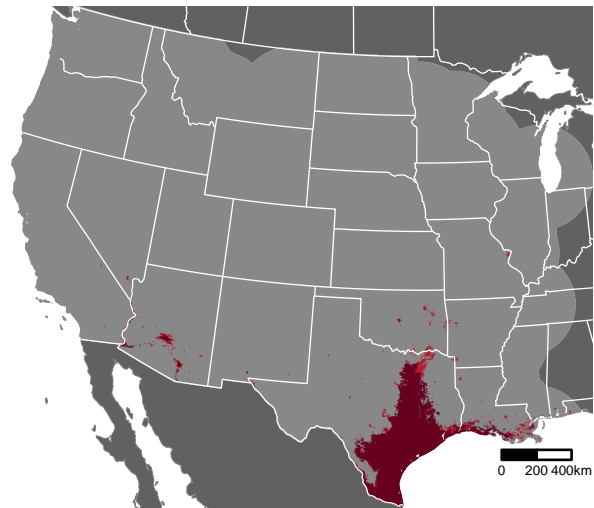
### GTGR Current Prediction



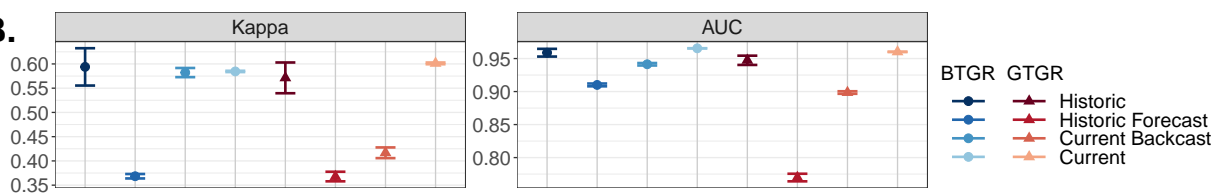
### BTGR Historic Prediction



### GTGR Historic Prediction



### B.



491

492 **Figure 3.** Predicted suitability maps and discrimination ability of SDMs. (A) Maps display areas where predicted suitability  
 493 is greater than the maximum-sensitivity-specificity thresholds for each model [great-tailed grackle (GTGR) current: 0.4440,  
 494 boat-tailed grackle (BTGR) current: 0.4780, great-tailed grackle (GTGR) historic: 0.4635, boat-tailed grackle (BTGR) historic:  
 495 0.3935]. Darker shaded regions are predictions made using the historic environment (historic and current backcast) and lighter  
 496 regions are predictions made using the current environment (historic forecast and current). The northern edge of the boat-tailed  
 497 grackle range is expanded in a map insert for clarity. Overall, the areas of lighter color indicate changes in habitat availability

498 from 1979-2019, as predicted by each model. (B) The ability of each model to predict the presence or absence of boat-tailed  
499 grackles (blues) or great-tailed grackles (reds) using Cohen’s kappa (agreement between presence or absence classification for  
500 model and true presence or absence) and AUC (area under the sensitivity-specificity curve). The models were tested using  
501 either test data excluded from the training data set (historic and current predictions) or test data from the opposing temporal  
502 period (backcast and forecast predictions). Error bars signify one standard deviation in the values across 10 replicates. The high  
503 values of the boat-tailed grackle historic, current backcast, and current, and the great-tailed grackle historic and current models  
504 indicate that these models are accurate, while the lower values of the boat-tailed grackle Historic Forecast and the great-tailed  
505 grackle historic forecast and current backcast models indicate that the boat-tailed grackle historic and the great-tailed grackle  
506 historic and current models have poor transferability.

## 507 Hypothesis 1: Habitat Availability

508 We compared how habitat availability has changed for the boat-tailed grackle and the great-tailed grackle  
509 by predicting habitat suitability across each species range using environmental data from 1979 and 2019  
510 (Analysis 1). We validated these predictions using presence-absence data set aside from the current and  
511 historic datasets. If habitat availability was an important factor in determining the range dynamics of either  
512 species, then the current models should be sufficient to predict the expected range dynamics, the current  
513 and historic models should agree on the locations of suitable habitat, and the current models should be  
514 transferable to the historic dataset. Alternatively, if changes in habitat associations or connectivity were  
515 important for the species range dynamics, the current and historic models should disagree and be mutually  
516 non-transferable.

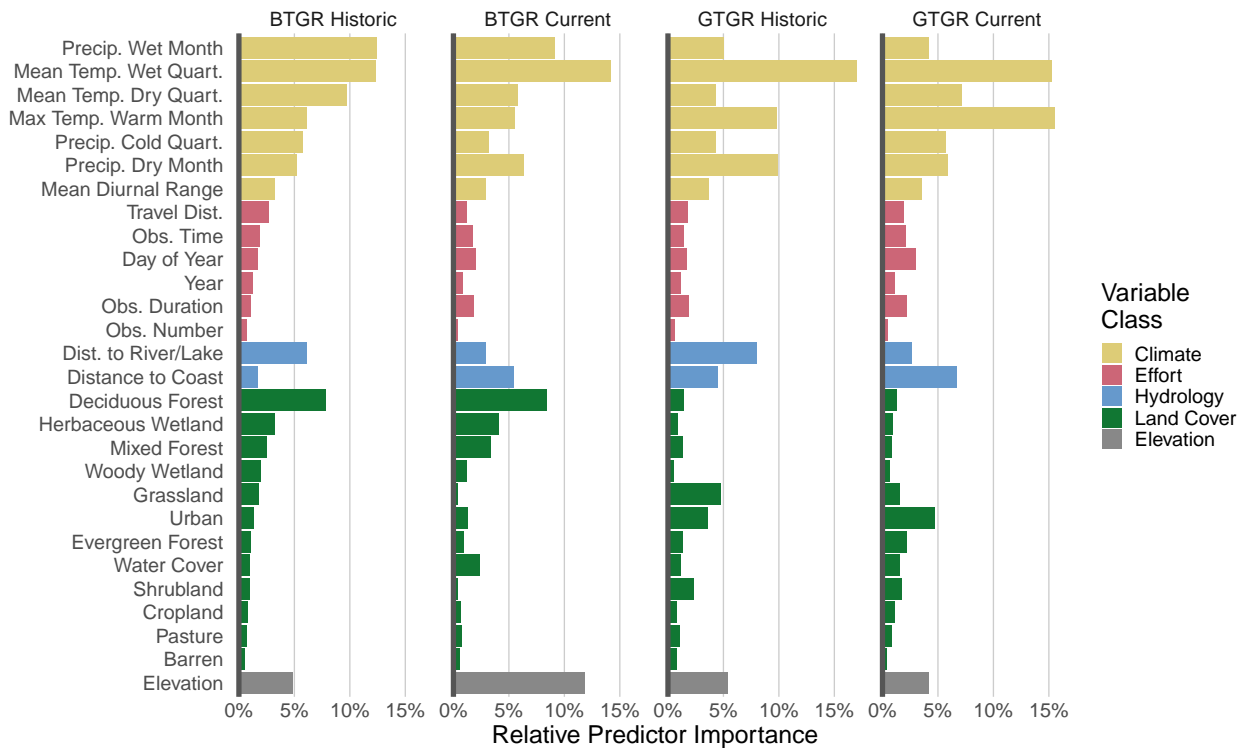
517 Habitat availability for the boat-tailed grackle has remained the same across most of its range according to  
518 both the current and historic models, and the current model is highly transferable. The boat-tailed grackle  
519 remained restricted to the coasts of the Gulf of Mexico and Atlantic Ocean, but habitat suitability increased  
520 within the interior of Florida and on the northern edge of the species range, increasing the total suitable  
521 area from 180,406 km<sup>2</sup> to 199,912 km<sup>2</sup> in the historic model, and from 111,218 km<sup>2</sup> to 163,243 km<sup>2</sup> in the  
522 current model (Fig 3A; see Fig S2 for suitability values). The models disagreed on the northern extent of  
523 suitable habitat, with the historic model reaching the southern tip of Delaware, while the current model  
524 predicted that suitable habitat reached farther north to Long Island. The current model recreated existing  
525 species range definitions, including a known break in the species range on the western edge of the Florida  
526 panhandle (Post et al., 1996). The current model was also highly transferable, with little difference between  
527 the prediction accuracy using the current or historic datasets ( $\Delta\text{Kappa} = 0$ ,  $\Delta\text{AUC} = -0.026$ , Fig 3B),  
528 while the historic model had lower transferability ( $\Delta\text{Kappa} = -0.226$ ,  $\Delta\text{AUC} = -0.049$ ). The accuracy of  
529 the current model indicates that environmental change is sufficient to predict changes in habitat suitability,  
530 and the low transferability of the historic model could be due to greater geographic bias caused by the  
531 smaller sample size (Fig S1). Our models agree with observations that the boat-tailed grackle range has  
532 remained largely stable except for an expansion along the northeastern coast of the US and suggest that  
533 habitat availability could play a role in the range dynamics of the boat-tailed grackle.

534 Habitat availability for the great-tailed grackle has expanded, but the current and historical models disagree  
535 on the extent and location of this expansion and are mutually non-transferable. The historic model restricted  
536 the great-tailed grackle range to 198,175 km<sup>2</sup> in southern Texas, matching previous reports of the species  
537 range in the 1970s (Wehtje, 2003), and predicted minor reductions in range to 181,281 km<sup>2</sup> (Fig 3A, Fig S2).  
538 The current model instead predicted suitable habitat existed in both time periods across the known great-  
539 tailed grackle range expansion (Wehtje, 2003) in the central and southwestern US, with further expansions  
540 within central California, Colorado, Kansas, and southeastern Texas. Suitable habitat expanded from 322,750  
541 km<sup>2</sup> in 1979 to 547,694 km<sup>2</sup> in 2019, however this expansion included areas that were suitable within  
542 the historic model. Neither model had high transferability (current:  $\Delta\text{Kappa} = -0.184$ ,  $\Delta\text{AUC} = -0.061$ ;  
543 (historic:  $\Delta\text{Kappa} = -0.203$ ,  $\Delta\text{AUC} = -0.177$ , Fig 3B). The disagreement between our models indicates that  
544 environmental change alone cannot explain the range expansion of the great-tailed grackle. Each model  
545 accurately predicted the species range within its own time period, but failed to predict the known changes in  
546 that range. Together, our models predict that the great-tailed grackle range has more than doubled in the  
547 past 40 years, but the habitat associations found in one time period are incapable of predicting the changes in

548 occupied habitat over time. These changing habitat associations could indicate that the great-tailed grackle  
 549 is occupying novel habitat, either because the species can tolerate a wider variety of habitats or has overcome  
 550 barriers such as dispersal barriers or temporal lag, the time required for populations of a species to establish  
 551 in previously unoccupied suitable habitat (Essl et al., 2015).

## 552 Hypothesis 2: Habitat Associations

553 We compared the changes in habitat associations of boat-tailed grackles and great-tailed grackles by mea-  
 554 suring the importance of each environmental predictor to the current and historic models for each species  
 555 and quantifying the marginal effect that changing the value of these predictors had on habitat suitability.  
 556 Differences in which predictors are most important or how predictors influence habitat suitability describe  
 557 differences in the realized niches predicted by our models (Analysis 2). We also quantified how frequently  
 558 each species was observed on different land cover classes between the current and historic datasets to test for  
 559 changes in the breadth of land cover classes used by either species. Finally, we performed a niche similarity  
 560 test to determine if the environments occupied by each species in the historic and current time periods are  
 561 more different from each other than would be expected by chance (Analysis 3). Changes in the environments  
 562 either species was observed on would indicate that the species has novel habitat associations.

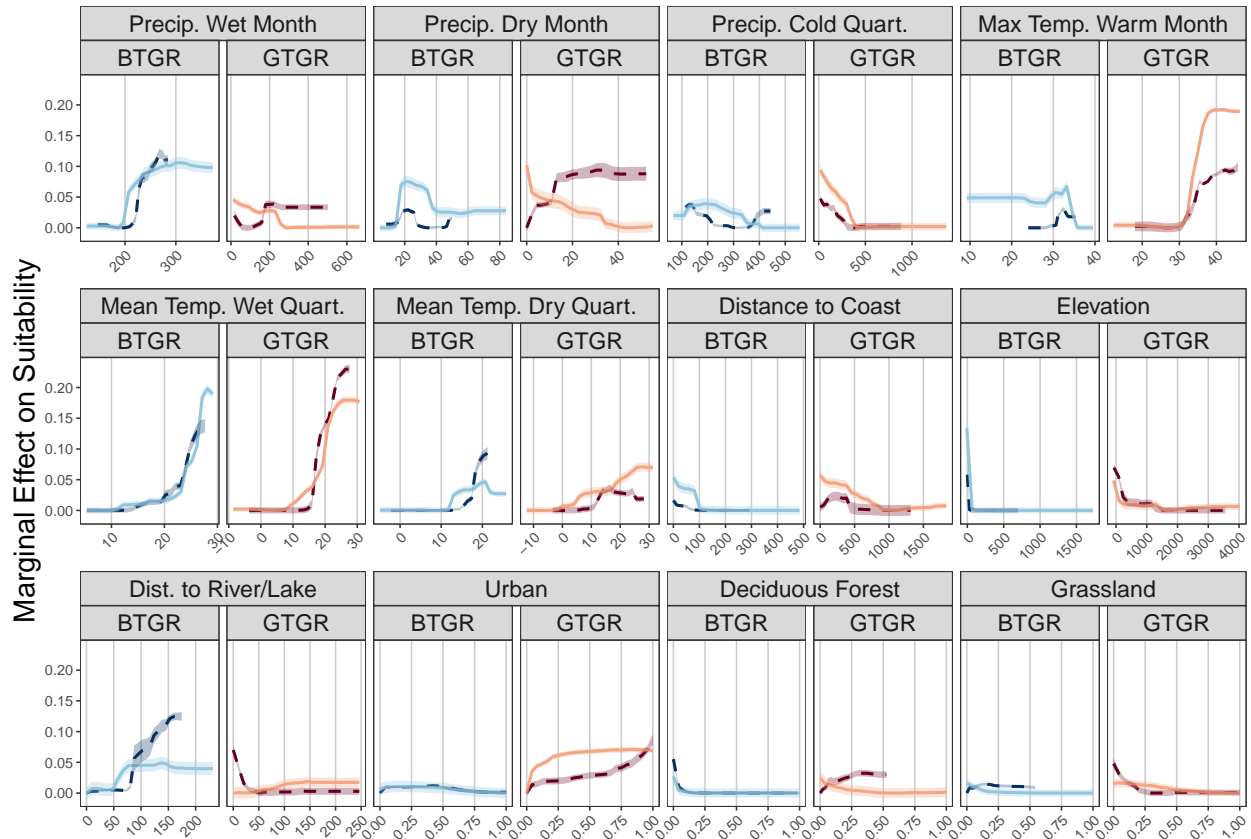


563

564 **Figure 4.** Importance of environmental predictors for the boat-tailed grackle (BTGR) and the great-tailed grackle (GTGR)  
 565 historic and current species distribution models (SDMs). Relative predictor importance measures how informative the predictors  
 566 were for classifying presence or absence points within each model (% total GINI index). The predictor colors indicate whether  
 567 a predictor was a measure of climate (yellow), observer effort (red), distance to water (blue), land cover classification (green),  
 568 or elevation (gray).

569 The most important predictors for the current boat-tailed grackle model were mean temperature of the  
 570 wettest quarter (accounting for 14.2% of the total average GINI index), elevation (11.8%), precipitation of  
 571 the wettest month (9.1%), and deciduous forest land cover (8.4%; Fig 4). Habitat suitability increased as the  
 572 mean temperature of the wettest quarter and precipitation of the wettest month increased and was highest  
 573 when both elevation and deciduous forest land cover were close to zero (Fig 5; see Fig S3 for the full set of

574 partial dependence plots). Our model predicts that the ideal habitats for boat-tailed grackles are warm, low  
 575 elevation habitats with high precipitation and low forest cover.



576  
 577 **Figure 5.** Partial dependence curves for the 12 most important environmental predictors across all boat-tailed grackle (BTGR)  
 578 and great-tailed grackle (GTGR) models. The curves represent how changing each environmental predictor changes the en-  
 579 counter rate for the modeled species. The historic models are represented by the darker dashed lines and the current models  
 580 are represented by the lighter solid lines. Shaded regions indicate one standard deviation. The differences between the historic  
 581 and current models for each species present how realized niches of each species as predicted by our models have changed.

582 The historic model for the boat-tailed grackle disagreed on the importance and effect of only a few predictors,  
 583 supporting consistent habitat usage in the species. Both the historic and current models placed high impor-  
 584 tance on the mean temperature in the wettest quarter (12.4%; Fig 4), precipitation of the wettest month  
 585 (12.4%), and deciduous forest cover (7.9%). However, the historic model prioritized the mean temperature of  
 586 the driest quarter (9.7%, 5.8% in the current model) and not elevation (4.8%). Among these predictors, only  
 587 the mean temperature of the driest quarter had a different effect in the historic model than in the current  
 588 model (Fig 5). Habitat suitability increased as the mean temperature of the driest quarter increased in both  
 589 models, but the current model predicted that suitability would decrease beyond the observed temperature  
 590 range of the historic model. Differences between the historic and current models do not support a change in  
 591 habitat associations of boat-tailed grackles over time.

592 Boat-tailed grackles were found in every land cover class except deciduous forests and ice/snow in both  
 593 the historic and current time periods. Boat-tailed grackles were found more often in urban areas in the  
 594 current time period, and less often in the land cover class that was the second most common in the historic  
 595 time period: woody wetlands (Fig S4). Boat-tailed grackles were also found less often in croplands, which  
 596 corresponds with a decrease in croplands across the checklist range. We found no evidence of change in  
 597 habitat occupancy based on land cover classes for boat-tailed grackles, agreeing with the results of our  
 598 SDMs. The niche similarity test for the boat-tailed grackle did not find a significant difference in the



599 environmental space occupied by the boat-tailed grackle over time (Warren's  $I = 0.647$ ;  $p$ -value = 0.446, Fig  
600 S5B), which further supports the hypothesis that the boat-tailed grackle did not change the environments  
601 it occupies between the historic and current time periods.

602 The most important predictors for the current great-tailed grackle model were maximum temperature of  
603 the warmest month (15.5%; Fig 4), mean temperature of the wettest quarter (15.3%), mean temperature  
604 in the driest quarter (7.2%), and distance to coasts (6.8%). Habitat suitability increased as the maximum  
605 temperature of the warmest month, mean temperature of the wettest quarter, and mean temperature of the  
606 driest quarter increased, while suitability was negatively related to the distance to coasts (Fig 5, Fig S3).  
607 Our model predicts that the ideal habitats for great-tailed grackles are warm areas not too far from coasts.

608 The historic model for the great-tailed grackle disagreed on the importance and effect of several predictors,  
609 supporting a change in habitat associations. The historic model agreed with the current model on the high  
610 importance of the maximum temperature of the warmest month (9.8%, Fig 4) and mean temperature of the  
611 wettest quarter (17.0%). However, the historic model prioritized the precipitation in the driest month (9.9%  
612 vs. 5.9% in the current model) and the distance to fresh water (7.9% vs. 2.7% in the current model), and  
613 not the distance to coasts (4.5%) nor the mean temperature in the driest quarter (4.3%). Habitat suitability  
614 increased as precipitation in the driest month increased, while the current model predicted the opposite  
615 trend (Fig 5). Habitat suitability was also greatest near fresh water, while the current model predicted  
616 little effect of the distance to fresh water. The two models also disagree on which land cover class was most  
617 important for great-tailed grackles. Urban cover was most important for the current model (4.8% vs. 3.6%  
618 in the historic model), while grassland cover (4.7% vs. 1.5% in the current model) was most important  
619 for the historic model. While habitat suitability increased as urban cover increased for both models, the  
620 current model reached its maximum suitability by 25% urban cover, while the historic model did not reach  
621 similar suitability until almost 100% urban cover. The faster rate of suitability increase in the current model  
622 indicates that great-tailed grackles were found across a wide variety of urban habitats, from moderate to  
623 highly urbanized areas, while the historic model indicates that great-tailed grackles were preferentially found  
624 in highly urbanized habitat. Our models predict that the great-tailed grackle is currently found in more arid  
625 habitat with greater variability in urban cover than 40 years ago.

626 Great-tailed grackles were found in every land cover class except deciduous forests, mixed forests, and  
627 ice/snow in the historic sample, and every land cover class except deciduous forests and ice/snow in the  
628 current sample. There were more great-tailed grackle observations in the current sample on urban areas,  
629 croplands, and grasslands and less observations in water, shrublands, pastures, and evergreen forests (Fig  
630 S4). While the most common land cover classes great-tailed grackles were found on had shifted, there was  
631 no evidence that great-tailed grackles expanded the breadth of land cover classes they could occupy. These  
632 results are consistent with our SDMs, which only found differences in the range of urban habitats that great-  
633 tailed grackles occupied. The niche similarity test for the great-tailed grackle found a significant difference  
634 in the environmental space occupied by the great-tailed grackle over time (Warren's  $I = 0.641$ ;  $p$ -value =  
635 0.001, Fig S6B). The observed value for Warren's  $I$  was lower than the simulated values, further supporting  
636 the hypothesis that the great-tailed grackle changed the environments it occupies between the historic and  
637 current time periods.

### 638 Hypothesis 3: Connectivity

639 To determine whether changes in connectivity between habitat patches caused by environmental change  
640 could explain the rapid expansion of the great-tailed grackle but not the boat-tailed grackle, we estimated  
641 the change in accumulated current across the range of each species between 1979 and 2019 (Analysis 4).  
642 Accumulated current summarizes the amount of movement through a cell, thus cells with higher current  
643 values are more suitable for movement and increase connectivity. We binned current values into high or low  
644 connectivity using the 75th percentile (Bonnin et al., 2020). Most cells within the 75th percentile of current  
645 values based on the 1979 resistance surface remained within the 75th percentile for both species. Decreases  
646 in the distances between patches of cells with high current between the two time periods would indicate that  
647 habitat connectivity has increased.

648 Connectivity decreased for the boat-tailed grackle along the interior portion of its range (farther from the  
649 coasts) in the southern Atlantic states and the southern coast of Texas (Fig S7). However, connectivity  
650 increased along the Florida panhandle, the northern coast of North Carolina, and the areas surrounding  
651 New York City (New York State, New Jersey, and Connecticut). There were no isolated patches of high  
652 connectivity for the boat-tailed grackle, and changes in connectivity did not connect or isolate any habitat  
653 patches. Our model does not predict major connectivity changes occurring across the range of the boat-tailed  
654 grackle.

655 Connectivity decreased for the great-tailed grackle within the state of Arizona and along the northern extreme  
656 of the cells within the 75th percentile (Oregon, Nevada, Colorado, and Kansas). However, connectivity  
657 increased along the eastern extreme (Texas and Oklahoma) and the northern edges in Arizona and New  
658 Mexico (Fig S7). Only one region of high connectivity in Montana was isolated from the core of connected  
659 cells, and no areas became isolated or connected between 1979 and 2019. Similar to the boat-tailed grackle,  
660 our model does not predict major connectivity changes occurring across the range of the great-tailed grackle.

## 661 Discussion

662 We investigated how changes in habitat availability, habitat breadth, and connectivity relate to differential  
663 range dynamics in a sister-species pair. We found that the rapidly-expanding great-tailed grackle has in-  
664 creased the variety of occupied habitats in the past 40 years. The current realized niche of the great-tailed  
665 grackle contains more arid climate conditions and is less dependent on bodies of fresh water than in the past  
666 realized niche. We did not find evidence for an increase in the connectivity of previously isolated patches  
667 of suitable habitat. Overall, our results for the great-tailed grackle are consistent with hypothesis 2, that  
668 an expansion in the realized niche of the great-tailed grackle may have contributed to the geographic range  
669 expansion of the species (Fig 1). While this expansion might predate the period we investigated, which could  
670 be the case if these behavioral traits are part of the inherent repertoire of great-tailed grackles in line with  
671 hypothesis 4, the change in the range does not seem to reflect a lag to move into previously occupied habitat  
672 as the novel habitats the great-tailed grackle now occupies did exist within dispersal distance of the historic  
673 range for the species. In contrast, the boat-tailed grackle has remained within the same habitat conditions.  
674 Climate change in the northern extreme of the boat-tailed grackle range increased the area of predicted suit-  
675 able habitat, matching observed expansions of the species in that area. Similar to the great-tailed grackle,  
676 we found no changes in connectivity. Accordingly, the range dynamics of the boat-tailed grackle match  
677 expectations based on changes in habitat availability, our hypothesis 1 (Fig 1).

678 Our current boat-tailed grackle model is consistent with past work showing that boat-tailed grackles are  
679 highly restricted to coastal areas, and that an expansion into northern coastal areas could be due to climate  
680 changes. Boat-tailed grackles rarely occur far from saltwater in the northern portion of their range, but  
681 can nest inland across Florida (Selander & Giller, 1961; Post et al., 1996). Our current model recreated  
682 this distribution and predicted that elevation and distance to coastline were highly important environmental  
683 limitations. The historical model did not recreate the same high suitability within the interior of Florida  
684 and had both elevation and distance to coastlines as less important. However, our historic model also had  
685 lower transferability and could have reduced accuracy due to a low sample size, which can inflate the impact  
686 of geographic bias in samples (Elith et al., 2010; Anderson & Gonzalez, 2011; Guillera-Aroita et al., 2016;  
687 Yates et al., 2018). Our niche similarity test also supports consistent habitat use for the boat-tailed grackle  
688 in both time periods. Both SDMs predict increased suitability in the northern portion of the species range,  
689 which matches past observations (Selander & Giller, 1961) and general trends observed in several bird species  
690 that track their optimal conditions as anthropogenic climate change has altered environments (Vitousek et  
691 al., 1997; Thomas, 2010; Chen et al., 2011; Tomiolo & Ward, 2018).

692 The changes in species range we found in the great-tailed grackle matched those predicted by previous  
693 researchers. Selander & Giller (1961) note that, along the northern range edge, great-tailed grackles have  
694 expanded into new arid prairie habitat but were highly restricted to human settlements and farms in these  
695 areas. Great-tailed grackles require access to open habitat and standing water across their range (Selander &  
696 Giller, 1961), and human land use change and irrigation could meet these needs. Our models did find higher

697 habitat suitability values for the great-tailed grackle close to bodies of freshwater in the historic but not the  
698 current time period, suggesting that great-tailed grackles occupy habitats farther from natural open water  
699 sources. The differences between the current and historic models were also supported by our niche similarity  
700 test, which indicated that great-tailed grackles occupied a significantly different area of environmental space  
701 in the current time period relative to the historic time period. The current great-tailed grackle model also  
702 predicted higher suitability in areas with more cropland and pasture, but neither land cover class had high  
703 predictor importance. Instead, precipitation in the wettest and driest months marked the greatest difference  
704 between the current and historic models. Wehtje (2003) proposed that lower nest predation and abundant  
705 food in human modified environments could allow the great-tailed grackle to support populations within  
706 otherwise suboptimal climate conditions. The great-tailed grackle could use the same land cover classes in  
707 both time periods, but current populations have novel or preexisting ways to use human altered environments  
708 to expand their realized climatic niche. It is possible that the fundamental niche of the great-tailed grackle  
709 has remained the same, while the realized niche has expanded due to anthropogenic environmental change.  
710 Our results show that the great-tailed grackle is currently found across a wider variety of broad-scale habitats  
711 than 40 years ago. Further work on local-scale habitat use across the range of the great-tailed grackle could  
712 explore the causes of the trend we have observed.

713 It remains unclear why the great-tailed grackle has expanded its niche while the boat-tailed grackle has not.  
714 Both the boat-tailed grackle and the great-tailed grackle are highly adaptable species with similar foraging  
715 habits. Human-associated species like boat-tailed grackles and great-tailed grackles that use urban habitats  
716 are typically more behaviorally flexible and better suited to use new environments than other species (Sol  
717 et al., 2002; 2005; 2013; Wong & Candolin, 2015). There could be meaningful differences in the degree of  
718 flexibility between these species or other factors that limit the ability of the boat-tailed grackle to expand to  
719 new habitats. The greater nest-site specificity of the boat-tailed grackle could be a limiting factor, though  
720 nest-site plasticity does exist in the species (Post et al., 1996). Further studies are needed to compare  
721 ecologically relevant differences in flexibility, exploration, dispersal, and reproductive behaviors between  
722 these two species.

723 Our results demonstrate vastly different niche dynamics within closely related species and illustrate the  
724 divergent responses species can have to anthropogenic change. The distinct niche dynamic of each species  
725 represents opposing responses to anthropogenic change: the boat-tailed grackle has shifted its range in  
726 response to climate change, while the rapidly expanding great-tailed grackle has acclimated to new climates  
727 possibly due to human land-use change. Species with similar responses to the boat-tailed grackle could be  
728 more vulnerable to future climate change (Thomas, 2010), while the great-tailed grackle parallels rapidly  
729 expanding introduced species, despite being native to North America (Peer, 2011). The expansion habitats  
730 used by the great-tailed grackle also confounds our ability to project how the species range will change in the  
731 future, and could have implications for a projected expansion in the common grackle (*Quiscalus quisqualis*,  
732 Capainolo et al., 2021). Identifying the mechanism of range dynamics in both species expands the knowledge  
733 of the complex and changing factors that shape species ranges globally.

734 The high accuracy of our SDMs when cross validated on their own datasets and the transferability of the  
735 current boat-tailed grackle model support the use of SDMs as tools to study how species ranges change  
736 over time. While improving model transferability remains a challenge for SDMs (Vaughan & Ormerod,  
737 2005; Yates et al., 2018), using a combination of climate and land use data can improve model accuracy  
738 and transferability in some situations (Elith & Graham, 2009; Regos et al., 2019). Our results also stress  
739 the importance of testing model transferability before assuming niche conservatism for all species. While  
740 the niches of species commonly remain consistent (Liu et al., 2020), assuming species will retain their niche  
741 through time can limit the usefulness of SDMs. When model transferability is tested, SDMs become a more  
742 effective tool for studying species ranges to both understand fundamental questions in ecology and evolution  
743 and set conservation priorities in the face of ongoing anthropogenic changes (Elith et al., 2010; Grenoulet  
744 & Comte, 2014; Sofaer et al., 2018; Chen et al., 2018).

745 SDMs are accompanied by several limitations that are important to consider. SDMs are correlative in nature  
746 and are susceptible to biases in sample and parameter selection (Regos et al., 2019; Sofaer et al., 2018). Here,  
747 we used geographic undersampling and a balanced random forest design to reduce the impact of sampling  
748 bias and selected both climate and land cover parameters to include biologically relevant variables, but

749 other potentially causative variables could remain. We note that our results capture correlations between  
750 species occurrence and environmental factors, and thus cannot determine a causal link between where either  
751 species is found and the environment. Habitat occupancy change could occur independently of environmental  
752 change, such as if all suitable sites were not yet occupied due to temporal lag. Increased occupancy as the  
753 species reaches already suitable sites would correlate with further environmental change and be captured by  
754 our species distribution models. Our models similarly cannot distinguish lagged responses to environmental  
755 trends that pre-date our dataset from responses to within-dataset trends. The temporal limits of our study  
756 could influence our results as the species ranges could react to changes beyond the scales we investigated.  
757 Environmental change that occurred before 1970 could have influenced the observed ranges of the species  
758 during 1970-1979 due to temporal lag in the species occupying areas within their fundamental niches. Because  
759 our models were trained on species occurrences, the niches described by our model depend on a combination  
760 of environmental factors that are physiologically or behaviorally favored by the species (the fundamental  
761 niche for the species), dispersal behavior and limitations, and biotic factors that influence where the two  
762 species will occur (Soberón & Nakamura, 2009). We included a broad set of climatic, land use, topographic,  
763 and hydrologic factors within our SDMs to capture the environmental factors that could influence occurrence,  
764 but these factors may be incomplete, or may be too coarse to capture local scale habitat use. Our connectivity  
765 analysis investigated whether environmental change could influence the dispersal limitations for either species,  
766 but assumed that dispersal ability and habitat use remained constant over time. Further work is needed to  
767 investigate variation in dispersal behavior within the great-tailed grackle and boat-tailed grackle to determine  
768 the possible influence of dispersal behavior in the range dynamics for both species (see Q1 and Q2 of Logan  
769 et al. (2021) for project proposals). Recent work promotes the inclusion of biotic factors in SDMs such as  
770 pathogen, predator, or competitor species because interspecific dynamics can play a major role in determining  
771 species ranges (Gaston, 2003; Paquette & Hargreaves, 2021; Stephan et al., 2021). Determining the relevant  
772 biotic factors for each species remains challenging, but future work could investigate how the presence of  
773 nest predators such as the fish crow (*Corvus ossifragus*), which overlaps in range with boat-tailed grackles  
774 but not great-tailed grackles (Post et al., 1996), could also prevent the boat-tailed grackle from expanding  
775 its range.

776 In conclusion, this investigation found that across the range expansion of the great-tailed grackle, the species  
777 now occupies a wider variety of habitats than 40 years ago, while the boat-tailed grackle is found within  
778 the same habitats over time, even as environments have changed. Despite the many similarities between  
779 these two species, they occupy distinct niches and appear to have divergent responses to anthropogenic  
780 change. While the boat-tailed grackle range currently conforms to climate change, the great-tailed grackle  
781 has expanded across new human-altered environments. The potential causes for the observed widening of  
782 habitat use in the great-tailed grackle, but not the boat-tailed grackle demand further investigation of the  
783 ecology, gene flow, and behavior of both species that could have created such different range dynamics. We  
784 encourage others to also consider behavior when attempting to understand what limits species ranges (e.g.,  
785 Greggor et al. 2016). Here we have detailed how environmental and habitat use change can play important  
786 roles in range expansions and range stability, and future work will elucidate the factors shaping species  
787 ranges in our rapidly changing world.

## 788 Data Availability

789 All data and code used in this study are available at the associated KNB repository (Summers et al., 2022)

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## 792 Conflict of Interest Disclosure

793 We, the authors, declare we have no financial conflict of interest relating to the content of this article. CJ  
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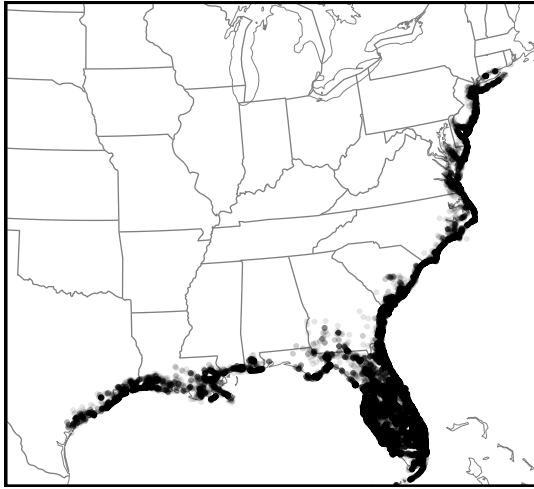


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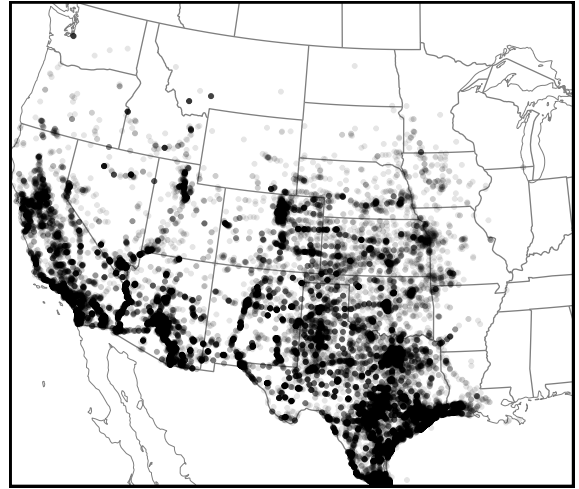
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1038 **Supplemental Figures**

BTGR Current



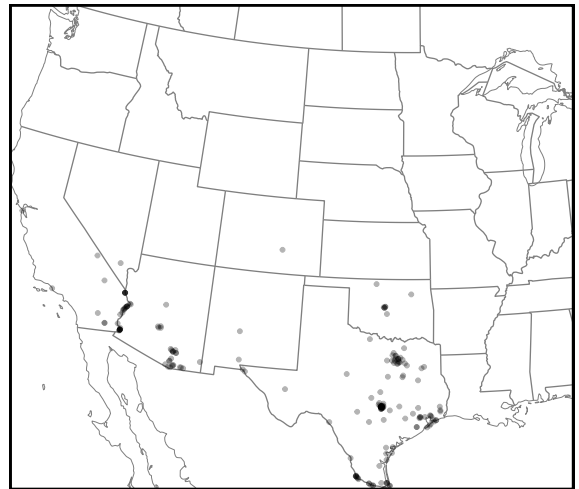
GTGR Current



BTGR Historic

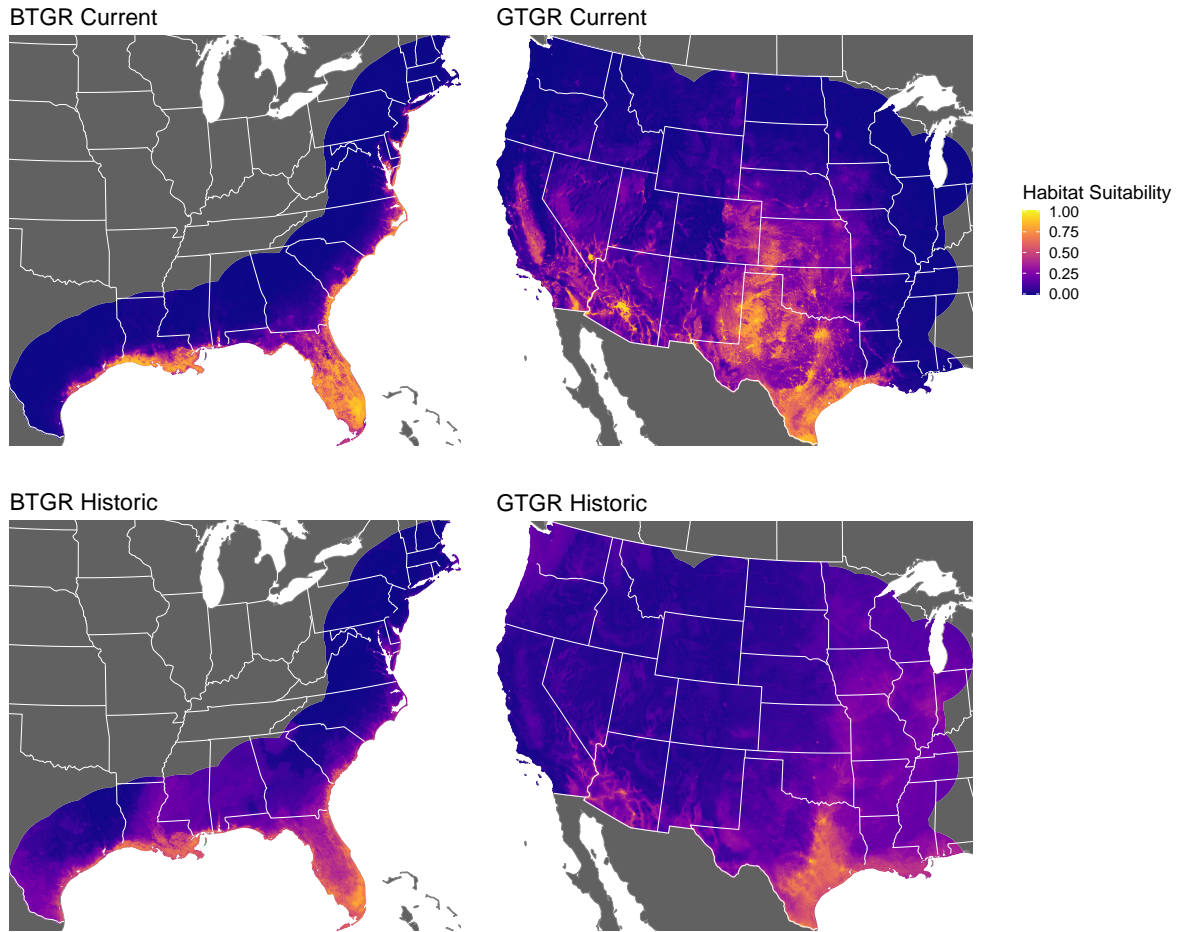


GTGR Historic



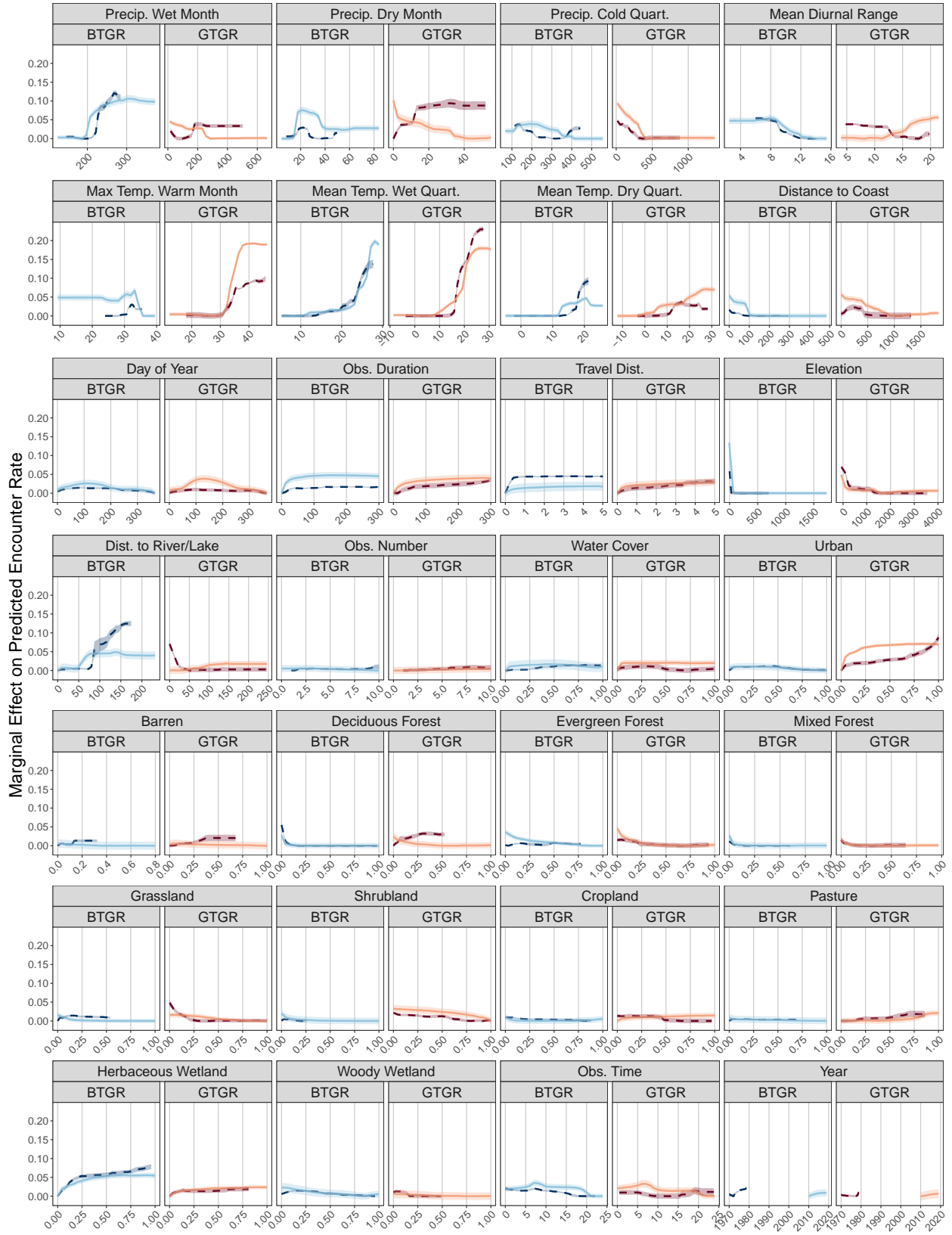
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1040 **Figure S1.** Map of observation locations for boat-tailed grackles (BTGR) or great-tailed grackles (GTGR) from historic  
1041 (1970-1979) and current (2010-2019) eBird records. These locations are filtered for record quality.



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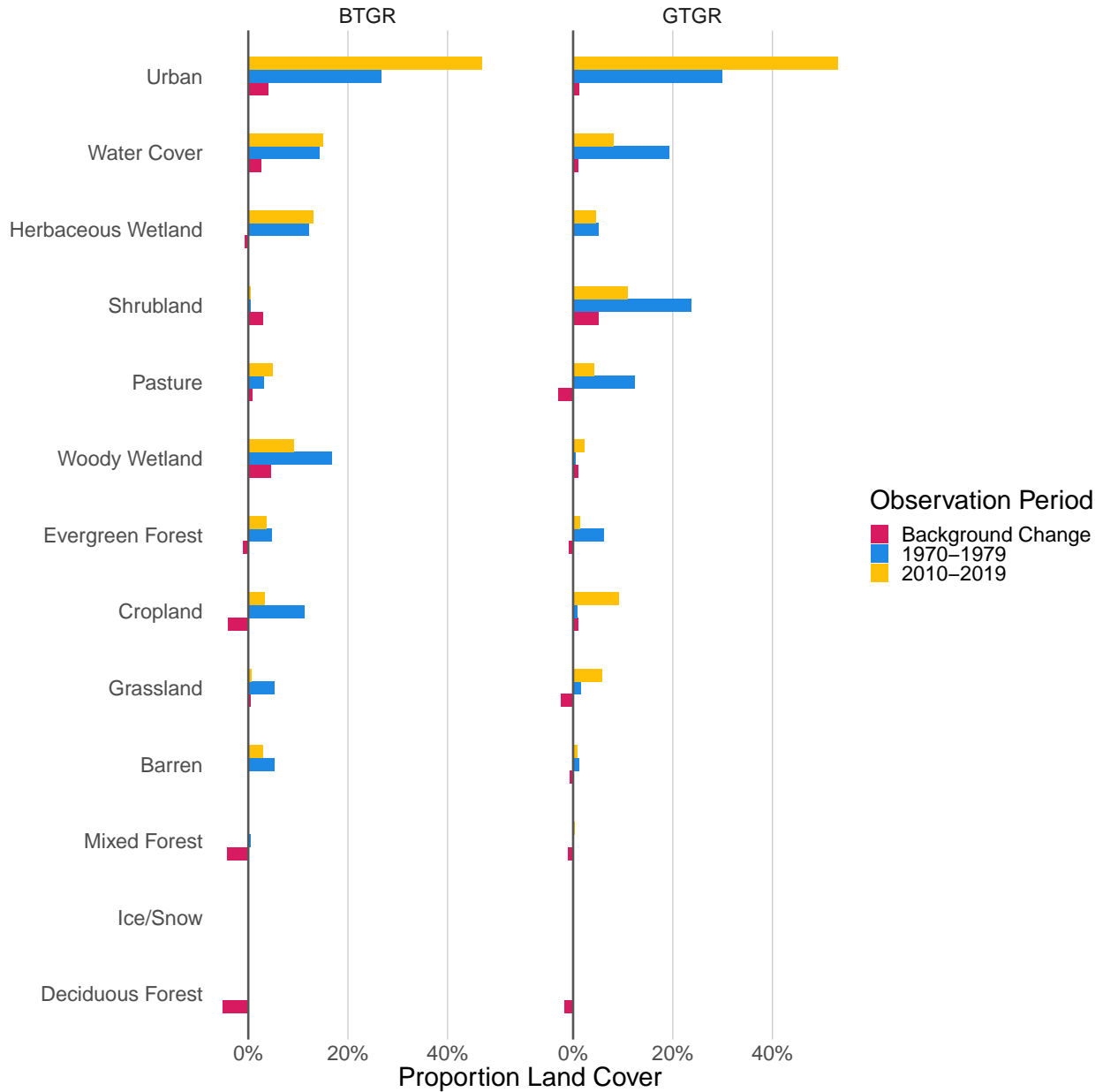
1043 **Figure S2.** Predicted habitat suitability using random forest models for boat-tailed grackles (BTGR) and great-tailed grackles  
 1044 (GTGR). Brighter colors indicate higher habitat suitability. The presented results are the average of the 10 replicates.



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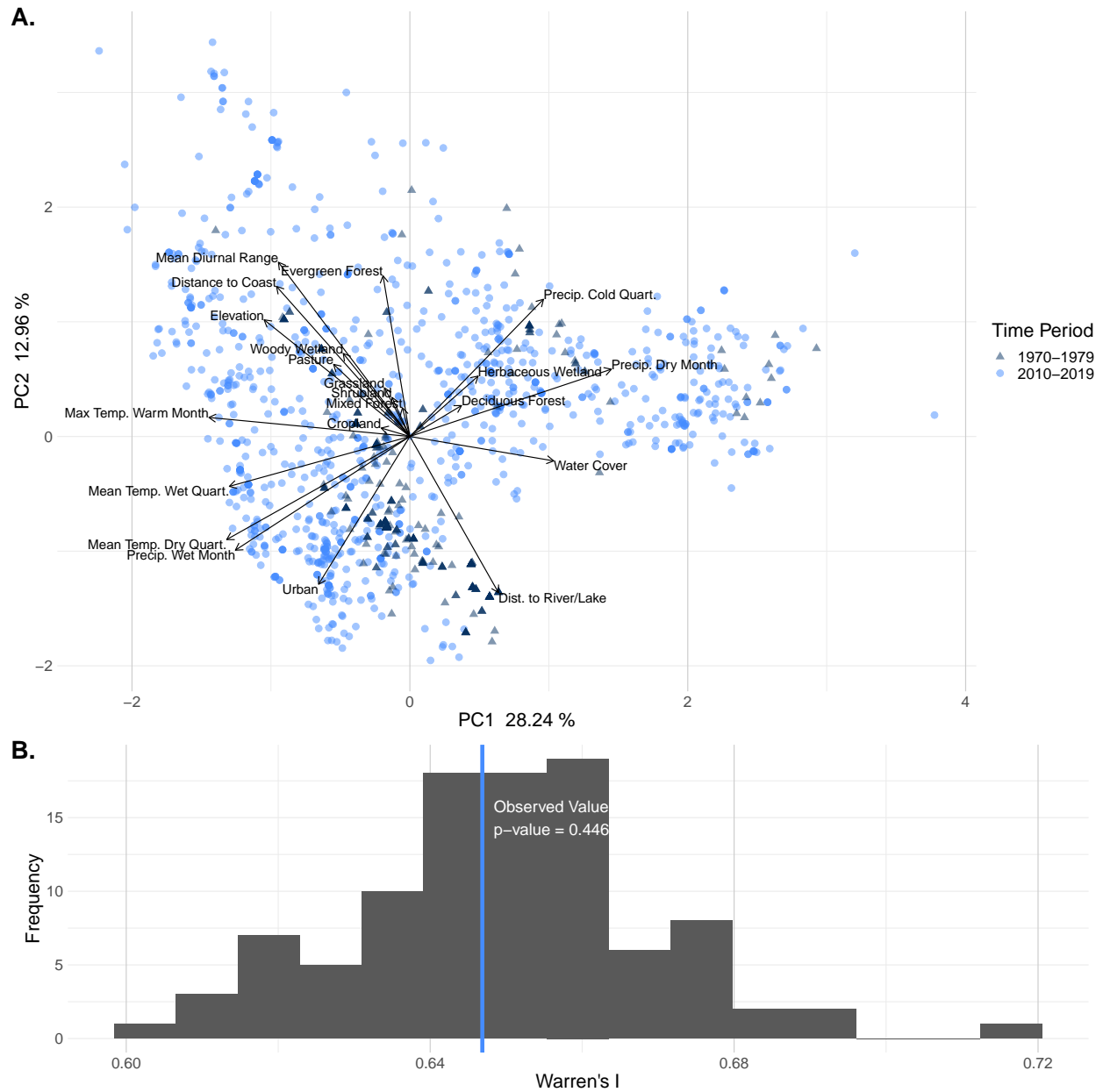
1046 **Figure S3.** Partial dependence curves for environmental predictors across all models (boat-tailed grackle: BTGR; great-tailed  
1047 grackle: GTGR). The curves represent how changing each environmental predictor changes the encounter rate for the modeled

1048 species. The historic models are represented by the darker dashed lines and the current models are represented by the lighter  
 1049 solid lines. Shaded regions indicate one standard deviation. The differences between the historic and current models for each  
 1050 species present how the species niche has changed based on our models.



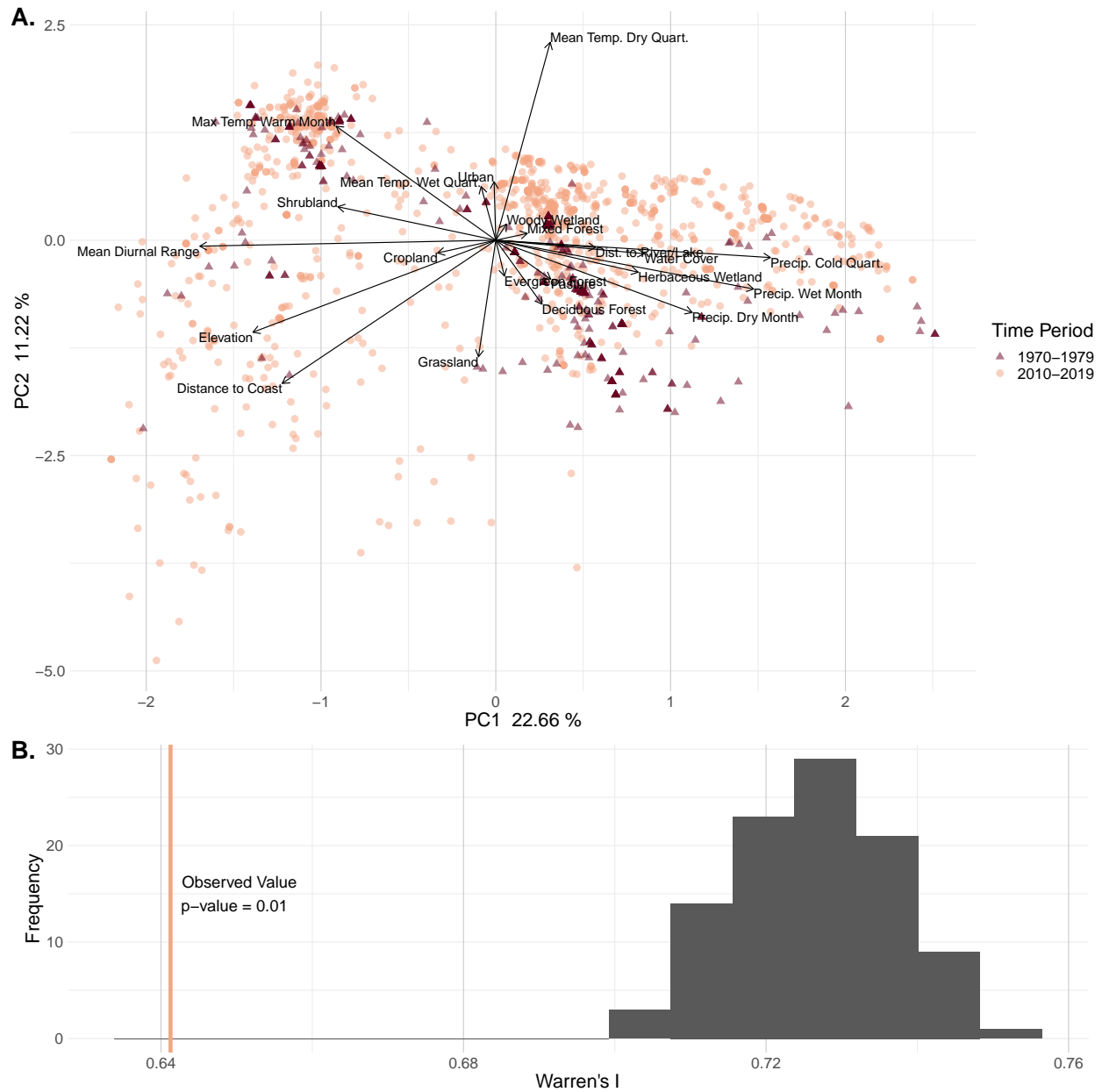
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1052 **Figure S4.** Land cover classes with observations of boat-tailed grackles (BTGR) and great-tailed grackles (GTGR) in 1970-  
 1053 1979 and 2010-2019 compared to the change in percent land cover area between each year range. The proportion of land cover  
 1054 measures what percent of observations for each species were located on each land cover class in the corresponding time frame.  
 1055 Both species were found more often in urban environments in the current time period, which also corresponds with a slight  
 1056 increase in the urban background area. Both species were also found less often in their previously second most common land  
 1057 cover type (woody wetland for boat-tailed grackles and shrubland for great-tailed grackles).



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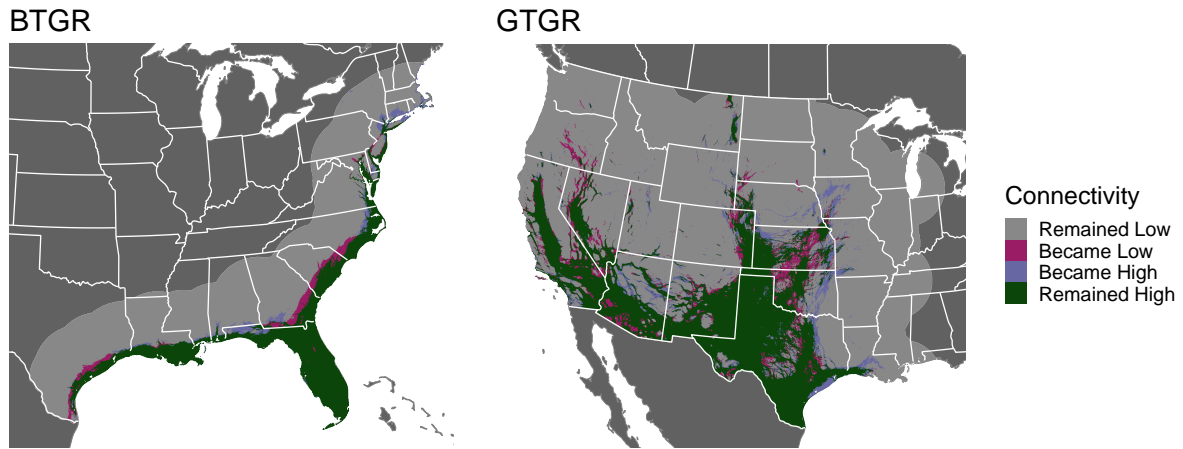
1059 **Figure S5.** Results of the niche similarity test between the historic (1970-1979) and current (2010-2019) time periods for the  
 1060 boat-tailed grackle. (A) Species occurrence points plotted along the first two principal component (PC) axes used for the niche  
 1061 similarity test. The percent variance captured by each principal component is presented in the axis label. The black lines  
 1062 expanding from the origin indicate the rotation values for the environmental predictors along the two principal components.  
 1063 The current time period observations were randomly subsampled to 1000 points for visual clarity. (B) Values of Warren's I  
 1064 from the niche similarity test based on the observed data (solid line) and 100 simulations (histogram). Higher values of Warren's I  
 1065 indicate greater niche similarity. The p-value presented for the observed value is based on the null hypothesis that the observed  
 1066 value presents equal or greater niche similarity than the simulations.



1067

1068 **Figure S6.** Results of the niche similarity test between the historic (1970-1979) and current (2010-2019) time periods for the  
 1069 great-tailed grackle. (A) Species occurrence points plotted along the first two principal component (PC) axes used for the niche  
 1070 similarity test. The percent variance captured by each principal component is presented in the axis label. The black lines  
 1071 expanding from the origin indicate the rotation values for the environmental predictors along the two principal components.  
 1072 The current time period observations were randomly subsampled to 1000 points for visual clarity. (B) Values of Warren's I  
 1073 from the niche similarity test based on the observed data (solid line) and 100 simulations (histogram). Higher values of Warren's I  
 1074 indicate greater niche similarity. The p-value presented for the observed value is based on the null hypothesis that the observed  
 1075 value presents equal or greater niche similarity than the simulations.





1076

1077 **Figure S7.** Change in connectivity between 1979 and 2019 measured as change in accumulated current for boat-tailed grackles  
 1078 (BTGR) and great-tailed grackles (GTGR). Current values were divided into high and low categories based on whether the  
 1079 values were above or below the 75th percentile of current values for each map. Colors indicate whether the current values  
 1080 remained low between the two time steps (gray), went from high to low (magenta), went from low to high (blue), or remained  
 1081 high (green). The darker gray color indicates areas outside the range where checklists were selected for each species, and were  
 1082 excluded from the connectivity analysis. The regions that have remained highly connected are continuous for both species,  
 1083 which indicates that changes in connectivity are not responsible for range changes in either species.