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 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 habitat breadth or connectivity of a species changes. The ability of a species to rapidly expand their geographic range through changes in their habitat breadth, also known as niche shifts, has been linked to behavioral flexibility, the ability to change behavior when circumstances change. We tested how changes in habitat availability, habitat breadth, or habitat connectivity contributed 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 suitable habitat ranges,habitat breadth, and range-wide connectivity have changed for both species. We found that the two species occupy distinct habitats and that the habitat of the great-tailed grackle has shifted to include 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 a change in habitat breadth drove the rapid range expansion of the great-tailed grackle, while climate change shaped minor shifts in the available range of the boat-tailed grackle. The expansion in habitat breadth of 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 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 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 species are 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 loss of habitat (IUCN 2021). These declines have been linked to a broad pattern of niche conservatism, where species remain restricted to their niche, here also referred to as habitat breadth, despite movement to new geographic areas or environmental change (Holt & Gains, 1992; Wiens et al., 2010; Liu et al., 2020).The ecological underpinnings of niche conservatism, and what factors allow some species to shift their niche, remain difficult to identify (Wiens et al., 2010). Theoretical models and empirical results point to population dynamics, gene flow, evolutionary trade-offs, and behaviors such as habitat choice as possible reasons that species do not adapt to new conditions and expand their ranges (Holt & Gains, 1992; Holt, 2003; Wiens et al., 2010). However, there are some examples of changes in the breadth of habitat that a species uses, known as niche shifts, driving species range expansions (Broennimann et al., 2007; Hill et al., 2017; Sherpa et al., 2019).

Species expanding into new areas are assumed to have overcome some of the trade-offs or limitations that lead to niche conservatism. The causes of niche shifts can include behavioral flexibility, the ability to change behavior when circumstances change (see Mikhalevich et al., 2017 for theoretical background on our flexibility definition) (Chow et al., 2016; Griffin & Guez, 2014; e.g., Lefebvre et al., 1997; Sol et al., 2002; 2005; 2007; Sol & Lefebvre, 2000). This idea predicts that flexibility, exploration, and innovation facilitate the expansion of individuals into completely new areas and that their role diminishes after a certain number of generations (Wright et al., 2010). Experimental studies have shown that latent abilities are primarily expressed in a time of need (A. M. Auersperg et al., 2012; Bird & Emery, 2009; Laumer et al., 2018; Manrique & Call, 2011; e.g., Taylor et al., 2007). Therefore, we do not expect the founding individuals who initially dispersed out of their original range to have unique behavioral characteristics that are passed on to their offspring. Instead, we expect that the actual act of continuing a range expansion relies on flexibility, exploration, innovation, and persistence, and that these behaviors are therefore expressed more on the edge of the expansion range where there have not been many generations to accumulate relevant knowledge about the environment. There is also evidence that some species can behaviorally shift their niche in response to anthropogenic climate change or can expand their range by using human altered environments (Wong & Candolin, 2015; Wolff et al., 2020). Human-modified environments are increasing (Goldewijk, 2001; e.g., Liu et al., 2020; Wu et al., 2011), and species associated with these habitats show differences in their behavior (Chejanovski et al., 2017; e.g., Ciani, 1986; Federspiel et al., 2017).

However, range dynamics are also influenced by factors beyond niche: environmental change leading to a recent increase in the amount of available habitat can facilitate a geographic range expansion (Hanski & Gilpin, 1991; Wiens, 1997), and change in habitat connectivity can alter species range limits (Holt, 2003; Platts et al., 2019). A species may not need to be behaviorally flexible to move into new areas if they can continue to use the same types of habitat they are accustomed to. For example, a species may expand its range because changes in climate have caused more geographic areas to fall within its niche or if previously isolated habitat patches become connected. Thus, it is important to identify how changes in the availability of habitats, their habitat breadth, and the dispersal abilities of species contribute to range shifts to understand whether niche shifts are truly happening and to identify the underlying causes of range shifts.

Here we investigated the drivers of different range dynamics in two closely related grackle species, the great-tailed grackle (*Quiscalus mexicanus*, hereafter GTGR) and boat-tailed grackle (*Quiscalus major*, hereafter BTGR). These species offer an opportunity for simultaneous investigation of the roles of behavior and increased habitat availability for a rapidly increasing geographic range expansion. GTGR has rapidly expanded its range northward over the course of the 20th century (Post et al., 1996; Wehtje, 2003), moving its northern range edge from Southern Texas to Nebraska (Fig 1B). In contrast, BTGR has experienced only minor changes to the northern edge of its range (Wehtje, 2003) despite both species having similar foraging habits and successfully using human-altered environments (Selander & Giller, 1961; Post et al., 1996; Johnson & Peer, 2020). Detailed reports on the breeding ecology of these two species indicate that range expansion in BTGR but not GTGR may be constrained by the availability of suitable nesting sites (Selander & Giller, 1961; Wehtje, 2003). BTGR may be limited by the need for coastal marshes or isolated groves near water for nesting sites (Post et al., 1996), while GTGR can nest in agricultural lands, marshes, and urban areas with vegetation and surface water (Johnson & Peer, 2020). GTGR inhabits a wide variety of habitats (but not forests) at a variety of elevations (0-2134m), while remaining near water bodies, while BTGR exist mainly in coastal areas (Selander & Giller, 1961). There is also evidence that GTGR has preferred different habitats over time and across their range. Ornithologists have recorded GTGR breeding primarily in natural and human-made wetlands, while those within the recently expanded range readily breed in urban parks (Wehtje, 2003). However, this apparent difference in habitat breadth has yet to be rigorously quantified.

The range expansion in GTGR and range stability in BTGR could be an example of a sister-species pair where one has shifted its niche while the other follows niche conservatism. We characterized the historic (1970-1979) and current (2010-2019) niches of GTGR and BTGR using species distribution models (SDMs) to test three predictions (Fig 1A): (1) *changes in habitat availability:* GTGR and BTGR use different habitats, and the habitat of GTGR, but not that of BTGR, has increased in suitability and connectivity over the past few decades. This supports both the hypothesis that the availability of habitat, not inherent species differences, explains why GTGR are able to much more rapidly expand their range than BTGR and the hypothesis that environmental change has facilitated the range expansion of GTGR. An alternative to this prediction is that there are no changes in habitat availability, but some inherent trait allows GTGR to expand even though both species have unused habitat available to them. This would support the hypothesis that the original behavior of GTGR was already well adapted to facilitate a range expansion. (2) *changes in habitat breadth (i.e., niche)*: over the past few decades, GTGR has increased the habitat breadth that they can occupy, whereas BTGR continues to use the same limited habitat types. This would support the hypothesis that a niche shift, possibly due to changes in behavioral traits facilitated GTGR's geographic range expansion. (3) *changes in habitat connectivity:* species distribution models generally do not account for additional factors such as dispersal limitations when estimating suitable habitat. Therefore, we plan to conduct a separate analysis to examine possible changes in connected habitat. This would again support the hypothesis that environmental change has facilitated the range expansion of GTGR.

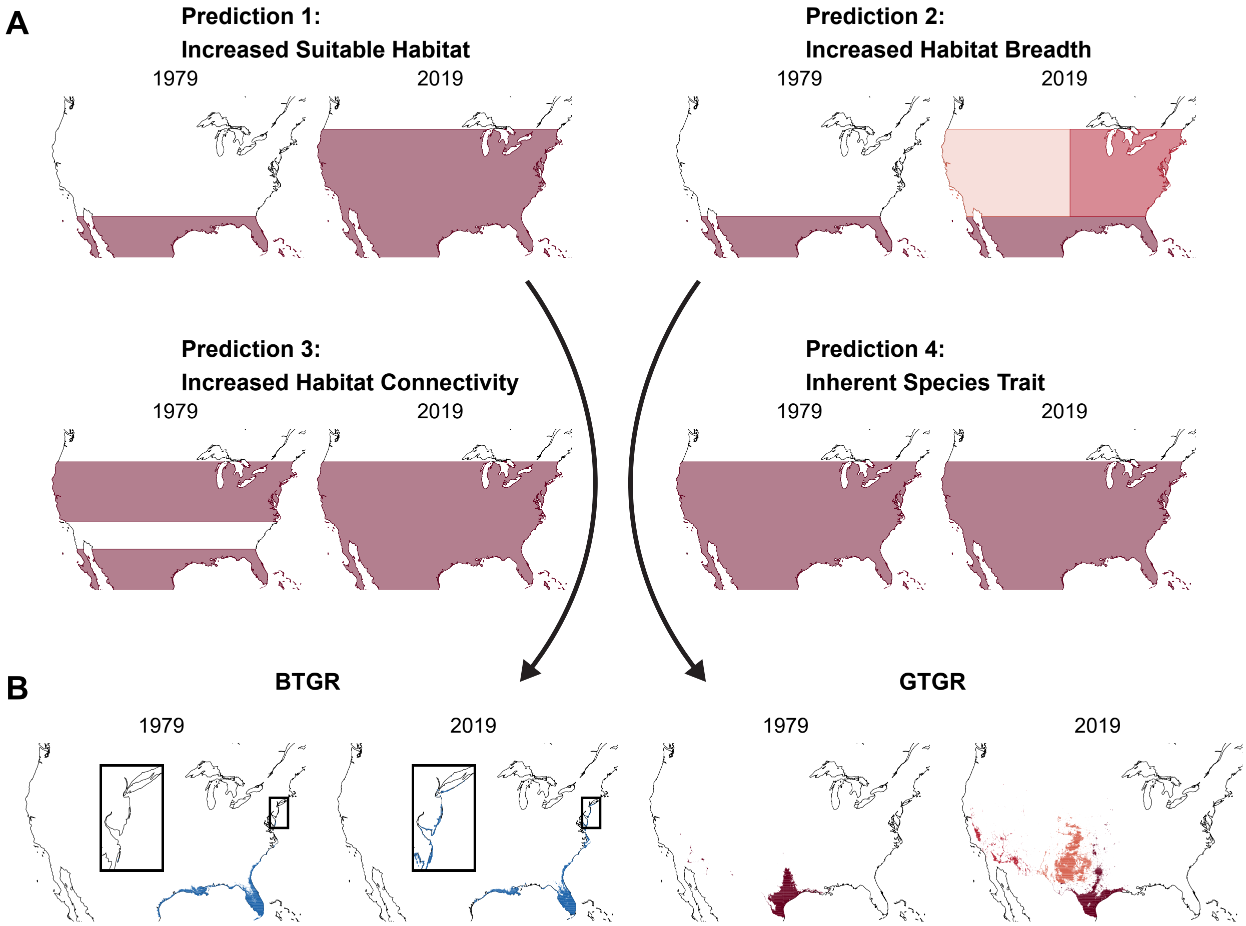

Figure 1. Comparison between the predicted patterns depending on the forces that facilitated range expansion and the habitat suitability predicted by the SDMs. (A) The pairs of plots display the predictions for the historic and current models if increased suitable habitat (P1), increased habitat breadth (P2), increased habitat connectivity (P3) or other inherent species trait(s) (P4)

drove range expansion. (B) The suitable habitat predictions for the historic and current models based on environmental data from 1979 and 2019. We used the maximum-sensitivity-specificity thresholds for each model (GTGR Current: 0.4440, BTGR Current: 0.4780, GTGR Historic: 0.4635, BTGR Historic: 0.3935) to assign habitat as suitable. The different colors in the GTGR map indicate that different environmental conditions existed within the 2019 expanded range that were not found in the 1979 range. The arrows connect the species ranges to the most supported predicted range dynamics.

We used ecological niche modeling to examine temporal habitat changes over these past few decades using observation data for both grackle species from existing citizen science databases. We determined the change in habitat availability using predictions produced by both our current and historic models for each species based on environmental data from 1979 and 2019 (Fig 2). We also tested the ability of our current and historic models to predict species presence and absence using data from the opposite time period to validate the predicted changes in suitable habitat (Torres et al., 2015; Regos et al., 2018; Yates et al., 2018). Then, we compared how the importance and effect of environmental predictors and occupied land cover types changed between our current and historic models. Finally, we used a circuit theory-based connectivity model to test for changes in habitat connectivity between 1979 and 2019. In combination, our analysis allowed us to determine whether the range of GTGR, but not BTGR, might have increased due to an increase in habitat availability, connectivity, or occupancy of suitable habitat, or because GTGR, but not BTGR increased their habitat breadth through a niche shift.

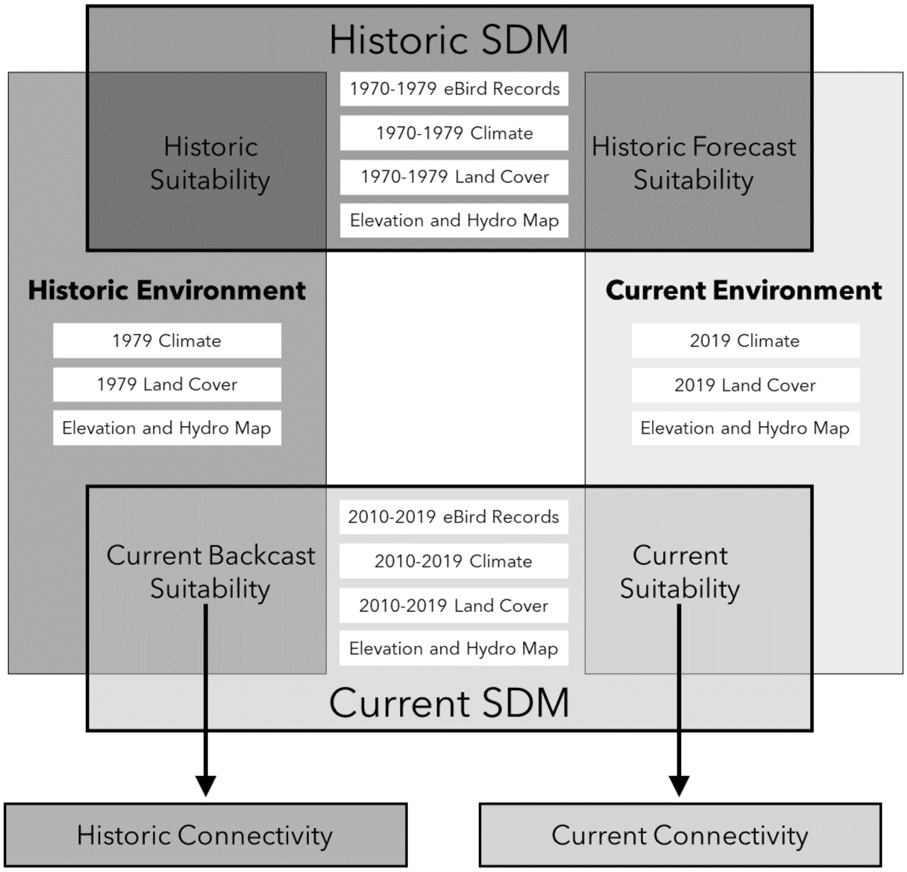

Figure 2. Overview of modeling approach and steps. The white boxes list the data used to generate the SDMs and environments used for predicting habitat suitability. The overlap between shaded boxes indicates that a habitat suitability prediction was created using the overlapping SDM and environmental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

Methods

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 Ecology in 2020. The hypotheses, predictions, and methods in this manuscript come from the preregistration, and we detail all changes to the methods below.

Preregistered Analysis Plan

Response Variable: Presence/absence of GTGR and BTGR

Explanatory Variables

1. **Land cover** (e.g., forest, urban, arable land, pastureland, wetlands, marine coastal, grassland, mangrove) - we chose these land cover types because they represent the habitat types in which both species exist, as well as habitat types (e.g., forest) they are not expected to exist in (Selander & Giller, 1961) to confirm that this is the case. If it is the case, it is possible that large forested areas are barriers for the range expansion of one or both species. We planned to download global land cover type data from MODIS (16 terrestrial habitat types) and/or the IUCN habitat classification (47 terrestrial habitat types). The IUCN has assigned habitat classifications to GTGR (https://www.iucnredlist.org/species/22724308/132174807#habitat-ecology) and BTGR (https://www.iucnredlist.org/species/22724311/94859792#habitat-ecology), however these appear to be out of date and we updated them for the purposes of this project.

    - **Further details:** We limited our study extent to the contiguous United States, which should not affect our investigation of distribution changes because the entire range of BTGR and the northern expanding edge of GTGR range are both within the contiguous United States. We verified this assumption by comparing species distribution models using 2010-2019 observations and MODIS land cover data with and without the limited spatial extent. Restricting the training data to the contiguous United States caused no drop in the AUC when predicting habitat suitability within the US relative to the unrestricted model.
    - **Deviations from the preregistered plan:** We used the National Land Cover Database (NLCD) and historical land cover modeling data from Sohl et al., 2016 instead of MODIS for our land cover dataset because the former datasets have a greater temporal range. MODIS data exists for a continuous period of 2001-present, and could only be extended to 1993 using compatible data from the Global Land Cover Characterization (GLCC) land cover dataset . Using MODIS data would require limiting the temporal range of our study to 1993, yet the most rapid period of GTGR expansion occurs from 1967-1977 (Wehtje, 2003). We initially proposed to use data from 1968-1970 for our historical model, and data from 2018 for our present-day model. However, instead, we used land cover projections from Sohl et al., 2016 for our historical land cover data and the NLCD (2011, 2013, 2016; and 2019) for our modern land cover data, which allowed us to model species distributions closer to our proposed temporal range. Both datasets use a modified version of the Anderson Land Classification System (Hardy & Anderson, 1973), share the same geographic extent, and are high resolution (250m and 30m, respectively). The land cover classification system includes classes for forests, urban areas, pasture and crop lands, wetlands and grasslands.

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

3. **Climate** (e.g., daily/annual temperature range) - GTGR was originally from the tropics (Wehtje, 2003), which generally have a narrow daily and annual climate range, and now exist in temperate

regions, which have much larger climate ranges. Accordingly, the daily/annual temperature range could allow us to determine the role of potential climatic limits in explaining ranges and range changes for both species. If there are limits, this could inform the difference between the range expansion rates of the two species. We considered the 19 bioclimatic variables from WorldClim.

- **Further details:** We converted monthly climate data for each time period from WorldClim (Fick & Hijmans, 2017) into the set of 19 climate variables included in the BioClim dataset using the biovars function from the dismo package in R (Hijmans et al., 2017). We tested the 19 BioClim variables across the ranges of both species for collinearity using the vifcor function from the usdm package in R (Naimi et al., 2014) with a correlation threshold of 0.7. We excluded the variable with the greater variable inflation factor within overly correlated pairs, resulting in a set of 7 climate variables: mean diurnal temperature range, maximum temperature of the warmest month, mean temperature of the wettest quarter, precipitation of the wettest month, precipitation of the driest month, and precipitation of the coldest quarter.

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

   - **Further details:** We separated the coastlines and bodies of freshwater due to the associations BTGR has with salt water (Post et al., 1996) and GTGR has with freshwater (Selander & Giller, 1961).
   - **Deviations from the preregistered plan:** We used the river, lake, and coastline shapefiles from the Natural Earth database (http://www.naturalearthdata.com/) as the basis for water bodies instead of the USGS National Hydrography database. The USGS National Hydrography database does not differentiate between minor and major bodies of water, resulting in near complete coverage of the contiguous US map with bodies of water. The Natural Earth database incorporates data on rivers and lakes from the North American Environmental Atlas at a 1:10 million scale. The lower resolution data allowed for the computation of distances between the more than 1 million sample points and all water bodies. Natural Earth shapefiles have also been used in other SDMs to calculate distances to water bodies (Mi et al., 2017).

5. **Connectivity:** Distance between points on the northern edge of the range to the nearest uninhabited suitable habitat patch to the north in 1970 compared with the same patches in ~2018. We identified the northern edge of the distribution based on reports on eBird.org from 1968-1970, which resulted in recordings of GTGR in 48 patches and recordings of BTGR in 30 patches. For these patches, we calculated the connectivity (the least cost path) to the nearest uninhabited suitable habitat patch in 1970 and again in ~2018. Given that GTGR are not found in forests and that the elevation limits for GTGR (Selander & Giller, 1961), and observing the sightings of both species on eBird.org, large forests, tall mountain ranges and high elevation geographic features could block or slow the expansion of one or both species into these areas and their surroundings. For each point, we planned to calculate the least cost path between it and the nearest location with grackle presence using the leastcostpath R package (Lewis, 2022). This would allow us to determine the costs involved in a grackle deciding whether to fly around or over a mountain range/forest. We would define the forest and mountain ranges from the land cover and/or elevation maps.

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

Species Distribution Models

One model, including all explanatory variables, was run for GTGR and a separate model wwas run for BTGR. For the explanatory variables, MaxEnt produces a continuous prediction of habitat suitability for each grid cell (0 is least suitable and 1 is most suitable). We planned to use MaxEnt and also use jackknifing procedures to evaluate the relative contribution/importance of different environmental variables to the probability of species occurrence. We planned to optimize the model by trying different regularization coefficient values, which controls how much additional terms are penalized (Maxent's way of protecting against overfitting), and choosing the value that maximizes model fit. Most MaxEnt papers use cross-validation and the area under the curve (AUC) to evaluate model performance, and we planned to do the same.

For every model we fit, we selected one presence and one absence from a 2.5 km hexagonal grid per week to geographically subsample the data and reduce imbalance in observation effort. We then separated the subsampled checklists into a set to train our model (80% of checklists) and a set for model validation (20% of checklists). We used a balanced random forest approach, where absence points are selected at an equal frequency as presence points, which addressed the imbalance in the ratio of presence and absence points (Strimas-Mackey et al., 2020). We accounted for stochasticity in the geographic subsampling, dataset separation, and balanced random forest processes by repeating model creation 10 times independently for each time period and species. We used the ranger package in R to create each model (Wright & Ziegler, 2017).

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

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

Analysis instructions

1. Download and preprocess eBird data. Conduct spatial filtering to account for sampling bias
2. Clean the species occurrence data: remove any uncertain records or geographic outliers
3. Import climactic variables from WorldClim and landscape data from MODIS and crop to region of interest
4. Match environmental data to grackle occurrence records
5. Fit models with maxent to get predicted distributions and estimate importance/contribution of each environmental variable

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

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

- **Deviations from preregistered plan:** For our historic models, we used checklists from 1970-1979, and for the current models we used checklists from 2010-2019 (eBird Basic Dataset, Jan 2021) instead of 1960 and 2018, respectively. The temporal ranges for our dataset were selected for both sufficient sample size and overlap with the period of maximum GTGR range expansion (Wehtje, 2003). To determine the minimum number of samples needed to make our present and historical models comparable, we created species distribution models using subsamples of the 2010-2019 eBird dataset with different numbers of positive observations. We found that retaining >= 300 observations allowed our models to have a ΔAUC of less than 0.1. Using this limit, we set the temporal range for our historical model to 1970-1979 because this range had > 300 observations of both species and contains the most rapid period of GTGR range expansion. We also limited our spatial extent to the contiguous United States to ensure consistent coverage of historic and current environmental data.

Analysis 1 (P1: habitat suitability): has the available habitat for both species increased over time? We fit species distribution models for both species in 1970 and in 2018 and determine for each variable, the range in which grackles are present (we define this as the habitat suitability for each species). Then planned to take these variables and identify which locations in the Americas fall within the grackle-suitable ranges in 1970 and in 2018. We then be able to compare the maps (1970 and 2018) to determine whether the amount of suitable habitat has increased or decreased. If we would be able to find data for these variables before 1970 across the Americas, we would additionally run models using the oldest available data to estimate the range of suitable habitat earlier in their range expansion.

- **Final analysis:** We included the discrimination ability of our SDMs as metrics for how accurately our models predict grackle-suitable habitat and whether one model could be used to predict suitable habitat in both the historic and current time periods for each species. We tested discrimination ability using the 20% of data excluded from the training set of each model. We measured Kappa and AUC for each model. We also used these metrics to quantify model transferability; the ability of a model to perform accurately using datasets independent of the training dataset. Model transferability has been used to measure the consistency of habitat preferences over time (Torres et al., 2015; Wu et al., 2016; Regos et al., 2018). Low transferability would indicate that the backcast or forecast suitability predictions do not accurately represent the species range and that habitat preference changes influenced the likelihood of occurrence. We used the 20% excluded from the opposite time period (1970-1979 for the current backcast and 2010-2019 for the historic forecast) model to test the transferability of our models over time. We also compared the geographic extents of suitable habitat based on the historic and current models for both species to determine whether the models agree on the range dynamics for their species (Fig 2). We used the sensitivity-specificity-sum-maximum threshold (Liu et al., 2005) to classify suitable habitat. We applied the suitability threshold to the contemporary prediction maps and the backcast/forecast prediction maps to generate predicted suitable habitat ranges in 1979 and 2019. We then mapped changes in habitat suitability classifications to determine the range dynamics predicted by each model.

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

Analysis 2 (P1: different habitats): does the range of variables that characterize suitable habitat for GTGR differ from that of BTGR? We fit species distribution models for both species in 2018 to identify the variables that characterize suitable habitat. We planned to examine the raw distributions of these variables from known grackle occurrence points or extract information on how the predicted probability of grackle presence changes across the ranges for each habitat variable. The habitat variables for each species would be visualized in a figure that shows the ranges of each variable and how much the ranges of the variables overlap between the two species or not.

- **Final analysis:** To determine changes in habitat preferences over time, we quantified the importance of each environmental predictor using the Gini index and calculated the partial dependence of each model to the environmental predictors. The Gini index quantifies the classification information gained when a predictor was included in our random forests, with more informative predictors receiving greater values (Strimas-Mackey et al., 2020). We calculated partial dependence by averaging the predicted habitat suitability across 1000 randomly selected checklists where one predictor was set to one of 25 evenly spaced values across its observed range. We repeated the partial dependence calculation across all of the 25 values to create a partial dependence curve for every predictor. To compare partial dependence across predictors, we subtracted all partial dependence values by the minimum habitat suitability for each curve to obtain the marginal effect of each predictor.

- **Deviations from the preregistered plan:** We did not compare the distribution of environmental values at observation points. Instead, we used predictor importance and the partial dependence of habitat suitability on each predictor because they are more informative metrics of habitat breadth. Predictor importance and the partial dependence of habitat suitability on each predictor take into account differences in sampling effort across geographic areas and predictor covariation. Comparing the distribution of environmental values at observation points would not have accounted for these confounding effects and would not take full advantage of the information available through our SDMs.

Analysis 3 (P2: habitat breadth): has the habitat breadth of both species changed over time? We planned to count the number of different land cover categories each species is or was present in for 1970 and 2018. To determine whether this influences their distributions, we would calculate how much area in the Americas is in each land cover category, which would then indicate how much habitat is suitable (based solely on land cover) for each species.

- **Final analysis:** We compared the proportion of observations located on each land cover class in addition to the number of different land cover classes that each species was observed on. Changes in the number of land cover classes either species was observed on would indicate that the habitat breadth had expanded, while changes in the frequency of land cover classes would indicate changes in the preference for different land cover classes.

- **Deviations from the preregistered plan:** We compared species observations from 1970-1979 and 2010-2019 instead of only using observations from 1970 and 2018 to use all data available.

Analysis 4 (P3: habitat connectivity): has the habitat connectivity for both species increased over time? If the connectivity distances are smaller in 2018, this would indicate that habitat connectivity has increased over time. We planned to calculate the least cost path from the northern edge to the nearest suitable habitat patch. To compare the distances between 1970 and 2018, and between the two species, we would run two models where both have the distance as the response variable and a random effect of location to match the location points over time. The explanatory variable for model 1 will be the year (1970, 2018), and for model 2 it would be the species (GTGR, BTGR). If we would be able to find data for these variables before 1970 across the Americas, we would additionally run models using the oldest available data to estimate the range of connected habitat earlier in their range expansion.

- **Final analysis:** We used Circuitscape version 4.0.5 (Anatharaman et al., 2020) to determine whether changes in access to habitat due to connectivity could explain range shifts in BTGR or GTGR. Circuitscape uses electrical circuit theory, treating a landscape as an electrical circuit with different landscape features offering different levels of resistance. We created our resistance surfaces using the results of our SDMs, which is a common practice when experimental data on species movement through a landscape is not available (Beier et al., 2011; Justen et al., 2021; de Sousa Miranda et al., 2021). We converted habitat suitability to resistance using a negative exponential function because this function performs well for avian species (Trainor et al., 2012). Our final resistance surface had values ranging from 1 to 100, with 1 as the minimum resistance value. To calculate connectivity across the entire species range, we used a method that does not require a priori selection of habitat patches. Connectivity estimates are more dependent on node location when close to a node, so we created a buffer surrounding the ranges for each species and selected random points from the perimeter of this buffer for our nodes in Circuitscape (Koen et al., 2014). The buffer removed the correlation between node location and connectivity values within the checklist ranges, resulting in connectivity values that were only dependent on the resistance map. We used a buffer that was 600 km removed from the edge of the checklist ranges and used 18 randomly selected nodes. We then simulated current between each node using the pairwise function in Circuitscape and used the summed accumulated current as our metric of connectivity. We defined regions within the 75th percentile of the accumulated current values as high connectivity areas because the rank of suitability values, rather than the magnitude of suitability values, are the most transferable feature of SDMs (Guillera-Arroita et al., 2015). We chose the 75th percentile as our threshold based on Bonnin et al., (2020).

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

Results

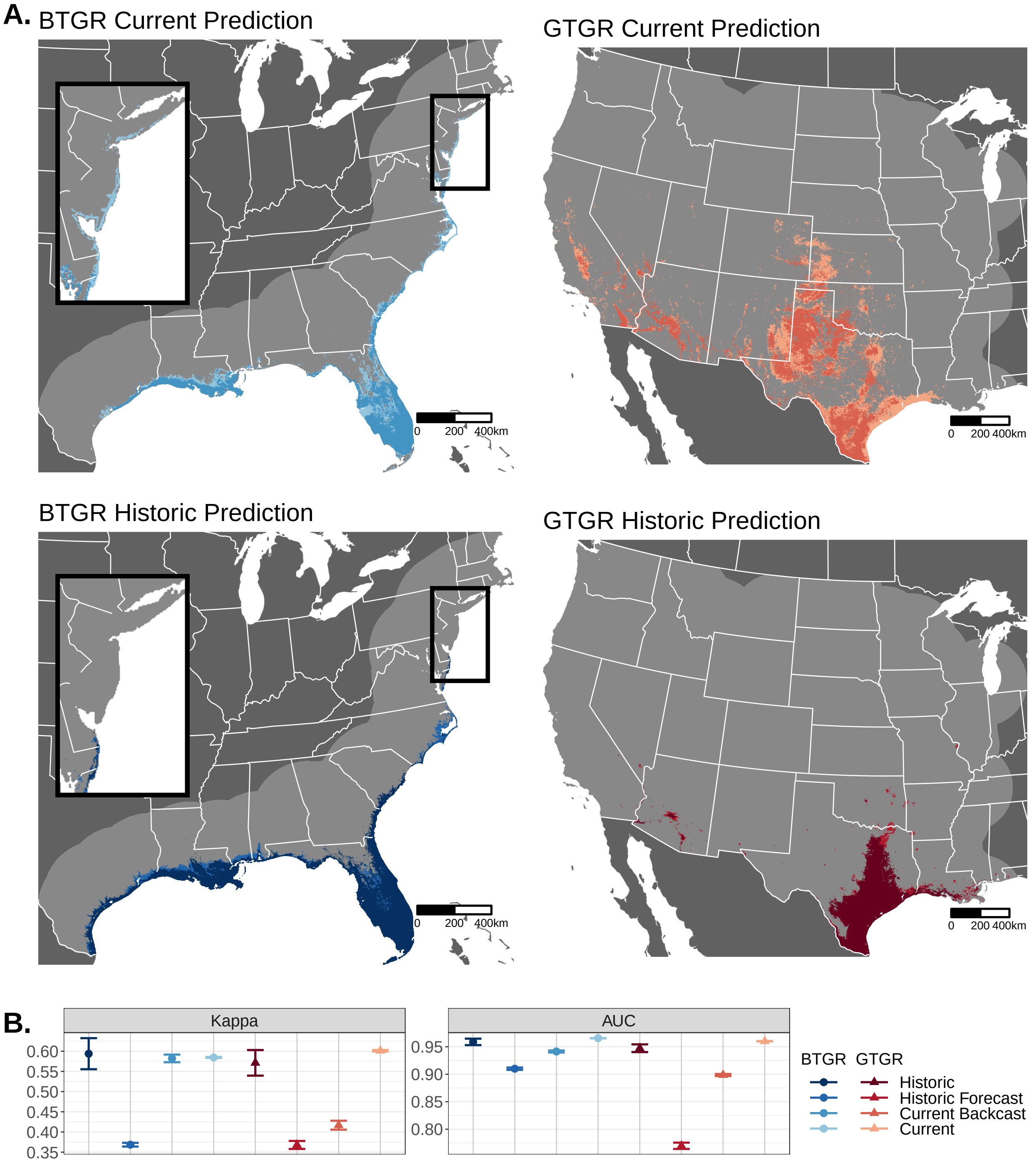

Figure 3. Predicted suitability maps and discrimination ability of SDMs. (A) Maps display areas where predicted suitability is greater than the maximum-sensitivity-specificity thresholds for each model (GTGR Current: 0.4440, BTGR Current: 0.4780, GTGR Historic: 0.4635, BTGR Historic: 0.3935). Darker shaded regions are predictions made using the historic environment (Historic and Current Backcast) and lighter regions are predictions made using the current environment (Historic Forecast and Current). The northern edge of BTGR range is expanded in a map insert for clarity. Overall, the areas of lighter color indicate changes in habitat availability from 1979-2019, as predicted by each model. (B) The ability of each model to predict the presence

or absence of BTGR (blues) or GTGR (reds) using Cohen's kappa (agreement between presence or absence classification for model and true presence or absence) and AUC (area under the sensitivity-specificity curve). The models were tested using either test data excluded from the training data set (historic and current predictions) or test data from the opposing temporal period (backcast and forecast predictions). Error bars signify one standard deviation in the values across 10 replicates. The high values of BTGR Historic, Current Backcast, and Current, and GTGR Historic and Current indicate that these models are accurate, while the lower values of BTGR Historic Forecast and GTGR Historic Forecast and Current Backcast indicate BTGR Historic and GTGR Historic and Current models have poor transferability.

Habitat Availability

We first compared how habitat availability has changed for BTGR and GTGR by predicting habitat suitability across each species range using environmental data from 1979 and 2019. We validated these predictions using presence-absence data set aside from the current and historic datasets. If habitat availability was the most important factor in determining the range dynamics of either species, then the current models should be sufficient to predict the expected range dynamics, the current and historic models should agree on the locations of suitable habitat, and the current models should be transferable to the historic dataset. Alternatively, if changes in habitat preference or connectivity were important for the species range dynamics, the current and historic models should disagree and be mutually non-transferrable.

Habitat availability for BTGR has remained the same across most of its range according to both the current and historic models, and the current model is highly transferable. BTGR remained restricted to the coasts of the Gulf of Mexico and Atlantic Ocean, but habitat suitability increased within the interior of Florida and on the northern edge of the species range, increasing the total suitable area from 180,406 km2 to 199,912 km2 in the historic model, and from 111,218 km2 to 163,243 km2 in the current model (Fig 3A; see Fig S2 for suitability values). The models disagreed on the northern extent of suitable habitat, with the historic model reaching the southern tip of Delaware, while the current model predicted that suitable habitat reached farther north to Long Island. The current model recreated existing species range definitions, including a known break in the species range on the western edge of the Florida panhandle (Post et al., 1996). The current model was also highly transferable, with little difference between the prediction accuracy using the current or historic datasets (ΔKappa = 0, ΔAUC = -0.026, Fig 3B), while the historic model had lower transferability (ΔKappa = -0.226, ΔAUC = -0.049). The accuracy of the current model indicates that environmental change is sufficient to predict changes in habitat suitability, and the low transferability of the historic model could be due to greater geographic bias caused by the smaller sample size (Fig S1). Our models show that the BTGR range has remained largely stable except for an expansion along the northeastern coast of the US and that habitat availability was likely the major driver of range dynamics in BTGR.

Habitat availability for GTGR has expanded, but the current and historical models disagree on the extent and location of this expansion and are mutually non-transferrable. The historic model restricted the GTGR range to 198,175 km2 in southern Texas, matching previous reports of the species range in the 1970s (Wehtje, 2003), and predicted minor reductions in range to 181,281 km2 (Fig 3A, Fig S2). The current model instead predicted suitable habitat existed in both time periods across the known range expansion of GTGR (Wehtje, 2003) in the central and southwestern US, with further expansions within central California, Colorado, Kansas, and southeastern Texas. Suitable habitat expanded from 322,750 km2 in 1979 to 547,694 km2 in 2019, however this expansion included areas that were suitable within the historic model. Neither model had high transferability (current: ΔKappa = -0.184, ΔAUC = -0.061; (historic: ΔKappa = -0.203, ΔAUC = -0.177, Fig 3B). The disagreement between our models indicates that environmental change alone cannot explain the range expansion of GTGR. Each model accurately predicted the species range within its own time period, but failed to predict the known changes in that range. Together, our models predict that the GTGR range has more than doubled in the past 40 years, but indicate that changes to habitat preferences or connectivity likely played a larger role than habitat availability in shaping range dynamics.

Habitat Preferences

We next compared the changes in habitat preferences of BTGR and GTGR by measuring the importance of each environmental predictor to the current and historic models for each species and quantifying the marginal effect that changing the value of these predictors had on habitat suitability. Differences in which predictors are most important or how predictors influence habitat suitability describe differences in the niches predicted by our models. We also quantified how frequently each species was observed on different land cover classes between the current and historic datasets to test for changes in the breadth of land cover classes used by either species.

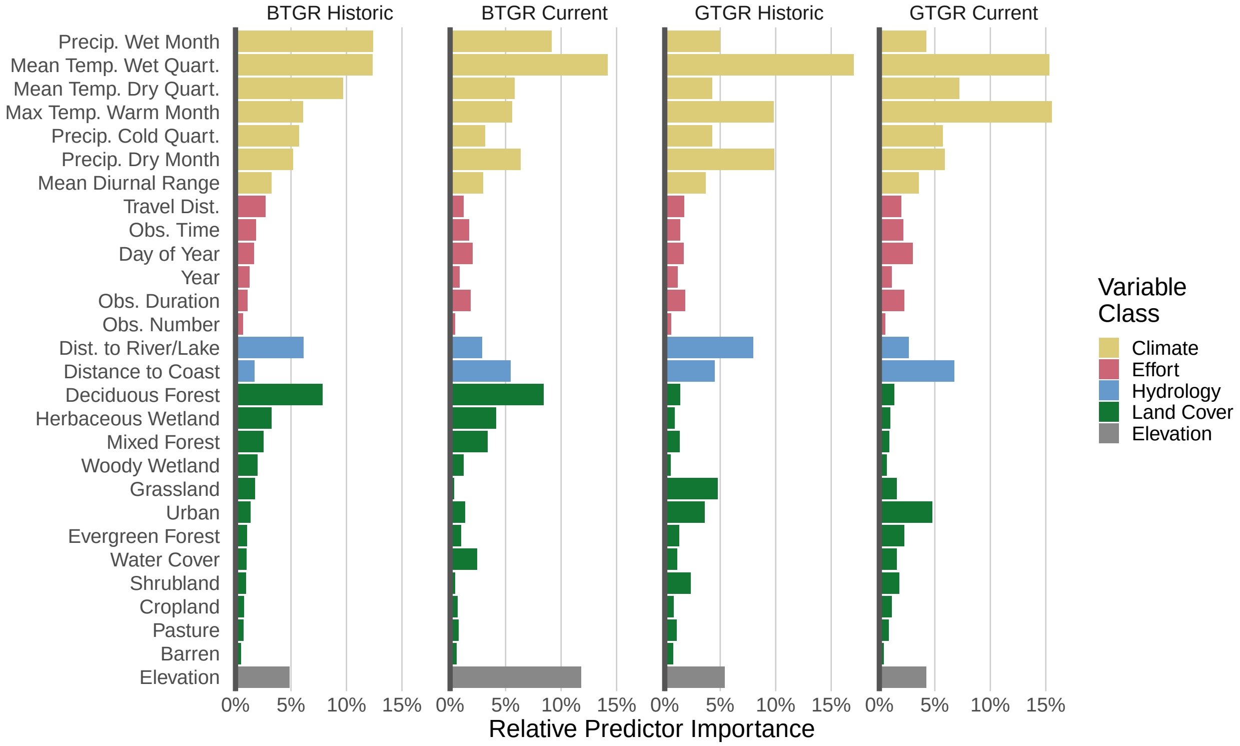

Figure 4. Importance of environmental predictors for BTGR and GTGR historic and current SDMs. Relative predictor importance measures how informative the predictors were for classifying presence or absence points within each model (% total GINI index). The predictor colors indicate whether a predictor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

The most important predictors for the current BTGR model were mean temperature of the wettest quarter (accounting for 14.2% of the total average GINI index), elevation (11.8%), precipitation of the wettest month (9.1%), and deciduous forest land cover (8.4%; Fig 4). Habitat suitability increased as the mean temperature of the wettest quarter and precipitation of the wettest month increased and was highest when both elevation and deciduous forest land cover were close to zero (Fig 5; see Fig S3 for the full set of partial dependence plots). Our model indicates that the ideal habitats for BTGR are warm, low elevation habitats with high precipitation and low forest cover.

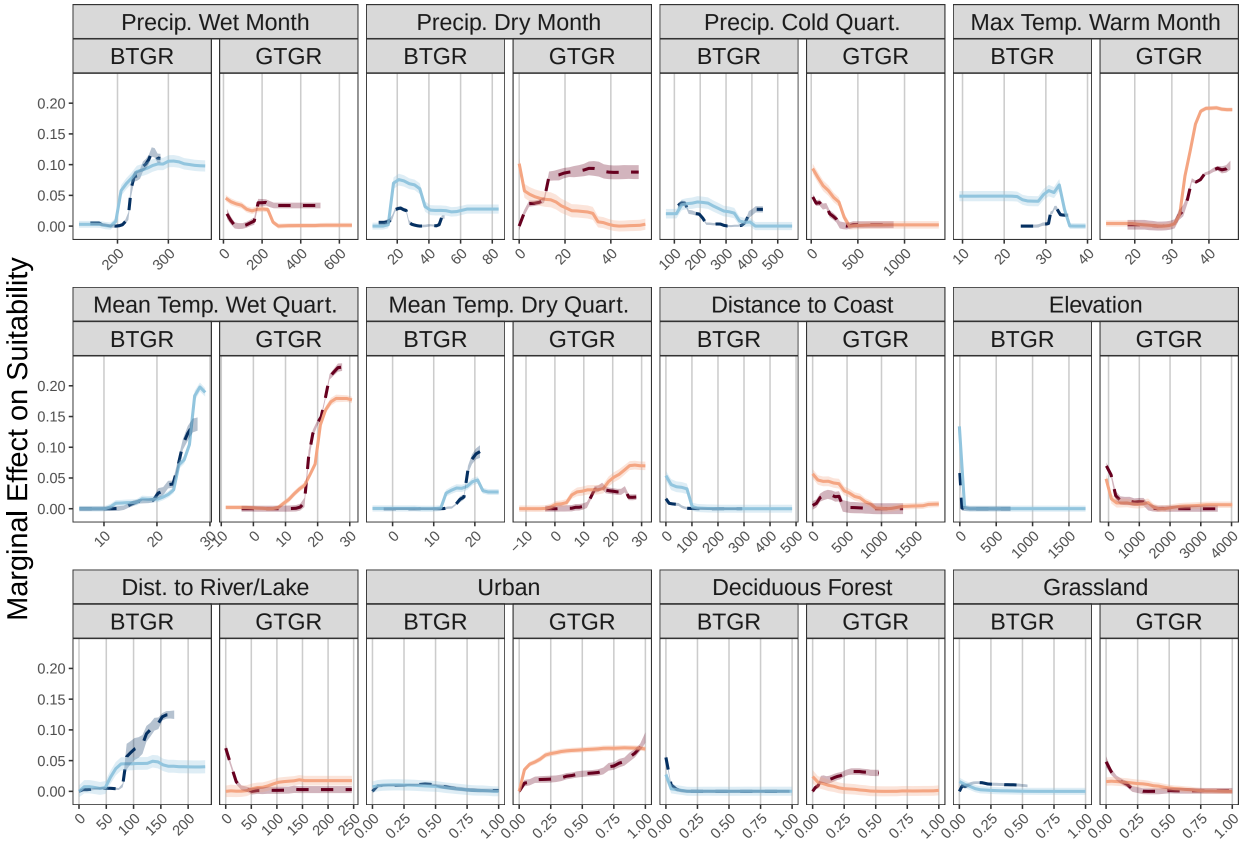

Figure 5. Partial dependence curves for the 12 most important environmental predictors across all models. The curves represent how changing each environmental predictor changes the encounter rate for the modeled species. The historic models are represented by the darker dashed lines and the current models are represented by the lighter solid lines. Shaded regions indicate one standard deviation. The differences between the historic and current models for each species present how the species niche has changed based on our models.

The historic model for BTGR disagreed on the importance and effect of few predictors, supporting niche conservatism in the species. Both the historic and current models placed high importance on the mean temperature in the wettest quarter (12.4%; Fig 4), precipitation of the wettest month (12.4%), and deciduous forest cover (7.9%). However, the historic model prioritized the mean temperature of the driest quarter (9.7%, 5.8% in the current model) and not elevation (4.8%). Among these predictors, only the mean temperature of the driest quarter had a different effect in the historic model than in the current model (Fig 5). Habitat suitability increased as the mean temperature of the driest quarter increased in both models, but the current model predicted that suitability would decrease beyond the observed temperature range of the historic model. Differences between the historic and current models do not indicate that the habitat preferences of BTGR have changed over time.

BTGR was found in every land cover class except deciduous forests and ice/snow in both the historic and current time periods. BTGR was found more often in urban areas in the current time period, and less often in the land cover class that was the second most common in the historic time period: woody wetlands (Fig S4). BTGR was also found less often in croplands, which corresponds with a decrease in croplands across the checklist range. We found no evidence of any change in habitat breadth based on land cover classes for BTGR, agreeing with the results of our SDMs.

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

The historic model for GTGR disagreed on the importance and effect of several predictors, supporting a niche shift for the species. The historic model agreed with the current model on the high importance of the maximum temperature of the warmest month (9.8%, Fig 4) and mean temperature of the wettest quarter (17.0%). However, the historic model prioritized the precipitation in the driest month (9.9% vs. 5.9% in the current model) and the distance to fresh water (7.9% vs. 2.7% in the current model), and not the distance to coasts (4.5%) nor the mean temperature in the driest quarter (4.3%). Habitat suitability increased as precipitation in the driest month increased, while the current model predicted the opposite trend (Fig 5). Habitat suitability was also greatest near fresh water, while the current model predicted little effect of the distance to fresh water. The two models also disagree on which land cover class was most important for GTGR. Urban cover was most important for the current model (4.8% vs. 3.6% in the historic model), while grassland cover (4.7% vs. 1.5% in the current model) was most important for the historic model. While habitat suitability increased as urban cover increased for both models, the current model reached its maximum suitability by 25% urban cover, while the historic model did not reach similar suitability until almost 100% urban cover. The faster rate of suitability increase in the current model indicates that GTGR can use a wide variety of urban habitats, from moderate to highly urbanized areas, while the historic model indicates that GTGR only prefer highly urbanized habitat. Our models indicate that GTGR has shifted toward more arid habitat with greater variability in urban cover.

GTGR was found in every land cover class except deciduous forests, mixed forests, and ice/snow in the historic sample, and every land cover class except deciduous forests and ice/snow in the current sample. There were more GTGR observations in the current sample on urban areas, croplands, and grasslands and less observations in water, shrublands, pastures, and evergreen forests (Fig S4). While the most common land cover classes GTGR was found to have shifted, there was no evidence that GTGR has expanded the breadth of land cover classes it could occupy. These results are consistent with our SDMs, which found the greatest change in preferences for climate factors.

Connectivity

To determine whether changes in connectivity between habitat patches could explain the rapid expansion of GTGR but not BTGR, we estimated the change in accumulated current across the range of each species between 1979 and 2019. Accumulated current summarizes the amount of movement through a cell, thus cells with higher current values are more suitable for movement and increase connectivity. We binned current values into high or low connectivity using the 75th percentile (Bonnin et al., 2020). Most cells within the 75th percentile of current values based on the 1979 resistance surface remained within the 75th percentile for both species.

Connectivity decreased for BTGR along the interior portion of its range (farther from the coasts) in the southern Atlantic states and the southern coast of Texas (Fig S5). However, connectivity increased along the Florida panhandle, the northern coast of North Carolina, and the areas surrounding New York City (New York State, New Jersey, and Connecticut). There were no isolated patches of high connectivity for BTGR, and changes in connectivity did not connect or isolate any habitat patches. Our model does not support connectivity changes contributing to the range dynamics of BTGR.

Connectivity decreased for GTGR within the state of Arizona and along the northern extreme of the cells within the 75th percentile (Oregon, Nevada, Colorado, and Kansas). However, connectivity increased along the eastern extreme (Texas and Oklahoma) and the northern edges in Arizona and New Mexico (Fig S5). Only one region of high connectivity in Montana was isolated from the core of connected cells, and no areas became isolated or connected between 1979 and 2019. Similar to BTGR, our model does not support connectivity changes contributing to the range dynamics of GTGR.

Discussion

We investigated how changes in habitat availability, habitat breadth, and connectivity contributed to differential range dynamics in a sister-species pair. We found that the rapidly-expanding GTGR has increased their habitat breadth in the past 40 years, whereas BTGR goes where there is available habitat, which is consistent with the hypothesis that changes in behavioral traits may facilitate GTGR's geographic range expansion (Fig 1). We found that the range dynamics of BTGR could be explained by changes in habitat availability due to climate change. The current GTGR niche contains more arid climate conditions and is less dependent on bodies of fresh water than in the past. Meanwhile, climate change in the northern extreme of BTGR range increased the area of suitable habitat, matching observed expansions of the species in that area. We found no evidence that changes in connectivity could have connected isolated patches of suitable habitat for either species.

Our current BTGR model is consistent with past work showing that BTGR is highly restricted to coastal areas, and that an expansion into northern coastal areas could be due to climate changes. BTGR rarely occurs far from saltwater in the northern portion of their range, but can nest inland across Florida (Selander & Giller, 1961; Post et al., 1996). Our current model recreated this distribution and predicted the elevation and distance to coastline as highly important environmental limitations. The historical model did not recreate the same high suitability within the interior of Florida and had both elevation and distance to coastlines as less important. However, our historic model also had lower transferability and could have reduced accuracy due to a low sample size, which can inflate the impact of geographic bias in samples (Elith et al., 2010; Anderson & Gonzalez, 2011; Guillera-Arroita et al., 2016; Yates et al., 2018). Both models predict increased suitability in the northern portion of the species range, which matches past observations (Selander & Giller, 1961) and general trends observed in several bird species that track their optimal conditions as anthropogenic climate change has altered environments (Vitousek et al., 1997; Thomas, 2010; Tomiolo & Ward, 2018).

The changes in species range we found in GTGR matched those predicted by previous researchers, but we found that the range expansion was primarily due to changes in the climate niche expanded into rather than land cover preferences. Selander & Giller (1961) note that, along the northern range edge, GTGR has expanded into new arid prairie habitat but was highly restricted to human settlements and farms in these areas. GTGR requires access to open habitat and standing water across their range (Selander & Giller, 1961), and human land use change and irrigation could meet these needs. Our models did find that GTGR preferred habitat close to bodies of freshwater in the historic but not the current time period, suggesting that GTGR can now survive farther from open water. The current GTGR model also predicted higher suitability in areas with more cropland and pasture, but neither land cover class had high predictor importance. Instead, precipitation in the wettest and driest months marked the greatest difference between the current and historic models. Wehtje (2003) proposed that lower nest predation and abundant food in human modified environments could allow GTGR to support populations within otherwise suboptimal climate conditions. GTGR could use the same land cover classes in both time periods, but current populations have novel ways to use human altered environments to expand their climate niche.

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

Our results demonstrate vastly different niche dynamics within closely related species and illustrate the divergent responses species can have to anthropogenic change. Phylogenetic signal of niche conservatism is strongest within short evolutionary timescales (Pearman et al., 2008), yet we found distinct niches for sister-species ~2 million years diverged (Powell et al., 2008) and evidence for a further niche shift within one species. The distinct niche dynamic of each species also represents opposing responses to anthropogenic change: BTGR has shifted its range in response to climate change, while the rapidly expanding GTGR has acclimated to new climates possibly due to human land-use change. Species with similar responses to BTGR could be more vulnerable to future climate change (Thomas, 2010), while GTGR parallels rapidly expanding introduced species, despite being native to North America (Peer, 2011). The habitat breadth expansion of GTGR also confounds our ability to project how the species range will change in the future, and could have implications for a projected expansion in the common grackle (*Quiscalus quiscalus*, Capainolo et al., 2021). Identifying the mechanism of range dynamics in both species expands the knowledge of the complex and changing factors that shape species ranges globally.

The high accuracy of our SDMs when cross validated on their own datasets and the transferability of the current BTGR model support the use of SDMs as tools to study how species ranges change over time. While improving model transferability remains a challenge for SDMs (Vaughan & Ormerod, 2005; Yates et al., 2018), using a combination of climate and land use data can improve model accuracy and transferability in some situations (Elith & Graham, 2009; Regos et al., 2019). Our results also stress the importance of testing model transferability before assuming niche conservatism for all species. While niche conservatism is a common pattern across species, assuming species will retain their niche through time can limit the usefulness of SDMs. When model transferability is tested, SDMs become a more effective tool for studying species ranges to both understand fundamental questions in ecology and evolution and set conservation priorities in the face of ongoing anthropogenic changes (Elith et al., 2010; Grenoullet & Comte, 2014; Sofaer et al., 2018; Chen et al., 2018).

SDMs are accompanied by several limitations that are important to consider. SDMs are correlative in nature and are susceptible to biases in sample and parameter selection (Regos et al., 2019; Sofaer et al., 2018). Here, we used geographic undersampling and a balanced random forest design to reduce the impact of sampling bias and selected both climate and land cover parameters to include biologically relevant variables, but other potentially causative variables could remain. Recent work promotes the inclusion of biotic factors in SDMs such as pathogen, predator, or competitor species because interspecific dynamics can play a major role in determining species ranges (Gaston, 2003; Paquette & Hargreaves, 2021; Stephan et al., 2021). Future work could investigate how the presence of nest predators such as the fish crow (*Corvus ossifragus*), which overlaps in range with BTGR but not GTGR (Post et al., 1996), could also prevent BTGR from expanding its range.

In conclusion, this investigation found support for the hypothesis that the range expansion of GTGR and range stability of BTGR is an example of niche shifting and niche conservatism in a sister-species pair. Despite the many similarities between these two species, they occupy distinct niches and had divergent responses to anthropogenic change. While BTGR range conformed to climate change, GTGR expanded across new human-altered environments. Our results are consistent with the hypothesis that behavioral flexibility may have allowed GTGR to expand their range by using new habitats. Further studies on how ecology, gene flow, and behavior created such different niche dynamics will shed light on the mechanisms that limited the BTGR but not the GTGR. This work will elucidate the role of behavior in shaping species ranges in our rapidly changing world.

Data Availability

All data used in this study are available at the following KNB repository:

Jeremy Summers. The role of climate change and niche shifts in divergent range dynamics of a sister-species pair. urn:node:KNB. urn:uuid:60291cb3-139e-43e2-ac8a-3182993b2e3f.

All code used in in this study is available at the following github repository: https://github.com/jtsummers53/grackle_SDM_project

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Conflict of Interest Disclosure

We, the authors, declare we have no financial conflict of interest relating to the content of this article. CJ Logan and D Lukas are Recommenders at PCI Ecology, and CJ Logan is on the Managing Board at PCI Ecology.

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Supplemental Figures

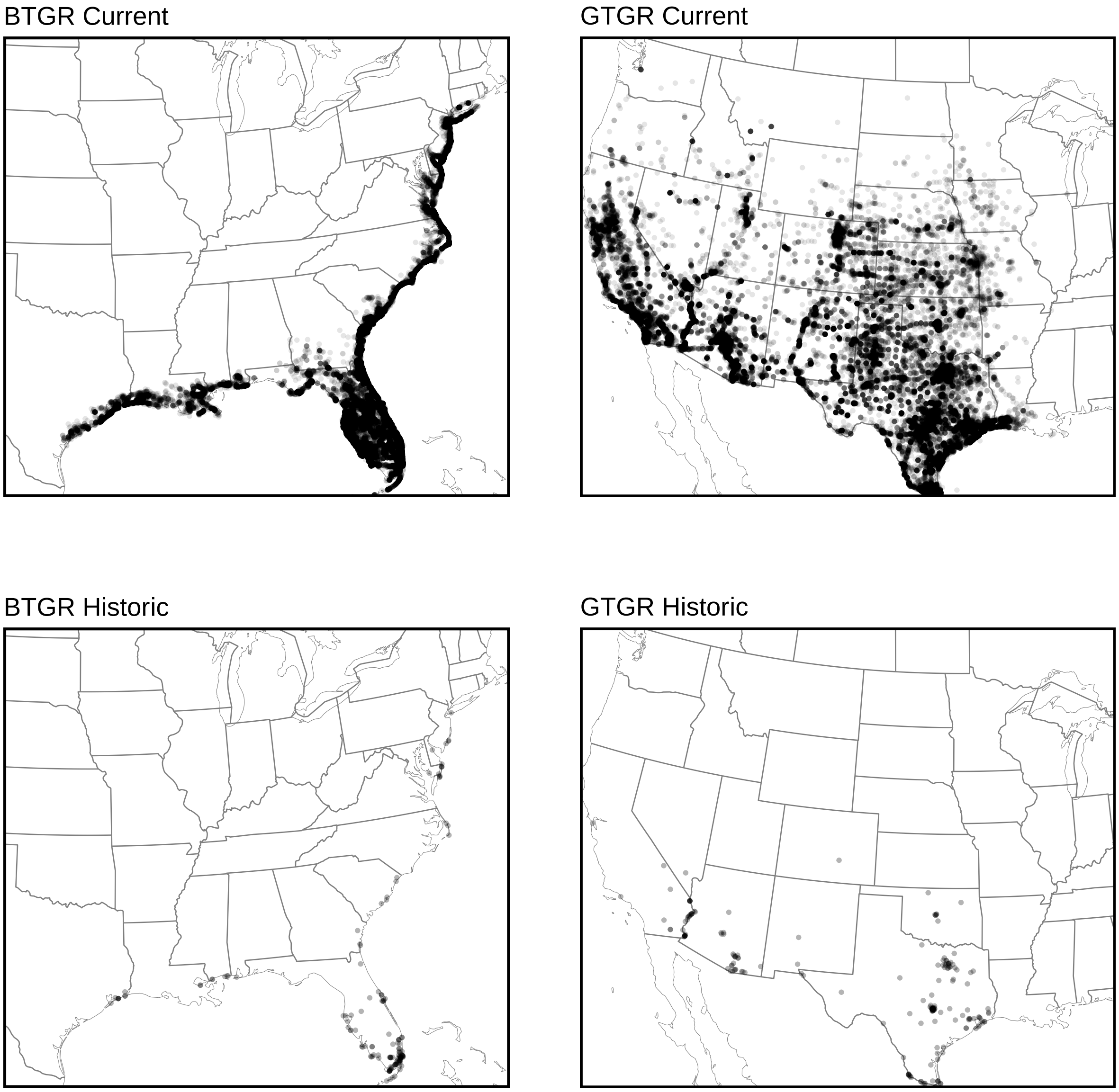

Figure S1. Map of observation locations for BTGR or GTGR from Historic (1970-1979) and Current (2010-2019) eBird records. These locations are filtered for record quality.

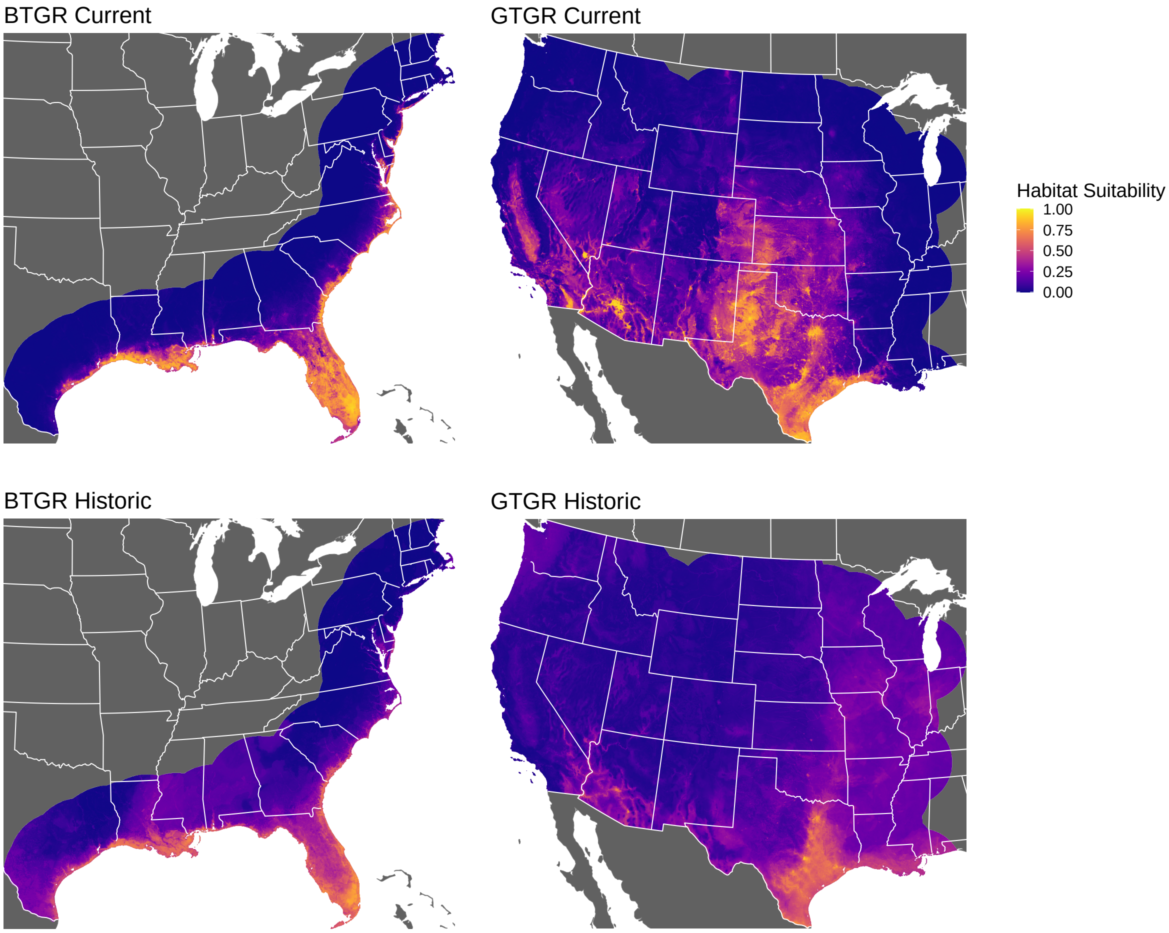

Figure S2. Predicted habitat suitability using random forest models. Brighter colors indicate higher habitat suitability. The presented results are the average of the 10 replicates.

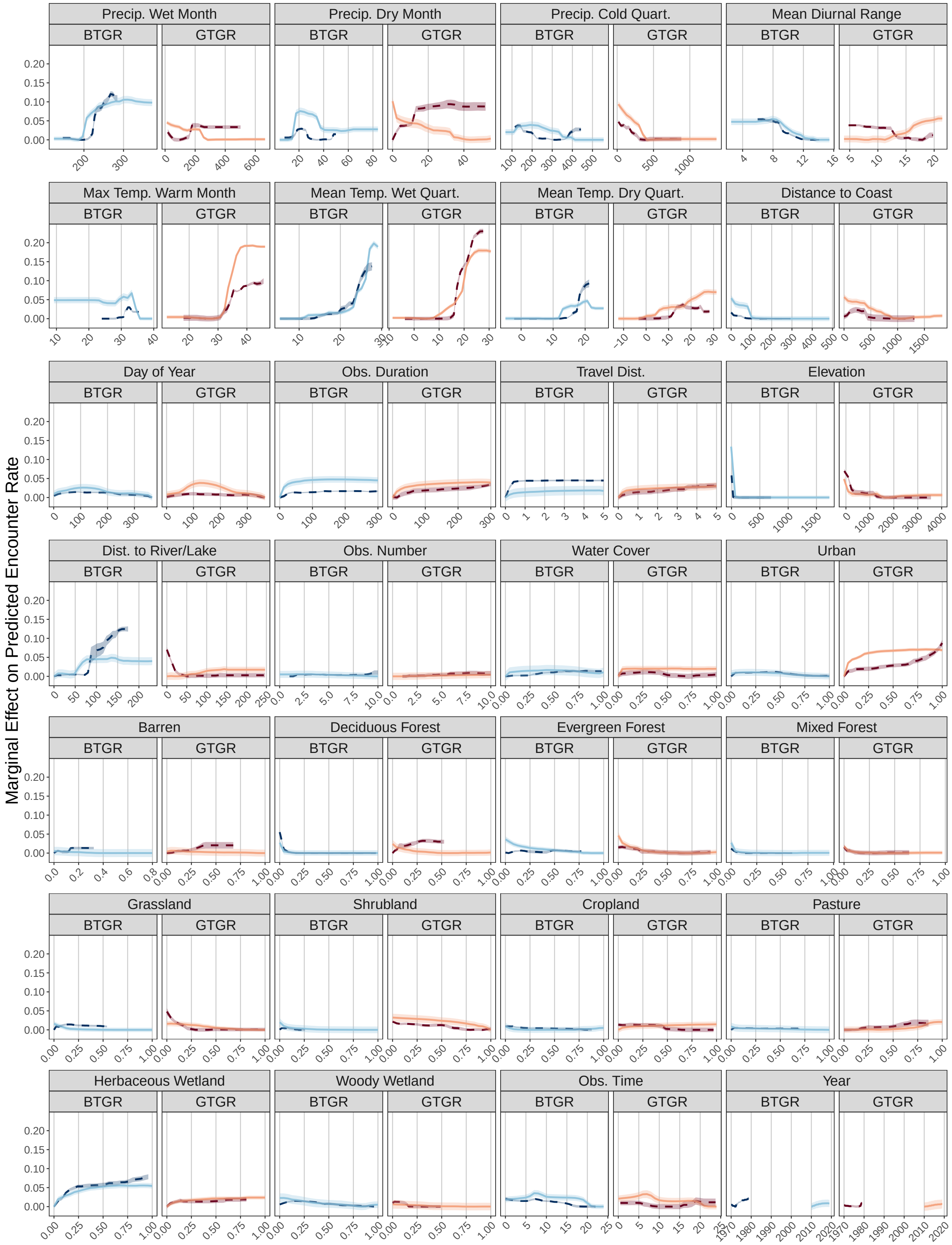

Figure S3. Partial dependence curves for environmental predictors across all models. The curves represent how changing each environmental predictor changes the encounter rate for the modeled species. The historic models are represented by the darker dashed lines and the current models are represented by the lighter solid lines. Shaded regions indicate one standard deviation. The differences between the historic and current models for each species present how the species niche has changed based on our models.

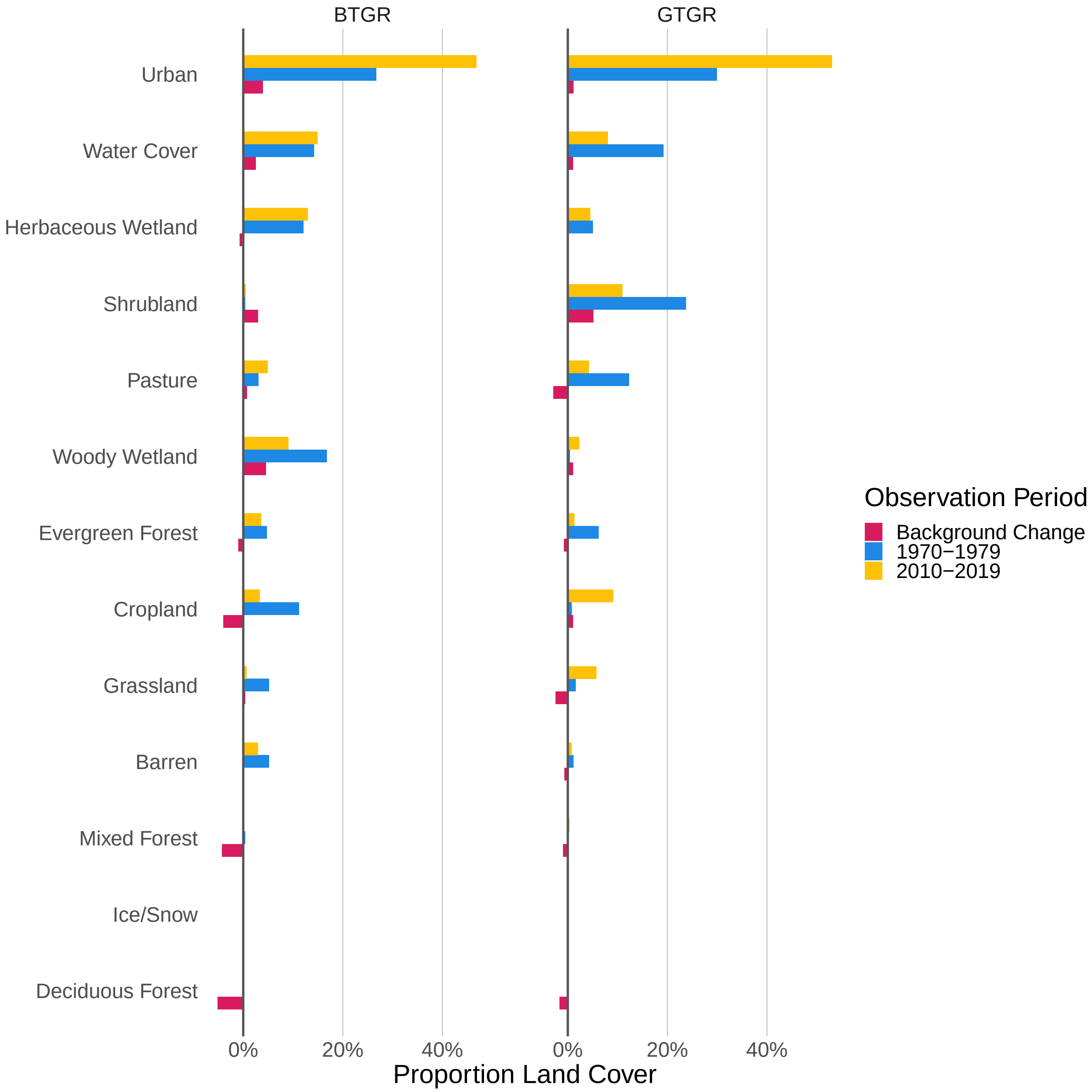

Figure S4. Habitat breadth of BTGR and GTGR in 1970-1979 and 2010-2019 compared to the change in percent land cover area between each year range. The proportion of land cover measures what percent of observations for each species were located on each land cover class in the corresponding time frame.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

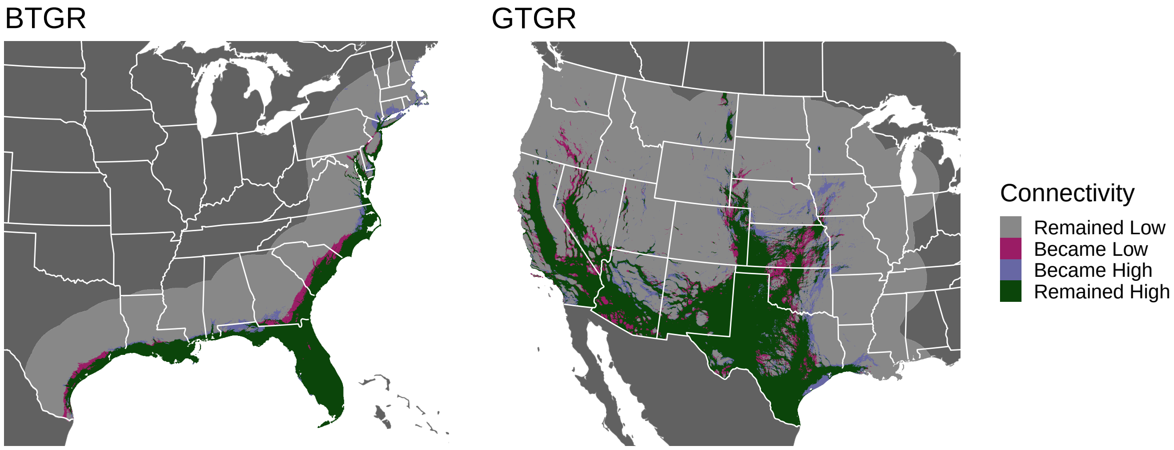

Figure S5. Change in connectivity between 1979 and 2019 measured as change in accumulated current. Current values were divided into high and low categories based on whether the values were above or below the 75th percentile of current values for each map. Colors indicate whether the current values remained low between the two time steps (gray), went from high to low (magenta), went from low to high (blue), or remained high (green). The darker gray color indicates areas outside the range where checklists were selected for each species, and were excluded from the connectivity analysis. The regions that have remained highly connected are continuous for both species, which supports that changes in connectivity are not responsible for range changes in either species.