Recommender: Revisions needed in your preprint

Dear authors,

Thank you very much for a very nice study. It has now been reviewed by two recognized researchers working on the field. As both reviewers say, and I agree, your study is very valuable and is well-conducted. However, the reviewers have also raised some interesting points that should be addressed or clarified and I think that accounting for them will increase the quality of the preprint.

Therefore, I invite you to respond to these comments and to revise your text accordingly.

I am looking forward your revised text,

Esther

We are thankful to both reviewers and to you for the positive feedback and helpful comments. Please find our replies to the reviewers' comments below (replies are in italics). In response to the reviewers' feedback, we have done an additional analysis and have significantly rewritten our manuscript to improve clarity, reduce over-interpretation of our results, and provide additional explanations and details of our methods. We have uploaded an updated version of our manuscript to EcoEvoRxiv at the provided doi link (https://doi.org/10.32942/osf.io/879pe), as well as a track-changes version uploaded along with our reply that presents all changes to the text relative to the original manuscript.

We hope that you find the revised version to be improved by the review process!

All our best,

Jeremy Summers, Dieter Lukas, Corina J. Logan, Nancy Chen

Reviews

Reviewed by anonymous reviewer, 01 Aug 2022 02:30

General comments:
This is a reliable and transparent study that compares the land cover and climate predictors of the geographic ranges of two similar bird species, only one of which has undergone a dramatic expansion of its geographic range over the past 50 years. The study compares correlations between site occupancy and environmental (land cover and climate) variables in the recent past and in the 1970s. The geographic range data were generated through the citizen science program 'eBird'.

Although the data and the analyses appear reliable based on my expertise (which is limited, see below), the authors sometimes overstate the possible scope of their inferences by making claims that fail to sufficiently acknowledge that correlation does not equal causation. It is clear that the authors understand this limitation of their data – they simply need to be more consistent in acknowledging these limitations (I point out some specific cases below). I lack expertise in the statistical methods used in this manuscript to quantify habitat associations. I therefore am not providing specific comments regarding these methods.

> *We thank the reviewer for their time in providing thoughtful feedback for our manuscript. We agree that the original language of the manuscript did not sufficiently communicate the limitations of our work due to the correlative nature of our analyses. We have addressed specific instances of causal language (see comment responses below) and have reviewed the entire text to ensure our conclusions remain within the bounds of our methods.*

Specific comments:
12: it seems to me that the pronoun for 'species' is 'it' rather than 'they'. If you want to use 'they', we suggest you switch from the singular 'species' to something like "members of a species" (here and elsewhere in the manuscript)

> *We have changed our use of "species" to singular throughout the manuscript. Thank you.*

75: I prefer to avoid acronyms, as they hinder understanding by readers who are not reading the manuscript from start to finish (because these readers often miss the explanation of the acronym; we think most readers fall into this category). And even those people reading from start to finish may sometimes have trouble remembering acronyms.

> *We have replaced the acronyms GTGR and BTGR with the full common name (great-tailed grackle and boat-tailed grackle) throughout the manuscript. We keep these acronyms in the figures to prevent large areas of text dominating the figures and define them in each figure legend.*

95: with regards to your first hypothesis (changes in habitat availability), does this encompass grackles responding slowly to something like the increase in urban parkland etc. that happened long ago? This is an increase in habitat availability, but if rate of population growth of grackles is low, the response to this increase in habitat might not happen until long after the new habitat is available.

> *We thank the reviewer for raising this important point. Our analysis cannot distinguish the role of time lags in range expansion, which means that factors predating our study period could also explain the observed range expansion. Our habitat availability test does investigate whether the environment within the expanded range has become more similar to the environment within the pre-expansion range of the species. However, changes to the expansion range that pre-date our study are not captured by our habitat availability test, preventing us from directly associating the range expansion with specific environmental changes. Currently there are no presence-absence based methods that can entirely account for temporal lag in species ranges. Including spatial autocorrelation between species*

observations within models can potentially improve model fit in situations with temporal lag (see De Marco P, Diniz-Filho JAF, Bini LM. 2008. Spatial analysis improves species distribution modeling during range shift. Biology Letters. 4(5):577-580) but it appears models generally perform similarly with or without spatial autocorrelation (see Thibaud E, Petitpierre B, Broennimann O, Davison AC, Guisan A. 2014. Methods in Ecology and Evolution. 5:947-955). The niche similarity test we performed partially addresses the issue by determining that there are significant environmental differences between the pre- and post-expansion ranges. This analysis only compared analogous environments between the historic and current datasets, which provides support that the great-tailed grackle did not occupy the same environments historically despite those environments occurring within 600 km of known species occurrences. Overall, our methods cannot examine the role of lagged effects of environmental change predating 1970, but they can describe the realized niche occupied by the great-tailed grackle over time. We added this caveat to the Discussion (see lines 754-758).

103: how do you distinguish a change in breadth of what is tolerated (niche) from a change in breadth in what is occupied (if you were evaluating a variable that correlated with habitat occupancy but which is NOT part of the niche)?

Our species distribution models capture the realized niches for the species, which includes effects of what is physiologically tolerated (fundamental niche), what is within dispersal abilities, and what is within biotic constraints for the species. The realized niche corresponds to what is occupied by the species, while the fundamental niche corresponds to what is tolerated. Our species distribution models thus cannot differentiate changes in fundamental niche, dispersal, or biotic interactions that could have contributed to changes in species ranges. However, our connectivity models partially address the dispersal abilities of the species, and we find that neither species had areas of their range isolated by low suitability habitat. However, our connectivity models do not account for changes in the dispersal abilities or behavior themselves, which remains an alternative explanation for the current range expansion. We have adjusted the language of our manuscript (see line 102 as an example) to focus on our modeling of the realized niche of the species, and we define what we mean by realized niche in the context of our manuscript (see lines 35-40).

107-108 “we plan to conduct “ - is this wording left over from your pre-registration? Now that you have completed the work, shouldn’t you now say something like “we conducted “?

Yes, this wording is left over from the pre-registration; thank you for pointing out this error. We have changed the wording to “we conducted”.

132: I subscribe to the perspective that figures (together with their legends) should be able to stand independent of the paper. For that reason, we encourage you to define SDM in the legend.

We agree and have defined SDM as well as GTGR and BTGR in the figure legends.

141: thank you for explaining deviations from your pre-registration

Thank you.

167: “occurs “ should be “occurred”

Done.

328: typo: “We then be able to”

Thank you, done.

236: please define/ explain MaxEnt -not everyone reading this paper will be familiar with this method

Very good point, thank you. We have added a brief explanation of MaxEnt and a relevant citation (see line 263).

264: same for random forest

We have added a brief explanation of random forests and how they are used to create species distribution models (see line 277).

321: your reasons for selecting this range of dates (1970-79) is sound - sufficient sample size is essential. However, given that this was a period of rapid range expansion, it seems that any new habitat preferences (for instance, a switch to urban habitats) would have happened at the start of this range expansion (and therefore before many of these observations were recorded). I think this is an important point to acknowledge.

We have added a statement in the Discussion (see line 752 and the previously mentioned lines 754-758) that acknowledges that the temporal limits of our study could influence our results due to a lagged relationship between environmental change and the observed species ranges.

340: you state the “low transferability” would mean “habitat preference changes”, but this is not necessarily the case. In fact, all it would take for this to not be the case would be a change in a correlation between occurrence and a modeled variable that does not actually influence occurrence (and surely it is inevitable that many variables show changing correlations with species occurrences as ranges shift or environments change)

Thank you for raising this important point. We have changed the statement (see line 372-374) to specify that low transferability indicates that the relationship between occurrence probability and our environmental predictors have changed, without concluding that changes in habitat preference are the only cause for this change.

353: “does the range of variables that characterize suitable habitat “ - “suitable” should be changed to “occupied”. This change should be made throughout since we cannot assume that unoccupied habitat is unsuitable. Further, occupancy does not demonstrate suitability, as organisms can occupy unsuitable habitats in which they do not breed (‘sinks’)

This is a good point that indicates that we should better define our use of "suitable habitat" in the manuscript. We have added a statement that we are referring to habitat suitability as the "predicted suitability of habitat for occupancy by the modeled species" (see line 107), which matches the use of suitability in other species distribution model papers (see for example Guillera-Arroita et al., 2015; Jiménez-Valverde et al., 2020). This definition of suitability is useful in our manuscript to describe areas with high predicted occupancy likelihood that may or may not truly be occupied by the modeled species. These areas may be "suitable for occupancy" due to environmental similarity to occupied sites, but may not be occupied due to dispersal limitations or environmental or biotic factors not included in our models.

359: similarly, we cannot assume that correlation equals preference

We agree that "preferences" infers too much causality in our results. We have substituted "habitat preference" with "habitat association" throughout to communicate the correlative nature of our results (see lines 371, 385, 392 as examples).

385: again, I think you are overstating your ability to infer preference from these data

We have removed the reference to habitat preferences here and instead stated that the data indicate whether the species occupy novel habitat over time.

410: I do not understand this explanation about the buffer removing correlation among points. Is it possible to add more explanation here?

We have added further explanation for the purpose of our buffer when selecting nodes for the connectivity models (see line 472-479). This explanation states that because circuit-theory based connectivity models calculate connectivity as the amount of current flowing through a cell as current moves from one node to another, the cells surrounding nodes will have elevated current values. By placing nodes offset from the ranges we wish to calculate connectivity over, we prevent the elevated current values near nodes from interfering with our connectivity values across our area of interest. The appropriate distance was determined by testing multiple buffer distances until connectivity values within the area of interest no longer depended on the location of the random nodes along the buffer.

474: what about the possibility that habitat availability had already changed (certain types of anthropogenic habitat had already expanded) but that there was a lag in response from the birds (for instance due to limited population growth rates)? This hypothesis seems reasonable when we recognize that the variables in the models are correlates of occurrence rather than known targets of preference.

We have edited our concluding sentence in this section to better articulate the alternative hypotheses based on our habitat availability results (see line 548). We emphasize that our results indicate that the habitat associations captured by our models have changed over time (not concluding that these associations capture the true niche for the great-tailed grackle) and that factors such as occupying novel

habitat, temporal lag, or dispersal barriers could have resulted in these associations changing.

513: it seems that local patterns of habitat availability could influence which habitats individuals are more likely to be found in at the local scale (for instance, a habitat that is less desirable might only be occupied locally if more desirable habitat is locally rare). Therefore, a shift in geographic range or a change in habitats over time could potentially change the average proportional habitat occupancy at the scale of the entire range even in the absence of a shift in preference

We agree with this interpretation of our land cover occupancy results. To better compare if observed habitat occupancy change could be due to chance we have completed an additional test, a niche similarity test, that compares the occupancy rates across environments between our historic and current samples (see lines 418-442). This test takes into account the abundance of the environmental variables across the sample, capturing both sampling bias and inequality in habitat presence. This new test does not state whether preference has truly changed, but tests whether observed habitat usage has changed against a null expectation of consistent habitat use. We found that the area of environmental space occupied by the great-tailed grackle is significantly different between the historic and current time periods, while no significant difference was found for the boat-tailed grackle. Together, these results support our hypothesis that the great-tailed grackle, but not the boat-tailed grackle, expanded its realized niche over time.

545: I think you are missing a word in this line

Thank you, we have changed the text in this line (see line 630).

545: “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.” I have several concerns here.
As a behavioral ecologist, I am concerned with the use of the word “preferences”. As you acknowledge elsewhere in the paper, based on the available data, I know about use, not preference.

Also, the hypothesis that the range shift might represent a change in preference for climate does not seem strongly supported even at a correlative level. A range expansion as extensive as that of the great-tailed grackle will inevitably lead to occupation of a broader set of climates. This will presumably almost inevitably lead to changes in the climate predictors of occurrence even in the absence of a causal role of the correlated climate variables.

Additionally, although I have no objection to your use of relativity coarse land cover categories (for obvious practical reasons), I suspect that these categories may miss habitat variability that is important to great-tailed grackles. My informal experience with this species in the Great Plains and Intermountain West of North America is that local populations often occupy very local sites that differ only modestly from the surrounding landscape where great-tailed grackles are absent. Thus, it seems possible that individuals of this species may be responding to more subtle variation in habitat than that captured by the land cover

categories in your analyses. So, I would be hesitant to draw conclusions about the impact of land cover in general (even if you can draw conclusions about broad categories of land cover).

> *We entirely agree with your concerns surrounding the presentation of our results, and have adjusted our language throughout the manuscript (see previous response on our use of "habitat associations") to clearly articulate that our results present a change in apparent habitat use rather than preference. We have removed our reference to the importance of land cover as compared to climate factors. The niche similarity test that we have added to our manuscript also provides more robust correlational evidence in support of our hypothesis that the great-tailed grackle is occupying novel habitat across its range expansion. Because this test only compares analogous environments between the 600 km radius of great-tailed grackle observations in the historic and current time periods, the niche similarity test supports that the great-tailed grackle is occupying distinct habitat types that also existed near known observations in the historic period, but were unoccupied at that time. We have also expanded our section in the Discussion (see line 706-712) where we present possible interpretations of our results. We agree that the apparent widening in habitat use of the great-tailed grackle could be caused by several factors, and that the use of local scale resources not captured by our models could likely contribute to the wider set of climate conditions that the great-tailed grackle occurs in. Under this interpretation, the fundamental niche of the great-tailed grackle has remained the same, but the realized niche contains a larger set of environments due to human-caused environmental change facilitating expansion of the great-tailed grackle into new areas.*

569: I suggest you avoid causal language ("contributed to") and instead describe your results in correlative terms.

> *We have replaced "contributed to the range dynamics of" with "does not predict major connectivity changes across the range of" to clarify that our results are model predictions of landscape connectivity, and to not assume a causal link between our predictions and the range dynamics of either species.*

592: again, please avoid making causal claims that exceed the scope of your data

> *We have removed our reference to the range expansion being "caused" by any of the observed relationships with habitat use.*

603: I like this hypothesis (that site occupancy depends on an interaction between variables). I don't know how easily this could be modeled using your current methods, but it would be interesting to explore.

> *We have expanded slightly on this hypothesis, as we agree it follows as the simplest explanation. However, we added a note that our current data could not determine the cause of the increase in habitat use of the great-tailed grackle, and suggest that local-scale habitat use assays across the species range would better explore this hypothesis. Given that our current data includes 32 total variables when counting all land cover classes, we did not include interaction terms to prevent overfitting caused*

by variable inflation. Our results provide an a priori reason to further investigate interactions between urban land cover, bioclimatic variables, and freshwater sources. Future work would also benefit from using fine-scale data on human-created water sources to more directly test this hypothesis.

605: I don't think you can claim that great-tailed grackles have expanded their niche. It seems equally plausible that they have simply expanded (and are continuing to expand) to occupy a relatively newly created habitat that they would have chosen and thrived in had it been available 500 years ago.

We agree that we cannot conclude from our results that the fundamental niche of the great-tailed grackle has changed, but both the situation you describe and our results present the great-tailed grackle expanding its realized niche. The realized niche of a species is limited by the habitats available, unlike the fundamental niche which encompasses all conditions the species could tolerate. Within the situation you have described, a species distribution model would also perform poorly because the current range includes non-analogous environments, environments that our historic species distribution model had not encountered. We limited our niche similarity test to analogous environments to allow for comparisons between the habitats occupied during the historic and current time periods and found that the great-tailed grackle, but not the boat-tailed grackle, is occupying novel habitat in the current time period. We have also edited the language of our manuscript to specify that we are modeling the realized niche of our species and how that differs from the fundamental niche (lines 759-762).

637: I like this paragraph, but right now you focus on one theme of your topic sentence, but largely ignore another (the limits of inference from this sort of correlative model)

We have expanded this paragraph to detail the factors that contribute to the realized niche of a species and which factors we could, or could not capture with our methods. These factors include temporal lag in the ability of our focal species to occupy suitable sites, the physiology and behavior of our study species, dispersal ability of our study species, and biotic interactions that may exclude or promote occupancy of our study species. We also acknowledge that we may have excluded biologically relevant environmental factors in our species distribution models or may have missed relevant trends in factors that pre-date our study period. We also added that our connectivity models were used under an assumption of a consistent niche and dispersal ability for our study species.

647: I remain unconvinced regarding the difference in niche shifts between these two species. Maybe one just has a narrower climate tolerance. we like a simple explanation as a default

Our species distribution models and niche similarity tests indicate that the boat-tailed grackle occupies the same habitats over time while the great-tailed grackle has occupied novel habitat in the current time period. These differences constitute a shift in the realized niche of the great-tailed grackle, and no niche shift in the boat-tailed grackle. We agree that there are likely significant differences in the environmental tolerances for either species, and these differences could explain why the boat-tailed

grackle has not occupied new habitat over time. The fundamental niche for both species could have remained the same over time, and the narrower climate tolerance of the boat-tailed grackle would have prevented the species from expanding its realized niche. However, we did find that the boat-tailed grackle has changed the geographic areas it occupies over time; the species occupies more northerly areas in the current time period when compared to the historic time period. Unlike the great-tailed grackle, these newly occupied areas are within the same environmental space as areas previously occupied by the boat-tailed grackle, and became more similar to the historic range of the boat-tailed grackle over time. While we cannot determine the reason that the boat-tailed grackle continues to occupy the same habitats over time, the two species have experienced different degrees of realized niche shifts, with the boat-tailed grackle occupying novel geographic areas, and the great-tailed grackle occupying both novel geographic areas and novel environmental conditions. We have rephrased this section to focus on the different patterns of habitat use change that our data does support.

650: we agree that the results of this work are consistent with the hypothesis that behavioral flexibility has allowed the range expansion of the great-tailed grackle. However, it is not clear that the work presented here does much to evaluate this hypothesis.

We agree that our work does not evaluate this hypothesis, and instead focus on how proposed future work will address remaining questions on the observed widening of habitat use in the great-tailed grackle. The current article was one piece of a larger preregistration (http://corinalogan.com/Preregistrations/gxpopbehaviorhabitat.html) where Question 4 focuses on testing and comparing behavioral flexibility in great- and boat-tailed grackles, which will fill in another piece of the answer to this question. The latter work is in progress so we will have more answers soon, which will appear in a different article.

655: thanks for making your data and code publicly available. we would encourage you to also make your code available somewhere in addition to GitHub (someplace with a mission that includes long-term archiving)

We uploaded our data and code to a KNB repository (see line 790).

Reviewed by anonymous reviewer, 01 Sep 2022 13:56

The preprint by Summers et al attempts to assess the role of competing processes on the range dynamics of two sister bird species. Overall, the questions are relevant, the case study is adequate to answer those questions, and the methods are in the right direction. we have though a number of comments, most of them related to the second prediction (changes in habitat breadth(niche)):

We thank the review for their positive assessment of our questions and methods and appreciate the feedback provided on improving the framing of our manuscript and proposing an additional test to better evaluate our second hypothesis. We have completed thorough revisions that specify our focus on the realized niche of our focal

species, clarify the presentation of our hypotheses, and have completed a niche similarity test to better evaluate changes in habitat occupancy over time.

1. The authors use “habitat breadth” to refer to the “niche” of the species, which is unnecessarily confusing and awkward. I am sure the authors know that in Ecology “niche (or habitat) breadth” has a very specific, and well-settled, meaning. Roughly, it refers to the amount of different environmental conditions that can be tolerated by a species, and leads to the gradient of habitat specialist-generalists. Two species can have completely different niches and however have the same niche breadth. In this sense we would ask the authors to substitute “habitat breath” for “niche”.

We agree that limiting our terminology to “niche” increases the clarity of our manuscript. We have removed the usage of “habitat breadth” and replaced this term with “niche”, where appropriate. When describing observed changes in which habitats are occupied by either species, we changed “habitat breadth” to “habitat usage” because this term is more strictly accurate than “niche”. When referring to the habitat preferences described by our species distribution models, we use the term “realized niche”, and define this term in the text (see lines 35-40) to maintain clarity and accuracy.

2. A related and subsequent issue is the differentiation between realized vs fundamental niche (or any other niche subset from Soberon´s niche BAM diagram). The authors should make some discussion on the Methods section (at least) on the niche “type” they are estimating in their work, and with Random Forest in particular. Because RF uses presence/absence they might be estimating something closer to the realized that the fundamental niche.

We have added references to the realized niche throughout the paper (see lines 759-762), as we are indeed measuring the realized niche using our methods. The reviewer is correct that the niche shift that we observe is a shift in the realized niche (matching the definition of niche shift found in Guisan et al., 2014). Our Random Forest models cannot account for changes in dispersal ability or in biotic interactions, thus these factors will constrain which environmental conditions our models will predict are suitable for each species, resulting in the realized niche rather than the fundamental niche.

3. A shift in the environmental conditions tolerated by a species can be due to a change in the pure physiological tolerances or due to the participation of both physiological and behavioral changes (due to phenotypic plasticity or not). I am completely out of my expertise here, but we would ask the author to tackle this issue in a clearer way. The authors do that in L47-64, but this paragraph is not concluding or clear.

We have added references to studies that investigated changes in niches leading to range shifts linked to changes in physiological tolerances. These studies indicate that changes in physiological tolerances often occur over long time spans, presumably not fast enough to explain the recent range expansion of great-tailed grackles. We argue that behavioral flexibility might operate over faster time spans, which is why we are focusing on this trait in this manuscript. We have added these explanations in lines 48-52.

4. On the Analysis section it is confusing to me the relationship between the three predictions made in the Introduction (L92-109) and the four analysis proposed. I do not understand the meaning of P1-P4, with P1 having two different meanings (“habitat suitability” and “different habitats” on L324 and L352 respectively). The subheaders of the Results section also have different names than the predictions. It would be easier if each prediction had its own analysis subsection that should be named consistently across all sections of the ms. Also, the term “prediction” for L92-109 is also confusing, since they are hypotheses rather than predictions.

> *We agree that the presentation of our hypotheses in the introduction can be more clear. We have changed the labeling for our hypotheses from “prediction” to “hypothesis” and have made the names for each hypothesis match the labeling used in our results section. We have also added a paragraph to the introduction that overviews how each analysis addresses the hypotheses that we present.*

5. Habitat availability hypothesis is adequately addressed by means of a Random Forest model. However, the niche shift hypothesis is admittedly addressed is a weaker way. At least in the way it is presented right now. In the present way the main evidence of a niche shift is the differences in the relative importance of environmental predictors, which is slightly indirect and not a test by itself. It would be needed a null model to make it a test. The second line of evidence is the proportion of occurrences of different habitat types, but in my opinion this approach is too coarse (and it is not a test either). The third line of evidence are the results from P1 (Fig. 3). we would explicitly add it as a line of evidence in this section, and not only of Habitat availability hypothesis. In my opinion, a more solid approach to test for a niche shift would be to use the existing methods to describe niche shift, particularly those proposed by Broennimann).

> *Thank you for the suggestion of additional tests to better investigate our niche shift hypothesis. We have added a niche similarity test (see lines 418-442) to determine if either species occupies significantly different habitat between the historic and current distributions. This test compares the observed environmental differences between the historic and current ranges to a simulated null model. We used Warren’s I as our primary metric to compare niche overlap due to potential bias in Schoerner’s D that would systematically underestimate overlap within our simulations caused by the large difference in range for the historic and current great-tailed grackle observations (Rödder & Engler, 2011). We found no significant difference in the niche occupied by the boat-tailed grackle over time, but did find a significant difference in the niche occupied by the great-tailed grackle over time, supporting our hypothesis that the great-tailed grackle, but not the boat-tailed grackle, has expanded the habitats it occupies as part of its range expansion.*

6. I find that the connectivity hypothesis needs some conceptual reworking. If landscape connectivity changes it is because the availability of suitable habitat has changed, which in turn it is because environmental conditions have changed (P1) or because the species niche have changed (P2) or both. In my opinion connectivity analysis and discussion should be better framed within changes in climate or niche.

We have added text (see line 118 and see line 459) to clarify that our landscape connectivity hypothesis is dependent on environmental change (Hypothesis 1) and not changes to the species niche (Hypothesis 2). Our landscape connectivity analysis uses suitability estimates from our current models only, thus testing the case that if each species could occupy their current realized niches, would past environmental conditions limit the ranges for each species due to landscape heterogeneity.

7. Finally, the authors use “niche conservatism” as one of the framing concepts of the ms. For me, it is not convincing at all. Niche conservatism it is not just that the niche of a given species does not change in a few decades in comparison to another that it does. It is the general tendency of species to retain their ancestral niche attributes and the implications this has in a wide array of dimensions (speciation, biogeography, etc, see Wiens and Graham 2005). As such we would suggest to play down the role of niche conservatism in this work.

We agree that the framing of “niche conservatism” that we used in the original manuscript did not include the typical usage of the term, and we re-framed the introduction of the manuscript to focus on changes in the realized niche of species as “niche shifts”. This change has helped clarify the manuscript as a whole, as our three main hypotheses (that an increase in previously suitable habitat, a change in habitat use, or an increase in connectivity of suitable habitat contributed to the range expansion of the great-tailed grackle) most directly deal with environmental change alone, change in the realized niche (which includes factors such as dispersal ability and biotic interactions which we could not isolate with our analyses), and change in habitat connectivity due to environmental change.