




Peer Community In Ecology

Drivers of range expansion in a pair of sister grackle species

Esther Sebastián González  based on peer reviews by 2 anonymous reviewers

Jeremy Summers, Dieter Lukas, Corina J. Logan, Nancy Chen (2023) The role of climate change and niche shifts in divergent range dynamics of a sister-species pair. *EcoEvoRxiv*, ver. 3, peer-reviewed and recommended by Peer Community in Ecology.

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The spatial distribution of a species is driven by both biotic and abiotic factors that may change over time (Soberón & Nakamura, 2009; Paquette & Hargreaves, 2021). Therefore, species ranges are dynamic, especially in humanized landscapes where changes occur at high speeds (Sirén & Morelli, 2020). The distribution of many species is being reduced because of human impacts; however, some species are expanding their distributions, even over their niche (Lustenhouwer & Parker, 2022). One of the factors that may lead to a geographic niche expansion is behavioral flexibility (Mikhalevich et al., 2017), but the mechanisms determining range expansion through behavioral changes are not fully understood.

The PCI Ecology study by Summers et al. (2023) uses a very large database on the current and historic distribution of two species of grackles that have shown different trends in their distribution. The great-tailed grackle has largely expanded its range over the 20th century, while the range of the boat-tailed grackle has remained very similar. They take advantage of this differential response in the distribution of the two species and run several analyses to test whether it was a change in habitat availability, in the realized niche, in habitat connectivity or in the other traits or conditions that previously limited the species range, what is driving the observed distribution of the species. The study finds a change in the niche of great-tailed grackle, consistent with the high behavioral flexibility of the species.

The two reviewers and I have seen a lot of value in this study because 1) it addresses a very timely question, especially in the current changing world; 2) it is a first step to better understanding if behavioral attributes may affect species' ability to change their niche; 3) it contrasts the results using several complementary statistical analyses, reinforcing their conclusions; 4) it is based on the preregistration Logan et al (2021), and any deviations from it are carefully explained and justified in the text and 5) the limitations of the study have

been carefully discussed. It remains to know if the boat-tailed grackle has more limited behavioral flexibility than the great-tailed grackle, further confirming the results of this study. **References**

Logan CJ, McCune KB, Chen N, Lukas D (2021) Implementing a rapid geographic range expansion - the role of behavior and habitat changes. <http://corinalogan.com/Preregistrations/gxpopbehaviorhabitat.html>

Lustenhouwer N, Parker IM (2022) Beyond tracking climate: Niche shifts during native range expansion and their implications for novel invasions. *Journal of Biogeography*, 49, 1481–1493. <https://doi.org/10.1111/jbi.14395>

Mikhalevich I, Powell R, Logan C (2017) Is behavioural flexibility evidence of cognitive complexity? How evolution can inform comparative cognition. *Interface Focus*, 7, 20160121. <https://doi.org/10.1098/rsfs.2016.0121>

Paquette A, Hargreaves AL (2021) Biotic interactions are more often important at species' warm versus cool range edges. *Ecology Letters*, 24, 2427–2438. <https://doi.org/10.1111/ele.13864>

Sirén APK, Morelli TL (2020) Interactive range-limit theory (iRLT): An extension for predicting range shifts. *Journal of Animal Ecology*, 89, 940–954. <https://doi.org/10.1111/1365-2656.13150>

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Reviews

Evaluation round #2

DOI or URL of the preprint: <https://doi.org/10.32942/osf.io/879pe>

Version of the preprint: 2

Authors' reply, 27 January 2023

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Decision by **Esther Sebastián González** , posted 22 December 2022, validated 22 December 2022

Minor changes needed before recommendation

Dear authors,

Please, I am very sorry this took so long. I was waiting for a second review that finally did not come. However, one of the reviewers was able to re-read your study and is very happy with the changes performed. He/she only has some minor comments that I think can help to improve a little bit more the quality of the paper.

On my side, I only have a few minor comments to add to those of the reviewer:

- Lines 61-64. Is there any empirical evidence of this? If so, please add a reference, it is not clear to me if this is something that is known of something you expect.
- Lines 80-99. You specify in the abstract that the great-tailed grackle is more

- Behaviorally flexible than the boat-tailed grackle, but this information is not included in the introduction, and I think it is important to fully understand your story. Maybe you can add a brief sentence about it in this paragraph.
 - Lines 153-154. You briefly explain how you tested hypotheses 1-4, why didn't you include hypothesis 4 here? Maybe you can add a brief explanation also.
 - Line 225: There is a missing space in "usedata"
Looking forward to a revised version.
- Esther

Reviewed by anonymous reviewer 2, 01 December 2022

The authors have improved the manuscript in important ways, and I am satisfied with the revision. Most important, the authors are much more consistent in acknowledging the limitations associated with their correlative data set.

I include some specific suggestions below. Most of these are minor.

16 – it seems that you should mention interior Florida here also

57 – is the word "certain" needed here? It seems misleading to me. How about just "some number of generations"?

63 – "thus therefore" – it seems one of these should be deleted

125 – This wording is a bit confusing / awkward: "This hypothesis would support the hypothesis"
Maybe change to something like "Support for this hypothesis would be consistent with the broader hypothesis..."
or "Support for this hypothesis would, by extension, also support the hypothesis that..."

225 – "usedata" to "use data"

354-355 – you state here that this time period precedes the rapid range expansion, but earlier, you state that rapid range expansion happened within this range (1967-1977 – line 193)

421 – change "are significant when compared to a null space" to "differ significantly compared to a null space"

562 – This wording: "would indicate that the species has novel habitat associations" implies a comparison between species, but I think you are comparing between time periods within species. Therefore, shouldn't this sentence read something like "would indicate that the species has novel habitat associations in one time period relative to the other time period"

671 – "into previously occupied" should, I believe, be "into previously unoccupied"

713 – I suggest inserting "realized" before "niche"

723-733 – in this paragraph you could integrate some of the growing evidence that a relatively large subset of bird species do not seem to be changing their geographic ranges in response to climate change (at least in simple, predictable ways). For instance:

Currie and Venne DOI: 10.1111/geb.12538

Neate-Clegg et al. DOI: 10.1111/csp2.291

782 – insert comma after "boat-tailed grackle"

Evaluation round #1

DOI or URL of the preprint: <https://doi.org/10.32942/osf.io/879pe>

Version of the preprint: 1

Authors' reply, 19 November 2022

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Decision by [Esther Sebastián González](#) , posted 02 September 2022

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

Reviewed by anonymous reviewer 2, 01 August 2022

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.

Specific comments:

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

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; I think most readers fall into this category). And even those people reading from start to finish may sometimes have trouble remembering acronyms.

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.

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)?

107-108 “we plan to conduct “ - is this wording left over from you pre-registration? Now that you have completed the work, shouldn't you now say something like “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, I encourage you to define SDM in the legend.

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

167: “occurs “ should be “occurred”

328: typo: “We then be able to”

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

264: same for random forest

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.

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)

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’)

359: similarly, we cannot assume that correlation equals preference

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

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

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.

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

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

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, we 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 relatively 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).

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

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

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.

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.

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)

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

650: I 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.

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

Reviewed by anonymous reviewer 1, 01 September 2022

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. I have though a number of comments, most of them related to the second prediction (changes in habitat breadth(niche)):

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 I would ask the authors to substitute “habitat breath” for “niche”.

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 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 I 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.

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 have also different names than the predictions. It would be easier if each prediction have 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.

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). I 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).

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.

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 I would suggest to play down the role of niche conservatism in this work.