Manuscript ECM22-0164 — Response to reviewers

January 26, 2023

To the editorial board,

Thank you for the opportunity to submit a revision of our manuscript for your consideration. Our major changes include the following:

1. As suggested by Dr. Godoy and Reviewer 1, we have re-framed the article such that readers understand from the Introduction that encroachment at our study site appears stalled. This background information shifts the emphasis from predicting encroachment speed to understanding the mechanisms that explain the apparent stasis, and asking under what conditions encroachment might proceed.

2. As suggested by Reviewer 2, we have broadened our Discussion by connecting our creosotebush study system to other cases of woody encroachment, using the demography-dispersal framework as a unifying lens to understand diverse encroachment systems.

We describe these and other changes in greater detail below, where we reproduce comments from the associate editor and reviewers and provide our point-by-point responses. All of our changes are denoted in the manuscript with Mahogany font. We think the review process has greatly strengthened our manuscript. We hope you agree.

On behalf of myself and all coauthors,
Tom Miller

Response to Dr. Oscar Godoy

Comment 1: *"The main limitation I see and it is in line with the first reviewer is the mismatch between the research questions and the study site. This work aims to test the population mechanisms by which shrub expansion occurs or it is prevented but you acknowledge at the same time at the beginning of the discussion that there is no current dynamics in the system. That is, it has reached a quasi steady state in which neither expansion nor contraction is observed. In sum, it is difficult to marriage the idea that you are going to understand the dynamics of shrub encroachment in an area there has been pushing dynamics in the past but not right now. Because of this fundamental limitation, I strongly believe the manuscript needs to be reconsidered. One potential suggestion could be the following: Shrub encroachment can be pulled or pushed and this occurs by different population mechanisms. However, these processes do not occur continuously, it goes in pulses. In the Chihuahuan desert, it has occurred an expansion during the last century but now it has stopped, and we want to understand why the expansion process is no longer in action as well as to predict future dynamics according to the mechanisms by which the study species (Larrea tridentada) is governed.*

I think this is a more honest perspective of what it is going on in the system and allow the reader to obtain a better view of the current process and the importance of obtaining a mechanistic knowledge to both understand current stationary conditions and predict future expansions. Should you consider this alternative, I would be very happy to reconsidered a careful revised version of the manuscript. "

Response: We have followed the suggestions of Dr. Godoy and Reviewer 1 to re-frame the paper such that the stalled nature of the encroachment wave is presented in the Introduction. This re-framing, summarized in a new Introduction paragraph beginning line 114, shifts the emphasis from predicting encroachment speed to understanding the mechanisms that explain the apparent stasis, and asking under what conditions encroachment might proceed. We have also revised the title to reflect this change.

Response to Reviewer 1

Comment 2: *"This paper attempts to offer a new perspective to shrub encroachment by analysing it from a point of view of population dynamics. Framing the study under this concept, authors bring the idea that shrub encroachment may be pulled or pushed,*

formulating clear and relevant hypothesis in a very intriguing conceptualization. The topic is clearly important, the approach is novel and the manuscript is clear and technically sound and correct."

Response: We appreciate the positive feedback, and the time and effort that the reviewer invested in our paper.

Comment 3: *"That said, this manuscript has one major problem. The whole study is performed in one only site in which the shrub population is actually in an steady state of no expansion (as authors recognised). This is a major conceptual flaw, from my point of view, as it entirely conditions the mechanisms to be tested. Testing which are the mechanisms of expansion of a system that is not expanding yields some results that are not relevant for the study purpose.*

I strongly suggest the authors to re-frame completely the idea and focus it on which are the population dynamics mechanisms of shrublands in quasy-steady state. This is not going to change a lot the relevance and interest of their results, but I think it prevents almost completely the framing into the field of shrub encroachment (maybe dynamics post equilibria of shrub encroachment may make more sense?). As is, the paper is very misleading and leaves the reader a bit flat."

Response: We understand the reviewer's point and we decided to re-frame the introduction such that the "quasi-steady state" of the encroachment wave is provided as background. We have made changes to the Introduction (lines 90, 114) and Discussion (lines 551, 703) to convey this shift. We have moved the re-survey data to Figure 2, described in the Introduction.

Despite the shift in emphasis described above, we continue to use the concepts and literature of shrub encroachment as the entry point to our study. In our opinion, this is the appropriate and necessary frame of reference given the large body of literature documenting historical expansion of creosotebush, both regionally and at our study site, and concerns about future encroachment. We respectfully disagree with the reviewer's assertion that mechanisms of expansion are "not relevant" for a wave that is not presently spreading. That is akin to saying that mechanisms of population growth are not relevant for a population at carrying capacity. Carrying capacity is the special case of population growth where births equal deaths, and similarly, a stalled wave is the special case of expansion in which every step forward is matched by a step backward. For this reason, the demography-dispersal

framework and push/pull concepts remain the appropriate frame of reference for our work. In our revision, we attempted to balance the reviewer's concerns about leaving the reader feeling flat, which we think are fair, with our continued use of shrub encroachment as the study's thematic anchor.

Comment 4: *"I have to recognise in any case that I sincerely enjoyed the paper, I find the approach clearly novel and interesting and the authors never lied to the reader (they correctly discuss why the mechanisms found may not be entirely applicable). Simply, for me it makes little sense to frame the paper under the umbrella of shrub encroachment expansion with the proposed study site. It is a pity, actually. I think the work has potential to be replicated in sites with ongoing shrub expansion, yielding groundbreaking results."*

Response: We are pleased that the reviewer finds our approach novel and interesting, and we agree about the potential to apply this framework more broadly. In response to a similar point from Reviewer 2, we have added new material to the Discussion elaborating on this point (beginning line 673).

Response to Reviewer 2

Comment 5: *"This manuscript by Drees et al. combined observational data from field surveys, seedling transplant experiments, and spatial integral projection models to explain the expansion of creosotebush into Chihuahuan Desert grasslands. Overall, the experiment was well-designed and the manuscript is very well-written. Congratulations to the authors for a nice work, showing that the expansion of creosotebush in this ecosystem is pulled by peak fitness at the leading edge at a slow rate."*

Response: We appreciate this reviewer's positive comments and the time they invested to provide constructive feedback on the manuscript.

Comment 6: *"My only major comment for the authors to consider is to have some discussions about whether these findings/mechanisms presented in this study can be applied to other ecosystems encroached by other species, for example, the encroachment of juniper encroachment in sagebrush steppe, the encroachment of honey mesquite into southern US rangelands, or the encroachment of acacia species into African savannas. If not, then what other factors may play, in terms of differences in expansion compared to creosotebush encroachment? Adding this in the Discussion section may, to some extent, broaden the scope of this manuscript."*

Response: We appreciate this suggestion and we enjoyed the opportunity to dig into other case studies from the literature. We have added a new paragraph to the discussion (beginning line 673) that draws on the literature to provide points of similarity and contrast with other woody encroachment systems. We also use this paragraph to highlight the value of our demography-dispersal framework as a broadly applicable approach to diverse systems, as Reviewer 1 suggested.

Comment 7: *"Line 14, What kinds of observational data?"*

Response: We have revised this sentence to clarify (line 14).

Comment 8: *"Line 23, "showing little to no change in spatial extent", it would be nice to put a number in cm here to show the expansion of shrub cover over 12 years, supporting the model predicted rate (8 cm/yr)."*

Response: Because shrub cover was estimated every 10 meters, this is the minimum increment at which we could detect change in the shrub boundary. Therefore are not confident that a rate of change from these data would be very meaningful, since we think the little change that occurred is consistent with measurement error (now mentioned at line 673).

SCOTT: check this response. At first blush it looks like the difference between 2001 and 2013 could be attributed to the tape being a little off. But 10 meters seems like a long way off. Is it possible that the apparent advance of the farthest shrubs is real??

Comment 9: *"Line 45, A more recent citation here would be, Morford, S. L., Allred, B. W., Twidwell, D., Jones, M. O., Maestas, J. D., Roberts, C. P., & Naugle, D. E. (2022). Herbaceous production lost to tree encroachment in United States rangelands. Journal of Applied Ecology."*

Response: Added – thank you.

Comment 10: *"Line 67, Whether interspecific interactions also play roles in determining the demographic rates? For example, the competition of creosotebush and black grama for resources at the front edge."*

Response: This paragraph introduces the ideas of positive or negative density feedbacks, which in this context relate strictly to intra-specific processes. For this reason

we have not modified this sentence. However, we address the reviewer's broader point at line 646, where we discuss inter-specific interactions with resident grasses.

Comment 11: *"Lines 159-166, the authors may provide additional information on grazing intensity, fire regimes, drought, and other environmental conditions of this site, at least during the period of this study. As the authors have indicated in Lines 104-106, all these factors have been believed to drive the expansion of creosotebush. If these factors changed quite a lot during this study, then the test of seed dispersal and density-dependent demography as alternative drivers may not be validated."*

Response: Our study area did not experience cattle grazing or fire during the study period, and study years included one unusually wet and one unusually dry monsoon season. This information has been added beginning at line 178.

Comment 12: *"Lines 263, 277, 290, 298, I am wondering whether the authors could provide references or why different parameters were modeled with different distributions (e.g., Bernoulli random, Gaussian random, etc.)"*

Response: We have added information to each of these sections to provide some rationale for these choices (lines 278, 292, 314, 327). However, these are very standard distributions used in modeling demographic vital rates, described in detail in the methods papers that we cite, so we do not elaborate very much here.

Comment 13: *"Lines 462-466, what are the criteria you used to define the size of shrubs (large vs small)? It seems that you did not have this information in the Methods and Materials, or I missed this point."*

Response: This information was embedded in the figure legend so we have now moved it to the main text (line 468). For visualization purposes only, data were split into four size groups evenly spaced from minimum to maximum size.

Comment 14: *"Line 504, seed dispersal is one thing, but seed germination rate may also play a significant role in recruitment."*

Response: We agree. Our recruitment analysis combines seed germination and early seedling survival into a single step, since we lack data that would allow us to parse things more finely. We now clarify this (line 324).

Comment 15: *"Line 642, I guess this is quite important in terms of the establish-*

ment of woody seedlings, especially considering the interspecific competition between woody and herbaceous species. Sankaran, M., Ratnam, J., & Hanan, N. P. (2004). Tree–grass coexistence in savannas revisited–insights from an examination of assumptions and mechanisms invoked in existing models. Ecology Letters, 7(6), 480-490."

Response: We agree this is potentially important and we appreciate the suggested reference, which we have added (line 651).

Comment 16: *"Figure 1, Please indicate the unit for grass cover on the right y-axis."*

Response: The revised figure now indicates that grass cover is mentioned as the proportion of ground covered by black grama.

Comment 17: *"Figure 2, I would recommend having a figure legend to show what different colors indicate. In addition, why points in Panel A and C were in different sizes? What does this indicate?"*

Response: We have added a legend to Figure 2 as recommended. The figure caption in our previous submission failed to indicate that point size in panels A and C represent the sample size associated with each binned mean. We have fixed this in our resubmission.