Peer Community In Evolutionary Biology

Phenotypic evolution during range expansions is contingent on connectivity and density dependence

Inês Fragata *based on peer reviews by 3 anonymous reviewers*

Cite this recommendation as:
Fragata, I. (2021) Phenotypic evolution during range expansions is contingent on connectivity and density dependence. *Peer Community in Evolutionary Biology*, 100133. https://doi.org/10.24072/pci.evolbiol.100133

Understanding the mechanisms underlying range expansions is key for predicting species distributions in response to environmental changes (such as global warming) and managing the global expansion of invasive species (Parmesan 2006; Suarez & Tsutsui 2008). Traditionally, two types of ecological processes were studied as essential in shaping range expansion: dispersal and population growth. However, ecology and evolution are intertwined in range expansions, as phenotypic evolution of traits involved in demographic and dispersal patterns and processes can affect and be affected by ecological dynamics, representing a full eco-evolutionary loop (Williams et al. 2019; Miller et al. 2020).

Range expansions can be characterized by the type of population growth and dispersal, divided into pushed or pulled range expansions. Species that have high dispersal and high population growth at low densities present pulled range expansions (pulled by individuals from the edge populations). In contrast, populations presenting increased growth rate at intermediate densities (due to Allee effects - Allee & Bowen 1932; i.e. where growth rate decreases at lower densities) and high dispersal at high densities present pushed range expansions (driven by individuals from core and intermediate populations) (Gandhi et al. 2016). Importantly, the type of expansion is expected to have very different consequences on the genetic (and therefore) phenotypic composition of core and edge populations. Specifically, genetic variability is expected to be lower in populations experiencing pulled expansions and higher in populations involved in pushed expansions (Gandhi et al. 2016; Miller et al. 2020). However, it is not always possible to distinguish between pulled and pushed expansions, as variation in speed and shape can overlap between the two types. In addition, it is difficult to experimentally

manipulate the strength of the Allee effect to create pushed versus pulled expansions. Thus, several critical predictions regarding the genetic and phenotypic composition of pulled and pushed expansions are lacking empirical tests (but see Gandhi et al. 2016).

In a previous study, Dahirel et al. (2021a) combined simulations and experimental evolution of the small wasps Trichogramma brassicae to show that low connectivity led to more pushed expansions, and higher connectivity generated more pulled expansions. In accordance with theoretical predictions, this led to reduced genetic diversity in pulled expansions, and the reverse pattern in pushed expansions. However, the question of how pulled and pushed expansions affect trait evolution remained unanswered.

In this follow-up study, Dahirel et al. (2021b) tackled this issue and linked the changes in connectivity and type of expansion with the phenotypic evolution of several traits using individuals from their previous experiment. Namely, the authors compared core and edge populations with founder strains to test how evolution in pushed vs. pulled expansions affected wasp size, short movement, fecundity, dispersal, and density dependent dispersal. When density dependence was not accounted for, phenotypic changes in edge populations did not match the expectations from changes in expansion dynamics. This could be due to genetic trade-offs between traits that limit phenotypic evolution (Urquhart & Williams 2021).

However, when accounting for density dependent dispersal, Dahirel et al. (2021b) observed that more connected landscapes (with pulled expansions) showed positive density dispersal in core populations and negative density dispersal in edge populations, similarly to other studies (e.g. Fronhofer et al. 2017). Interestingly, in pushed (with lower connectivity) landscapes, such shift was not observed. Instead, edge populations maintained positive density dispersal even after 14 generations of expansion, whereas core populations showed higher dispersal at lower density. The authors suggest that this seemingly contradictory result is due to a combination of three processes: 1) the expansion reduced positive density dispersal in edge populations; 2) reduced connectivity directly increased dispersal costs, increasing high density dispersal; and 3) reduced connectivity indirectly caused demographic stochasticity (and reduced temporal variability in patches) leading to higher dispersal at low density in core populations. However, these results must be taken with a grain of salt, since only one of the four experimental replicates were used in the density dependent dispersal experiment. In range expansions experiments, replication is fundamental, since stochastic processes (such as gene surfing, where alleles maybe rise in frequency due by chance) are prevalent (Miller et al. 2020), and results are highly dependent on sample size, or number of replicate populations analysed.

Having said that, results from Dahirel et al. (2021b) highlight the importance to contextualize the management of invasions and species distribution, since it is thought that pulled expansions are more prevalent in nature, but pushed expansions can be more important in scenarios where patchiness is high, such as urban landscapes. Moreover, Dahirel's et al. (2021b) study is a first step showing that accounting for trait density dependence is crucial when following phenotypic evolution during range expansion, and that evolution of density dependent traits may be constrained by landscape conditions. This highlights the need to account for both connectivity and density dependence to draw more accurate predictions on the evolutionary and ecological outcomes of range expansions. **References**

Allee WC, Bowen ES (1932) Studies in animal aggregations: Mass protection against colloidal silver among goldfishes. Journal of Experimental Zoology, 61, 185–207. https://doi.org/10.1002/jez.1400610202

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Williams JL, Hufbauer RA, Miller TEX (2019) How Evolution Modifies the Variability of Range Expansion. Trends in Ecology & Evolution, 34, 903–913. https://doi.org/10.1016/j.tree.2019.05.012

Reviews

Evaluation round #2

Authors' reply, 22 September 2021

We thank the recommender and staff for the work around these revisions. Please find below a quick summary of the minor revisions done in this round:

-Comment: "My biggest comment is that the first paragraph of the introduction (L36 to L44) is a bit disconnected. I could not follow the reasoning behind it"

Answer: we have rewritten the first paragraph in a way that is hopefully more cohesive

- Comment: "warm-up iterations–> burn-in iterations":

Answer: Stan's warmup phase works slightly differently from the usual burn-in in MCMC procedures (hence the different name). In particular there is active tuning of the search algorithm parameters during that phase

All other minor change suggestions have been included verbatim or near-verbatim.

Decision by Inês Fragata, posted 13 September 2021

I think this version is now much clearer in how it differs from other works and how it is actually pushing the field forward, as well as on the limitations that it has. I really like the overview figure and it was much easier to follow up the different experiments and the generations they were performed.

I have one medium comment and several minor suggestions/comments, almost exclusively on the writing. Once these are addressed, I will be happy to write the recommendation!

My biggest comment is that the first paragraph of the introduction (L36 to L44) is a bit disconnected. I could not follow the reasoning behind it.

L36: Maybe start with: "The distribution ranges for many species are …"

L37-38: This sentence is a bit disconnected from the first, because it is not clear what the "their dynamics "referes to? is it the range expansion dynamics?

L43: is likely key –> is important (there are several citations backing up this importance!)

L83-85: Maybe rephrasing the beginning of the sentence might help: "The position of a range expansion on the push-pulled continuum…"

L88: exploring this is in our opinion the –> exploring this is, in our opinion, the

L89: given the distinction –> given that the distinction

L94: rephrase the beginning to: The few (theoretical and empirical) studies focusing on this subject hint that….

L123- 124: Maybe something like: "Using this data we examine the phenotypic changes underlying the different types of range expansions, in space and time."

L185 – Really cool figure 2!

L223: (except one where this was 15) –> (except one with only 15)

L252: complementary from short-term –> complementary to the short-term

L253: as while –> since

L254: behaviour, this –> behaviour, and this

L272: were this time manipulated –> were manipulated

L289-290: data in a bayesian –> data using a bayesian

L295: warm-up iterations–> burn-in iterations

Also please add the number (or interval) of burn-in iterations used in general

L384: Moving to the effect of rearing density–> Additionally, fecundity was not (…)

L389: There was no such density –> There was no density

L391: experimental landscapes are in almost –> experimental landscapes were in almost

L404: before –> previously

L434: remove the from "the trade-offs"

L436: Add commas "may reduce and in some cases prevent" –> may reduce, and in some cases prevent,

L438: matter a lot to   –> may be key to

L440: Whether or not trade-offs matter–> Irrespective of the impact of trade-offs,

452:     led to the appearance of a link –> showed/ suggested/ indicated a link

L465: there is actually

L477: Start the sentence with the however and remove it from the middle of the sentence and add a that after given.

However, it is difficult to say whether (..) range expansions, given that many dispersal models (..)

L481: show that shifts

L487 – 490: I would revert the order of the sentence:

Our results at the expanding edge are consistent with existing theory, since strong enough increases (…)

L490-491: Start with however: "However, in core populations dispersal became (…)"

L517: Separate the sentences: "life histories. Further "

518: would be better equipped –> would be important

Evaluation round #1

Authors' reply, 23 August 2021

Decision by Inês Fragata, posted 23 April 2021

Revisions needed

 Dear Authors, Your work has been assessed by three reviewers and me. Whereas we generally agree that the work is very interesting and clearly has an added value to the study of the eco-evolutionary dynamics of range expansion, there are some changes that would improve the current manuscript and are needed to clarify some aspects of your experimental design.   **### General comments** I think that the manuscript is very interesting and relevant, but there are several things that need to be improved. Reviewers 1 and 2 provide several comments that will allow you to do this. I am adding below comments of my own, with the intent of also helping on this matter. I think the supplementary material is great! **### Specific comments # Introduction** As reviewer 1 stated there are some literature, especially theoretical, that can be added to the introduction and later on discussed (reviewer 1 provides most of these examples).

Some additional references that may (or not) be of use also:

-      Miller TEX, Angert AL, Brown CD, Lee-Yaw JA, Lewis M, Lutscher F, Marculis NG, Melbourne BA, Shaw AK, Szűcs M, Tabares O, Usui T, Weiss-Lehman C, Williams JL. Eco-evolutionary dynamics of range expansion. Ecology. 2020 Oct;101(10):e03139. doi: 10.1002/ecy.3139. Epub 2020 Sep 2. PMID: 32697876.

-      Zaker N, Ketchemen L, Lutscher F. The Effect of Movement Behavior on Population Density in Patchy Landscapes. Bull Math Biol. 2019 Dec 23;82(1):1. doi: 10.1007/s11538-019-00680-3. PMID: 31919597.

-    Williams, J.L. and Levine, J.M. (2018), Experimental evidence that density dependence strongly influences plant invasions through fragmented landscapes. Ecology, 99: 876-884. `https://doi.org/10.1002/ecy.2156`

-      Urquhart, C.A., Williams, J.L. Trait correlations and landscape fragmentation jointly alter expansion speed via evolution at the leading edge in simulated range expansions. Theor Ecol (2021). `https://doi.org/10.1007/s12080-021-00503-z`

-      **# Methods**
You should add a figure that explains better your experimental design (i.e. how many strains and replicates per strain x type of connectivity you have) and also a table explaining which traits were sampled in each generation and which replicates from each population were used. I think this is a really important piece of information that you need to add to the manuscript, it was super confusing to understand what you did in each generation and knowing that you selected a replicate at random was not helpful at all. Another important piece of information that you should is also the size of the landscapes (i.e. the number of patches). This information is available in your initial paper, but I think it should also be here. In your analyses, have you considered using the number of the edge patch as a covariate? I am assuming that different landscapes had different sizes. If so, adding the expansion size as covariate (or the number of the edge patch were you took the individuals from) allows to test if the several traits analysed were in some way correlated to how much the population expanded. Another suggestion that I have is to do a multivariate analysis with all traits assuming that, in general, you used the same replicate population across time (and with the BIG caution note that the traits were analysed in different generations). This is because invasive populations often have the invasion syndrome and I wonder if here, by checking each trait individually, you might miss the sign. I know this is more unconventional, so really up to you to see whether this makes sense in your system. Please clarify why do you use two measures of dispersal. In line with reviewer 1, I find the use of the word context very confusing, as it can relate to different things. I think that you should specify the comparisons you are doing and not give a general nomenclature (both here and in the results). In your analyses have you nested experimental replicate in the interaction between experimental landscape and strain? This will be important to guarantee the level at which the intercept is varying.   **# Results** You should use more precise language in the description of the results. To improve plot readability on all figures, I would put a line to mark the median value of the stock populations (like you do in fig 4C) across all other facets in the plot. This way the comparison between stock and the evolved populations would be easier.

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In addition, it will also make it easier to see how different the two evolved populations are from each other. **# Discussion** I think the discussion needs to incorporate a bit more some predictions from theoretical studies. I think that it would be great if you add some of predictions to the introduction and then revisit them in the discussion, to give a greater depth to these results. As reviewer 2 pointed out, beware the fact that you only analyzed one single replicate for some traits, which limits your ability to generalize your results. L374: 376 – The sentence staring by "This is despite…" is a bit confusing, i am not sure if it is a comma missing or the structure of the sentence that is not correct. L439:441 - The sentence staring by "By contrast…" is also a bit weirdly phrased

Reviewed by anonymous reviewer 1, 06 April 2021

Dahirel and colleagues present the results of an experimental study to examine the effects of connectivity and density dependence on trait selection during range expansion. The purpose of the study is well motivated and clear. Based on a previous experiment and theory for pushed vs pulled expansions, we would expect that the high connectivity (reference) landscapes would have higher fitness at the leading edge than the core, and/or negative or non-density dependent dispersal. The reduced connectivity landscapes should have lower fitness at the leading edge and/or positive density dependent dispersal. Although the results were somewhat complicated, the figures were clear. The authors did find that the density dependence of dispersal varied between treatments in the manner we would expect given high connectivity landscapes induced pulled waves, and reduced connectivity resulted in pushed waves. The manuscript would benefit from being more strongly grounded with theory – both clarifying in the introduction and stronger links in the discussion. Below I provide more specific feedback to improve the manuscript.

1. L67-71 I think this is a bit misleading, "spatial sorting" is typically used to refer specifically to traits that enhance dispersal, and there are a wider range of traits potentially under selection during spread that are not described by this term (the authors describe some of these in lines 74-75). Related, I disagree with the use of 'spatial selection' at L83 to refer to all of these processes – if the authors wish to equate spatial and natural selection (as it's arguably still debated in the literature), they will need to explicitly define this. Otherwise, I think it would be more suitable to use natural selection for traits like fecundity.

2. I was surprised the authors did not incorporate any of the literature that explicitly considers landscape connectivity in shaping range expansions. There are a number of previous studies that look at both density dependence during spread in fragmented landscapes, as well as how landscape connectivity alters evolutionary trajectories of leading edge populations. I've provided some suggestions below for papers that should be highly relevant, but I would suggest the authors incorporate more of the previous literature on this topic to better motivate their work. (e.g. Dowdall et al. 2018, J. of Mathematical Biology; Lutscher & Musgrave 2017, Ecology; Gralka & Hallatschek 2019, eLife; Williams et al. 2016, American Naturalist & Science)

3. In some places, the methods need clarifying to help the reader follow the complex story. Adding a summary of the traits studied and from which generation would help – this could be in the text (~L 155 – 168) and/or in a table. It wasn't clear why traits were tested at different generations, and not the latest one (12th generation, I believe?). I'm not sure it really matters for the results but I found it confusing. Please also add an explanation of why two different measures of dispersal were used, how are they related to each other, and what the expectations were for each treatment. (I'd also recommend putting these two sections next to each other in the methods).

4. For the measurements of wasp size, where 8 core-edge populations were selected at random, how did you choose from across the isolines? Maybe I missed something, but I thought the original design had 8 replicates of each of the three types.

5. Throughout the methods and results, I found the use of the word 'context' hard to keep track of (in particular the contrasts between core and edge and the two connectivity treatments). Upon revisiting this section of the methods, I see now that context is used more generically to mean both core vs. edge and reference vs. reduced connectivity. Since specific hypotheses are laid out for each, to me it does not make

sense to combine them into one word. To me it would be clearer to give each more precise names, or at least occasionally redefining context.

6. I struggled with some of the language in the results section around whether or not two groups were different from each other. What does it mean by 'some indication' or the 'only potential effect'? Is there an alternative way to make it clearer that the groups are not significantly different (using the appropriate Bayesian language here, of which I am not an expert), but the mean is higher in one treatment than another?

7. L 381-384 This was interesting to me and I wish the authors gave more information in the main text. From Figure S.2.1: wasps were smaller after the experiments than stock populations, and edge populations in reference landscapes were smaller than core populations as well as those from the reduced connectivity landscape. But there were no differences between edge and core in the reduced connectivity landscapes? Earlier, the authors state that body size is linked to fitness, which I assumed to mean that larger individuals reproduced more. It wasn't immediately clear why they expected the differences in body size they reported to be most important in the context of dispersal-competition trade-offs. I wondered if the authors could provide some further insight on how body size relates to competition (if at all) and perhaps whether this could be indicative of selection in the reference landscapes? Further in L385-400, can you relate any of these trait changes to the changes in speed from the first experiment?

8. In a few places in the discussion, the complexity of the results gets washed over (e.g. L377-379, 404-406) – while I appreciate trying to simplify, the arguments would be more powerful if the nuance were included.

9. L410-424 – can you provide an alternative hypothesis? What if the egg number-egg size tradeoff was not supported with further work?

10. L445 – In this paragraph, I think more can be said from theory in the metapopulation context that makes predictions about why dispersal might be lower when patches are more dispersed.

11. Overall, the discussion would benefit from a paragraph describing the limitations of this experiment to help put it into a larger context. There is just a little on L471-473.

12. The supplementary material sections include several sections – it would be clearer in the main text if the authors referred to specific figures rather than referring the reader to the entire section.

A few minor comments:

L24. The reader does not yet know what 'treatments' refers to – please be more precise here.

L92. The use of the word surprising in this case seemed a bit strong. To me, the lack of studies is not surprising – this is a new field and these kinds of experiments are very difficult to do. Instead, what about something like, "the next step' or 'the way forward' is to…

L 98-88. What does 'appears to move edge populations away from' mean?

L203. What is a tracklet?

L391. What does "but in the other in the second" mean?

L410. Appearance would be more appropriate than apparition here.

Reviewed by anonymous reviewer 2, 31 March 2021

Download the review

Reviewed by anonymous reviewer 3, 22 March 2021

I just completed the review of the manuscript with the title "Landscape connectivity alters the evolution of density-dependent dispersal during pushed range expansions". It is well-written and describes adequate and well though off experimental procedures to answer an interesting research question about species range expansion in the context of environmental change.

I have an overall question concerning the main conclusions of the preprint: could it be that, as a species expands its range, the lower densities at the expanding range edge cause an initially pushed expansion to

move towards a pulled one?

Introduction

The introduction provides an adequate framework for the study. It is well structured, explaining the research context and knowledge gaps and it is based on relevant research. The motivation of the study, as well as the objectives, are clear and relevant in the current context of environmental change.

Materials and methods

Data and code were made available to the reader. The description of the methods is detailed enough to allow replication and the statistical analysis are adequate. I think that the methods would benefit from a new figure, describing schematically the experimental design. As such, it is my recommendation that the authors consider creating a figure were the experimental steps are schematically represented.

Results

Paragraph around line 355 – I understand what the authors meant. However, when they write "…leading to negative density-dependent dispersal…" that is not always absolutely right, from what I can understand. In the wasps from the "core" in the "reference" landscape and the wasps from the "edge" in the "reduced connectivity" landscape, there is a positive density-dependence. The authors should clarify this paragraph.

References

References are adequate.

Discussion

Lines 390-391 – Please clarify this sentence.