

The manuscript entitled “Shifts from pulled to pushed range expansions caused by reduction of landscape connectedness” presents the results of both individual-based simulations and experiments with minute wasps to investigate the role of “reduced connectedness” on populations undergoing a range expansion. The main messages are: (i) in addition to density-dependent growth and/or dispersal (studied previously), “reduced connectedness” can also lead to “pushed” expansions; (ii) the “pushed” expansions that can occur do not always match the current descriptions of pushed waves, in that they travel faster than pulled waves, as expected, but also lose genetic diversity faster, in contrast with current descriptions/understanding.

While the manuscript introduces a very interesting hypothesis, I am left doubtful on whether the results are sufficient to prove this hypothesis. More specifically, while the word connectedness is used in both titles and in the main text, which suggests a relationship with topology of the structured environment, the way in which it is implemented in the simulations is by reducing the basal diffusion coefficient of a sFKPP equation. As previously shown (see Hallatschek and Korolev, Fisher Waves in the Strong Noise Limit, PRL, 2009), this results in an increased relevance of population noise compared to the deterministic component of the reaction-diffusion equation (also seen in simulations), which breaks the assumptions that lead to the traditionally used Fisher velocity  $v_F$  as estimated for the “pulled” front velocity. In this reference, it is shown that the actual front velocity becomes slower than the predicted  $v_F$  as diffusion decreases, leaving me to wonder how the results presented in fig. 2 have been produced and whether they are an artifact of the way the simulations are analysed or  $v_F$  is estimated.

I also have major reservations regarding the experimental data, whose results in front speed are too qualitative, somewhat in disagreement with the theoretical predictions, and also not well controlled, since variations in growth rate are not accounted for. As a result, I don’t believe the manuscript should be recommended for publications. I list all my other minor concerns in details below:

1. There are several instances where key concepts or parameters were not well defined or explained, which made it initially difficult to understand the work, for example:
  - “(Reduced) Connectedness” – Despite being the titular concept in the paper, I initially found it quite difficult to understand what this actually meant in the context of this work. When it is first introduced (Ln. 90) the idea of “physical links” is used, which relates well to the experiments discussed later, but not to the simulations used, where “reduced connectedness” in practice means that the base dispersal rate  $D_0$  is lower. This made it difficult initially to appreciate the significance of Fig. 1, which with hindsight does actually motivate the work reasonably well.
  - A more minor point, but the parameters discussed in the simulations (such as  $K$ ,  $r_0$  and  $D_0$ ) are described as being biologically plausible (with citations), but this is not obvious to me given that we don’t know how large a “patch” is, or how long a “step” is, and all of the parameters have no units.
2. I found it generally quite difficult to follow the methods section, particularly all of the statistical analyses that are used throughout the work.

- In the simulations, the maximum dispersal in a timestep is limited to one patch, whereas in the experiments this is not true. Is this difference not important, and if not, why impose the condition in the simulations?
  - Why using a statistical analysis for the simulations? The data should be plenty to be able to give the average front velocity. How is this front velocity determined (position of the front vs position of the half point)? Why using an exponential decay to fit the asymptotic velocity when it's known to approach it via power-law (see Birzu, 2019).
  - I don't understand the description in S3 about determining whether the reduced connectedness did limit movement/dispersal. Additionally, it seems like the difference is (averaged over everything) significantly less than one patch. Given that eggs can only be laid in integer patches, is this difference significant, especially given that no difference is within the error bounds? Also, was the 'growth rate' in the experiments unaffected, i.e. did they get the same number of new wasps with each generation in the two regimes? These points are important, because it's used in the discussion to justify why the reduced connectedness expansions must be pushed – see later comment.
  - Specifically, on how the experiments were carried out, it says when the first adults start to emerge from the previous generation's eggs, new eggs are provided, and after 48 hours, the adults and old eggs are removed. My question is how do you know the new adults didn't infect some of the uninfected old eggs, which are then removed 2 days later? This could affect effective growth rates etc, which again could impact the argument later about  $V_F$  in the discussion.
3. A few thoughts on the results section:
- One of the reference velocities ( $K=225$ ) is lower than  $V_F$ , which isn't addressed other than to say it's "very close," but I would argue that this statement may or may not be justified depending on the error. From the figure, the result doesn't seem statistically compatible with the Fisher velocity predicted.
  - I think it would be interesting, if possible, to see the diversity decay rates in terms of an effective population size, and how these related to the actual population sizes that are in the simulations/experiments. This concept is alluded to later in the discussion, but not actually shown for most of the data/rates in the paper.
4. I have a few issues with the argument outlined in the discussion about why the experimental expansions in the reduced connectedness regime must be "more pushed." The basis of the argument is that the velocity is the same in both cases, and that  $V_F$  must be lower in the reduced connectedness case, leading to a larger  $V/V_F$  ratio in the reduced connectedness case, meaning it must be "more pushed." My issues are:
- The velocities are the same, but with very large error bounds (Fig. 3b)
  - They say that  $V_F$  must be lower in the reduced connectedness case because the initial dispersal is lower.
    - As I mentioned earlier, I'm not sure how significant the lower dispersal is when the difference is much less than one patch, and has comparably large errors to those on the velocities (indeed, the error bounds include zero difference).

- This also assumes, as they say, that everything else, such as the growth rate at low densities remains the same. I'm surprised this doesn't appear to have been checked given how fundamental it is to the argument. Given the variability/errors in all the other measurements, I wouldn't be surprised if this also varied significantly, and may cancel out any reduction in dispersal.
- 5. I also don't completely understand the argument put forward to explain why the genetic diversity decays *faster* in the reduced connectedness case, even though velocities would indicate that it is pushed, and therefore should decay slower.
  - Basically, I'm not convinced as to why the cases where there is no movement into the first unpopulated patch ( $N_{x+1,t+1}=0$ ) should be removed. Their argument for this is that there is no "new" population in this case, and so it is not relevant, whereas I would argue for every step where this is true, the previous new population becomes larger. Consider the toy example below

t=1	$N_{x=1}=\text{lots}$	$N_{x=2}=0$	$N_{x=3}=0$
t=2	$N_{x=1}=\text{lots}$	$N_{x=2}=5$	$N_{x=3}=0$
t=3	$N_{x=1}=\text{lots}$	$N_{x=2}=20$	$N_{x=3}=0$
t=4	$N_{x=1}=\text{lots}$	$N_{x=2}=30$	$N_{x=3}=2$

In this example going to the t=2 step would give a new population of size 5, and to the t=4 step would give you a new population of size 2, with the step to t=3 being discarded. I think though, given that no movement occurred in step from t=2 to t=3, then the "new" population size at position x=2 is in the end 20, because the 5 that were there first did not advance the front, and so going from step t=3 to t=4 those 5 no longer have any advantage over the other 15. At t=3, I think the effective population size at the front is therefore 20, so I think by removing these steps the effective population size measured is being artificially reduced, which is key to the argument used to explain why diversity decreases faster (smaller population=faster loss of diversity).