GENERAL COMMENTS

This MS presents theoretical evidence about the effects of conditions previously encountered by an invasion front on its future advances. The study shows that these demographic effects, named by the authors as colonisation debt, occur in environments with heterogeneous carrying capacity, and populations with positive density-dependence and local dispersal.

Overall, the MS is very well written. The background is well presented. They clearly explain what is novel in their study compared to previous ones about factors affecting invasion speed in one-dimensional landscapes: considering environmental gradients as monotonic variations of the carrying capacity in space. Moreover, they propose a hypothesis based on the novel concept of 'colonisation debt': colonisation debt should only occur in invaders affected by positive density dependence. They test the hypothesis using a stochastic model, and also provide experimental evidence supporting the colonisation debt.

The design of the simulations is appropriate to test their hypothesis. Overall, the approach seems consistent. Simulation results strongly support the relationship between positive density dependence and colonisation debt. The experiment also shows the occurrence of colonisation debt in an organisms with positive density-dependent dispersal. The absence of colonisation debt in a species without positive density-dependence remains experimentally untested in this study.

In the discussion, the range of situations where the impacts of colonisation debt should be higher is clearly explained: species with local dispersal (absence of long-distance dispersal), and steeper gradients. The authors also suggest future research lines uncovered in their study: to take into account the genetic background of the individuals. Here, I missed a brief mention to studies focused on the evolutionary dimension of range expansion and colonisation (evolutionary rescue applied to the colonisation of novel habitats). Finally, they very well suggest benefits of considering colonisation debt for management of actual invasions or other range shifts.

Strengths of the MS:
1. Presentation of a novel concept and an associated hypothesis
2. Combination of theoretical and experimental approaches
3. Results strongly support their hypothesis
4. Clarity across the entire MS

Weaknesses:
-The absence of colonisation debt in an organism without positive density-dependence not experimentally tested.

DETAILED COMMENTS

Pag 2; line 30
“density-dependent growth” is too general, also including negative density-dependence at high densities when resource become a constraint. Thus, I would provide here a more specific definition for Allee Effects: “positive density-dependent growth at low densities”

Pag 2; line 45
“in the absence of any density-dependence”
Do you include here also negative? If not, replace by “in the absence of positive density-dependence”

Pag 4; equation for Ki
Could you check the conditional statements please?
I am not sure they are correct.
I guess if you define j as the closest patch to the left of i, then i cannot be equal to j. So, I think the left bound of the first interval should be exclusive.
Also, I found it weird including i within the definition of the interval for the increasing part.
I think the following definitions would be more clear to the readers:
decreasing part: if i belongs to]j,j+q]
increasing part: if i belongs to]j+q,j+q+2q]
Maybe I am wrong, but I recommend the authors to revise the definitions of the intervals in the equations.

Pag 5, lines 129-130
Letters i and j are already used in Eq. after line 107 (Ki) with other meanings, so I suggest the authors to use different letters here to avoid confusion (e.g. in 107 you say Kj = Kmax and here Kj = Kmin).

Pag 6, line 146
Why you did not use Kmin = 90 in the simulations to better mimic your experimental model?

Figure 7
“Patches with K = Kmin = 45 and K = Kmax = 450 are represented as belonging to both gradients”. Why did you classify Kmin as part of an upward gradient? If the patch is in the invasion front, so the flow of migrants should come from the left side.; thus, a patch with Kmin should only be represented as belonging to a downward gradient. The same applies to Kmax. An alternative option would be to remove patches with Kmax and Kmin from the analysis. But including them as belonging to both gradients does not make sense to me. I would check this.

Pag 8; Line 177
For more clarity, replace “at K = 45” by “in the patch with K=45 (i.e. Kmin)”

Pag 8; Figure 4
A colour legend would be useful here

Pag 9; line 208
Replace “affected by” by “when there is”

Table 1
I recommend to order columns based on AIC (from best to worst model).