Dear Managing Board,

Please find our revised version of the manuscript '*Colonisation debt: when invasion history impacts current range expansion*', archived on biorXiv. We have considered the recommender's and the reviewers' comments concerning the previous version of our manuscript. We tried to address their concerns at best, and thank them for helping clarifying some aspects of the manuscript. In addition to the version available on bioRxiv, we also joined a version with the modifications noted in red in the manuscript. We truly hope that this new version of the manuscript will be considered appropriate for recommendation by *PCI Ecology*.

Yours sincerely,

Thibaut Morel-Journel, on behalf of the authors

Recommender

I was expecting a more explicit treatment of environmental gradients, like one of the reviewers. It would be great if your model included the need for shifts in the environmental conditions used by the species that are common in range margins and/or during invasions. I now understand that this goes beyond the model you are presenting here, but I encourage you to pursue this objective further in the future.

Response : Indeed, denomination of "environmental gradient" was a poor choice for this study, as this term encompasses a variety of changes in environmental factors across space. As pointed out by the recommender and one of the reviewers, range shifts can be generated by changes in environmental conditions, the most notable example being climate envelopes. Besides, these range shifts can be akin to pushed invasions, in which genetic diversity is notably conserved because the environment circumscribes the species by acting as a barrier to dispersal and establishment outside of the envelope (Garnier and Lewis, 2016). The gradient then corresponds to conditions that are increasingly unsuitable for colonisation by the species towards the limits of the range, where the environment is essentially deleterious for the species, preventing any colonziation.

The environmental gradients in carrying capacity considered in this study correspond rather to variations in the amount of habitat available, which is always susceptible of supporting an invasive population, even if it is potentially only of small size. The environmental conditions encountered are therefore never deleterious enough to prevent any colonization by itself, although additional density-dependence mechanisms can stop the invasion front, at least temporarily. In the context of this study, there is therefore no assumption of maximum extent that can be reached by the invasive population at a given time. Hence, the invasion is always pulled without any density-dependence mechanism. A discussion of the distinction between the gradients we consider here and the environmental gradients constraining ranges was included in the new version of the manuscript.

I tend agree with one the reviewers that your in silico experiments should be backed up by analyses without the descending gradients, to tease apart the role of these gradients when carrying capacity is low.

Response : We performed additional simulations considering a single gradient of carrying capacity, either ascending or descending, for the same values of slope as tested in the main simulations (from $q = 1$ to $q = 10$). These results are presented extensively in the supplementary material, and discussed in the main text. Although there is a higher variability in invasion speeds over a single gradient, the results confirm the existence of the colonisation debt: for a same carrying capacity, instantaneous speed is faster in a downward gradient (when the preceding patches are larger) than in an upward gradient (when the preceding patches are smaller).

And also that the way you classify gradients according to carrying capacity is potentially confusing.

Response : As explained in the first response to the recommender's comment, the study aims at assessing the impact of varying carrying capacities over space, in link with variations in habitat quantity for the invasive species. As the term "environmental gradients" is indeed tied to a specific context, we chose to remove it from the manuscript. However, we do study gradients of carrying capacity, i.e. gradual changes over space

characterized by their slopes. We clarified in the manuscript the type of gradient considered here, and the differences with environmental gradients as considered to define species ranges.

Reviewer 1

I'm less convinced that the authors' interpretations and framing of their results is appropriate given some of the choices made in their model. At minimum, a reframing of the results is warranted, but some additional simulations that decouple the gradient length and steepness may further strengthen the results.

Response : The link between gradient length and slope is constrained in the study by the need to keep a constant carrying capacity across all landscapes (and a constant slope for a given gradient): the slope is defined as $(K_{max} - K_{min})/q$. Therefore, the length cannot be modified without changing the slope, unless the minimal or maximal carrying capacity is also changed. In this study, we chose to consider landscapes with the same average carrying capacity overall, for which we fixed K_{min} and K_{max} as constant values for every landscape. We underline in this version of the manuscript the link between slope and length, and explain why gradients are therefore only discussed in terms of slope, but not length.

I would also have liked to see the experimental results presented more thoroughly, and worked more clearly into the discussion.

Response : We added an additional figure in the new version of the manuscript, which aims at showing the concordance between the experimental and model results, i.e. that the carrying capacity of the patch on the front alone is not enough to predict the invasion speeds observed experimentally and that the carrying capacity of the patch behind the front brings additional information about invasion speed. A section specifically concerning the experimental results was also added to the discussion.

The authors have modelled a periodic landscape as a series of successive gradients, where both the steepness and length vary. In their results, the short / steep gradients are strongly influenced by the opposite gradient behind the minimum or maximum carrying capacity patch. In my view, it is not possible then to attribute any changes in invasion speed to the gradient steepness or direction in these cases. It seems like the authors get around this in discussing the role of the gradient direction only in the shallower gradient scenarios, but this is not clearly specified. Even in this case, the influence of positive density dependence is much stronger on the upward patches just after the minimum carrying capacity patch. Some additional simulations that explore this effect without the descending gradient behind might help tease apart the role of the gradient, a low carrying capacity core and the periodicity of the environment. At minimum, the possibility of each of these could be further explored.

Response : We performed additional simulations with a single gradient across space, every patch before being at K_{min} and every patch after at K_{max} for an upward gradient, and the opposite for a downward gradient. In this configuration, we still detected differences between upward and downward gradients indicative of colonisation debt, albeit with more variability, since we considered a single gradient rather than multiple ones for estimating speeds. As expected the artifacts previously identified as resulting from the succession of gradients (generally for $q < 3$) were not visible for a single gradient. The differences between these simulations and those presented in the manuscript are discussed and these results are presented in details in the supplementary material.

As is, I'm not sure calling these "gradients" is quite right. This language makes me expect you are modelling an environmental gradient, as in a range shift for example.

Response : As explained in the response to the recommender, we expanded on the way we use "gradient" in this manuscript, to make it clearer that these gradients concern carrying capacity, i.e. variations in the amount of habitat available rather than habitat quality.

The experiment got lost a bit in the results and discussion. As is, I'm not sure the inclusion of the experiment is fully justified. Some stronger connections between the experimental results and simulations are warranted, and perhaps including some further analysis (if possible) using similar methods as the simulations. For example, looking specifically at the role of gradient steepness.

Response : Besides the additional figure concerning the experimental results, we have added a section to present them more thoroughly. The figure presents the instantaneous speed as a function of carrying capacity on the front, similar to the analysis of the simulation outcomes. This results highlights that the invasion reaches

lower speeds in the shallow gradient compared to the steep one for a same carrying capacity ($K = 90$), with the analysis supporting the role of the carrying capacity of the previous patch in this difference.

It is unfortunate that the authors did not also include a treatment with a shallow, upward gradient as the difference between the up- and down-ward gradients seems like an important result, and with both gradients the difference between periodicity and a straight gradient could have been studied further.

Response : Unfortunately, invasions in upward gradients, i.e. starting with an initial introduction in the smallest patch, would have had a very high extinction probability. On the one hand, experimental invasive population dynamics are highly stochastic, and a single population in a small patch would have had very high risks of extinction. On the other hand, *T. chilonis* also suffers from a very strong over-competition when the number of eggs is limited compared to the population size, increasing further the extinction risks. We added this information in the methods section of the main text and in the supplementary material.

3 -I'm not sure I agree with this assertion, at least this is not the only way that density dependence can affect invasions.

Response : This sentence was intended to indicate that linking the carrying capacity to invasion speed is a way positive density-dependence shape population range expansion, not necessarily the only way. It was modified in this version of the manuscript.

15 - The switch in terminology here to "extinction debt" is confusing.

Response : We apologize for this mistake, which was corrected in this version of the manuscript. It should read as 'colonization debt'.

The first two paragraphs here lack focus, and may be too general for the audience that is likely interested in these results. Consider revising down to one paragraph.

Response : The first two paragraphs were shortened and merged to more simply introduce the article.

35 - this sentence is unclear, consider revising. Do you mean that density dependence causes emigration from the core and therefore expansion?

Response : We thank the reviewer for pointing out that this sentence was unclear in this version of the manuscript. It was modified to convey more clearly the following message: density-dependent growth and density-dependent dispersal have been shown to create a causal relationship between expansion speed and the size of populations in the core, because larger core populations provide more individuals to the front populations, thus preventing the reduction of growth or dispersal caused by density-dependence.

46 - consider removing one of "however" and "yet"
245 - There's an extra word here.
86 - Consider adding a reference here.
Methods - Some additional info about growth and dispersal might be worth adding to the main text, in particular the authors should make it clear that dispersal is local and the positive density dependence comes in the form of an Allee effect for growth and changes in dispersal probability for dispersal.
Figure 3 – Consider making the lines / circles / crosses more prominent

Response : We thank the reviewer for these suggestions, which were taken into account in the new version of the manuscript.

51-52 - I don't agree with this assertion. In at least some of these papers, carrying capacity is not explicitly modelled but is an emergent property of the population dynamics. So reducing growth also changes the carrying capacity. The point on 52 about binary patches is more meaningful and accurate.

Response : We thank the reviewer for pointing out the link between growth rate and carrying capacity. This was included in the new version of the manuscript.

54 - Again, this is not necessarily true. You can have variable carrying capacity emerge from population dynamics alone. Consider hedging here, at least.

Response : We did not intend to state that the carrying capacity could not vary due to factors other than resource availability, but that resource availability was a factor impacting the carrying capacity. This has been clarified in the current version of the manuscript.

62 - I'd like more here about what the significance of this relationship is. The authors do a nice job of this in

the conclusion, it could come a bit here too.

Response : The relationship between carrying capacity and invasion speed has been observed in previous studies of invasion in landscapes with constant carrying capacities. Based on these studies, we therefore expect a decrease in invasion speed if positive density-dependence is involved. This was explicitly stated in the current version of the manuscript.

65-68 -Wouldn't this depend strongly on the mode of dispersal and/or dispersal distances? With limited dispersal distances or local dispersal and a downward gradient, populations might saturate habitat close to the core quickly and then get stuck by the low carrying capacity patches? I know this is not what the results show, but I wonder if there is a threshold carrying capacity below which there can be pinning without long distance dispersal?

Response : As pointed out by the reviewer, pinning can occur with positive density-dependence when dispersal is only local, depending on the relationship between the dispersal abilities of the individuals and the size of the area of low carrying capacity patches (Keitt et al., 2001; Morel-Journel et al., 2022). We considered here conditions for which front stops were not permanent at small population sizes. However, shallower gradients create larger areas of low carrying capacities, which could stop the invasion if large enough. This perspective was included in the paragraph of the discussion relative to the dispersal distance.

69 - Would the ability for populations to grow large at the front lead to accelerating speed with positive density dependence? There is previous research on acceleration with evolution, but here it's shown that acceleration can be just from positive density dependence in heterogeneous landscapes. This is an interesting result that I think is worth elaborating on here and in the results / discussion.

Response : Indeed, our model predicts increasing invasion speeds with density-dependence, but only because the carrying capacity itself increases in upward gradients. Besides, the marginal increase in speed is expected to become smaller as the carrying capacities reaches very large values. Indeed, positive density-dependent growth and dispersal are most impactful in small populations, so that their impact are expected to fade out as the carrying capacity increases (Fig.1). The acceleration observed is therefore limited in space and/or time.
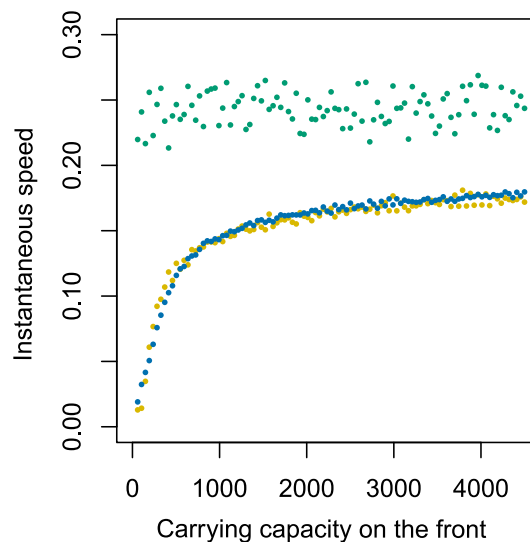

Figure 1: Instantaneous speed as a function of carrying capacity of the patch where the front is located, for a single gradient of increasing carrying capacity with $K_{max} = 4500$ and $q = 100$. The dots correspond to averages over 500 simulations, without any density-dependence mechanism (green), with Allee effects (yellow) and with density-dependent dispersal (blue).

73-75 - Does this mean that population dynamics at the edge might reflect habitat quality in the core, vs. just at the edge, with positive density dependence? Or that the previous patches matter more than the current patch? Consider clarifying here.

Response : With density-dependence, population dynamics at the edge are still impacted by carrying capacities

of the edge patch, but they are also impacted by the dynamics of core populations behind the front. A sentence was added to clarify this point.

83 - Some justification for this choice of landscape would be helpful. Why not just a single gradient in either direction, which would mimic environmental gradients in nature?

Response : The periodic landscape was chosen to maintain an identical average carrying capacity across every landscape, as there is a known impact of the overall carrying capacity on invasion speed with positive density-dependence (Haond et al., 2021). Considering a periodic landscape maintains the average carrying capacity at a constant value, thus removing this impact and allowing us to focus on the heterogeneity in carrying capacity itself. The methods section was amended to underline this point.

124-136 - I'm curious about the different measures of speed. Are they correlated? I would expect the landscape level speed to average out across simulations over time, but early on it should be correlated with the gradient speed?

Response : Indeed, we expect landscape speed to be correlated with gradient speed early on, but the time-scale considered for the simulated invasions was large enough so that the average carrying capacity encountered over the course of the whole invasion was systematically close to the landscape average ($K = 247.5$), which was the same for every treatment.

The local measure of speed taken at the midpoint was interesting, but I didn't see this come through in the results.

Response : The measure of speed taken at midpoint is presented in the part of the results about the impact of gradient slope on simulated speed and in Fig. 4B of the manuscript.

143 - I'm curious why the authors chose the downward landscape and not to include an upward gradient as well?

Response : The population dynamics of *Trichogramma chilonis* are highly stochastic, especially at small carrying capacities. Thus, the extinction risks of an experimental invasion starting in a patch with K=45 or even K=90 would have been very high, preventing the observation of any expansion. Given the material constraints of the experiments, we chose not to consider this case. This point is now addressed in the methods section of the manuscript.

Results - It would be nice if the experimental results came through more. I'd like to see a figure from the experiment and perhaps some further analysis linking experimental and simulation results. I also wondered about including a figure showing speed as a function of carrying capacity in the current patch vs. the patch directly behind.

Response : We thank the reviewer for this suggestion. A figure presenting the instantaneous speeds observed in the experiment as a function of carrying capacity, corresponding to the figure of instantaneous speeds in the model, was added to the main text. We hope that this figure will help to highlight the greater difference between the instantaneous speeds as the slope decreases. Besides, the results were rewritten to bring out more the comparison between the outcomes of the model and of the experiment. The aim of our analysis was to identify whether or not the patch behind the front also had an impact on invasion speed, as the impact of the carrying capacity of the front patch was expected. The result show that this is indeed the case: both the patch on the front and the patch behind impact speed.

164 - Is this just because of the periodicity in the landscape? Do changes in speed due to q average out as carrying capacity goes up and down?

Response : As pointed out by the reviewer, the constant landscape speed is likely observed because the average carrying capacity across the whole landscape was constant. This was one main objective of the use of such landscapes, because the impact of average landscape carrying capacity on invasion speed with density-dependence has already been observed in homogeneous landscapes (Haond et al., 2021, e.g). As we aimed in this study at studying the impact of heterogeneity, comparing landscapes with identical average carrying capacity ensured that it would not impact our results. This result concerning landscape speed suggests that this is indeed the case. The introduction was modified to provide more explanation, and the results concerning landscape speed were extended to highlight this result.

Discussion - In other research, for example Garnier Lewis 2016 (in the Bulletin of Mathematical Biology), it is shown that environmental gradients can mimic positive density dependence in that they can create pushed

waves. I thought it was interesting that here the biological mechanisms induced something beyond what we see with just the gradient. I wondered whether the density independent simulations still spread as pushed waves in the gradients? And would be interested to hear the authors interpretation of their results in this context in the discussion. With longer gradients, more akin to environmental gradients studied with range shifts, would we see something different?

Response : We thank the reviewer for this very interesting suggestion. The study by Garnier and Lewis (2016) presents pushed invasions (characterized by the maintenance of genetic diversity over space) in a context of slowly shifting climatic envelopes due to climate change. Conversely to biological invasions as presented in this study, the size of the colonized range correspond to (and is constrained by) the envelope, which is entirely colonized. In this context, the slow-moving climate envelope limits the colonization of new habitats by the populations on the edge, even without density-dependence mechanisms. Garnier and Lewis (2016) notably indicate that the pushed nature of the wave requires the speed of the envelope to be slow enough for the wave to remain pushed. In our context, heterogeneity is not temporal but only spatial, and the invaded area can always increase in size. In this context without constraint, our simulation results show that the invasion is pulled (i.e. independent from carrying capacity) without any density-dependence mechanism. The existence of a gradient of carrying capacity over space is not enough to generate pushed waves, but would require an actual constraint like the climatic envelope.

218-21 - I'm not sure I follow this, consider rewording and expanding on this explanation. I would expect that with density dependent dispersal populations would establish in the smallest patches, but then stall there due to low dispersal. Whereas, with density dependent growth populations might lag in establishing at all in the smallest patches. I don't think this is what was found though?

Response : Because of the push from the previously colonised patches in the downward gradient, the invasion always reaches the patch after the smallest one, with a population large enough to not go extinct because of positive density-dependent growth but still rather small. With density-dependent growth, this population produces dispersing individuals that are detected but fail to establish in the next patch. With density-dependent dispersal, this populations does not produce enough dispersing individuals for them to be detected in the next patch. This discrepancy creates the difference in the lag (of 1 for density-dependent dispersal and 2 for density-dependent growth). This was developed in the new version of the manuscript for more clarity.

224 - I found this confusing, the shallower gradients are also the longer ones, is that correct?

Response : Indeed, we apologize for the confusing phrasing of this sentence. We mean here that the impact of colonization debt at the scale of a single patch is less visible in shallower gradients because the difference in carrying capacity between two consecutive patches is smaller. Therefore, for a same carrying capacity on the front, the difference between the carrying capacities of the patches behind the front in upward and downward gradients becomes smaller. This part of the manuscript was rewritten for more clarity.

Reviewer 2

The absence of colonisation debt in a species without positive density-dependence remains experimentally untested in this study.

Response : As pointed out by the reviewer, we could not test experimentally for the absence of colonization debt in the absence of density-dependence. The experimental setup we used is specifically suited to the model species considered (*Trichogramma chilonis*). We initially considered another strain, which displayed density-independent dispersal. Unfortunately, this part of the experiment did not succeed, so we were restrained to consider only the strain experiencing density-dependent dispersal.

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).

Response : We thank the reviewer for this remark, which is especially interesting in the case of waves constrained by positive density-dependence mechanisms, that increase the genetic diversity on the front compared to invasions without any mechanism. This added genetic diversity might itself facilitate evolutionary rescue in the populations on the front, potentially allowing these populations to evolve to mitigate the density-dependence mechanisms generating the pushed invasions in the first case. We added a paragraph in the discussion to consider these aspects.

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 5, lines 129-31: 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 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"

Response : We thank the reviewer for these remarks, according to which the new version of the manuscript has been modified.

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.

Response : We thank the reviewer for pointing out that the second statement was indeed erroneous. We also agree that considering i = j is inconsistent with the definition of j and can be confusing. The intervals have been corrected.

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

Response : We assumed that the reviewer meant to order the rows according to their AIC, which has been done in the new version of the manuscript.

Why you did not use Kmin = 90 in the simulations to better mimic your experimental model?

Response : As pointed out, the minimal patch size considered for the steep landscape is 90 rather than 45. We chose to do so in the experiment because of the strong demographic stochasticity of *Trichogramma chilonis*, which makes population dynamics at K = 45 rather unstable. Therefore, small patches would have been difficult for *T. chilonis* to reliably pass through during the 15 generations of the experiment. This is now explained in more details in the methods section. However, we did not have the same limitation for shallow landscapes, for which Kmin = 45. Similarly, we exploited a larger range of carrying capacities for simulations, from $K_{max} = 450$ to $K_{min} = K_{max}/10 = 45$. However, results were similar with $_{min}$ = 90, albeit not as strong (Fig.2).
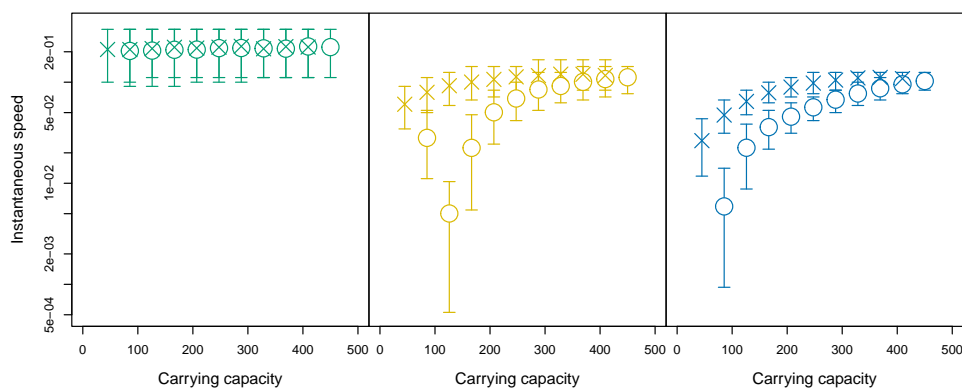

Figure 2: Instantaneous speed as a function of carrying capacity, for $q = 10$ (rows) and either no mechanism (green), Allee effects (yellow) or density-dependent dispersal (blue), for carrying capacities varying between $K_{min} = 90$ and $K_{max} = 450$. Mean values over all patches with the same carrying capacity are represented by crosses if the patch is in a downward gradient, and as circles if the patch is in an upward gradient.

Figure 3: "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.

Response : We thank the reviewer for this remark. We modified Figure 3 (now Figure 4) to include patches at K_{min} in the downward gradient only and those at K_{max} in the upward gradient only, and the sentence was removed from the legend.

References

J. Garnier and M. A. Lewis. Expansion under climate change: The genetic consequences. *Bull Math Biol*, 78: 2165–2185, 2016. ISSN 0092-8240. doi: 10.1007/s11538-016-0213-x.

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