



Peer Community In Evolutionary Biology

The push and pull between theory and data in understanding the dynamics of invasion

Ben Phillips based on peer reviews by **Laura Naslund** and 2 anonymous reviewers

Maxime Dahirel, Aline Bertin, Marjorie Haond, Aurélie Blin, Eric Lombaert, Vincent Calcagno, Simon Fellous, Ludovic Mailleret, Thibaut Malausa, Elodie Vercken (2020) Shifts from pulled to pushed range expansions caused by reduction of landscape connectivity. bioRxiv, ver. 1, peer-reviewed and recommended by Peer Community in Evolutionary Biology. [10.1101/2020.05.13.092775](https://doi.org/10.1101/2020.05.13.092775)

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Exciting times are afoot for those of us interested in the ecology and evolution of invasive populations. Recent years have seen evolutionary process woven firmly into our understanding of invasions (Miller et al. 2020). This integration has inspired a welter of empirical and theoretical work. We have moved from field observations and verbal models to replicate experiments and sophisticated mathematical models. Progress has been rapid, and we have seen science at its best; an intimate discussion between theory and data. An area currently under very active development is our understanding of pushed invasions. Here a population spreads through space driven, not by dispersal and growth originating at the leading tip of the invasion, but by dispersal and growth originating deeper in the bulk of the population. These pushed invasions may be quite common – they result when per capita growth and dispersal rates are higher in the bulk of the wave than at the leading tip. They result from a range of well-known phenomena, including Allee effects and density-dependent dispersal (Gandhi et al. 2016; Bîrzu et al. 2019). Pushed invasions travel faster than we would expect given growth and dispersal rates on the leading tip, and they lose genetic diversity more slowly than classical pulled invasions (Roques et al. 2012; Haond et al. 2018; Bîrzu et al. 2019). Well... in theory, anyway. The theory on pushed waves has momentarily streaked ahead of the empirical work, because empirical systems for studying pushed invasions are rare (though see Gandhi et al. 2016; Gandhi, Korolev, and Gore 2019). In this paper, Dahirel and colleagues (2020) make the argument that we may be able to generate pushed invasions in laboratory systems simply by reducing the connectedness of our experimental landscapes. If true, we might

have a simple tool for turning many of our established experimental systems into systems for studying pushed dynamics. It's a nice idea, and the paper goes to careful lengths to explore the possibility in their lab system (a parasitoid wasp, *Trichogramma*). They run experiments on replicate wasp populations comparing strongly- v poorly-connected arrays, and estimate the resulting invasion speeds and rate of diversity loss. They also build a simulation model of the system, allowing them to explore in-silico a range of possible processes underlying their results. As well as developing these parallel systems, Dahirel and colleagues (2020) go to careful lengths to develop statistical analyses that allow inference on key parameters, and they apply these analyses to both the experimental and simulation data. They have been motivated to apply methods that might be used in both laboratory and field settings to help classify invasions. Ultimately, they found reasonable evidence that their poorly-connected habitat did induce a pushed dynamic. Their poorly connected invasions travelled faster than they should have if they were pulled, they lost diversity more slowly than the highly connected habitat, and replicates with a higher carrying capacity tended to have higher invasion speeds. All in line with expectations of a pushed dynamic. Interestingly, however, their simulation results suggest that they probably got this perfect result for unexpected reasons. The strong hint is that their poorly-connected habitat induced density dependent dispersal in the wasps. Without this effect, their simulations suggest they should have seen diversity decreasing much more rapidly than it did. There is a nuanced, thoughtful, and carefully argued discussion about all this in the paper, and it is worth reading. There is much of value in this paper. Theirs is not a perfect empirical system in which all the model assumptions are met and in which huge population sizes make stochastic effects negligible. Here is a system one step closer to the messy reality of biology. The struggle to align this system with new theory has been worth the effort. Not only does it give us hope that we might usefully be able to discriminate between classes of invasions using real-world data, but it hints at a rule that Tolstoy might have expressed this way: all pulled invasions are alike, each pushed invasion is pushed in its own way.

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Reviews

Evaluation round #2

DOI or URL of the preprint: <https://doi.org/10.1101/2020.05.13.092775>

Version of the preprint: version 3

Authors' reply, 15 December 2020

Dear Dr Phillips,

We thank you for your swift decision on our manuscript, and are happy to see it soon recommended by PCI!

The new version is now online on bioRxiv; all final changes have been done according to the revision notice. Just to detail the couple changes that may need to be detailed:

1- (former) line 328: we replaced by $vF < vF_{\text{continuous}}$ to be clearer 2- all requirements were already fulfilled but one. We added a two-sentence short "Ethical note" paragraph to the Methods, after the description of the experiment.

We also corrected a few typos we noted during final typesetting.

All the best,

Maxime Dahirel, on behalf of all authors

Decision by **Ben Phillips**, posted 15 December 2020

Last changes before recommendation

Dear Author,

Congratulations! Your preprint submitted to PCI Evol Biol has been accepted and is about to be recommended.

Before doing so, we need that you modify your article according to this list of modifications:

Mandatory modifications

1- Please take into account this last minor changes:

L28: suggest, "where invasion speed conforms to pushed expectations, but the decline in genetic diversity does not."

L101: "describe [in] Fig 1"

L328: should this be $vF_{\text{true}} < vF_{\text{discrete}}$?

L332 "between pulled and [fully] pushed expansions"

L522: Suggest, "In our simulations, these pushed expansions..."

2- Please make sure that:

-Data are available to readers, either in the text or through an open data repository such as Zenodo (free), Dryad or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data.

-Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) are available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be reused.

-Details on experimental procedures are available to readers in the text or as appendices. Include information

about ethical approval for animal experimentation. Provide information about the compliance of their work with ethical standards of their national ethical committees and report the reference number of the ethical committee approval. If the study did not require ethical approval, include some sentences explaining why the approval was not needed.

-Authors have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this preprint declare that they have no financial conflict of interest with the content of this article." If appropriate, this disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: "XXX is one of the PCI Evol Biol recommenders."

3- Please make the following changes:

-Add the following sentence in the acknowledgements: "Version 4 of this preprint has been peer-reviewed and recommended by Peer Community In Evolutionary Biology (<https://doi.org/10.24072/pci.evolbiol.100118>)"

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Note that this DOI is not the DOI of your article, but the DOI of the recommendation text. The DOI of your article remains unchanged.

4- If not yet done, please send us a picture for which you own the rights that could serve as a thumbnail/illustration for your article on the web site of PCI. It can be a figure of the article.

Optional instructions (we strongly advise you to follow them)

1- We suggest you to remove line numbering from the preprint and put the tables and figures within the text rather than at the end of your MS.

2- Then, we strongly advise you to use the PCI templates (word docx template or latex template) to format your preprint in a PCI style. Here is the links of the templates: <https://peercommunityin.org/templates/>

□ For word template:

Do not hesitate to modify the template as you want (and send it back to us if you made significant improvements).

-the text to be replaced by your own text starts with XXX, eg XXXXTitle of the article.

-XXXXthe "citeas" □ *Dahirel, M., Bertin, A., Haond, M., Blin, A., Lombaert, E., Calcagno, V., Fellous, S., Mailleret, L., Malausa, T., and Vercken, E. (2020). Shifts from pulled to pushed range expansions caused by reduction of landscape connectivity. bioRxiv, 2020.05.13.092775, ver. 4 peer-reviewed and recommended by PCI Evolutionary Biology. <https://doi.org/10.1101/2020.05.13.092775>*

-XXXXthe date of deposit in the preprint server □ *date of the deposit of the latest version*

-XXXXthe surnames and names of the reviewers we sent you □ *Laura Naslund and two anonymous reviewers*

-XXXXthedoiwesentyou □ <https://doi.org/10.24072/pci.evolbiol.100118>

-XXXXthe surname and name of the recommender □ *Ben Phillips*

-In the acknowledgements, add this sentence □ "Version 4 of this preprint has been peer-reviewed and recommended by Peer Community In Evolutionary Biology (<https://doi.org/10.24072/pci.evolbiol.100118>)"

-Please be careful to choose the badges "Open Code" and "Open Data" only if appropriate (in addition to the "Open Access" and "Open Peer-Review" badges).

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-main.tex and sample.bib should be filled.

-in main.tex, the recommender's name is "Ben Phillips" and the reviewers' names are Laura Naslund and two anonymous reviewers -In sample.bib, indicate the right version of your preprint. It is version 4

-Preambleevolbiol.tex should be modified (comment lines 115, 119) to select badges. Please be careful to choose the badges "Open Code" and "Open Data" only if appropriate (in addition to the "Open Access" and "Open Peer-Review" badges).

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I hope this is clear. Do not hesitate to ask for any help if needed.

Once you have made these modifications, you should upload the new version of the article on the preprint server. Please tell us when you have done so. Thanks.

Best,

The Managing board of PCI Evol Biol

Evaluation round #1

DOI or URL of the preprint: <https://doi.org/10.1101/2020.05.13.092775>

Authors' reply, 12 December 2020

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Decision by [Ben Phillips](#), posted 27 September 2020

I apologise for the slight delay in providing a decision. I received two very high quality reviews within 30 days, but (as requested by the author) waited to take into account a third review from an open peer review exercise. This also was an excellent review and I have included it as part of the formal review process here.

This is a thought-provoking manuscript, and represent a lot of careful thinking, experiment, and analysis. I congratulate the authors on the work. I found the conceptual broadening of what might constitute a pushed wave to be interesting, and certainly a worthy topic for exploration.

Both of the reviewers I commissioned, however, had substantial concerns, so I cannot recommend the manuscript at this time. I would instead suggest a major revision with option to resubmit.

These reviewers' primary concerns lay with the modelling. Both reviewers 2 and 3 raise serious concerns around calculation of v_F . *Given the fundamental importance of v_F to the argument of the manuscript, these are concerns that need to be seriously considered. On one hand we have a concern that the model is not appropriate for the continuum description, giving a biased v_F ; and on the other we have a concern that the stochastic component of the model will also generate a bias in v_F .* These concerns need to be addressed before the manuscript can be recommended.

The reviewers also both had concerns about the interpretation of the experimental data. The big surprise here is that the invasion speed appears unaffected by connectedness, and the authors argue that v_F must be lower. Both had concerns about the arguments for this, and R3 had the additional useful suggestion that the ceteris paribus assumptions could/should be checked.

R2 and R3 also express concern about the exponential approach to v . Given the long-term approach to v over time in stochastic invasions, I see why you have taken this approach (and thought it a good idea), but R3 points out that a power law might be the more appropriate scaling.

Both reviewers clearly felt that the work could benefit from greater attention to the work of Gandhi et al, Birzu et al, and Hallatschek and Korolev. I thought this was good advice. For my part, I would also suggest that the experimental work of Williams et al 2016 (Science 353:482), and the theoretical work of Peischl et al 2015 (Am Nat 185:E81) might also be relevant (for different reasons).

I hope these reviews have been helpful. If the issues around calculation of v_f can be resolved, and a more thorough case made for the interpretation of the experimental results, the manuscript could be recommended.

Additional requirements of the managing board:

As indicated in the 'How does it work?' section and in the code of conduct, please make sure that:

- Data are available to readers, either in the text or through an open data repository such as Zenodo (free), Dryad or some other institutional repository. Data must be reusable, thus metadata or accompanying text must carefully describe the data.
- Details on quantitative analyses (e.g., data treatment and statistical scripts in R, bioinformatic pipeline scripts, etc.) and details concerning simulations (scripts, codes) are available to readers in the text, as appendices, or through an open data repository, such as Zenodo, Dryad or some other institutional repository. The scripts or codes must be carefully described so that they can be reused.
- Details on experimental procedures are available to readers in the text or as appendices.
- Authors have no financial conflict of interest relating to the article. The article must contain a "Conflict of interest disclosure" paragraph before the reference section containing this sentence: "The authors of this preprint declare that they have no financial conflict of interest with the content of this article." If appropriate, this disclosure may be completed by a sentence indicating that some of the authors are PCI recommenders: "XXX is one of the PCI XXX recommenders."

Reviewed by anonymous reviewer 1, 11 September 2020

Pulled and pushed behavior of population waves, the parameters controlling this behavior, transitions between both types of population waves, and the evolutionary consequences have garnered quite some interest in recent years. Dahirel and coauthors contribute to this work by asking how changing migration between patches / metapopulations affects the classification of the population wave and the genetic consequences. I find their study thought provoking and would like to thank the authors for providing me with the opportunity to dive deeper into the topic than I would have otherwise done. I would also like to applaud the authors for sharing the source code and many details of the analysis openly.

While I enjoyed reading the manuscript, I found it hard to properly convince myself, within the time available, of some of the key arguments. In the following, I will first outline my main questions and concerns, inevitably biased by my own research focus (range expansions, continuum limit, not working on pushed/pulled transitions).

1) The authors investigate range expansions occurring within a set of patches or metapopulations. 'Connectedness' thereby refers to migration rate between patches (or structure facilitating migration in case of experiments). My main concern is that the parameter regime / setup the authors use is not suitable for a continuum description, around which key arguments are or at least might be based. Specifically, I think this is a concern for computing v_f (around line 264 in the manuscript). Were r_0 or D_0 slightly higher, v_f would reach the maximum possible value of 1. I think there are two possibilities: Either I am wrong, in which case slight modification of the manuscript could prevent other readers from making the same erroneous conclusion. Or I am at least partially right, in which case a thorough discussion of connected metapopulations vs. continuum limit and discussion of applicability of results by Gandhi et al. and Birzu et al. to this study would be needed.

2) I struggle following the paragraphs in which different treatments are compared in simulations because sometimes both v and v_f change. Why did the authors not choose to keep one constant (compare to Gandhi et al., 2019)?

3) Given the high stochasticity in the system and the authors' aim to make inference from limited information (as is the case out in the field), the use of Bayesian inference appears reasonable. However, I am afraid that this approach makes the paper less accessible and 'less sticky', at least to readers like me, who understand the concept of Bayesian analysis but are not able to scrutinize the details. This approach might also make the findings more vulnerable to misinterpretation than necessary. One example is the exponential approach to v . Is this assumption supported by the data? Is this assumption actually necessary to extract v ? I suggest the authors include more of the raw data (front profile, speed as function of time) in the manuscript without sacrificing any of their Bayesian inference. Fig. 3 is a good example of how statistical rigor (to the extent I can judge) and intuition can be combined.

4) Heterozygosity - experiments: I'd appreciate a quick

introduction on what is measured and the consequences of wasp mating. Could the authors also share their interpretation of Table S4.2? 5) Heterozygosity – simulations: Why did the authors choose to use only two alleles? 6) Is non-neutral evolution of the wasp population a concern that can be ruled out?

A number of minor comments: • Line 82: Is the statement that disaccharides lead to an Allee effect correct in this generality? • Line 146: Visualise the function? • Line 154: Is there a prefactor N missing? • Line 189: I would have enjoyed a picture of the setup. For the general reader, this might be the first paper with this experimental setup they come across. Similarly, a flow diagram of the experiment might help visualize the experiment. • Line 197: What does "16:8 L:D" mean? • Line 199: Is there a concern of infecting the same egg twice? • Line 208: 'until emergence of first adults'. Why not wait for all adults? • Lines 248: With this definition of v_t , *approaching v might take a long time. Why not define a moving average of the local speed which would allow one to disregard the initial phase of approaching v ?* • Line 270: *How much does v_F change when changing from r_0 to r_1 and r_2 and D_0 to D_1 and D_2 ? (See also next point.)* • Line 315: *As the reference scenario's speed is very close to v_F , the dependence on K is a bit surprising. A brief comment might be helpful. Relatedly, what do the authors attribute the fact to that v_F for $K=225$ (v_F estimate, v estimate, others)?* • Line 375: *Dependence on K : Can it be ruled out that it's an indirect effect of changing K ?* • Line 450: *I unfortunately cannot follow the argument in this paragraph.* • *Supplementary Figure S7.1: What is the rationale behind using Bayesian inference here? Aren't the data directly available from simulations?* • *Supplementary Material S7: Is 'based on our second model' referring to 'reduced connectedness + DDD'?*

Reviewed by anonymous reviewer 2, 24 August 2020

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Reviewed by [Laura Naslund](#), 24 September 2020

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