

Decision for round #1 : Revision needed

All reviewers found the work novel and of general interest. I share that opinion. They also provided detailed comments and suggestions to improve the manuscript. Most major concerns converged among reviewers to questions of clarity/reproducibility, reference to previous work, and interpretation of results. The detailed suggestions found in reviewers' reports will most certainly contribute to improving the manuscript. Reviewers were concerned the work would not be reproducible because of lack of details on the various packages and code used to run simulations. Most reviewers also raised concerns over some interpretations of results generated from a specific model. Part of the problem was a concern over the sensitivity of results to the specific model used. Some more specific potential issues were also suggested, such as the dependence of results on the assumed correlation between dispersal and fecundity, or the validity of concluding to lower competition in highly fragmented landscapes. Finally, all reviewers suggested additional references to previous work to better set the broader context for adding evolutionary dynamics to the study of extinctions in metapopulations with habitat destruction. In my opinion, addressing these, and all other comments from reviewers, will increase the potential impact of this study.

We thank you and the reviewers for the time and work done on this manuscript and for the constructive and positive feedback. We have tried to address all comments and feel that the manuscript is vastly improved as a result. We apologize for the time it took to send this revision, largely due to the completion of my PhD manuscript and to my moving to a postdoc position.

Reviews

Reviewed by Eva Kisdi, 01 Jul 2022 14:07

This paper investigates the evolution of dispersal via numerical simulations in a spatially explicit system, assuming that dispersal is traded off with competitive ability. The paper has potential, but some simulations can be criticized for having very few individuals. The interpretation of results and comparison to earlier work should also be improved.

(1) Many results pertain to the case when 99% of the landscape is unsuitable. In this case, there are only 25 patches that can support an individual. How much genetic drift plays a role at such low numbers? How much are the results repeatable over different lattices? With only 25 patches, there is considerable randomness in their actual locations and distances.

We agree that stochastic processes (eg, the stochasticity of extinctions) will lead to genetic drift and that the importance of drift will likely be very important on the brink of extinction (eg, at 99% fragmentation). We feel however that having such a stochastic/drift component is important here, as we try to uncover not only dispersal evolution, but its effects on metapopulation maintenance (eg, the evolutionary rescue perspective), the importance of stochastic processes being all the more relevant close to extinction.

Each simulation scenario is here repeated on 20 different landscapes and we indeed observe more variability around the mean dispersal at 99% which may be partly due to genetic drift but also just to different spatial patterns (figure 2). However, even taking this variability into account (see variance in figure 2), the observed increase in dispersal cannot be due to randomness and genetic drift alone.

We have clarified our consideration of different landscapes in the new version of the manuscript:

Line 211: we have added “To assess repeatability, twenty...”

We have also added a paragraph in the discussion to clarify the role of selection and drift, in the light of your comment (see L365-374)

(2) The authors say that fragmentation decreases overall occupancy and therefore reduces competition (line 311). Figure 3, however, shows almost 100% occupancy of habitable patches even at a very high level of fragmentation.

By “overall occupancy”, we mean the occupation of the entire grid, suitable and non-suitable patches. But we agree that our argument on competition is maybe not quite clear. What we mean is that when fragmentation is high and as occupancy on the entire grid is decreased, for a given empty patch, there are potentially less colonizers (ie less filled patches) that can access it. Hence competition for access to this patch is reduced, as fewer contrasted strategies can access a given patch.

Line 330-332: We have added “Thereby, when a patch is emptied, the number of possible colonizers (ie, of suitable filled patches) is reduced.”

(3) The comparison to earlier results in lines 295-309 neglects the fact that in the present model, higher dispersal also means higher fecundity: A dispersive strategy can colonize many patches in the absence of the competitively superior strategy. Many previous models assumed, however, that fecundity is constant and dispersal affects only the spatial allocation of offspring. Environmental heterogeneity selects against dispersal in these models because dispersing offspring end up, on average, in a worse place than where they come from. Dispersal would not be selected against in these previous models if the dispersing offspring were extra offspring in addition to those who do not disperse. In the present model, this latter situation is the case and dispersal would be highly favoured also without the competition-colonization trade-off. (The competition-colonization trade-off explains in the present model why low dispersal may be present.)

I believe the same difference explains why fragmentation decreases dispersal in many natural systems (lines 321-323). If a parent has only so many offspring, then wasting them to disperse into mostly uninhabitable patches is selected against. Instead, the authors' model focuses on a highly fecund organism, which can afford to disperse some of its offspring even if most dispersed offspring perish in unsuitable patches. This is because most of the non-dispersed offspring would perish to kin competition anyway (Hamilton and May 1977); it does not matter how many offspring remain in the patch, the patch will be inhabited by one surviving individual, i.e., it's siblings will die.

The same issue arises also when comparing dispersal dimorphism to Bonte et al (2010): they assumed that the total number of offspring is independent of the dispersal strategy, the present model assumes otherwise. The other papers cited here consider the probability of dispersal with a global dispersal pool, not dispersal distance on a lattice. The comparison should therefore be done more carefully.

We largely agree with the reviewer. However, while the decoupling of dispersal distance and propagule number has been useful in previous works to understand the evolution of dispersal itself, it is still a debatable assumption. As we propose in the text, many biological systems (propagules of social insect colonies, seed size vs number) suggest otherwise. We have tried to rework the text to better highlight that our model assumes such a situation. Also, we would like to stress that even with our hypothesis, evolution of high dispersal is actually only happening in restricted scenarios (large & random fragmentation).

We agree that in the discussion, we compare our results to previous models sometimes based on different assumptions (and not only on this issue). We feel that it is however important to discuss previous works, even if they differ in some ways, to give a broader take on the issues we tackle.

However, we agree that we need to highlight these differences more and explain how they might affect our results.

For this purpose, we added a paragraph in the discussion about these modelling differences, including the impact of the correlation between fecundity and dispersal. (L311 – 328)

(4) The two reasons given in lines 367-372 are in fact the same: with sufficiently strong aggregation, like the cases described in line 383-392, fragmentation does not affect the population and therefore neither drives it extinct nor selects for different dispersal. Strongly aggregated habitat removal is like comparing two lattices of different sizes but both large – they give the same results.

Line 398: We have removed “for two reason” and “First”

Line 400: We have removed “Second,”

(5) The paper would much benefit from restructuring. The ms investigates evolution in a temporally constant environment and evolutionary rescue in a deteriorating environment. It would help if these were two main sections and the reader would not need to jump back and forth between the two scenarios. The results and their interpretations should be given in one place (currently all interpretation is left to the Discussion). It is a lot easier to grasp and remember results when they make sense! that is, when they are properly explained at the same place where they are described. For one example, the Results section only states the fact that no evolutionary rescue is seen in aggregated landscapes. The explanation is easy; but the reader learns it only almost a hundred lines later, in the second half of the Discussion.

Other comments

- I wonder how much the evolution of dispersal strategies with distance >1 depends on whether the landscape percolates (this may be a highly nontrivial question).

Looking at our landscapes and the resulting evolution, we suspect the reviewer may be right. However, we feel that it is not a central point we want to make, so we did not reanalyze all data to assess this aspect.

- The authors say that evolutionary rescue is a threshold phenomenon. This is not entirely true, even if there is a jump in Figure 4.

We agree and we modified this sentence L280-402

- In theory papers, a section "Materials and methods" really covers the description of the model, so it is better to give it a more suitable title.

We modified the title of the section. L155

- Lines 174-186 repeat what has already been said.

We removed lines and replaced it by "(see introduction)" L183

- The legend of figure 2 seems to be mistaken, panels c and d are not what the legend says.

Yes, we modified it.

- Panels a and d of figure 3 are not informative.

We feel that the observation of phenotype dynamics may be important for readers to assess the maintenance of polymorphism over time.

- Note a typo on the horizontal axis in Figure 4, the last number is presumably 0.1, not 0.01.

We have corrected.

- The writing could be improved at some places. E.g. "variations of various selective pressures" does not read well. In line 87, "Fragmentation" is confusing as it may refer to the splitting of colonies described in the previous sentence (replace with habitat fragmentation or start new paragraph). In line 313, " fragmentation intensifies the strength of the competition for space" is confusing because the previous sentence said fragmentation decreases competition. The plural of "offspring" is also "offspring"; "evolution" has no plural.

We have proof-read the text and tried to correct mistakes whenever we could. Including the corrections proposed by the reviewer here.

Reviewed by David Murray-Stoker, 24 Jul 2022 16:53

Summary Finand et al. (bioRxiv 2022.06.08.495260, submitted to PCI Ecology) used mathematical simulations to understand (1) how habitat fragmentation and configuration affects the evolution of dispersal traits and (2) how temporal variation in habitat fragmentation to determine when evolutionary rescue of the metapopulation could occur. The authors demonstrate that increased habitat fragmentation selects for increased dispersal ability, but this effect depends on habitat configuration (i.e., aggregation); contrasting dispersal abilities coexisted under high fragmentation with minimal or no habitat aggregation. Additionally, the simulations showed that faster evolution of dispersal ability increases persistence of the metapopulation, but habitat aggregation reduces this effect. This study provides a solid foundation for further theoretical and empirical research, with direct relevance to conservation and restoration ecology. The authors were also clear and upfront about the limitations of their models, with directions for future work set. In summary, I found this to be a strong and sound study with appeal to both general and applied ecological research. I have offered 3 major comments to improve the clarity of the research and situate the results in the broader ecological context, with several minor comments regarding alternative interpretations of statements and edits to the text.

We thank the reviewer for his appreciation and for the time he devoted to our manuscript. We tried to cover all his comments.

Major Comments

1. Transparency on how the simulations were conducted.

1.1. The authors were very clear in defining what the simulations were testing and how parameters were defined; however, there was a conspicuous absence describing all of the software and programs used for the simulations. For full transparency and reproducibility, all software programs required for the analysis should be cited.

1.1.1. The authors cite the `NLMR` and `landscapetools` packages, both of which are implemented in R; however, this might not be known by other readers.

We agree and apologize. We indeed forgot to indicate that our work was done using R. We have added "Simulations and analysis were done with R 3.9." L156

1.2. As the authors conducted a simulation study, it is essential that the analytical code for the simulations is deposited in a stable depository (e.g., Zenodo, figshare).

1.2.1. Analytical code is frequently required for simulation studies in peer-reviewed journals and should also be provided if the authors intend to publish this work in Peer Community Journal

Our code is available on github: https://github.com/bfinand/Model_dispersal_evolution

We have added a section "Data availability" at the end of the manuscript to indicate this L442-444

2. Clarification on the evolution of dispersal as an adaptive process.

2.1. My understanding of the simulations is that the evolution of dispersal is treated as an adaptive process (i.e., natural selection) when non-adaptive processes (e.g., genetic drift, gene flow, and mutation). Although the terminology in the model description for Scenario 2 describes the speed of evolution as different mutation rates (lines 227-230), later discussion (e.g., lines 291-294, 300-301, 305-308, 390-392) implies the evolution of dispersal as adaptive. I think it is important for the authors to clarify how mutation and the evolution of dispersal is considered (i.e., is it adaptive or non-adaptive processes underlying the evolution?).

We agree this is a very important point and we did several modifications to the text (see below but also the answers to reviewer 1). Our model is stochastic and does include mutation and drift, the latter being highly important when the metapopulation is on the brink of extinction. Gene flows is the only force that is here very simplified, as the model we used is phenotype based.

2.1.1. Genetic drift can be important in fragmented habitats with small population sizes, while gene flow could homogenize populations at high dispersal and potentially lead to divergence at low dispersal and/or increased habitat isolation.

We agree that genetic drift is important in our model and especially at high fragmentation percentage due to the small population size. To better assess how it may lead to additional variability, we undertook 20 replicates for each parameter combinations. Studying the replicates highlights higher variability close to extinction in the evolutionary process, while selection of high dispersal remains prevalent. Gene flows are simplified in our model as it is a phenotypic approach.

We have added a paragraph in the discussion to clarify our take on the evolutionary process L311-328

2.1.2. I apologize to the authors in advance if my understanding of the term "mutation" is incorrect in the context of the simulations.

3. Expand the base of the foundational literature.

3.1. The authors make reference to Tilman et al. (1994) when describing previous work (e.g., lines 73-94) and as the broader context in which their results are placed (e.g., lines 295-309). I think it is

not only possible but necessary to expand the foundational literature on the competition-colonization tradeoff in relation to habitat fragmentation and dispersal.

3.1.1. Tilman et al. (1994) is an influential piece of research, but it is not the only study that considers how the competition-colonization tradeoff affects dispersal strategies under habitat fragmentation, as suggested by the authors (lines 90-92).

3.2. A quick search on Google Scholar (search terms = competition colonization trade off, habitat fragmentation, dispersal) yielded several relevant articles, including: Tilman, D. et al. 1997. Habitat destruction, dispersal, and deterministic extinction in competitive communities. *The American Naturalist* 149:407-435. Link Yu, D. W., and H. B. Wilson. 2001. The competition-colonization trade-off is dead; Long live the competition-colonization trade-off. *The American Naturalist* 158: 49-63. Link Calcagno, V., et al. 2006. Coexistence in a metacommunity: the competition-colonization trade-off is not dead. *Ecology Letters* 9: 897-907. Link

3.3. The authors do make good use of empirical research examining the competition-colonization tradeoff to introduce (e.g., lines 47-72) and situate their results in the broader context (e.g., lines 310-327).

Indeed the reviewer is right. The competition-colonization trade-off has inspired many developments. Most of these works, including the ones proposed here are focusing on ecological outcomes (eg, coexistence of species in fragmented landscapes). Our aim is here not to focus on these ecological dynamics, but rather to use the trade-off to uncover resulting eco-evolutionary dynamics of dispersal (which is not done into these articles).

3.3.1. I would argue that Cheptou et al. (2008) is a great example of an empirical study investigating how habitat fragmentation alters the evolution of dispersal in relation to the competition-colonization tradeoff

We agree with the reviewer and we cite this work as an important empirical inspiration (eg L57,59,83,343)

3.4. In summary, I think the authors should make more use of the fairly extensive body of work on the competition-colonization tradeoff, habitat fragmentation, and dispersal, including the use of work already cited in the manuscript. Tilman et al. (1994) is foundational by chronological precedent and influential, but there are other studies that have built upon that foundation. I trust the authors to identify and include work that is most relevant to their own research in the revision, but I think it is important to increase the relevant body of work cited in Finand et al.

We agree that we need to be fair on this. However, our manuscript is centered on the evolution of dispersal, the competition-colonization being the choice of constraint rather than the object. Therefore, we would like to keep the focus of the discussion of these evolutionary processes.

Minor Comments

1. Lines 47-49: I do not think the introduction is the most appropriate space, but as Fahrig has been cited, it would be interesting to discuss how the rResults from the simulations relate to the Habitat Amount Hypothesis (Fahrig 2013). Specifically, how does the number or percentage of suitable patches affect metapopulation persistence, regardless of spatial arrangement? References 2 Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography* 40: 1649–1663. Link Haddad, N. M., et al. 2017. Experimental evidence does not support the Habitat Amount Hypothesis. *Ecography* 40: 48-55. Link Watling, J. I., et al. 2020. Support

for the habitat amount hypothesis from a global synthesis of species density studies. Ecology Letters 23: 674-681. Link

We thank the reviewer for highlighting this important debate. However, note that these articles are about the maintenance of species diversity in space, and a bit far from the dispersal evolution questions we want to tackle. We however have a companion work on similar questions of biodiversity (impact of habitat fragmentation on ant communities) and will need these references in this context.

2. Lines 52-53: Habitat fragmentation can affect habitat suitability in terms of site isolation and the ability for organisms to disperse to the sites; however, my initial reading interpreted “non-suitable habitats” as degraded or environmentally unsuitable. I think it would be helpful for the readers if the authors clarified how the habitats are unsuitable due to fragmentation.

In our study, we define the fragmentation as the proportion of hostile vs suitable patches (L49). So, the fragmentation is the creation of unsuitable patches.

3. Lines 124-125: I am not certain if evolutionary rescue is necessarily an adaptive trait but instead an emergent response. Populations can adapt to intense selection imposed by the environment, and, if the population is able to adapt, there has been evolutionary rescue. In other words, evolutionary rescue is a response to adaptive evolution by populations. Note: I am using the definition of evolutionary rescue defined by Bell (2017), which was cited by Finand et al.

We agree and we have modified the sentence to clarify it L126

4. Lines 141-144: This comment is not intended to guide a new analysis in the present manuscript, but I was wondering if the eventual competition between colonizers could affect the dynamics? It could be an interesting topic to investigate in a future study, but I do not think it is necessary for the present manuscript.

We think that as long as the competitive hierarchy is respected, results should not change. However, former works on the ecological side (eg, the Yu & Wilson or the Calcagno paper mentioned earlier by the reviewer). For instance, Calcagno suggests that relaxing the hierarchy may somewhat impede coexistence, meaning (for us) that polymorphism would become less likely. But studying further this question would indeed require a whole new analysis.

5. Lines 157-160: I think this definition of habitat fragmentation closely follows the Habitat Amount Hypothesis eventually developed by Fahrig (2013). The definition of fragmentation used by the authors does not explicitly state: (1) how adjacent and occupied patches are treated, (2) if the spatial arrangement (i.e., degree of connectivity and isolation) affects the intensity of habitat fragmentation, and (3) how does increased aggregation of suitable patches (i.e., habitat size) affect the dynamics? I think these are important assumptions that should be clarified by the authors in relation to their working definition of habitat fragmentation.

We have reworked the text to clarify this aspect. We mention how adjacent and occupied patches are treated L159

To clarify the point made by the reviewer, we have added “While we keep a simple definition of fragmentation (proportion of unsuitable patches), note (1) that higher frequency of unsuitable patches

decreases overall connectivity; (2) that we also manipulate the effect of fragmentation on local contexts by considering varying degrees of aggregation. " L164-169.

6. Lines 247: The authors can remove "...which is congruent with Tilman et al. (1994)."

Line 247: we have removed "which is congruent with Tilman et al. (1994)."

7. Lines 252: The authors can remove "Aggregation therefore qualitatively changes the results of mean field models (such as Tilman et al., 1994)." from the results and save it for the discussion.

As reviewers have opposite points of view about this (see comment of reviewer 1), we have decided to keep some simple interpretation in results and take a step back in the discussion.

8. Lines 311-313: Reduction in occupancy doesn't mean a reduction in competition. Depending on patch size, isolation, and quality, competition could actually be increased in a fragmented patch. I would argue that the average competition level should be the average of competition from each patch.

We modified this sentence to clarify our take on competition. L330-332

9. Lines 323-325: Does spatial heterogeneity decrease dispersal or select for variation in dispersal abilities?

It decreases dispersal but it can also select for variation at the same time. For instance, figure 3c shows 2 pics of dispersal distances.

10. Figure 1: I think readers would benefit from a more comprehensive figure caption that allows the figure to 'stand alone.' Without guidance from the authors, it took a considerable amount of time to properly understand the content, and I think expanding the caption would help the reader understand the figure and, more broadly, the approach to and interpretation of the simulations.

We agree and we have modified the figure captions. We have extended the captions and we tried to provide enough details for the various figures to stand alone.

Reviewed by anonymous reviewer, 23 Aug 2022 15:06

Dear authors,

I have carefully read the paper. The paper deals with the evolution of dispersal in the presence of a colonization-competition tradeoff in the context of a spatially explicit model. The rationale of it is very clear, but model specification is poor. I point to some aspects of the model that I think they are poorly described:

1. **How is the definition of the colonization-competition tradeoff set up? In Tilman (1994), the tradeoff is chosen in a very particular way for the whole community of S species to coexist.**

We have modified the caption of Figure 1 to explain better the link between competition and colonisation. Basically, when competition happens among phenotypes, the one with the smallest dispersal distance wins the competition.

2. Is the dynamics time discrete?

Yes. We have added L175-176 “Dynamics time is discrete and each time step is divided...” to clarify this.

3. How many possible different dispersal strategies are considered?

To clarify this point, we have added “Mutation incurs incremental variations in dispersal distance of 1, upward or downward with equal probability. Dispersal distance distance of zero would mean staying in the patch (hence going extinct at some point) while distances below 0 are not possible and discarded. We do not set any maximum for the dispersal distance. Note however, that while this situation is never reached in our simulations, a dispersal distance above 25 would mean global dispersal over the whole grid and further increases would not lead to additional benefits, only to being less competitive”. We have clarified this in L191-195

4. How the quasi stationary state is checked for? In other words, why 50000 time steps? Aren't the length of the transients depending on parameter values?

Because of the stochasticity of the model (see eg comments on drift above), a strict equilibrium is never reached. However, dynamics usually become coherent quite fast (see fig 2). All simulations were run and checked for consistency. We have clarified this on L214

In principle, I like the verbal descriptin found in the ms, but a more detailed description would be needed. In any case, what the ms currently lacks is an argument defending that the details of model specification are not relevat for the reported results. In other words, their results are robust to slight changes in model definiton.

Indeed, the results of the models very often depend on their specification. We have tried to discuss some of the modelling assumptions that seemed critical to us, also using some of the comments made above (eg, about the relationship between dispersal and fecundity in the discussion L311-328).

In the introduction section, a better connection with previous literature should be achieved. What gives credit to a simulation model is its connections (in some reasonable limits) to existing models. The approach the authors take stems from a stochastic version of Levins metapolation model with habitat destruction. Previous models of this kind have been analyzed in the literature:

Otso Ovaskainen, Kazunori Sato, Jordi Bascompte, and Ilkka Hanski (2002). Metapopulation models for extinction threshold in spatially correlated landscapes. *Journal of theoretical Biology*, 215: 95-108.

Jordi Bascompte and Miguel A. Rodríguez (2001). Habitat patchiness and plant species richness. *Ecology Letters*, 4: 417-420.

Jordi Bascompte and Ricard V. Solé (1996). Habitat fragmentation and extinction thresholds in spatially explicit models. *Journal of Animal Ecology*, 65: 465-473.

Alonso, D., & Mckane, A. (2002). Extinction dynamics in mainland-island metapopulations: an N-patch stochastic model. *Bulletin of Mathematical Biology*, 64(5), 913–958.

<https://doi.org/10.1006/bulm.2002.0307>

Solé, R. V., Alonso, D., & Saldaña, J. (2004). Habitat fragmentation and biodiversity collapse in neutral communities. *Ecological Complexity*, 1(1), 65–75. <https://doi.org/10.1016/j.ecocom.2003.12.003>

Allouche, O., & Kadmon, R. (2009). A general framework for neutral models of community dynamics. *Ecology Letters*, 12(12), 1287–1297. <https://doi.org/10.1111/j.1461-0248.2009.01379.x>

Some of these papers should be cited, because also deal with extinction thresholds in metapopulation models.

We thank the reviewer for these additional articles. We have added some of these papers in the discussion from L385-392. Note however that most of these works are on how the spatial context affects ecological dynamics, while we would like to keep a focus on eco-evolutionary dynamics of dispersal in this manuscript.

I would advice that the authors should start with a simple mean-field one-species model able to recover model results when destruction/recovery and colonization/extinction processes are at random. This would connect to Levins model. From here, introduce S equivalent species, which would correspond to the S-species open Levins model analyzed by Allouche and Kadmon (2009) or Sole etal (2004). Then, introduce S different strategies according to a given colonization-extinction tradeoff, still in the contex of ODE-based patch occupancy metacommunity models, which should correspond to Tilman (1994) with habitat destruction. Then, continue by the introduction of explicit space (a system of N sites or patches), that can be in three states, either destroyed (D), or free but suitable for colonization (A), and fully colonized by a species that belong to any of the S stragies (S_i). And finally, introduce the possibility of evolution.

While we see the value of the methodology proposed here, especially the idea of better communication with a progressive complexity, we feel that the current set of simulation allows a good take on the question we want to tackle (ie, how fragmentation and its structuring lead to various evolution of dispersal).

This close relation of the simulation model presented in the ms to previous literature should be emphasized. It is what gives credit to the model. In some of these limits, do your simulations match model predictions? If yes, you are in a good shape.

Otherwise, in principle, the reader (or this reviewer) should be able to check every line of code to see to what extend results hold or depend on the details of model specification.

BTW, in the context of open science, the model code should be made availabe to check and reuse, by giving credit to the authors, of course.

We agree that highlighting predictions and discussing how our results relate to the previous litterature is very important to assess whether the model works properly. We have tried to propose clear predictions in the introduction and to discuss our results thoroughly in the last part of the manuscript.

Our code is available on github: https://github.com/bfinand/Model_dispersal_evolution

We have added a section “Data availability” at the end of the manuscript that points out the link to the code L442-444

Reviewed by Shripad Tuljapurkar, 05 Sep 2022 21:30

Review of Evolution of dispersal and the maintenance of fragmented metapopulations

by: Basile Finand et al.

This paper starts by pointing out that the "mean-field" approach to landscapes, where one considers only the fraction of "suitable" patches, is limited. What also matters is where patches are relative to each other -- i.e., aggregation. The paper then looks at these two dimensions, here called fragmentation and aggregation, as they effect the competition/colonization trade-off first shown by Tilman.

The main phenotype considered is "dispersal" ability, and the authors then also consider phenotypic "evolution" by assuming that random mutations cause a random step change in dispersal distance.

The main results are that fragmentation and aggregation have distinct effects on the competition/colonization trade-off (as described here). In addition, evolution can change dispersal phenotypes fast enough to affect a "rescue" from increasing fragmentation.

Here are my comments.

1. Considerable effort has been taken with the writing so that technical and even biological details are summarized as simply as possible, as is the actual simulation procedure. This is good, but more specifics may be needed, and some of my questions are driven by that.

We thank the reviewer for the time devoted and the appreciation of our work.

2. Line 49-50 "fragmentation is defined by the proportion of hostile locations (patches) and we systematically vary its degree of spatial aggregation..."

How about fragmentation in the sense of distance between suitable patches? Is that subsumed in the definition here?

In our study, we define the fragmentation as the proportion of hostile vs suitable patches (L50). Following this definition, increased fragmentation decrease the possibility of dispersal among suitable patches. The aggregation that we also manipulated impacts this connectivity of patches. An increase of aggregation clumps patches together and favors local connectivity.

To clarify this, we have added "While we keep a simple definition of fragmentation (proportion of unsuitable patches), note (1) that higher frequency of unsuitable patches decreases overall connectivity; (2) that we also manipulate the effect of fragmentation on local contexts by considering varying degrees of aggregation." L166-169

3. I am confused by the term "aggregation," The pictures here do provide an intuitive sense of what "aggregation" may be -- but the reference to R packages does not help.

How about some (simple) statistics, say the spatial correlation, or the conditional probability of finding a similar patch as a function of distance?

Aggregation is exactly that. It is defined by the spatial autocorrelation on the grid.

To clarify, we have added Line 164-166

4. Does the "scale" of aggregation/fragmentation matter? And how does that connect to the scale of the "patch", if a patch only supports one individual?

The fragmentation and aggregation is defined at the level of the landscape, constraining how patches (one patch=one individual) are arranged. The fragmentation controls the number of suitable vs unsuitable patches and the aggregation, defined by the Hurst exponent, controls the configuration of these patches and especially the spatial autocorrelation. Manipulating the Hurst coefficient allows variation in the size of patch groups. We hope that the modification done with the last comment will clarify it.

5. Line 73 - 78 suggests that Dispersal = Colonization ability? True?

Yes, we have added "(here our measure of dispersal)" L76 to clarify it.

Line 190 says, "competitive hierarchy favors the strategy that has the smallest dispersal distance." Is competition also determined by dispersal?

Yes, individuals who disperse the least are the most competitive. We have tried to clarify this further in the new presentation of Figure 1.

Presumably then one can say that the results trade-off increased dispersal (good as fragmentation increases) vs. decreased dispersal (competition; good as aggregation increases).

6. Line 262 -- "random few suitable patches" makes no sense.

Sorry for this. Line 263: We have deleted "Random"

7. The cited paper by Sciani et al. talks about the R package. While that is good, more detail and discussion (in terms of the underlying theory of how one represents and models landscapes, say the work by Gardner) is essential. Remember that simulations are not proofs, especially simulations that rely on a poorly described process (FBMs, fractals).

We agree that the way we constructed the landscape is essential to understand results. We have added some information about the way we considered aggregation L165-169.