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.

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.
    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
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?).
        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.

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).
      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
   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.

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 results 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

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

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.
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.
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.
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.
6. Lines 247: The authors can remove “...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.
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.
9. Lines 323-325: Does spatial heterogeneity decrease dispersal or select for variation in dispersal abilities?
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.

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Note: If any of the above comments are unclear, please do not hesitate to contact the editor or contact me directly.