Peer Community In
Ecology

Unity makes strength: clustered extinctions have stronger, longer-lasting effects on metacommunities dynamics

Elodie Vercken based on reviews by Frederik De Laender and David Murray-Stoker

A recommendation of:

Spatial distribution of local patch extinctions drives recovery dynamics in metacommunities

Camille Saade, Sonia Kéfi, Claire Gougat-Barbera, Benjamin Rosenbaum, and Emanuel A. Fronhofer *(2021) , bioRxiv, 2020.12.03.409524, ver. 4 peer-reviewed and recommended by Peer Community in Ecology* **10.1101/2020.12.03.409524**

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Recommendation

In this article, Saade et al. (2021) investigate how the rate of local extinctions and their spatial distribution affect recolonization dynamics in metacommunities. They use an elegant combination of microcosm experiments with metacommunities of freshwater ciliates and mathematical modelling mirroring their experimental system. Their main findings are (i) that local patch extinctions increase both local (α-) and inter-patch (β-) diversity in a transient way during the recolonization process, (ii) that these effects depend more on the spatial distribution of extinctions (dispersed or clustered) than on their amount, and (iii) that they may spread regionally. Microcosm experiments are already quite cool just by themselves and have contributed largely to conceptual advances in community ecology (see Fraser and Keddy 1997, or Jessup et al. 2004 for reviews on this topic), but they are here exploited to a whole further level by the fitting of a metapopulation dynamics model. The model allows both to identify the underlying mechanisms most likely to generate the patterns observed (here, competitive interactions) and to assess the robustness of these patterns when considering larger spatial or temporal scales. This release of experimental limitations allows here for the analysis of quantitative metrics of spatial structure, like the distance to the closest patch, which gives an interesting insight into the functional basis of the effect of the spatial distribution of extinctions.

A major strength of this study is that it highlights the importance of considering the spatial structure explicitly. Recent work on ecological networks has shown repeatedly that network structure affects the propagation of pathogens (Badham and Stocker 2010), invaders (Morel-Journel et al. 2019), or perturbation events (Gilarranz et al. 2017). Here, the spatial structure of the metacommunity is a regular grid of patches, but the distribution of extinction events may be either regularly dispersed (i.e., extinct patches are distributed evenly over the grid and are all surrounded by non-extinct patches only) or clustered (all extinct patches are neighbours). This has a direct effect on the neighbourhood of perturbed patches, and because perturbations have mostly local effects, their recovery dynamics are dominated by the composition of this immediate neighbourhood. In landscapes with dispersed extinctions, the neighbourhood of a perturbed patch is not affected by the amount of extinctions, and neither is its recovery time. In contrast, in landscapes with clustered extinctions, the amount of extinctions affects the depth of the perturbed area, which takes longer to recover when it is larger. Interestingly, the spatial distribution of extinctions here is functionally equivalent to differences in connectivity between perturbed and unperturbed patches, which results in contrasted “rescue recovery” and “mixing recovery” regimes as described by Zelnick et al. (2019).

Furthermore, this study focuses on local dynamics of competition and short-term, transient patterns that may have been overlooked by more classical, equilibrium-based approaches of dynamical systems of metacommunities. Indeed, in a metacommunity composed of several competitors, early theoretical work demonstrated that species coexistence is possible at the regional scale only, provided that spatial heterogeneity creates spatial variance in fitness or precludes the superior competitor from accessing certain habitat patches (Skellam 1951, Levins 1969). In the spatially homogeneous experimental system of Saade et al., one of the three ciliate species ends up dominating the community at equilibrium. However, following local, one-time extinction events, the community endures a recolonization process in which differences in dispersal may provide temporary spatial niches for inferior competitors. These transient patterns might prove essential to understand and anticipate the resilience of natural systems that are under increasing pressure, and enduring ever more frequent and intense perturbations (IPBES 2019). Spatial autocorrelation in extinction events was previously identified as a risk for stability and persistence of metacommunities (Ruokolainen 2013, Kahilainen et al. 2018). These new results show that autocorrelated perturbations also have longer-lasting effects, which is likely to increase their overall impact on metacommunity dynamics. As spatial and temporal autocorrelation of temperature and extreme climatic events are expected to increase (Di Cecco and Gouthier 2018), studies that investigate how metacommunities respond to the structure of the distribution of perturbations are more necessary than ever.

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Reviews

Toggle reviews

Revision round #2

2021-04-14

Author's Reply

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Decision round #2

Dear Authors,
Thank you for your revision and for addressing carefully the comments of the reviewers and myself. You have been doing a great job, and I reckon that most
I still have one remaining concern that needs to be addressed before I can recommend your manuscript.
Although the core topic of your manuscript is related to the effect of spatial structure in metacommunities, I feel that the issue of space is not fully appreciated in its present version yet.

When analyzing a larger landscape, you find (i) no difference for metrics measured in unperturbed patches in comparison with smaller landscapes; (ii) for other metrics, a larger effect of the spatial distribution in larger landscapes, which is driven by a quantitative modification of metrics measured in clustered extinctions.

These two points highlight the fact that the position of a given patch relative to perturbed or unperturbed patches is crucial here, and should be acknowledged and discussed more explicitly.
Regarding the first point (i): you analyze only unperturbed patches that are adjacent to a perturbed patch, so the local environment of these patches is more or less the same regardless of landscape size. This actually looks like the equivalent of an edge effect. It is quite interesting, and might be worth commenting.
For the second point (ii): it does seem that the size of the cluster has a strong effect (no modification for dispersed extinctions, that do not change in larger landscapes), which is further supported by the analysis of recovery dynamics on Fig S18 and S19. The distance to an unperturbed patch (which is correlated to the size/depth of the perturbation cluster) has a clear effect on the recovery dynamics. I do believe that the use of quantitative indicators in the analysis of the simulations in large landscapes (not in addition to the clustered/dispersed factor, but in replacement of it) could give more insight on the general role of space here, outside of the specific clustered/dispersed modalities. Patches from all modalities could be pooled and analyzed with regard to their actual local environment. Multi-model comparison methods could be used to determine which indicator is most informative as different indicators are likely to be correlated (e.g., the distance to the closest perturbed/unperturbed patch or the number of perturbed/unperturbed patches in the neighbourhood).

I reckon that the discussion could be improved with a part addressing explicitly these issues related to a more quantitative interpretation of spatial structure, and would give the opportunity to make better use of Fig. S7-S8 and S18-S19, the latter not being called in the main text yet. Some parts of the discussion already address the issue of space (e.g. L. 435-439, 472-476, 548-551, 561-567, 591-586), but they are scattered over different paragraphs and could be brought together for more clarity.

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Revision round #1

2021-02-03

Author's Reply

Download author's reply (PDF file)Download tracked changes file

Decision round #1

Dear Authors,   I would like to apologize for the delay in getting back to you. I have been waiting for a 3rd review for more than 3 weeks now, so I decided to proceed with the first two reviews only, to avoid keeping you waiting any longer.   Both reviewers were very positive about your work, which they found thorough and clearly written. The elegant link between experimental results and model simulations was particularly appreciated. I reckon that most of the comments we had should be easily addressed, but please pay particular attention to the suggestions concerning results presentation, the analysis of dynamical response variables, and the analysis (or at least discussion) of effects of temporal synchrony in perturbations.   I will be most happy to recommend your manuscript once you have addressed these comments. Thank you for sharing your work with us.   Best regards,   Elodie Vercken.   My own comments: - I wondered why you used the terms “spatial clumping” rather than “spatial autocorrelation” - The size of the landscape sets a strict limit to the range of spatial clumping that can be explored. I reckon you could use the model to investigate larger landscapes, to check whether the dominant influence of the spatial distribution of extinctions over extinction rates holds in less constraint configurations. - Also, I think it would be informative to compare the distributions of some functional indicators between experimental modalities (e.g. distance to the closest extinct patch, proportion of extinct patches in a 1-patch neighbourhood), as it would help to interpret the results (see for instance l. 464-465). Would it be possible to analyze the different response variables with such quantitative covariates, rather than "clumped vs dispersed"? - It seems that the results are sensitive to dispersal (l. 287-290); Maybe it would be interesting to run a sensitivity analysis relative to dispersal on the model outcomes. It might also interact with landscape size, as the influence of higher dispersal rates should be stronger in larger landscapes. - Figures : why is the modality "no extinction" represented on Fig 2 and not on Fig 1? (also, legend says that these represent diversity in extinct patches or extinct landscapes, so something is not right here). - Fig 3: why are only non-extinct patches adjacent to an extinct one included in the analysis? It does raise again the issue of landscape size, and the potential large-scale influence of extinction events. - I did not understand how you estimate the consistency between experimental results and the different modelling scenarios. For instance, L. 340-341, you state that the "competition-colonization trade-off" scenario is more consistent with experimental results, while based on the effect sizes on Fig 3a and Fig 4a, I would tend to say that the "empirical interactions" scenario is a better fit?   **Additional requirements of the managing board**: We would like to receive your revision within 2 months. If you need more time, just tell us. 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."

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Reviewed by Frederik De Laender, 2021-01-20 11:02

The manuscript "Spatial distribution of local patch extinctions drives recovery dynamics in metacommunities" presents the effects of the extent and spatial clustering of an extinction event on the recovery of local and regional diversity, productivity, and on the recovery rate, in a metacommunity of competing species. It is based on a microcosm experiment and a mathematical model. Spatial clustering had a larger effect than the extent of extinction events.

The introduction is effective in setting the scene for this study, but I believe it could be made clearer, at the end of the intro, which phase of recovery dynamics are targeted here with respect to the diversity and productivity data (just after the disturbance? One generation later? Etc). That was not clear to me, and I also did not find this back in the methods. The methods are clear and well-described (apart from the time points associated with the diversity and productivity data). The results are well-structured (although I provide some detailed comments below). I find the discussion repeats the results a bit too much, which makes the discussion section relatively long and renders some of the interesting bits less visible.

As a general comment to the paper, which I generally liked and found to be based on an impressive amount of work and well thought-through designs, I have to say it took me a while to realize that the main variables (e.g. Fig1) were measured during a recovery trajectory. This also raises the question of how representative these measurements are for the 'recovery dynamics' as a whole. If possible (e.g. if the necessary data have been measured in the experiments) I think it would be cool to try to plot the rate of change (or some other summary stat) of (some of) these variables during the recovery period instead of the variables themselves. This might be even more effective in addressing the main questions.

Another general comment, which may seem a tad pedantic, but well: I would propose to replace ‘extinct patches’ with ‘disturbed’ or ‘perturbed’ patches. That is because (1) a patch cannot go extinct, only populations or species can; and (2) it prevents some odd constructions like ‘alpha diversity in an extinct patch’ (which, technically, should be zero).

Finally, I wonder if it would be possible to compare the measured dispersal rates and the competition parameters to see if the empirical system exhibited features akin to a competition-colonization tradeoff.

Specific comments

L13: ‘persist’ suggests long-term persistence; not sure if this is what is meant here.

L37: In a scenario where all biomass disappears, how can one trophic level benefit? If all are removed, it does not matter which trophic level a species belongs to, right? Please clarify.

L46-52: Although I like the intro, I feel the focus of this bit is less clear and evokes some elements that are not core elements, so my suggestion would be to trim it down. At this point, it was also not clear what was meant by ‘spatially structured’.

L69: I propose to use something like ‘extent’ instead of ‘rate’, as there’s no time component, right?

Eq4: I advise to use single-letter expressions for variables (e.g. m instead of n_links).

L221: I advise to use ‘interaction coefficients’ or ‘competition coefficients’ instead of ‘competitive abilities’.

L227: It would be nice to have a rationale for the scenario of no species interactions. I’m sure a few things can be learnt from that additional scenario, but spelling them out would be useful.

L258: “extinction rate alone only had a marginal effect on the outcome of the experiment”. I’d say that for beta diversity it had.

Fig.1: why isn’t there a ‘no extinctions’ scenario plotted for the experiment?

Fig.1: the variable ‘recovery time’ seems to be factorial (5 levels). Was this the case and if so, why, and how was it dealt with in the statistical analyses?

Fig.2: depending on what you want to convey as the main result, there might be more effective ways to plot these data. One way could be to make a biplot for (some of) the variables at 4 extinctions vs. 8 extinctions, to show they are all located near the 1:1 line, regardless of interaction scenario (coded with a symbol key for example) or the spatial arrangement of extinction (e.g. using a color key). A second panel could do exactly the same but would now compare the variables between the two spatial extinction arrangements. Just a spontaneous thought though.

More on Fig.2: It seems interesting that beta diversity is higher in perturbed networks than in nonperturbed networks when there are no species interactions. Is that then purely due to difference in species abundances? In general, it could be insightful to plot one of these beta diversity indices that only look at compositional similarity and not at similarity of abundance.

L265-266: I would be a bit more precise. What is meant by ‘reproduced these results’? What are ‘these results’? I suspect it is the relatively small effect of the number of extinctions compared to that of spatial arrangement but it would be good to repeat this here.

L282-283: It could be interesting to compare the distributions of interaction strengths across model scenarios (possibly scaled by intrinsic growth), as it might explain the results for recovery rate.

Fig.3: This caption mentions “at the last two measurement points”: what are these and why was this info not mentioned in Fig.1 (and 2)?

The section starting L357 starts by mentioning the consistency of the results across response variables, but then focuses on the recovery rate only. It might be useful to, even if briefly, mention how exactly effects on the recovery rate explains the effects on the other variables.

L366-367: If the data are available to do so, it could be nice to substantiate this further by testing how the number of neighboring non-extinct patches affects recovery rate.

L400-401: I would find it more logical to state “extinct patches had a higher biomass”.

Reviewed by David Murray-Stoker, 2021-01-15 18:44

Summary

Saade et al. (bioRxiv 2020.12.03.409524) evaluated how the rate and spatial distribution of extinctions affected metacommunity diversity. Using a simplified ciliate metacommunity of three species in a factorial manipulation of extinction rate (0, 4, and 8 patches out of 16) and spatial distribution (dispersed vs. clustered) paired with numerical simulations, Saade et al. demonstrate that recolonization dynamics and community recovered depended more on spatial distribution or the interaction between spatial distribution and extinction rate than extinction rate alone. By combining the experiment with numerical simulations, Saade et al. were further able to identify that interspecific interactions and, specifically, a competition-colonization tradeoff as a possible mechanism. It is important to note that these numerical simulations were based on empirical measurements of the study organisms and more directly link the numerical to experimental (and vice versa) in the study. The authors were also very clear when discussing their results and the broader implications, presenting any uncertainty and tempering any broader claims with appropriate context; in doing so, I think it makes the link between this study to the broader body of work stronger because it accepts limitations while also presenting the strengths. This study contributes very strong evidence of how spatial configuration needs to be considered when looking at extinction or extirpation dynamics. This study also provides an important “proof-of-concept” that spatial distribution of extinctions should be considered to understand community recovery. In an applied sense, this study suggests that exclusion of spatial distribution from analysis or management of extinctions could be faulty. In summary, I found this paper very compelling, clearly written and ‘mentally replicable’ (i.e., while reading the methods and looking at the figures, I could replicate the study), and with no major criticism or comments. I only have a few minor suggestions to improve clarity and presentation of the results and some comments for the discussion.

Minor Comments

1. Line 187: What R package was used for the mixed-effects models? It would be good to know whether it was lme4 or nlme, for the sake of reproducibility.
2. Line 195: On which parameters was relative importance calculated and how was it determined? It is likely a simple thing I just missed, but this component spilled over to Table 1 and Table 2 where it was not clear exactly what information was being provided.
3. Line 258: Extinction rate is said to have a “marginal effect” on community recovery, and this seems accurate based on Table S2 but not Table 1. Looking at Table 1, I would consider the effect of extinction intermediate but Table S2 I can see how it is marginal. The in-text presentation could therefore appear misleading when calling the effect marginal yet readers only immediately seeing Table 1.
4. Table 1 and Table 2 captions: As written, I do not know exactly what the relative importance is derived from. Following my second comment (Line 195), a more detailed clarification in the methods would make a brief, if any, clarification in the table caption helpful.
5. Line 344: It is reported that “β -diversity was fairly low because the patches ended up being homogeneous” but the results are not shown. This happens again on Line 397. Would it be possible to add a figure to the supplement?

6. Line 517: Effects of metacommunity synchrony on extinction dynamics are discussed, but asynchrony and 'portfolio effects' could also be discussed. While the experiment only used synchronized extinction treatments, it would be good to at least mention asynchrony and how this could have affected results and conclusions.
    - More broadly, is it possible to use the metacommunity model to parameterize temporal asynchrony in the extinction treatments and numerical responses? Spatial asynchrony would also be interesting, along with the interaction of spatial and temporal asynchrony.
    - I completely understand that this is not really the point of the paper and going too far into this topic would dilute the message of the present study, but it would be good to at least note potential effects of asynchrony and potentially parameterize temporally and/or spatial asynchronous models.
7. Figure S5: It looks like the default graphing parameters re-organized the time points so that the x-axis does not go in chronological order. In ggplot (and wrappers like ggpubr), this could be done with the scale*x*discrete() function.