Editor

Dear Authors

I have now obtained three reviews by experts in the field. They see much value in your contribution but have also some critical comments. From my own reading i found this a well-written paper with only some minor points that have been trapped by the referees. Therefore, I invite you to resubmit a revised version of your contribution as a minor revision.

Kind regards
Werner Ulrich

Dear Editor,

We thank you, and the three reviewers, for the positive and constructive comments on our work. Please find our responses to reviewer's comments bellow.

Sincerely yours
The authors

Reviewer 1: Ludek Berec

Abstract: … asymmetry has a contrasting effect on the stability of asymmetric metacommunities … due to asymmetric transmission of perturbations caused by the asymmetric distribution of biomass … Quite a lot of asymmetries here makes the message a bit buried and confusing as regards causes and consequences.

We have rephrased these two sentences and reduced the occurrence of the term "asymmetric" in the same sentences to clarify the message.
"In particular, differences in interaction strength and resource supply between patches generate an asymmetry of biomass turnover with a fast and a slow patch." (l.7-9)
"Here, we demonstrate that asymmetry has a contrasting effect on the stability of metacommunities receiving localised perturbations." (l.11-12)
"This discrepancy between the responses is due to the asymmetric transmission of perturbations caused by the different distribution of biomass between the fast and the slow patch." (l.17-19)

Page 2, lines 38-40: Though the cited models relied on neutral or competitive communities, there are classic models exploring unstable predator-prey dynamics in patches connected by dispersal, showing regional coexistence of both species provided prey are better dispersers than predators. So, the claim here is not entirely correct.

Our paragraph was not clear. We now state early that the cited studies are about competitive metacommunities:
"For instance, in competitive metacommunity models, spatial heterogeneity provides…" (l.32)
And we mention the models you were referring to:
"In trophic metacommunities, spatial heterogeneity has also been identified as a stabilising factor (Steele, 1974; Hastings, 1977, 1978), but the underlying mechanisms are more complex due to the interplay between trophic and spatial dynamics." (l.38-40).

Page 2, lines 47-48 (also page 3, lines 75-76): … did not identify the mechanisms underlying this asynchrony … Isn't the asymmetry of interaction strength and the ensuing asymmetry of energy flow just the mechanism the authors call for? Isn't this exactly what the authors propose as the mechanism a few pages later and in the abstract? I admit I am a bit lost here in the arguments.

This paragraph was not clear and we rewrote it to highlight it two main points:
"subsequent studies suggested that increased asymmetry does not necessarily lead to increased stability. For example Ruokolainen et al. (2011) presented a model in which biomass fluctuations can become more variable with increasing asynchrony. Hence, the relationship between asymmetry and stability is not trivial and the mechanisms governing asynchrony through the difference in energy flow between the fast ans slow channels are not well understood." (l.50-55)

Specifically, the whole page 3 is interwoven by the words "asymmetry" and "asynchrony" which needs quite an effort to decipher and imagine. I admit I have troubles to dig the mechanism also from the concluding paragraph on lines 209-214. Please consider rewriting this hard-to-read part of the text.

We reorganised the introduction to make the text easier to read. In the previous version, we referred to the results of Rooney et al. (2006), Goldwyn and Hastings (2009) and Ruokolainen et al. (2011) in two distant paragraphs, which blurred the message. These two paragraphs have been merged into a single paragraph to state more clearly what we know from these studies and which gap we will fill with the help of the metacommunity framework.
At the end of the Results section, we deleted the concluding paragraph l.209-214 to avoid the repetition with the first paragraph of the discussion (see one of the last comments of reviewer 3).

Model: please provide a justification for choosing d1 = r = 0. Also, I consider assuming gamma = omega quite strange, could not the relationship between gamma and omega be motivated by some realistic examples e.g., from Rooney et al. (2006)?

We set d_1=0 to reproduce the setup with a mobile predator coupling two distinct energy channels as in Rooney's paper.
"We reproduce the two main features of Rooney et al's model." (l.103).
Even if d_1=0 seems to be an extreme case, "slightly mobile prey ($0<d_1<<d_2$) should not change the results because Quévreux et al. (2021) showed that the species for which dispersal has the strongest influence drives the coupling between the two patches". (l.104-106)
We set *r*=0 following Barbier et al's (2019) analysis. Varying *r* does not alter the overall biomass distribution and the stability patterns. Setting *r*=0 removes most of the constraints on predator persistence and enables us to freely explore the effect of the interactions. This is now explicitly stated in the caption of Table 1 and in the appendix.
"Finally, the mortality rate is set to zero (*r*=0) to remove the energetic limitations of the food chain and make interactions the dominant factors determining biomass distribution and stability patterns, as in Barbier et al., (2019)." (l.535-537).
We set the relation gamma=omega for modelling convenience because it allows species persistence for all combinations of *ea* and *ma*. As in Rooney et al. (2006), we varied them independently and found consistent patterns (see Figures S2-14 and 15 in the supporting information). Our aim concerning the parameters governing the asymmetry, is to explore a broad range of values to derive general patterns rather than to reflect a specific system.

Model: Also, you claim that the negative effect of predator on prey is captured by 'm a'. This sounds like epsilon and m determine different processes. But due to scaling, m affects all terms in the predator equation, including the positive effects of prey on predators "epsilon a', so I view this claim as somewhat misleading.

***m* is indeed affecting all terms in the equation due to the scaling but since it is in factor, we can neglect it and simply keep *ea* and *ma* because it affects in the same way all the demographic processes of predators. This is particularly clear for biomasses at equilibrium, which do not depend on this *m* in factor (see equations 9a-c in section S1-2 in the supporting information).**

Page 6, lines 125-126: The authors are right that the perturbation scaling in model (2) is akin to that of demographic stochasticity. But demographic stochasticity affects species much more at low abundances than at large ones. It is rather environmental stochasticity that has an even effect regardless of population abundance. Why the perturbation scaling in model (2) is chosen as it is? Does it follow from some first principles? Please provide some reasons for the selected form?

Your reasoning is correct when comparing the variance of perturbations to the equilibrium biomass but here we consider "the ratio of mean species biomass variance to perturbation variance, which is roughly independent of biomass and disentangles the effect of asymmetry on perturbation transmission from its effect on species abundance" (l.128-130). We have added further explanations justifying this choice: "Therefore, for different perturbations affecting different species with the same value of standard deviation σ_i, we generate a similar variance at the metacommunity scale regardless the abundance of the perturbed species and excite the entire metacommunity with the same intensity (see Figure S2-3 in the supporting information)." (l.130-133). We have added a new Figure S2-3 in the supporting information to illustrate this point.

Another issue I have with both Methods and Results is flooding by supplementary information. One needs to go there and back, and the amount of information is really inhibiting.

You are right that the Methods section refers a lot to the supplementary information but we did it on purpose as specified in the text: "We refer to the Appendix S1-1 for the thorough description of the food chain model and the analysis methods." (l.99). Indeed, we did not include all the details in the main text to avoid overwhelming the reader with information that is not essential to understand the results. In particular, we do not explain in detail in the main text the rescaling of the parameters and we only describe the overall metacommunity model in the main text. The references to the supplementary information concern technical details important for those who want reproduce the results but not for the overall understanding of the methods.
Concerning the results, we refer to the supporting information mostly to prove that our results are robust. Therefore the reader does not need to read the appendix to understand our results.
Overall, we believe the reader has "all the necessary information in the main text to fully understand our results. The supplementary information only serves to give additional technical elements to fully reproduce our work and proofs of the robustness of our results" (l.100-102).

Figure 1 does not have two panels, but in the text, it is referred to as Figure 1A and Figure1B.

Thank you for spotting this mistake, this has been corrected.

Is there a need to give over 60 references?

The reference count is inflated by Table 1 (8 references) and subsection "Implications for conservation" in the Discussion (18 references), which were not previously cited in the introduction. The core references in the other sections are much less numerous.

In conclusion, I view the text … I see the topic as interesting and the take-home message as clear and convincing. But I do find the study as quite heavy, with many detours and a load of supporting information that in my opinion decreases impact of this study. I would suggest streamlining the study and making the study more straightforward.

We agree the manuscript is quite dense and we have tried to make it easier to read. We have reorganised the introduction (see our response to your 4th comment) and we have simplified the results.
- We have moved the "Source-sink effect" section to the supporting information because these results were not at the heart of our demonstration. Instead, the distribution of biomasses is now represented in Figure 4 to support the description of Figure 3 (figure with the biomass CVs at different scales). This enables us to directly start the Results section with Figure 2, which presents one of our main findings.
- Figure 6 has been deleted: Figure 6A has been moved with the "Source-sink effect" section to the supporting information and Figure 6B has been merged with Figure 5B. This has helped us to remove some repetitions present in the previous version.
The "Stability in a heterogeneous world" section of the discussion also suffered from repetitions and vague sentences. We have rephrased the paragraph comparing our results with those of Rooney et al. to stress our finding that asymmetry *per se* is not stabilising:
"By considering the stability at different scales, our results contrast with this explanation. On the one hand, the asynchrony of prey dynamics, when they are perturbed in patch #2 (Figure 2), stabilises the dynamics of predators because their resource supplies are asynchronous. On the other hand, the dynamics of prey at the metapopulation scale are not stabilised by their asynchrony (Figure 3C) because of the low local stability in patch #2 (Figure 3B), which decreases the overall stability of prey. The potential stabilising effect of asymmetry depends both on the perturbed patch and the considered trophic level. Therefore, the overall stability at the metacommunity scale is governed by the relative contributions of the various populations in response to local perturbations, and asymmetry *per se* does not have a stabilising effect." (l.235-243).

Finally, the authors have already considered a similar system in Quévreux et al. (2021a) and many figures presented here are at a first glance analogous to those presented here. It is therefore more than needed to clearly discuss a difference between Quévreux et al. (2021a) and the current study. The only text in this direction appears to be that on lines 246-249, but I find this insufficient. I would like to see a paragraph in which the authors would say that this study is a sort of follow up to Quevreux et al. (2021a) (is it indeed so?), what Quevreux et al. (2021a) found and what is new and important in this study. This would I think set this study in the context even better.

The first paragraph of the discussion is actually dedicated to this comparison, but this was not sufficiently clear in the previous version. To solve this issue, we now refer to Quévreux et al., (2021a) right at the beginning of the paragraph:
"Quévreux et al. (2021a) showed that in a homogenous metacommunity the spatial correlations between patches can be obtained from the within-patch correlations, the dispersing species making the link between the two (see Figure S2-25 for a summary of the results of Quévreux et al., 2021a). In other words, knowledge of the dynamics at the local scale is enough to understand the stability pattern at the metacommunity scale. In a heterogeneous metacommunity, a similar approach does not work because patches do not contribute equally to the dynamics. In particular, a patch with fast energy flow can have an overwhelming impact […] Clearly, the dynamics at the metacommunity scale cannot be assessed by the dynamics at the local scale, as in Quévreux et al. (2021a), and they are an emergent property

resulting from the tight interplay between the strength of perturbation transmission in each patch." (l.221-231)

Reviewer 2: Phillip P.A. Staniczenko

The authors consider a two-species metacommunity model comprising two resource patches and two populations of a mobile predator species that moves readily between the two patches. One resource patch is a "fast" patch in which the basal prey species is quickly replenished, while the other is a slow "patch" with lower prey growth rate; there is also asymmetry in predator-prey interaction strength between the two patches, with higher interspecific effects in the "fast" patch. The authors study the effect on population dynamics of a pulse perturbation applied to the "fast" versus "slow" patch. They find that perturbing prey abundance in the "fast" patch leads to synchrony in the dynamics of the two prey populations, whereas perturbing the "slow" patch has little effect on the correlation in dynamics between the two patches.

The manuscript is well-written, the methods appear sound, and the results are interesting. The authors do an excellent job of placing their contribution in the context of previous studies that have explored the role of interaction asymmetry on metacommunity stability. They also provide extensive supplementary information and have made R code available on GitHub. Their main result, that the properties of which patch is perturbed can have an impact on overall metacommunity dynamics, is well-argued and theoretically and practically relevant.

We thank you for this very positive overall assessment.

I have no major concerns and, below, provide a few minor comments that the authors may find helpful when revising the manuscript.

-- Introduction. I think it would be helpful to clarify for the reader how the following three terms are defined for the purposes of the study: "interaction strength," "asymmetry of interaction strength," and "metacommunity stability."

The definitions have been added:
"(*i.e.* the increased attack rate in one energy channel compared to the other one, see Fig.1)" (l.45)
"The stability of the metacommunity is assessed by the response at different scales (*e.g.* CV of the biomass of a species at the local and regional scales) when prey receive stochastic perturbations in one of the two patches." (l.84-86)

-- Equation 1. It would be helpful to provide a brief explanation of the parameters and terms, e.g., what the superscripts mean in B_2^(2), and the authors could also consider annotating terms according to the familiar designations such as "predator mortality."

The nomenclature of biomass is now clearly defined.
"$B_1^{(k)}$ and $B_2^{(k)}$ are the biomasses of prey and predators in patch 1 respectively." (l.92)
We prefer to keep the designation of parameters at it is for our manuscript to be consistent with Quévreux et al. (2021a) and Barbier et al. (2019).

-- Equations 3 and 4. It would be helpful to provide a qualitative explanation for the steps required to go from Equation 3 to Equation 4.

We have added the demonstration in the supporting information and refer to it in the main text:

“Because the system is at steady state, the stationary variance-covariance matrix C* of species biomasses (variance-covariance matrix of X , see the demonstration in Appendix S1-5)” (l.141-142).

-- Figure 4, Panel B. I believe there is no separate plot for predator biomass CV in patch 2 because the predator populations are perfectly correlated between the two patches---nevertheless, I think it is worth reminding the reader of this point in the caption.

This is now explicitly mentioned in the caption of figure 4B: “Note that the curves for predators overlap because their high dispersal perfectly balances their biomass distribution between the two patches.”

-- L185. The authors note that “predators have the largest total biomass.” Surely we would expect, in a two-species predator-prey system, that the total biomass of the lower trophic level, the prey, should be higher? Can the authors comment on significance of predators having higher total biomass and how much results depend on this observation?

Predators can be more abundant than prey if they have a lower biomass turnover than prey (*i.e.* a high positive effect of prey on predators *εa* and a low negative effect of predators on prey *ma* (see Fig.S2-1A in the supporting information, see also Barbier et al. (2019) for detailed explanations). Barbier et al. (2019) cited the study of Trebilco et al. (2016 doi:10.1098/rspb.2016.0816) on the fish communities in kelp forest as an example of inverted biomass pyramid. Actually, having predator biomass higher than prey biomass is not the important results here, the key observation is that species with the highest biomass and/or CV drive the stability at the metacommunity scale. This was specified by the following sentence:
“Finally, stability at the metacommunity scale depends on the distribution of biomass and CV among species” (l.178)
But we have added the following sentence at the end of the paragraph to specify that other biomass and CV distributions are possible.
“Other values of *εa* and *ma* lead to other distributions of biomass and CV among species, which can make prey to drive the stability at metacommunity scale (see Figures S2-5 and S2-7 in the supporting information).” (l.183-185)

-- L201. The authors use the term “recover” to describe a decrease in abundance of prey species following a perturbation that temporarily increases abundance. “Recover” typically describes an improvement from the perspective of the focal species, so perhaps “response” is a better, more neutral term to use.

We have changed “recover” for “response” in the text.

-- Figure 5, Panel B. For the y-axis, “Direct effect,” would a log-scale be better to show more even weighting of effects < 0 compared to > 0?

The log-scale would be messy because we mix positive and negative values. We have kept the linear scale but we have added a dashed black line (y=0) to better show how close to zero are the direct effects. In addition, Fig.6B shows well the contrasted direct effects between patches #1 and #2 thanks to the width of arrows and explicit numerical values (see our response to your last comment).

-- Discussion, L219. The authors suggest that “perturbing prey in the slow patch desynchronises prey dynamics.” Personally, I’m not sure there is desynchronization taking place (i.e., change from synchrony to no synchrony), rather that the dynamics in the two patches continue to play out independently of one another.

We have replaced "desynchronises prey dynamics" by "decrease the synchrony of prey dynamics" in the entire text to acknowledge the fact that the dynamics become more asynchronous (no switch from synchrony to no synchrony as you pointed out).

-- Figure 6, Panel B. It would be helpful to mention in the caption the interspecific strength numbers---what they are and what they mean.

This has been done:
"The asymmetry of biomass distribution and interaction strength alters the direct effects between predators and prey (numeric values being the terms of the Jacobian matrix corresponding to each arrow)."

Reviewer 3: Diogo Provete

The paper by Quévreux et al. proposes a new model to understand how spatial heterogeneity promotes biomass assymetry via differential predation (variation in interaction strength) between local communities embedded in a metacommunity. This is an interesting paper that nicely fills an important gap in metacommunity theory by modeling how trophic interactions are affected by perturbations in prey populations. It's a follow up of two other papers from last year by the same authors. Since species in nature are constantly engaging in biotic interactions, a 2.0 metacommunity theory will not be achieved without understanding the role these interactions play in setting species distributions. A recent paper (Livingston et al. 2017 J Animal Ecol) has conducted an experiment to also test how predators and resource heterogeneity contribute to prey spatial dynamics. I think this is an excellent contribution, but I also have a few points to make:

Thank you very much for appreciating our work and for your constructive remarks.

1) There's key literature missing. I believe the model can dialogue with other concepts, such as the keystone community (Mouquet et al. 2012, Resetarits et al. 2018) in the sense that the 'fast' patch can act as a keystone community. These appear very briefly cited at the end of the discussion, in the context of implications for conservation. But due to the similarities in concepts, it would be good to talk about it in the introduction.

We now introduce the concept of keystone community in the introduction:
"In parallel to the keystone role of mobile predators, keystone communities (sensus Mouquet et al. (2013), which are equivalent to keystone patches), should have a major influence on synchrony and stability patterns." (l.79-81)
We have also extended the text dedicated to the concept in the discussion to include your relevant remark on the fast patch being the keystone community here:
"Keystone communities are usually identified as the patches that are highly connected to the other patches of the spatial network (Resetarits et al., 2018), but our results suggest that the dynamical properties of each patch can be important as well. For instance, the fast patch can be identified as a keystone patch because of its ability to synchronise the dynamics of the other patches." (l.317-320)

2) At the end of the introduction, in the paragraph about the movement of predators between patches, works by O Schmitz could be added, such as here and here.

Citations to O. Schmitz's work have been added.

Minor comments:

1) I think there's a missing word in this sentence (L. 129): "In the following, we assess the temporal variability of each population after stochastic perturbations affect the metacommunity in the vicinity of equilibrium"

We have corrected the sentence:
“In the following, we assess the temporal variability of the biomass of each population induced by stochastic perturbations affecting the metacommunity.” (l.134-135)

2) extra "equations' in L. 132: "from the variance-covariance matrix of perturbations VE (variance-covariance matrix of E) by solving the Lyapunov equation equation"

Corrected

3) provide source for silhouettes in Fig. 1

I have done the silhouettes myself with Gimp and Inkscape.

4) I'm not sure if the subheading "Underlying mechanisms" fits in the Results, so I think you should move it to the Discussion. Some of its content is even repeated in the 1st paragraph of Discussion

This subsection fits in the results because it describes Fig. 5 which contains raw results. We have deleted the last paragraph of the subsection to avoid the repetition in the following first paragraph of the discussion.

5) L. 306, another good citation would be Schiesari et al. 2019

Thank you for the reference!

I hope authors find my comments useful.