nature portfolio

Peer Review File

Quantifying the effects of response diversity dynamics on ecosystem stability

Corresponding Author: Professor Chih-hao Hsieh

This file contains all reviewer reports in order by version, followed by all author rebuttals in order by version.

Version 0:

Reviewer comments:

Reviewer #1

(Remarks to the Author)
This manuscript introduces a novel framework for quantifying dynamical response diversity in ecological systems, integrating nonlinear time series analysis (MDR-Smap) and applying it to a 40-year dataset from Lake Geneva. The authors propose that time-varying, context-dependent species responses, aggregated as functional dispersion (FDis), enhance biomass stability within trophic levels. The approach is methodologically ambitious and addresses a critical gap in biodiversity-stability theory. One core assumption and analytical choice warrant further clarification or revision to strengthen the study's mechanistic grounding.

1. The core response diversity metric used—functional dispersion (FD)—does not account for the direction (sign) of species' responses, thereby limiting its mechanistic alignment with ecological stability theory, which emphasizes the importance of compensatory (i.e., opposing) dynamics for stabilizing ecosystem functioning. While the manuscript briefly acknowledges this limitation (p.13), citing Ross et al. (2023), a more substantive discussion and methodological consideration would enhance the rigor of the stability argument. Specifically:
(a) Could FD be recalculated with sign-sensitive weighting or decomposed into components reflecting directional divergence?
(b) Are there observable patterns of sign heterogeneity within trophic levels, and do these correspond with observed stability trends?
(c) Could supplementary figures be added to visualize the temporal distribution of positive vs. negative species-level responses?
Addressing these questions would strengthen the causal interpretation linking response diversity to stability.

2. The manuscript concludes that response diversity stabilizes biomass within but not across trophic levels. However, given that FD implemented is sign-agnostic, this claim may overstate the evidence. If consumer species respond in a synchronized or unidirectional manner, FD may still yield high values without reflecting compensatory potential—possibly obscuring destabilizing dynamics. A more careful interpretation acknowledging this limitation would better reflect the scope and constraints of the current metric.

(Remarks on code availability)

Reviewer #2

(Remarks to the Author)
I found this a fascinating paper with the potential to have substantive impact on the field of community ecology. The most profound result is that diversity in the dynamics of responses to environmental change act in a way which stabilises food webs. This is an important result and has the potential to open up a new area of endeavour in community ecology, including achieving a better understanding of the mechanisms underpinning BD-EF relationships.

The analyses used are novel in this context but well established in a general sense, and provide a more permissive framework that accommodates more biology than would multivariate auto regression. The application of the DEV approach is a useful advance for describing resilience.

The focus is on ‘dominant’ genera (L134) in Lake Geneva. You need more detail on what was considered dominant and at least 2-3 sentences on the implications of omitting rarer taxa. This should be added to the summary of effects of taxonomic resolution at or around L359.

The paper is very dense and would benefit from the use of an experienced editor to try and simplify sentence structure and condense the text.

The paper is not very well written, and I have attempted to address the numerous grammatical errors. I propose a further detailed copyedit for grammar and clarity.

Title

I find ‘dynamical response diversity’ to be a clunky phrase. Could it be ‘Quantifying the effects of response diversity dynamics on ecosystem stability’

L27 The opening sentence is oddly phrased. Simplify as below:

“Variability in species’ responses to environmental changes (response diversity) is a critical feature in determining stability of ecosystem-level properties.”

L30 “context-dependence” should be “context-dependent”

L30 “species responses” should be “species’ responses”

L31 insert “other” between on and environmental

L33 Change “time-varying” to “time-variability in”

L35 Change “Using a 40-year monthly dataset from Lake Geneva” to Using a 40-year set of monthly data from Lake Geneva”

L42 Change “While the role of biodiversity in ecosystem stability has been widely demonstrated, the strength and even sign of biodiversity-stability relationships can vary within and among systems” to “The role of biodiversity in ecosystem stability has been heavily contested and the the strength and direction of biodiversity-stability relationships can vary within and among systems”

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L378 “Forward-looking” is an odd section title. Change to “Future research directions”

(Remarks on code availability)

Version 1:

Reviewer comments:

Reviewer #1

(Remarks to the Author)
All of reviewers’ concerns on the earlier version of the manuscript were addressed in a satisfying manner. I do not have anything else to add. Congratulations for this nice work.

(Remarks on code availability)

Referees' comments to the author(s):
Comments from reviewers are copied below with our point-by-point responses. We use black text for the reviewer's comments and blue text for our responses. Changes in the text of the revised manuscript are underlined.

Reviewer #1 (Remarks to the Author):

This manuscript introduces a novel framework for quantifying dynamical response diversity in ecological systems, integrating nonlinear time series analysis (MDR-Smap) and applying it to a 40-year dataset from Lake Geneva. The authors propose that time-varying, context-dependent species responses, aggregated as functional dispersion (FDis), enhance biomass stability within trophic levels. The approach is methodologically ambitious and addresses a critical gap in biodiversity-stability theory. One core assumption and analytical choice warrant further clarification or revision to strengthen the study's mechanistic grounding.
Response:
Thank you very much for your positive comments. Following the advice of Reviewer #1, we have provided additional clarification and conducted further analyses to strengthen the mechanistic grounding of the study.

1. The core response diversity metric used—functional dispersion (FD)—does not account for the direction (sign) of species' responses, thereby limiting its mechanistic alignment with ecological stability theory, which emphasizes the importance of compensatory (i.e., opposing) dynamics for stabilizing ecosystem functioning. While the manuscript briefly acknowledges this limitation (p.13), citing Ross et al. (2023), a more substantive discussion and methodological consideration would enhance the rigor of the stability argument. Specifically:
(a) Could FD be recalculated with sign-sensitive weighting or decomposed into components reflecting directional divergence?
Response:
We agree that accounting for the sign of species' responses is a critical aspect of response diversity. Following the advice, we have incorporated the "Divergence" index as proposed in Ross et al. (2023), implemented with the updated multivariate methodology (Polazzo et al 2024) into our analysis in the revision.
Page 12:
"**Considering positive and negative responses**

The dispersion index does not distinguish between negative versus positive responses[15], limiting its direct link to the mechanism by which response diversity stabilizes community dynamics. To partially address this limitation, we assessed sign heterogeneity in response (Methods); sign heterogeneity is prevalent in species' responses (SI Figs. 7 and 8), supporting the presence of portfolio effect as a stabilizing mechanism.

In addition, we examined the response divergence index[15,20] that accommodates signs of species' responses. Instability of total phytoplankton biomass was, on average, buffered by increasing response divergence of phytoplankton (Divg-PhytoToAll in SI Fig. 9). These results are qualitatively consistent with those based on the response dispersion index, though divergence results had greater variability and occasional subtle destabilizing effects (comparing SI Fig. 9 versus Fig. 4A). Response divergence of zooplankton (Div-ZooToAll) also exhibited, on average, stabilizing effects on total phytoplankton biomass (SI Figure 9), although both stabilizing and destabilizing effects were observed. Therefore, at cross-trophic levels, high response diversity in either predator or prey can have complex effects on stability of the phytoplankton community. In contrast, instability of total zooplankton biomass was not causally affected by response divergence (Divg-PhytoToAll and Div-ZooToAll; Table S1). Collectively, stabilizing effects of divergence are less clear than effects of dispersion. However, a key methodological limitation of the divergence index must be considered: it incorporates only extreme values (maximum and minimum) of species responses and ignores variance within the community, which is a critical component for the portfolio effect to operate and stabilize ecosystem properties. Consequently, although valuable for capturing sign heterogeneity, divergence provides an incomplete picture for demonstrating stabilizing effects of response diversity. Therefore, developing a comprehensive index that integrates both the sign and variance of responses remains a crucial yet challenging frontier for future research."

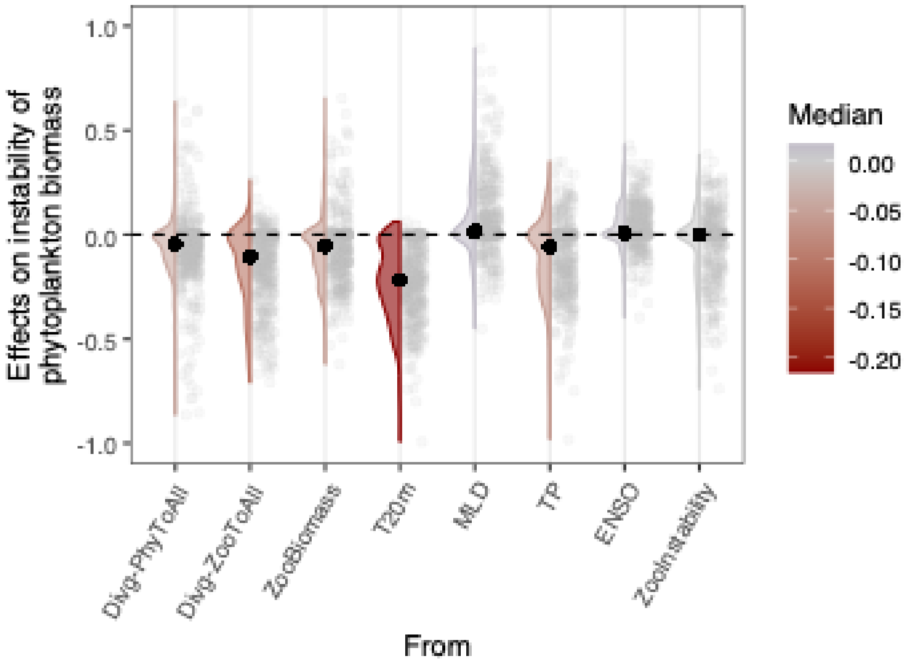
The explanation of the "Response divergence", Page 23:

"Sign heterogeneity in response plays an important role in the insurance effect of response biodiversity[15]. Here, we adopted the "response divergence" proposed in Ross et al[15] to accommodate the effects of positive and negative responses. The index is calculated as follows,

$$Divergence_j = \frac{(\max[J_{i,j}] - \min[J_{i,j}]) - \left| |\max[J_{i,j}]| - |\min[J_{i,j}]| \right|}{(\max[J_{i,j}] - \min[J_{i,j}])},$$

where $J_{i,j}$ is the Jacobian element estimated from the MDR-Smap (Fig. 1b). If the range of $J_{i,j}$ does not span zero, then all species respond in the same direction to the environment (no sign heterogeneity in response); in such cases, *Divergence* is 0. In contrast, when $J_{i,j}$ are perfectly symmetric around zero, *Divergence* is 1. In summary, "response divergence" ranges between 0 and 1, with 1 indicating perfect sign symmetry around zero of responses to the environment. The multivariate version of response divergence can be computed simply by averaging divergence measures across all forcing variables[20]. We note that this index of response divergence considers only the maximum and minimum of the $J_{i,j}$ but ignores the variance of $J_{i,j}$ that is critical for the portfolio effect to operate for stabilizing total biomass."

In summary, we recognize that a reliable sign-sensitive index for response diversity is not currently available. The development of an index that reflects directional divergence remains a considerable methodological challenge and an important direction for future research, beyond the aims of the present work.



SI Figure 9. Violin plots showing effects of response divergence and environmental variables on total phytoplankton biomass instability. **(a)** Instability of total phytoplankton biomass was, on average, buffered by increasing response divergence of phytoplankton, zooplankton, and lake water temperature, although considerable variation was observed. Effects of other influential variables showed no consistent sign over time. Total biomass instability was quantified using dynamic eigen-values (Methods). Influential variables were identified with Convergent Cross Mapping to assess dynamic causality (Table S1), and their effects on instability were estimated by MDR S-map across time intervals. Because instability is the target variable, negative effects estimated by MDR S-map indicate buffering against instability. Violin color and the position of the black point represent the median effect, while the grey dots beneath each violin represent the monthly estimates. Divg-PhyToAll represents the response divergence of the phytoplankton community to all other plankton genera and environmental variables, and likewise for Divg-ZooToAll. For the definition of other variable names, see SI Figure 1.

(b) Are there observable patterns of sign heterogeneity within trophic levels, and do these correspond with observed stability trends?

Response:

We have developed a new index to quantify sign heterogeneity in response. Our analysis reveals that sign heterogeneity is indeed prevalent in response to variables within and across trophic levels as well as to environmental variables (new SI Figures 7 & 8, included below). However, we did not find a simple, consistent correspondence between these patterns of sign heterogeneity and observed stability trends beyond those driven by seasonality. This result is theoretically expected: while sign heterogeneity is a necessary condition for compensatory dynamics and stability, it is not a sufficient condition. Other factors, such as the strength and variance of responses, are critical for stabilizing ecosystem properties.

We included this supportive analysis in the Discussion, Page 12, middle:

"The dispersion index does not distinguish between negative versus positive responses[15], limiting its direct link to the mechanism by which response diversity stabilizes community dynamics. To partially address this limitation, we assessed sign heterogeneity in response (Methods); sign heterogeneity is prevalent in species' responses (SI Figs. 7 and 8), supporting the presence of portfolio effect as a stabilizing mechanism.

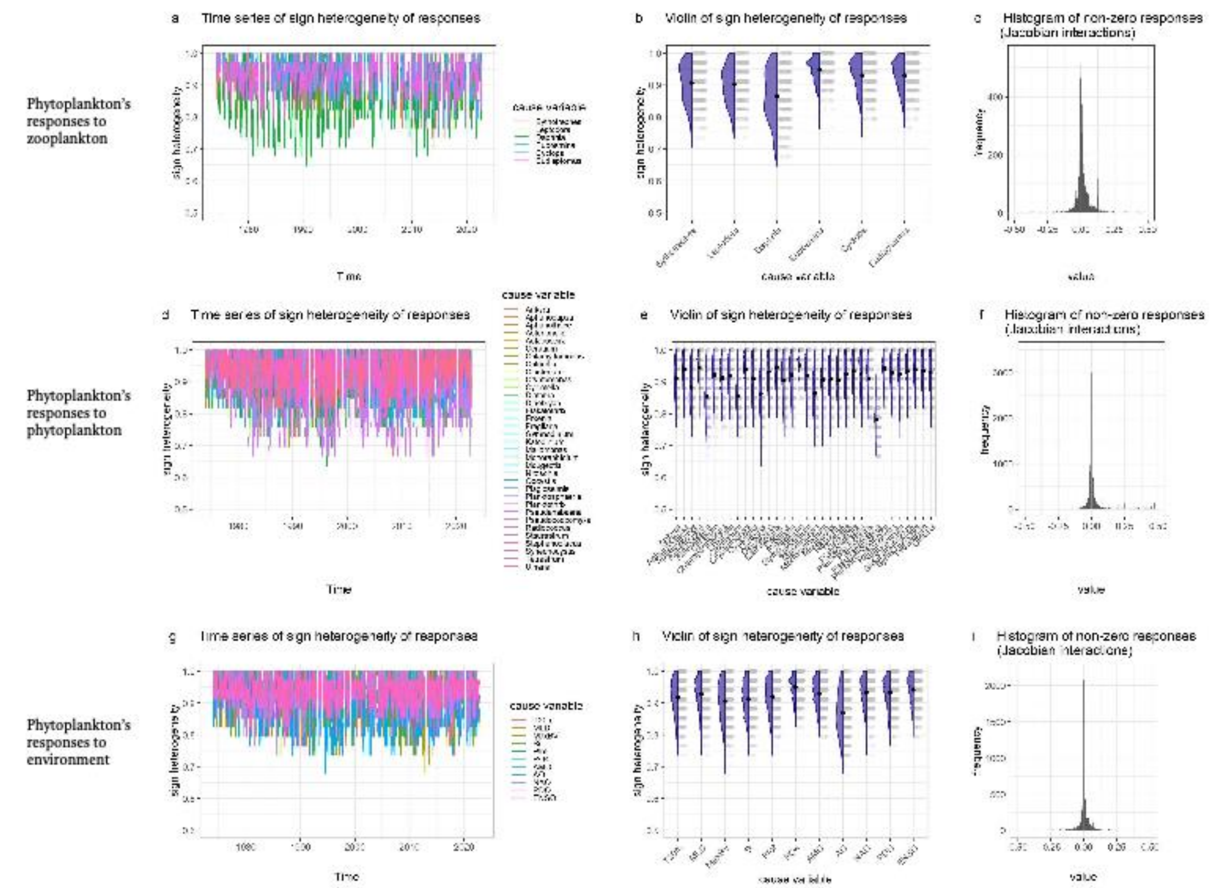
The explanation of the index of sign heterogeneity in response, Page 23:

"Index of sign heterogeneity in response at the community level

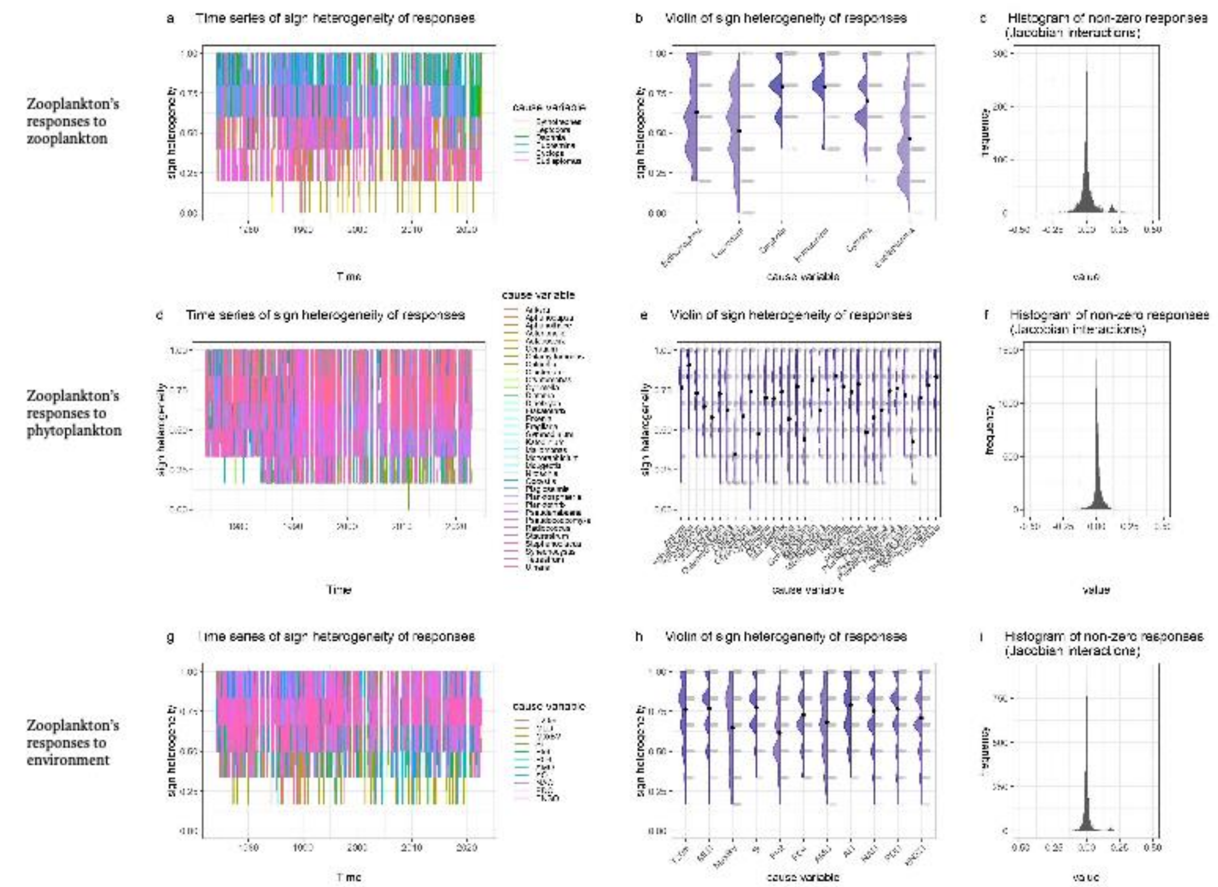
We quantified the sign heterogeneity of community responses to a given variable j using the following metric:

$$\text{Sign Heterogeneity}_j = 1 - \left| \frac{\sum_i \operatorname{sgn}\left(J_{ij}^{\text{non-zero}}\right)}{n_{j,\text{non-zero}}} \right|$$

Here, $J_{ij}^{\text{non-zero}}$ denotes the non-zero response of species i to variable j within the Jacobian matrix, and $n_{j,\text{non-zero}}$ is the number of all non-zero responses to variable j. The sign function sgn(·) returns 1, 0, or -1 for negative, zero, or positive inputs, respectively. The index ranges from 0 to 1: a value of 1 indicates an equal number of positive and negative responses (maximum sign heterogeneity), whereas 0 indicates all non-zero responses share the same sign (minimum sign heterogeneity). Cases where all responses are zero are excluded from the analysis."



SI Figure 7. Sign heterogeneity in phytoplankton responses. Panel **a**, **d**, and **g** illustrates the monthly time series of community-level sign heterogeneity in phytoplankton's response to each zooplankton genus, each phytoplankton genus, and each environmental variable, respectively. Values consistently above zero confirm the existence of sign heterogeneity in response. Violin plots (**b**, **e**, and **h**) summarize the distribution of the sign heterogeneity in response to each of the forcing variables. See *Index of sign heterogeneity in response at the community level* for the explanation of the computation. The overall long-term distribution of $J_{i,j}$ (**c**, **f**, and **j**) reveals that both positive and negative responses are prevalent. The sharp peak around zero indicates that weak responses are the most common. Zero responses are excluded from the analyses.



SI Figure 8. Sign heterogeneity in zooplankton's responses. Panel **a**, **d**, and **g** illustrate the monthly time series of community-level sign heterogeneity in zooplankton's response to each zooplankton genus, each phytoplankton genus, and each of the environmental variables, respectively. Values consistently above zero confirm the existence of sign heterogeneity in response. Violin plots (**b**, **e**, and **h**) summarize the distribution of the sign heterogeneity in response to each of the forcing variables. See *Index of sign heterogeneity in response at the community level* for the explanation of the computation. The overall long-term distribution of $J_{i,j}$ (**c**, **f**, and **j**) reveals that both positive and negative responses are prevalent. The sharp peak around zero indicates that weak responses are the most common. Zero responses are excluded from analyses.

(c) Could supplementary figures be added to visualize the temporal distribution of positive vs. negative species-level responses?
Response:
Yes, we have included SI Figures 7 and 8 to visualize the sign heterogeneity in response. See the response above.

Addressing these questions would strengthen the causal interpretation linking response diversity to stability.
Response:

Thank you for the very constructive suggestions. We have included new results and discussion for these issues in the revision. See our responses above.

2. The manuscript concludes that response diversity stabilizes biomass within but not across trophic levels. However, given that FD implemented is sign-agnostic, this claim may overstate the evidence. If consumer species respond in a synchronized or unidirectional manner, FD may still yield high values without reflecting compensatory potential—possibly obscuring destabilizing dynamics. A more careful interpretation acknowledging this limitation would better reflect the scope and constraints of the current metric.

Response:

As shown in SI Figures 7 and 8, sign heterogeneity in response is prevalent in the cross-trophic level response. Thus, the concern of the reviewer#1 regarding the potential synchronized responses is not an issue in this case study of the Lake Geneva plankton ecosystem. To clarify this, we have added the following discussion:

Page 12, bottom:

"Response divergence of zooplankton (Div-ZooToAll) also exhibited, on average, stabilizing effects on total phytoplankton biomass (SI Figure 9), although both stabilizing and destabilizing effects were observed. Therefore, at cross-trophic levels, high response diversity in either predator or prey can have complex effects on stability of the phytoplankton community. In contrast, instability of total zooplankton biomass was not causally affected by response divergence (Divg-PhytoToAll and Div-ZooToAll; Table S1)."

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The analyses used are novel in this context but well established in a general sense, and provide a more permissive framework that accommodates more biology than would multivariate auto regression. The application of the DEV approach is a useful advance for describing resilience.
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Thank you very much for your positive comments.

The focus is on 'dominant' genera (L134) in Lake Geneva. You need more detail on what was considered dominant and at least 2-3 sentences on the implications of omitting rarer taxa. This should be added to the summary of effects of taxonomic resolution at or around L359.
Response:
In the original version, the definition of 'dominant' genera was provided in Methods. In the revision, we have additionally clarified this definition in the main text and discussed the caveats of omitting rarer taxa, as requested.
Page 13, middle:
"Furthermore, we considered only dominant taxa, defined as those occurring in >20% of the monthly time points in this study. This choice reflects a methodological limitation in applying EDM that cannot accommodate taxa with time series including many zeros. Thus, effects (responses) of rare taxa on total biomass stability were omitted. Given that the biomass contribution of each rare taxon to total biomass is small, their influences on biomass stability are also likely to be minor."

The paper is very dense and would benefit from the use of an experienced editor to try and simplify sentence structure and condense the text.

The paper is not very well written, and I have attempted to address the numerous grammatical errors. I propose a further detailed copyedit for grammar and clarity.
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L57 Delete “Consequently,”
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L231 New paragraph at “Our results…”
L234 Delete “the”
L264 Delete “their”
L292 Change “variations” to “variability”
L378 “Forward-looking” is an odd section title. Change to “Future research directions”
Response:
All the suggestions have been incorporated in the revision, and the English was edited by Prof. John Kastelic, a professional editor. Thank you very much.