Original title The variability spectrum of ecological communities: How common and rare species shape stability patterns

New title The inherent multidimensionality of temporal variability: How common and rare species shape stability patterns

Authors Jean-François Arnoldi, Michel Loreau, Bart Haegeman

Dear Editors,

Please find attached the revised version of the above-mentioned manuscript. We have addressed the comments of the editor and the reviewers; see a point by point answer below. Changes in the manuscript are highlighted in blue. The line numbers correspond to those of the new version. We hope that you will find the revised manuscript suitable for recommendation by PCI Ecology.

With best regards,

Jean-François Arnoldi, Michel Loreau and Bart Haegeman

Response to comments of Editors

Thank you for submitting your preprint "The variability spectrum of ecological communities: How common and rare species shape stability patterns" to PCI Ecology. We have now received two reviews of your manuscript.

Both reviewers regard your work as a strong contribution to the understanding to the diversity-stability debate. We agree with the reviewers, it is indeed an insightful study that rigorously demonstrate that the nature of the perturbation matters, in the sense that it can dramatically changes the relationship between diversity and stability. We would therefore be happy to recommend it once the reviewers' comments are addressed.

Most reviewers comments are suggestions that will doubtlessly improve the overall clarity of the manuscript and so we regard the revision required as a minor one even though we acknowledge that the edition of a long paper could be time-consuming. One of the reviewer has provided a very detailed list of comments that should help you targeting parts that currently miss clarity. We would also like to highlight some of the reviewers' comments and expand on them:

We thank the Editors for their work, and for their constructive and encouraging comments.

* One reviewer points out that the paper is fairly long and that there is enough material for more than one paper. We agree. That said, we would be happy to recommend an even longer preprint that have a better balance between accuracy and pedagogy. The length issue may be one you will be dealing with depending on where you submit your manuscript, not an issue for a recommendation for PCI (as far as we understand the rules).

Although the manuscript length has not changed significantly compared to the previous version, we made substantial efforts to focus our message and shortened the discussion section to make it more factual and less speculative. Our paper is now essentially organized in two parts. The first establishes a general theory for variability, emphasizing its highly multidimensional nature, while the second part explains that a simple generic pattern can emerge in species-rich communities. The relevance of this pattern is then illustrated by explaining that it can shape diversity-stability relationships.

We revised the abstract accordingly (paraphrasing for conciseness): We show how variability can reveal inherent stability properties of ecological communities, with clear connections with other stability notions. This requires abandoning one-dimensional representations, and instead consider the whole set of variability values associated to a given community. Against the vertiginous dimensionality of variability, we show that a generic variability-abundance pattern emerges in species-rich communities, relating variability to the abundance

of perturbed species. The contrasting contributions of different species abundance classes can be responsible for opposite diversity-stability patterns, which can be understood from the behaviour of basic statistics of the abundance distribution.

* So far, the reader cannot reproduce the study, it is very important that the manuscript includes all the simulations details so the reader can reproduce your analysis. Note that one way to deal with this comment is to share your code.

The revised Appendix F includes a full description of the simulations. We also provide Matlab code as supplementary material.

* One reviewer mentions that you must differentiate previous mathematical findings from new ones. We agree, this would help understanding how to obtain equation B1. Another thought we had while reading the appendix is that you should consider adding a reference that introduces Stochastic Differential Equations to help readers not familiar with this to have a better understanding of the approach you developed.

During the revision we did an effort to clarify what are the new results of this paper, and what are the results that have been reported in previous papers, including our owns. Because we wanted to make the paper self-contained, we sometimes included arguments that are closely related to previously published ones. In the revisions we have more these connections as explicit as possible.

Some examples: line 179, Generalizing previous work (Arnoldi et al., 2016b; Arnoldi and Haegeman, 2016) to arbitrary perturbation type, we construct a measure of stability [. . .]; line 234, Although we know from previous work (Arnoldi et al., 2016b) that the smallest invariability value in response to immigration-type perturbations will always be smaller than $\mathcal{R}_\infty$, [. . .]; line 262, Worst-case invariability is close to asymptotic resilience, which corroborates previous findings showing that the long-term rate of return to equilibrium is often associated to rare species (Haegeman et al., 2016; Arnoldi et al., 2018)

Concerning the remark about stochastic differential equations, we have added a reference on line 104: In the perturbation term, $\xi_i(t)$ denotes a standard white-noise source (Arnold, 1974; Van Kampen, 1997). In Appendix A we write: Stochastic perturbations in continuous time are mathematically quite subtle (see, e.g., Turelli, 1977). However, in the setting of linear dynamical systems, the effect of a white-noise perturbation can be analyzed relatively easily. Because this analysis is not readily available in the ecology literature, we present here a short overview.

Finally, we would like to add a few comments as well as two typos:

* Circularity: Basically, the authors use a model where the higher the value of α, the more density dependent the perturbations are. Based on it, they found that the variability response for low values of α is driven by rare species whereas common species drive the response when α is high. Isn't it something expected? We think the authors should expand on this. This is not a problem but as written, it feels a little hidden behind the types of perturbations (demographic, immigration etc.)

The observation that the relative importance of rare vs common species changes when varying α is indeed obvious. However, our results are much stronger: we describe the exact dependence of variability on α and explain how this dependence modifies qualitatively the diversity-stability relationship.

We have made this precise in the revision, line 318 (paraphrasing for conciseness): The generic limit that yields the variability-abundance patterns of Figs. 4 and 5 is the one towards which a community of increasing complexity will tend. In the case of immigration-type perturbations species contribution to variability become proportional to the inverse of their abundance. The worst-case scenario follows the abundance of the rarest species, while mean-case invariability scales as an average species abundance thus rapidly declining with diversity. The responses to demographic perturbations are not determined by any specific species abundance class, so that no simple expectations based on typical trends of abundance

distributions can be deduced. We recover a simpler behaviour when looking at the response to environmental-type perturbation. It is now abundant species that drive variability, and mean-case invariability scales as a the inverse of average abundance, typically declining with diversity.

* Figures 4-6 examine slopes for different values of α. why not report the values of the slope along a gradient of α value

This representation would indeed describe more fully the dependence on α. However, we decided to keep the original figure, because we think it is easier to grasp, especially given the subtle difference with Taylor's law (see our response to the comment of the second reviewer about Taylor's law).

* There are several notations use throughout the appendix, most of them are common some other are introduced by the authors, so we would suggest that you add a table of notations when the set of appendix are introduced p 35.

We have added Table A1 presenting the main notation used in the appendices.

* May be a naive one: in appendix A, why not saying that u_k follows a multinormal distribution $\mathcal{N}(0, Cu)$?

Our results do not depend on assuming a multinormal distribution. We have kept the more general presentation.

* C_x instead of C in equation (A7)

* l. 287: We think it should be "5th to 95th" instead of "10th to 90th".

Changed (l.308).

We now invite you to respond to the reviewers' comments as well as the few comments we added and submit a revised manuscript for a potential recommendation by PCI.

Response to comments of Reviewer 1

In this theoretical study Arnoldi et al. investigate how the variability of community dynamics is affected by different types of perturbations. The stability-variability of ecological communities is set in relation to species equilibrium biomasses for different perturbation scenarios, and different abundance classes' roles in governing stability are acknowledged. Overall, the authors conclude that a multidimensional view on stability allows one to better appreciate the dynamical richness of ecological communities.

In general, I think this is a very strong and well conducted study. Adding a stochastic component into the thinking about complex ecological systems is interesting and much needed. However, I have a few points that should be addresses before recommending this study.

We thank the reviewer for her/his constructive comments. Many parts of the article have been substantially rewritten in order to improve clarity and address the points raised by the reviewer.

Major point: I miss an important reference to a similar study (Ives et al. 2003; Ecological Monographs). The similarity between this study and Ives et al. should specifically be addressed and discussed. Both studies compare the (output) variability of the stationary distribution to the (input) variability of process errors, in ecological models. Yet, Ives et al. uses linear discrete models.

The study of Ives et al. (2003) has indeed a number of points in common with ours. First, they also start from a simple linear community model to study stability properties. Second, they also introduce variability-based stability measures based on the ratio of output and input variability.

However, there are also major differences. First, the general objective of the Ives et al. study is very different from ours. They present a strategy to estimate community stability from time-series data, by inferring a linear community model as an intermediate step. In the current paper we take a less statistical and more conceptual approach: we develop a general theory of variability, and study its properties using the simple framework of linear community models. Second, more specifically, we stress the multidimensional nature of variability, while Ives et al. focus on a single variability metric, which can be seen as a single point in our variability distribution (note however that their metric does not enter exactly in our framework, mainly because they look at discrete-time dynamics, while we work in continuous time). In the paper we explain the importance of a multidimensional approach to variability. For example, as we argue in the discussion, it helps establishing connections with other stability measures such as return rates. This question of connecting stability measures is also raised by Ives et al. Finally, the second part of our paper, investigating the effects of rare and common species on different variability measures, and how this can lead to different diversity-stability relationships, takes a very different direction from the Ives et al. paper.

We believe that in the revised manuscript the general objective of our study is better articulated, and that the difference with related studies appears more clearly. For the Ives et al. study, we have explicitly indicated the connections. In particular, line 106: Community models of the form eq. (1) were studied by Ives et al. (2003) to analyze ecological time-series. In their approach, stability properties are inferred from the system response to specific perturbations. Here we build on a similar formalism, but explicitly explore a vast set of possible perturbations; line 177: To remove this linear dependence [of output variability on input variability], we define variability as $\mathcal{V} = \sigma_{\text{out}}^2/\sigma_{\text{in}}^2$, i.e., the average species variance relative to perturbation intensity (see Ives et al., 2003 for a similar definition of variability); line 400: [To reconstruct a variability distribution], the most direct approach consists in observing the same community under multiple environmental conditions. [...] However, there is more information to be extracted from time series than a single variability value. If high-quality time series are available, it might be possible to infer linear model dynamics, which can then be used to compute stability properties (Ives et al., 2003), and in particular, variability distributions.

Minor comments: It would be interesting to see how the mean and sd of equilibrium biomasses change as diversity increase in the networks. I would think that eq. biomasses decrease as diversity increase, thus affecting the perturbation magnitudes.

When increasing diversity, total biomass (sum over species) increases and average species biomass decreases. These relationships can be read off from Fig. H1, where the abundance statistics are linked to the different variability measures. Note, however, that changes in equilibrium biomass do not affect perturbation intensity σ_{in}^2, which only depends on the species-specific perturbation intensities σ_i^2 (see eq. 3).

It would be interesting to see how the two parts of stability, i.e. var_{out} and var_{in}, change when diversity in the communities change (i.e. producing figures similar to fig. 6). This would add valuable information about what is contributing the most to stability. I would suspect that var_{in} is highest for the environmental type of perturbation, followed by demographic and immigration types of perturbations.

Strictly speaking, there is no information to be gained by separating the numerator σ_{out}^2 and the denominator σ_{in}^2 of our variability measure, as the effect of σ_{in}^2 is trivial (see argument leading to eq. 4). However, it is true that the magnitude of direct effect of perturbations (the perturbation term in eq. 1) depends on species abundances and will consequently vary with diversity (except for immigration-type perturbations $\alpha = 0$). As the reviewer suggests, it would then be interesting to isolate this effect from the diversity-invariability relationships

shown in Fig. 6. As this cannot be done by studying σ_{in}^2 (see also response to previous comment), this would probably require the introduction of still another variability measure. We believe that such an extension would lead us too far from the main objective of the paper.

I agree that it is important to point out that different types of perturbations produce different stability patterns. Yet, since the stability measures presented here appear to be linearly related to each other (at least the mean responses), I would argue that a single measure of stability would hold a great deal of information about the stability of the whole community. For example, asymptotic resilience is linearly and negatively related to the mean stability for each perturbation scenario presented here (yet with different slopes; Fig. 6). Thus, a more simple one-dimensional representation of stability may be enough when calculating the stability properties of a community. Please comment on this!

This point indeed deserves clarification. In fact, we do not think that such a simpler representation is possible, because different variability measures are determined by different sets of species, and in general these sets of species, e.g., their abundances, are unrelated.

We explain this in the discussion, line 461: Ecologists have acknowledged the multiple-faceted nature of ecological stability. But here we are showing that a single facet (variability) is in itself inherently multidimensional, thus suggesting that links across stability facets may be quite subtle. For instance, short-term return rates may be linked with environmental variability, but environmental variability may have nothing to do with immigration-type variability, the latter possibly related with long-term return rates and driven by rare species. Even in our idealized mathematical setting, because measures can be determined by different species abundance classes, we should not expect a general and simple connection to hold between facets of ecological stability.

Response to comments of Reviewer 2

In this manuscript, the authors describe how the variability of modelled ecological communities are affected by stochastic perturbations.

One of the main findings is that the variability response to stochastic immigration perturbations is driven by rare species while the common species drive the response to environmental perturbations. While there have been previous suggestions of this differential responses of rare and common species to environmental fluctuations (e.g., using British birds, Saether et al. 2011, or within debates on forest tree communities dynamics, Chisholm et al. 2014), this is to my knowledge one of the first theoretical studies to investigate in great detail the role of species abundances, perturbation types and their interaction in shaping community-level variability. This work nicely builds on previous technical work by the authors, relating mathematically well-defined variability measures to more classic resilience measures, all of which are here described in a (relatively) accessible manner.

Other interesting finds of the paper include:
* how the variability (variance) vs mean abundance relationship is modulated by the strength of species interactions (which connects to how Taylor's law is modified by species interactions, see below)
* the effect of correlated or uncorrelated perturbations on community variability (for two-species systems)
* how diversity-stability relationships will be affected by these results: the relative contributions of the abundance classes can generate opposite diversity-stability patterns for different kinds of perturbations.

Overall I found the manuscript very interesting and also very rich in information, exploring in several interlinked directions how variability responses can be modified by both perturbation type and species abundances. The upside is that there are clearly several novel or synthetic insights into how ecological communities should function in a stochastic world. The downside is that the multifaceted nature of the manuscript, which is already fairly long, makes it difficult for the authors to be simultaneously pedagogical and very precise about the methods used. Most of my comments below probably stem from slightly different perceptions about how to balance these two worthwhile yet conflicting aims.

We thank the reviewer for his very thorough and constructive evaluation of our work. To address the "multi-faceted nature of the manuscript" we made substantial efforts to focus our message and shortened the discussion section to make it more factual and less speculative. Our paper is now essentially organized in two parts. The first establishes a general theory for variability, emphasizing its highly multidimensional nature, while the second part explains that a simple generic pattern can emerge in species-rich assembled communities. The relevance of this pattern is then illustrated by explaining that it can shape diversity-stability relationships (see response to comments of Editors).

I have two major technical comments regarding the connection of this work to Taylor law scaling / stochastic population dynamics theory, as well as about the strength of interactions actually considered (a little unclear so far, for lack of precise parameter values). Most of the comments can probably be dealt with by rewriting and adding additional information — no additional results are required. In fact, there might be ways to simplify the manuscript.

About the connection with Taylor's law, there should indeed be implications of our findings. However, it should be stressed that our observations are not equivalent to Taylor's law, but rather represent a dual pattern.

We have clarified this point as follows, line 295: The variability-abundance patterns shown in Figs. 4 and 5 should not be confused with Taylor's (1961) law. We plotted power-law relationships between average community variance and abundance of perturbed species, whereas Taylor's law describes a power-law relationship between a species variance and its mean abundance. In this sense, the variability-abundance pattern is *dual* to Taylor's law, i.e., the community response to single-species perturbations instead of that of individual species to a community-wide perturbation.

Although the results in most sections and appendices seemed very sound to me, I have been a little less convinced by the section "Implications for the diversity-stability relationship" so far. It relied on the assumption of independently perturbed species (I may be wrong about this though — please see the detailed comments). However, many communities for which we are interested in the diversity-stability relationship are synchronously perturbed by a common driver like temperature, shared by most species. This may imply a different diversity-invariability relationship that the currently positive one described for environmental-type perturbations. This seems corroborated by the worst-case variability response in Fig. 6 (right panel), where invariability decreases with richness which, if I am not mistaken, is obtained for fully correlated perturbations. Although from appendix E and Fig. 3 I gather that the authors attribute a special meaning to fully correlated, which can mean both synchronized and antisynchronized (if correct, this would be worth mentioning in the text, by the way). In any case, the worst-case variability does not corroborate the positive diversity-stability (sensu invariability) reported for environmental noise.

Consequently, I have been wondering if this section would not be better developed as a separate work, which would then allow to make more lifelike assumptions about the perturbation regime (or justify these better). But it is perhaps just a matter of making the assumptions more explicit. Please see the line-by-line comments for more specific interrogations.

We agree with the reviewer that much more can be said about the diversity-stability relationship, and that it would be better to leave a more thorough study for a separate paper. In the revised manuscript we present the diversity-invariability relationship (Fig. 6) as a practically relevant illustration of the patterns linking variability and abundance (Figs. 4 and 5); line 301: To illustrate some implications of the variability-abundance pattern, we now propose to revisit the diversity-stability relationship; line 406: We showed that species abundances greatly affect variability distributions. This new insight has broad consequences, for example (...)

About the criticism that we only consider a subset of perturbations when dealing with complex communities, it is true that in the section *Generic variability patterns*, species-specific perturbations are used to reveal the abundance-variability patterns. It should be noted however, that although this subset is indeed small compared to the entire perturbation set, it does cover a lot of the complexity of the variability distributions. For example, mean-case variability is equal to the mean of variabilities induced by single-species perturbations, and worst-case variability is realized by a single-species perturbation for perturbation types $\alpha = 0$ and $\alpha = 2$.

We added the following paragraph to clarify this point, line 288: Although we restricted our attention to a specific section of the perturbation set, the response to single-species perturbations of immigration and environmental types can still span the whole variability distribution, from worst-case (rarest and most abundant species perturbed, respectively) to mean- and best-case scenarios (most abundant and rarest species perturbed, respectively). For demographic-type perturbation the situation is more subtle as the response is independent of species abundance, and, in general, extreme scenarios will be associated to temporally correlated perturbations affecting multiple species.

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Finally, note that for the simulated perturbations in Fig. 6 we did not restrict to species-independent perturbations. The simulations span the entire set of perfectly correlated perturbations. We added the following sentence to clarify this point, line 305: For each community, we uniformly sample the boundaries of its perturbation set by drawing 1000 perfectly correlated perturbations (i.e., those that can realize the maximal response).

In the Discussion, it was difficult to get the point made by the "Theoretical consequences" section. There were some interesting elements but also a number of vague statements with little direct connection to the results. Thus, I have not felt that the Discussion was really doing justice to all the interesting findings enumerated in the previous sections. I would suggest to have a Discussion and a Conclusion much more factual, based on previous results and to-the-point, since the manuscript is already fairly long. Just for the sake of the example, I was puzzled as to how positive correlations in the perturbation direction can weaken community variability for environmental noise (quite unintuitive, since both species are given a big push) in the predator-prey example. Would this occur with more species? The Discussion does not tackle this sort of natural development of the results, and wanders, in my view, into too speculative constructions.

We agree that the previous version of the discussion, especially the part focused on theoretical implications, was rather speculative. We removed those ideas that were less connected with the results, and tried to make the discussion more factual and to-the-point.

General comments for authors

The first two main comments are relatively major, while the latter three pertain mostly to the writing style.

Scaling Taylor's law up to the community level

The authors mention only in passing Taylor's Law $\mathbb{V}(N_i) \propto \mathbb{E}(N_i)^\beta$ in the introduction and in the discussion. In my view, this is a missed opportunity and may appear very odd to readers familiar with population ecology. Taylor's law is not simply understood as a pattern in the data (as suggested l. 500-506) but also a scaling expected on theoretical grounds in single-species stochastic population models (see e.g. Linnerud et al. 2013 and related previous work by Lande et al. 2003).

What the authors do here, among other things, is bringing Taylor's law to the community level. This is evident from the formulas in Appendix B (B5) where the variability metric $\mathcal{V}$ is defined as proportional to the trace of the variance-covariance matrix of abundances. This means that all plots in Fig. 4 and 5 are log(Variance) vs log(Mean focal abundance) plots – as in all attempts to check Taylor's law (which consists mostly in the linearity of that relation rather than the particular value of that exponent, Keeling 2000). The difference in the log-log plots with most TL publications is that the authors plot the log of the community-level variance (sum of all species variances) rather than simply the variance of the perturbed species. But I do not see how this may change massively the results, all other things being equal (the authors are of course very welcome to prove me wrong here, if I am missing an important mathematical step).

We have clarified in the text that our observations are not strictly equivalent to Taylor's law, but a dual pattern. We mention this in the caption of Fig. 5, in the results (line 295) and in the discussion (line 430). For example, line 295: The variability-abundance patterns shown in Figs. 4 and 5 should not be confused with Taylor's (1961) law. We plotted power-law relationships between average community variance and abundance of perturbed species, whereas Taylor's law describes a power-law relationship between a species variance and its mean abundance. In this sense, the variability-abundance pattern is *dual* to Taylor's law, i.e., the community response to single-species perturbation instead of that of individual species to a community-wide perturbation.

In fact, one of the main result in Fig. 5 is that the classic scaling of Taylor's law $\beta = \alpha$ (authors' notation, corresponding to the top-left corner of Fig. 5), which has seen derived for independent stochastic populations (Linnerud et al. 2013), becomes $\beta = \alpha - 1$ with "strong" interactions (see the following comment for a discussion of how strong). This result is remarkable enough to be mentioned: relatively strong interactions can bring down Taylor's exponent by one unit.

As an aside: I have been wondering whether this result was showed only numerically here, or analytically as well? It would be good to make this clear.

It would be worthwhile to discuss these results in connection to those of Kilpatrick and Ives (2003) [cited in passing l. 502-504 but not discussed in the present manuscript]. They also showed a decrease in Taylor's law exponent for communities (albeit for less perturbation types, only environmental, and no trade-offs). Kilpatrick and Ives (2003) use very similar methods as well (it was unclear if the authors made this connection from the suggestion l. 504-505 of "simple models of the diversity-stability

The main difference between our work and the one of Kilpatrick and Ives (2003) is that we are looking at a pattern that is different from Taylor's law (we agree that continuous-time vs discrete-time is probably a minor difference). It would be interesting to explore with our approach how Taylor's law is affected by species interactions, extending the results of Kilpatrick and Ives (2003), but this is outside the scope of this paper.

We make this point more explicit in the discussion, line 436: This duality suggests that Taylor's law is, at the community level, strongly affected by species interactions. This is known (Kilpatrick and Ives 2003), yet our approach could help reach a more complete understanding of the ecological information contained in community-level Taylor's laws.

One of the innovations of the manuscript is the consideration of immigration-type perturbations (to my knowledge we know little about those). A corollary of the abovementioned connection between the authors' results and Taylor's law is that immigration-type perturbations generate TL exponents below one or even negative (Fig. 5). We almost never observe those. Would it mean that immigration-type perturbations are negligible in many communities? It is currently a bit unclear to me what we should expect when different perturbations are considered simultaneously though — would a given type necessarily dominate the community response? (these considerations would be interesting to bring in the Discussion)

The observed variance-mean scalings could potentially be connected to the relationship between forest community dynamics and debates on neutral theory. Neutral theory suggests strong impacts of immigration-extinction, under strong interactions as well due to the equal competition assumption. According to the authors, these assumptions would translate almost surely into negative TL exponents (or would this be incorrect?). Meanwhile, an environmental-perturbation variance scaling seems to be prevalent in the forest community-level data (Chisholm et al. 2014).

We think these are interesting suggestions. However, because we believe the link with Taylor's law to be outside the scope of this paper, we did not incorporate these suggestions in the revision.

How strong can be strong interactions?

The results of Figs. 4 and 5 assume that strong interactions proposed by the authors are somehow resembling interactions present in real data. However, I wonder what is meant exactly by "strong" since no parameter values are given for the assembled communities (see below my discussion of Appendix F).

Appendix G suggests that interactions should be as strong and multiple that species can somehow be "swapped", and yet the community as a whole keep the same properties. This resembles (at least very superficially) neutral theory where intra- and inter-specific competition have comparable strengths. However, a large body of current research (e.g., Adler et al. 2018, Barabas et al. 2017) highlights that a high degree of self-regulation, making interspecific interactions comparably much weaker than intraspecific, and therefore less influential over the community dynamics, must exist for both empirical and theoretical reasons. I have therefore sought to understand what assumptions regarding intra- / inter-specific interactions were made here. This is, in my view, a main limitation of this otherwise very nice manuscript: we are currently not able to reproduce the results since we do not have the exact parameter values or assembly algorithm.

In Appendix F, I found the following information (I would appreciate a table of parameter values for both the "weak" and "strong" interactions scenarios): "The mean interaction strength is set to 0.1 and its standard deviation to 0.1, thus allowing some occasional positive interactions (e.g. facilitation). Growth rates and carrying capacities are independently drawn from a normal distribution of unit mean and 0.2 standard deviation." If I am to rewrite the Lotka-Volterra model as

$$\frac{dN_i}{dt} = N_i\Big(r_i + \sum_{j=1}^{N} a_{ij}N_j\Big)$$

we then have $a_{ii} = r_i/K_i$, so 1 on average and $a_{ij} = r_i B_{ij}/K_i$, which is then around 0.1 on average. So 10 times stronger intra- than inter-interactions. If this is what constitutes "strong" interactions here (I assume that the reference set given is the one that corresponds to strong interactions), this seems very reasonable to me — this is not all unrealistic when comparing to e.g., Adler et al. 2018. However, this does not take into account the potential thinning out of communities during the assembly process. This may lead to weaker interactions in many cases — and perhaps stronger in some other cases, for reasons invoked in Haydon 2000. I would therefore be very curious to see which parameters are truly used for the communities that went through the assembly process.

We agree with the reviewer's analysis, and his conclusion that relatively weak interactions are sufficient to reach the case we called "strong interactions". In the revised manuscript we mention the values of interaction strength in the description of Fig. 4, line 245: We randomly draw species dynamical traits, starting with a configuration in which mean interspecific interaction strength is one tenth of the strength of species self-regulation, and we emphasize the relatively weak interactions when presenting Fig. 5, line 285: Importantly, our example demonstrates that this limit is reached already for relatively weak interactions (recall that in Fig. 4 and in the right-hand panels of Fig. 5, the interspecific interaction strengths are ten times smaller than the intraspecific ones.

More generally, we have rewritten the description of the multi-species model simulations, to make them fully reproducible. We have included a brief description in the main text, and give the full details in Appendix F. We also provide Matlab code as supplementary information., together with Matlab code as supplementary material.

Concerning "the potential thinning out of communities during the assembly", this effect was negligible in our simulations. More generally, Bunin (2017) presents a detailed analysis of this phenomenon for the random Lotka-Volterra models we use here.

Corollary question: I assume that the authors removed cases where a unique fixed point is unstable (e.g., species going to extinction, or a community settling on a limit cycle or strange attractors). But did the authors deal with cases with alternative stable states? (e.g., found in such models by Law and Morton 1993). Were these sufficiently rare here?

We have added the following sentence, line 249: [In simulations] some species would go extinct during assembly, but no limit cycles, chaotic behavior or multi-stability were observed."

Multidimensionality of stability

The abovementioned results are in many ways interesting and consistent enough to give (in my opinion) less importance in the manuscript to the more conceptual plea made by the authors, i.e., to look at stability from a multidimensional perspective. I certainly agree with them that this is needed, but it has been suggested before (e.g., Donohue et al. 2013, 2016). Also, it may not be best illustrated by the current focus on variability properties – this is only one aspect of stability. Or, perhaps the authors need to make crystal clear that they want to highlight only the multidimensional aspect of variability (which is but one component of stability). See line-by-line comments.

Yes, our focus here is on the multidimensional nature of variability. We have tried to clarify this throughout the text, e.g., line 461: Ecologists have acknowledged the multi-faceted nature of ecological stability. But here we are showing that a single facet (variability) is in itself inherently multidimensional, thus suggesting that links across stability facets may be quite subtle. For instance, short-term return rates may be linked with environmental variability, but environmental variability may have noting to do with immigration variability, the later possibly related with long-term return rates and driven by rare species. Even in our idealized mathematical setting, because measures can be determined by different species abundance classes, one cannot expect a general and simple connection to hold between facets of ecological stability.

Variability spectrum or variability distribution?

I am not sure that the wording variability spectrum adds a lot to the reader's understanding, especially given that the meaning of spectrum here is relatively vague and does not fully match physical (e.g., color spectrum of the fluctuations) or mathematical definitions (eigenvalue spectrum of an operator; at least I did not see an obvious connection). I would suggest to drop the term if spectrum is intended in a vague sense. Perhaps variability distribution or vector would do an equally good job? But these are just suggestions.

We changed "variability spectrum" to "variability distribution" throughout the manuscript. This also led us to change the title: The inherent multidimensionality of temporal variability: How common and rare species shape stability patterns. The new title should also communicate better the focus of the paper.

Demonstrated mathematically here, previously, or demonstrated numerically?

It was difficult to separate, as currently written, the results that were 1. mathematically proven for general communities (either here or in previous work) 2. conjectured based on a reasonable approximation (e.g., mathematically proven using a linear approximation of a nonlinear model) 3. found true only for simulations performed in the paper, i.e., for some specific parameter values of a given model.

The reader should be able to make easily the distinction between these categories, that are sometimes (if I understand correctly) blended in the same figures. Of course simplifications to the writing have certainly been performed to avoid a too lengthy or indigest text, but I was left wondering in many places if the results were proven by the authors and were, or from simulations, i.e. contingent upon parameter values. The writing style is relatively discursive, and while I am confident that the authors know very well their models and results, I had real difficulties pinpointing myself why some statements were true. I flag these issues in the line-by-line comments with ***. Just a few edits here and there may truly help the reader to pin down more easily to what category each result belongs to.

We added several references to previous work; see below for concrete examples.

Line-by-Line comments

* l. 32. There is quite some debate about whether EWS, including variance, can or cannot indicate regime shifts (see Dutta et al. 2018 for an overview using simulated models): variability can be indicative of ecosystem collapse but that is not always true. Please correct accordingly.

Agreed. Changed to "can be indicative" (line 31).

* l. 45 Here the authors express the idea that different values of perturbations will always lead to different variability values. Stricto sensu this is of course true: even if a dynamical system reacts weakly to perturbations, it is for instance unlikely that more perturbations will lead to less variability, provided no species goes extinct. But I wonder if this applies equally well to cases where the community locks on to a limit cycle or strange attractor. In those cases, a forced limit cycle can have an attractor that bears a large resemblance to the same system without or with a low perturbation regime (e.g., see how variances changes in Batt et al. (2013) once the limit cycle is reached). This is because the attractor, once reached, is largely constrained by the average parameter values and not their fluctuations. If this idea of stronger perturbations generating (much) larger fluctuations is only motivated by the assumption of a fixed point equilibrium, this might be worth stating somewhere relatively early in the introduction (currently the authors mention the assumption of a fixed point equilibrium l. 66 but the consequences of that assumption are not fully made explicit).

Our results do not apply to communities in more complex dynamical regimes, such as limit cycles or chaotic attractors. We have clarified this on line 57: For simplicity we will restrict to systems near equilibrium, by opposition to, e.g., limit cycles or chaotic attractors.

* l. 61. I would suggest to replace "but instead should reflect a system's propensity to withstand perturbations in general" by "but instead should reflect a system's propensity to withstand a whole class of perturbations". Indeed, not all possible types of perturbations are considered in this paper (as the authors rightly acknowledge a few lines below), correlated environments in particular are not considered.

Done as suggested (line 60).

* l. 87-88. In connection to the previous comment regarding l. 45, I would suggest to expand a bit here or earlier (unless the authors want to reserve a special place for this in the Discussion) on the consequences of that assumption for the results to come.

See above.

* Fig 1: This is a naive suggestion but in that figure, can "variability spectrum" be equated with vector" or "variability distribution"? Would this provide the same meaning? If so, it would simpler.

We replaced "variability spectrum" by "variability distribution" in all instances.

* l. 99 Eq. 1 I would suggest to use $\xi_i(t)$ as in the Appendix and leave $W_i(t)$ for the Wiener process rather than its "derivative". Or some other notation but please do not use $W_i(t)$ in place of $dW_i(t)$ — this will confuse anybody using SDEs.

Agreed, this was an oversight.

We have clarified this point as follows, line 109: Although environmental fluctuations often follow temporal patterns (Vasseur and Yodzis, 2004; Ruokolainen et al., 2009; Fowler and Ruokolainen, 2013) we will not consider autocorrelated perturbations. It would thus be interesting to extend the analysis to more general temporal structures of perturbations, as well as to nonlinear behaviors.

We now distinguish better linear stability and nonlinear community assembly. In the introduction, line 67: After having developed a general theory of variability which could be applied to any model community near equilibrium, we turn our attention to species-rich communities, assembled from nonlinear dynamics.. In the discussion, line 368: After having described a general (linear) theory for variability, which emphasizes its highly multidimensional nature, we turned our attention towards species-rich communities assembled by random (nonlinear) Lotka-Volterra dynamics.

Done.

We revised as follows, line 156: A disproportionate increases in fluctuation amplitude as perturbation intensity changes would reveal nonlinearity in the dynamics. In a linear setting, however, such effects cannot occur and there is only a linear dependency in perturbation intensity.

We replaced r by λ (l. 172).

We now define σ_{in}^2 as follows, line 174: For species-rich communities, we define the intensity of a perturbation as the average intensity per species (...).

We rephrased the sentence as, line 176: When increasing the $\sigma_i^2 s$ by a factor c, both σ_{in}^2 and σ_{out}^2 increase by the same factor.

We now write (line 179): Generalizing previous work (Arnoldi et al., 2016b, Arnoldi and Haegeman, 2016) to arbitrary perturbation type, we construct a measure of stability, called hereafter *invariability*.

We have rephrased this sentence as, line 181: The factor $1/2$ allows $\mathcal{I}$ to coincide, for simple systems, with asymptotic resilience (Arnoldi et al., 2016b). In particular, for the one-dimensional example considered above for which $\mathcal{R}_\infty = \lambda$, we indeed have that $\mathcal{V} = 1/2\lambda$ and thus $\mathcal{I} = \lambda = \mathcal{R}_\infty$.

Typo corrected.

Agreed. We replaced "variability spectrum" by "variability distribution".

This result is generally true for linear systems. The case of perturbing nonlinear systems is more subtle, and not considered here.

As far as we know, mean-case variability has not been studied before.

We have added the following comment at the end of this paragraph, line 229: For all perturbation types we see that positive correlations between the components of the perturbation (i.e., moving upwards on the disc) reduce variability (see Ripa and Ives, 2003 for related results).

The general relationship is indeed given in Arnoldi et al. (2016b). But this inequality only says that the worst-case invariability in response to immigration-type exogenous perturbations will be smaller than asymptotic resilience. We have modified this sentence as follows, line 234: Although we know from previous work (Arnoldi et al., 2016b) that the smallest invariability value in response to immigration-type perturbations will always be smaller than $\mathcal{R}_\infty$, in general (i.e., any perturbation type and/or any perturbation direction) there is, a priori, no reason to expect a relationship between $\mathcal{I}$ and $\mathcal{R}_\infty$.

* l. 248 and 251. *** The authors consider here a perturbation of a single species and suggest that "By superposition, this allows the study of perturbation scenarios in which species are affected independently." Would it be possible to provide a more precise reference or demonstration for this? While I understand the need to simplify the analysis and do it one species at a time, I am (so far) unconvinced that perturbing all species simultaneously would be exactly equal to perturbate species by species, even if perturbations are not correlated. What is exactly meant by "by superposition" — is this a precise mathematical definition or rather a physical analogy?

We mean here that the effect of a linear combination of independent perturbations can be reconstructed (by linearity) from the response to each perturbation in isolation. Perturbations that can not be described as such are those that present some inter-species correlations. We have changed the text as follows, line 253: Linear combinations of these perturbations will span all scenarios in which species are affected independently, but exclude scenarios in which they are perturbed in systematically correlated or anti-correlated way.

* l. 254-261. *** It is unclear whether these results arise only from simulations of the Lotka-Volterra community or also by examination of the linearised model of eq. (1). Fig. 4 suggests that it is both: please clarify the methods for the reader. The thematic structure of the paper (no classic Intro-Methods-Results-Discussion) requires that the methods are detailed unambiguously in each section. Alternatively, the authors could have a Methods section at the end or some more details in the Appendices.

We give the details of the model simulations in Appendix F. We have added a reference in the main text, line 247: (a complete description of the nonlinear model is given in Appendix F and Matlab simulation code is available as supplementary material).

* l. 264 In what sense are more common species more stable? They could very well fluctuate more, depending on their growth rates and intraspecific coefficients.

They are more stable in the sense that they are less sensitive to exogeneous perturbations. We have added this following comment, line 269: Despite being more stable than rare ones (they buffer exogenous perturbations more efficiently , see left-hand panel), common species are more strongly affected by environmental perturbations.

* l. 273-274. This idea with respect to the r-K trade-off seems very interesting and underdeveloped here. *** It is also symptomatic of the absence of detailed methods in the paper. I found myself wondering: how exactly was this trade-off modelled? Does it mean that when r is higher K is lower or the reverse? Both would make sense depending on the study system chosen. Neither Fig. 5 nor the main text p. 18 provide any answer as to exactly what relationship between r and K modelled (same for Appendix F). The reader needs to be able to replicate the results.

Here we simply chose $r \sim 1/K$, so that higher K implies lower r, and vice versa. In the revised manuscript we have tried to include the methods in full detail. In particular, we describe now the procedure to generate the r-K trade-off in Appendix F, and provide Matlab code as supplementary material.

In the main text, we have specified a r vs K trade-off, i.e., species with larger carrying capacities have slower growth rate (line 277). We have also added in the caption of Fig. 5 that species satisfy a r vs K trade-off ($r \sim 1/K$).

* l. 278-281 and Appendix F: here there is a mention of "sufficiently strong interactions". Are we talking about the interaction coefficients in the Lotka-Volterra model? Do strong LV coefficients also translate into strong elements in the community matrix? I would expect that the species abundance distribution would then create weaker community matrix coefficients for the rarer species. Or does this mention of sufficiently strong interactions already take abundances into account? The sense that is given to weak or strong interaction may have to be made more precise somewhere to avoid confusion.

We here use the standard terminology. Competition coefficients B_{ij} are per capita and do not depend on species abundances. The components of the community matrix A_{ij}, however, do depend on species abundance, because $A_{ij} = N_i B_{ij}$. We give the definition of competition coefficient B_{ij} in Appendix F.

* Fig. 5. In many ways this may be the most important figure of the article. I wonder if it might be worth it to have it on the untransformed scale somewhere in the Appendix: it is not true that variability is inversely proportional or proportional to variability here (cf. end of legend); if I understand correctly, it is log(variance) that is linear in log(abundance).

Because the slope of the linear relationship in log-log scales is 1 or -1, it implies inversely proportional ($y = C/x$) and proportional ($y = Cx$) relationships on untransformed scales. Because abundances and variability values span several orders of magnitude, a figure with untransformed scales is not particularly instructive.

* l. 287. Given what the authors report, I would refer more to a variability distribution rather than a spectra. But again that is a question of style.

Agreed, see above.

* l. 300. I am not sure that it is possible to tackle the diversity-stability question while perturbing only one species at a time. A proof of this superposition concept stated earlier would be most welcome to convince the reader here. Also, the environment usually force many species in the same direction (e.g., bad weather) — can the authors say in which direction a synchronous forcing may affect the results? This might be worth discussing later on.

Here we do not consider only species-independent perturbations. First, the numerical results are based on a vast sampling (1000 perturbations) from the complete set of perturbations. Second, we show the worst-case scenario, which is always associated with a perfectly correlated perturbation. On the other hand, the mean-case scenario is realized by a species-independent perturbation.

We clarified this in the text, line 305: For each community, we uniformly sample the boundaries of its perturbation set by drawing 1000 fully correlated perturbations (i.e., those that can realize the maximal response), of a given type. We then compute the bulk of the resulting (in)variability distribution (5 to 95 percentiles), as well as its mean and extreme realized values.

* l. 324-325 If the authors' meaning is that mean-case perturbations are more realistic because they allow for compensatory dynamics between species, I think this strongly disagree with the evidence (e.g., Vasseur et al. 2014). Please clarify the meaning of the sentence or discuss the assumption later.

We removed this confusing sentence.

* l. 341 Here it may be simpler to talk about a variability distribution rather than a spectrum (but again this is just a suggestion)

Agreed, see above.

* l. 360 diversity-invariability rather than diversity-stability?

Agreed.

* l. 362 The wording "immigration-type" perturbations suggests that one only adds new individuals to the local population. But what the authors model is white noise, so there's as much removal (emigration) as immigration. Mentioning this could help the reader understand better why rare species can be strongly affected by this type of perturbations (provided that my interpretation is correct of course ...).

We agree with the reviewer. The reason why we call this immigration-type is that it would correspond to a fluctuating influx of organisms, i.e., a perturbation of a constant immigration term. We have added this point when introducing the perturbation types, line 144: Because we focus on zero-mean perturbations, perturbations of this type contain as much emigration than immigration. The reasoning behind this nomenclature is that, in an open system, fluctuations of an otherwise constant influx of individuals would correspond to an immigration-type perturbation.

* l. 364 Does their contribution scale as the inverse of their abundance or their log-abundance? If we refer to Fig. 4 or 5 I believe it is the latter.

This sentence has been removed. To answer the reviewer's question, the left-hand panel in Fig. 4 shows that $\ln V \approx -\ln N + (\text{a constant})$, so that $V \approx (\text{a factor}) \times 1/N$.

* l. 371-374 Again, I believe the authors mean average log-abundance (or I am really misinterpreting the scales on Fig. 4).

See above.

* l. 374 ends on a rather speculative note if the result relies on independent perturbations.

This sentence has been removed. To answer the reviewer's question, the pattern shown does not rely on the species independence of pertubations, as simulations in fact span perfectly correlated perturbations.

* l. 384-386. This is speculation. To my knowledge autocorrelation in the perturbation can strongly affect EWS in other cases than a saddle-node bifurcation. See Dutta et al. 2018 for a discussion.

We removed this paragraph.

* l. 386-390. Even more speculative. It does not seem that the concept of "global instability" is well-defined. On the other hand, there are many kinds of possible local and global bifurcations in dynamical systems, and these can be excited (or not) by noise in very many ways. If the authors want to discuss this, I would suggest a rewrite of this paragraph to tackle the role of noise and forcing in dynamical systems with non-point attractors. But this might be simply too much for the paper and the authors might want to simply delete the paragraph.

We removed this paragraph.

* l. 415-422. From my perspective this paragraph is very speculative, which I feel is problematic when dealing with mathematical concepts. Assessing feasibility makes sense mostly for nonlinear systems, such as Lotka-Volterra. But in this case, a straightforward link between feasibility and asymptotic resilience is not obvious at all (e.g., Jansen & Sigmund 1998). There are some references showing a link between a locally stable interior fixed point and permanence sensu Jansen & Sigmund, such as Townsend et al. (2010). Clearly, if the authors want to go in that direction, they need to discuss theoretical work like this and do so precisely.

We followed the reviewer's advice and simply removed this part of the discussion. In general we tried to keep the discussion more factual and removed speculative assertions.

* l. 423-443. It is not quite clear to me what the point of this paragraph and section is. I would suggest to suppress it.

Deleted.

* l. 434-437. May's original complexity-stability bound is to my knowledge based on the community matrix, not the per capita interaction matrix. Hence I do not completely follow this remark.

Deleted.

*l. 443 I am uneasy with the progression towards more and more vague statements such as "demographic perturbations probe the collective response of ecosystems", because I can attach at least 3 or 4 different meanings to "probe" in that sentence. As the authors say two lines below, these reasonings go beyong the scope of the article. Perhaps it would be simply best to cut down the discussion and elaborate on those thoughts elsewhere.

Deleted.

In this section, I have been a little concerned by the implicit message that repeated references to "May's work" sends to fellow scientists — many other researchers have worked on the stability bound for random Jacobian matrices — perhaps best to cite articles in a factual manner rather than people. Conversely, this may not be correct to reduce the work of Robert May to asymptotic resilience: in fact he has done quite a bit on stochastic environments (May 1973).

Deleted.

l. 483-484. Based on Saether et al. 2011, Linnerud et al. 2013, I would tone down a little bit the novelty claims here. It has basically always been known, since the first works on demographic stochasticity, that rare populations would be much more vulnerable to it.

Agreed. The phrasing was unfortunate. We now write, line 418: The type of perturbations affects which species abundance class contributes most to variability. In turn, the physical size of the system considered affects which perturbation type dominates. This is well known for populations (Engen et al., 2008), and also transposes to the community level.

l. 493-495. About this non-trivial scaling of the variance, there are some existing results in a single-species context I think (e.g., Engen et al. 2008).

Thank you for this reference (see response to the previous comment).

l. 497-506. Should be rewritten according to the general comment on TL above.

In the revised manuscript we stress at multiple occasions that our results are not directly applicable to Taylor's law. For example, in the discussion we now write, line 429: To develop suitable methods, it might be helpful to first understand the link between the variability-abundance patterns and Taylor's (1961) law. A close connection is indeed expected: we studied the behavior of the community response to an individual species perturbation, while Taylor's law focuses on the individual species response to a perturbation of the whole community.

l. 508 and forward. The manuscript shows many clear results (the TL exponents decrease with increasing interactions, worst-case variability is realized by rare species for immigration-type perturbations and common species for environmental type, . . .). In my view, it would be a pity to have clear-cut results but a rather vague conclusion. I would suggest to either summarize well the findings and provide some directions for future work, or simply delete this conclusion.

Agreed. We rewrote the discussion to remain more factual and less speculative.

Appendices

I have few comments on those as they are overall very-well designed (they allowed me to better understand previous work by the authors). My only comment is that references, including to the authors' publications, should be included whenever a result from a previously published publication is reported. The reader needs to be able to differentiate already proven results (if repeated here for pedagogical purposes) from new ones (if provided).

Agreed. We have added several references to differentiate better new and old results.