

# Review of ‘The variability spectrum of ecological communities: How common and rare species shape stability patterns’

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## Summary for the editor and the authors

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.

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.

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 than 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.

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.

## 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  $\log(\text{Variance})$  vs  $\log(\text{Mean focal abundance})$  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).

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 been 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 relationships based on an assumed Taylor’s law”). In Kilpatrick and Ives (2003), a relationship between (species-level) variability and mean abundance is derived based on a linearization of a (discrete-time) Lotka-Volterra model with environmental noise. The main difference with the work of the authors seems to be discrete rather than continuous time, but I would be surprised if it has a major influence on the conclusions.

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).

### 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

$$\frac{dN_i}{dt} = N_i \left( r_i + \sum_{j=1}^n a_{ij} N_j \right) \quad (1)$$

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.

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?

## 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.

## 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.

## 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.

## Line-by-line comments

- 1. 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.
- 1. 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).

- 1. 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.
- 1. 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.
- Fig. 1: This is a naive suggestion but in that figure, can “variability spectrum” be equated with “variability vector” or “variability distribution”? Would this provide the same meaning? If so, it would be simpler.
- 1. 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.
- 1. 110 “The absence of temporal autocorrelation is not a critical assumption for what follows”: although it is perfectly fine to choose to model white noise as a first approximation in this manuscript, there are many good reasons (and references) suggesting that temporal autocorrelations in the forcing signal will strongly affect the responses of structured or multi-species models to perturbations (e.g. Ripa and Ives 2003; Greenman and Benton 2005a,b). I would therefore suggest to just state that the noise is uncorrelated here, or provide a demonstration (references, appendix, . . .) that temporal autocorrelation has indeed no bearing on the results.
- 1.118. Perhaps mention that stationary fluctuations = stability is limited to eq. 1 and not the nonlinear equations considered later?
- 1. 129 References for this scaling of responses to environmental noise could be inserted here, e.g. Engen et al. (1998) or Lande et al. (2003) – the reader has to take it in good faith otherwise.
- 1. 151-152. “This could reveal [...], this is not the case” -> It is a bit unclear what “this” mean in the sentence. I would suggest a rewrite along the lines of: “Large and nonlinear increases in fluctuation intensity in response to a small variation in a parameter would instead suggest nonlinearity in the dynamical system, but in the linear setting of eq. (1), such effects cannot occur by construction” – or similar.
- 1.161. I would refrain from denoting the strength of density-dependence  $r$  since this is the usual notation for the intrinsic population growth rate.  $\alpha, \beta, b$  or  $\gamma$  are commonly employed for denoting the strength of density-dependence, maybe  $b$  or  $\gamma$  here?
- 1.164. “average intensity felt by species” is a bit too interpretative. Replace by “average variance in growth rate” or similar? It would be clearer to say precisely what  $\sigma_{\text{in}}^2$  means though.
- 1.165. “then the maximal community response will be proportional to . . .”. Do you mean “the maximal community response  $\sigma_{\text{out}}^2$  will be proportional to . . .” or is there another quantity defined as maximal community response? This is the first introduction of the term. Please clarify.
- 1.169. \*\*\* Is  $\mathcal{I}$  defined from previous work (which I assume) - in this case, the authors should cite their previous work here.
- 1.170. \*\*\* Same comment. The reader (assuming the reader is a biologist with some mathematical training) has no way of knowing if this equality is mathematically proven, conjectured based on an approximation, . . .
- 1. 174 “In Appendix B we explain considering variance” -> it looks like a word is missing from the sentence.

- 1.196. I am concerned that calling the vector-valued variability responses ‘variability spectra’ and illustrating it graphically with blue, green, and red colors may induce some confusion with the spectral density of the time series within these communities. One idea would be to avoid the term spectrum and use distribution, but clearly that is up to the authors to decide which term they prefer.
- 1.198. \*\*\* This may be a naive comment: is this result for perfectly coherent perturbations true only for eq. (1) or more generally as well?
- 1.205. \*\*\* It is proven in Appendix C but has it been proven in a previous publication of the authors? Please include the reference.
- 1. 223-231. These are very interesting results. I wonder how they may connect to Ripa and Ives (2003), which could be developed in the discussion.
- 1.237. Do the authors mean that even in this very simple linear one-predator one-prey system, we cannot formulate analytically any relationship between asymptotic resilience and invariability for a given perturbation, like the one that you previously presented l. 170 (for a single-species system)? If so, I believe this should be stated more explicitly. How about the inequality stated in Arnoldi et al. (2016b) - I assume that the inequality at least holds?
- 1. 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?
- 1. 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.
- Fig. 4 l. 2 abundnace -> abundance
- 1. 264 In what sense are more common species more stable? They could very well fluctuate more, depending on their growth rates and intraspecific coefficients.
- 1.267. importnat -> important
- 1. 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.
- 1. 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.

- 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  $\log(\text{variance})$  that is linear in  $\log(\text{abundance})$ .
- 1.287. 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.
- 1.300. 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.
- 1. 315-315. Good analogy.
- 1. 320 “Finnaly” -> “Finally”, and “in all panels of Fig. 6”
- 1. 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.
- 1. 341 Here it may be simpler to talk about a *variability distribution* rather than a *spectrum* (but again this is just a suggestion)
- 1. 360 diversity-invariability rather than diversity-stability?
- 1. 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...).
- 1. 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.
- 1. 371-374 Again, I believe the authors mean average log-abundance (or I am really misinterpreting the scales on Fig. 4). 1. 374 ends on a rather speculative note if the result relies on independent perturbations.
- 1. 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.
- 1. 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.
- 1. 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.

- 1. 423-443. It is not quite clear to me what the point of this paragraph and section is. I would suggest to suppress it.
- 1. 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.
- 1. 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 beyond the scope of the article. Perhaps it would be simply best to cut down the discussion and elaborate on those thoughts elsewhere.

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).

- 1. 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.
- 1. 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).
- 1. 497-506. Should be rewritten according to the general comment on TL above.
- 1. 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.

## 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).

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