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Antagonistic effects of long- and short-term environmental variation on species coexistence

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1st revised submission:	30 June 2021
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Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2020-2643.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Reject – article is scientifically unsound

Scientific importance: Is the manuscript an original and important contribution to its field?
Acceptable

General interest: Is the paper of sufficient general interest?
Marginal

Quality of the paper: Is the overall quality of the paper suitable?
Marginal

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
Yes

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
Yes

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Is it accessible?
Yes

Is it clear?
No

Is it adequate?
No

Do you have any ethical concerns with this paper?
No

Comments to the Author
The authors present an interesting analysis of the expected outcome of a two species competitive interaction under different thermal regimes. Two-species approaches are useful initially to explore an idea, but are perhaps best considered unusual. Many assemblages are characterised by multiple species in a given setting with interactions between all of them. An example are the transitive hierarchies found in ant assemblages, but other come to mind too. Thus, the case made here is for a situation that perhaps best reflects only certain circumstances (and especially some of this originally envisioned by experimentalists such as Park and ecologists such as MacArthur.

The authors could spend some time making the argument clearer. For example, I could not follow the second sentence of the introduction. No comparison exists though two are expected given the 'Although' and the 'greater'. Such an early difficulty compromises ease of following an argument that must be clearly laid out from the start.

I wondered too whether the authors had actually made good sense of the arguments by Chesson and others of how even variable environments could be considered stationary, and that nonstationarity can be overcome by consideration of an asymptotic environmentally determined trajectory. I am not a specialist in this field, but it seems to me that the arguments are not made sufficiently clear to distinguish how the current approach actually adds to work done by Chesson and others.

In this regard, I missed too consideration of the fact that the effect of environmental thermal variation is not independent of the generation time of the species in question because that determines the extent to which the variation occurs either within or among generations, which in turn affects niche breadth, or at least niche breadth in terms of thermal performance curves which is, of course, thermal performance breadth.

Moreover, while the application for thermal performance curves seems a reasonable assumption, these curves are quite unlike other survival curves. Thus, these curves tend to be very different for traits related to variation in precipitation which show a much more characteristic S-shape, than the asymmetric curve characteristic of thermal performance.

In the explanations for the short- and long-term variation I found little consideration either of the changes that may occur to thermal performance curves over relatively short time scales or the fact that the authors have to consider ectotherms only and then assume that the temperatures equate to body temperature. The main reference they cite (Dillon et al. 2016 Integr. Comp. Biol.) makes all of this clear, yet the authors do not specify how they have treated these matters or whether they simply overlooked them. What was also not clear to me is whether the authors maintained the autocorrelation structure of the data with the short-term variation and long-term variation or whether they changed it to a greater extent in one versus the other. It would seem to me that the autocorrelation structure of the original time-series was maintained for the short-term variation increase, but not for the long-term. It's not clear how this is likely to influence the outcomes independently of the actual variation in the time series. In other words, the authors are not very clear about what they mean by increased variation versus increased stochasticity.

In considering the two model species, it appears that the performance breadths differ between the two species and no detail is given on the Topt. Thus, it's not clear to what extent the differences are simply a consequence of differences in these specific parameters of the models. Likewise, no information is given on whether K, r and d differed between species. One has to assume it's identical, but this seems unrealistic.

In the results I could not fathom the statement 'the proportion of species coexisting'. With two species either there is coexistence or there is not. Thus, the first paragraph was not at all clear to me. I also found the statements about continuous and discrete short-term and long-term variation poorly explained. This causes some difficulty in making a clear assessment of the outcomes. The pdf version I saw had no Figure 3, so I was not able to assess that outcome fully. In Figure 4, it seemed to me that a broader set of conditions would have revealed the fuller suite of outcomes and I wondered why the authors selected the various parameter values they did. This is never explained in the ms.

As a consequence of these initial difficulties, evaluating the generality of the outcomes is problematic. As matters stand I wondered what the effect of generation time and spatial dynamics would be. Mike Angilletta has shown how important spatial dynamics are for competitive outcomes influence by temperature and I saw little of that considered here.

Review form: Reviewer 2

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Marginal

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
Yes

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Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
See attached file for comments to the author. (See Appendix A)

Decision letter (RSPB-2020-2643.R0)

18-Dec-2020

Dear Dr Shen:

I am writing to inform you that your manuscript RSPB-2020-2643 entitled "Antagonistic effects of long- and short-term environmental variation on species coexistence" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A ‘response to referees’ document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
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Sincerely,
Dr Sasha Dall
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
Two thorough and helpful reviews have been received. One comments on considerable lack of clarity and explanation in the submitted ms, leading to them being unable to follow important elements of the arguments being put forward. The other reviewer has provided detailed comments in a separate file, in which they also raise a number of important areas for clarification, and specifically from a modelling perspective provide a series of direct questions, and some theoretical information which, if they can be responded to and clarified in the ms, could lead to an ms that does contain novel value and advance the field. On that basis I feel that rejection allowing resubmission is appropriate.

Reviewer(s)' Comments to Author:
Referee: 1
Comments to the Author(s)
The authors present an interesting analysis of the expected outcome of a two species competitive interaction under different thermal regimes. Two-species approaches are useful initially to explore an idea, but are perhaps best considered unusual. Many assemblages are characterised by multiple species in a given setting with interactions between all of them. An example are the transitive hierarchies found in ant assemblages, but other come to mind too. Thus, the case made here is for a situation that perhaps best reflects only certain circumstances (and especially some of this originally envisioned by experimentalists such as Park and ecologists such as MacArthur.

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Referee: 2
Comments to the Author(s)
See attached file for comments to the author.

Author's Response to Decision Letter for (RSPB-2020-2643.R0)

See Appendix B.

RSPB-2021-1491.R0

Review form: Reviewer 1

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Acceptable

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

> **Is it accessible?**
> Yes
>
> **Is it clear?**
> Yes
>
> **Is it adequate?**
> Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
See attached document for comments to the authors. (See Appendix C)

Decision letter (RSPB-2021-1491.R0)

02-Aug-2021

Dear Dr Shen:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

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In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

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Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Dr Sasha Dall
mailto: proceedingsb@royalsociety.org

Associate Editor Board Member
Comments to Author:
Thank you for your revisions. The paper has been re-examined by one of the original reviewers, who is complementary about the improvements made in the revision. However, they also raise a number of areas for further clarification, and I agree with the points and recommendations made. Please note that PRSB does not permit multiple rounds of revision, so please address these comments carefully.

Author's Response to Decision Letter for (RSPB-2021-1491.R0)

See Appendix D.

Decision letter (RSPB-2021-1491.R1)

13-Aug-2021

Dear Dr Shen

I am pleased to inform you that your manuscript entitled "Antagonistic effects of long- and short-term environmental variation on species coexistence" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

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All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Dr Sasha Dall
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor:
Board Member
Comments to Author:
Thank you for the clear and detailed responses to all of the reviewer's questions and suggestions

Appendix A

Comments to the authors

The authors investigate the effects of environmental fluctuations on different time scales on coexistence of two species in a Lotka-Volterra model. Special reference is made to nonstationary environmental change (e.g., climate change) and potential effects of this variation on species coexistence. The authors model differences in short- and long-term variation using a hierarchical model of the environment where the average of the distribution of temperature is also a random variable that changes on some time-scale. The authors conclude through simulations that short-term environmental fluctuations generally promote species coexistence and long-term fluctuations generally erode coexistence. They suggest that these results could be used to explain the varied effects of environmental fluctuations hypothesized in the literature, including references to Hutchinson's and May's thoughts, as well as the intermediate disturbance hypothesis.

I think these issues are very interesting to disentangle. There are a great many complexities in the study of environmental variability. As the authors can probably attest, one of the issues is that environmental variability can come in many forms (and be modeled in many ways), each of which may not have equivalent effects on some ecological outcome, such as species coexistence. The investigation of short- and long-term variation is a very interesting one. However, I could not understand how the model permits results that depend on the timescale of variation per se. Some of the modeling is not exactly clear, and needs to be clarified to better interpret and understand the results. I give an analytical treatment of the model to make clear the origin of my skepticism toward the disparate effects of timescales of variation. This is the major issue to be resolved.

There were some other conceptual and technical issues that I found concerning. The discussion of model types and the effects of environmental fluctuations in the introduction was not clear and seemed to include some errors. This was probably made confusing by the fact that terms like nonequilibrium were not defined, which is often used in disparate ways in the literature. I provide more detailed comments on the use of these terms in the introduction.

Major Issues:

1) Issue concerning the results

I'm not convinced that the effects presented in the figures are due to the time scales of variation *per se*, rather than the magnitude of variation. This skepticism is motivated by two points, which I expand on in detail below. The detail is for no other reason than that I feel I owe you, the authors, sufficient justification for my hesitancy in accepting the results. In this way, any errors I have made in my argument are clear to you and so can be adequately scrutinized.

The first argument is that an analytical treatment of the model reveals that temperature can only have effects on species interactions through changes in the average performance of species, $E[w]$, which should not depend on timescales of variation (asymptotically). The second is the fact that changes in variation at any particular timescale is confounded with changes in the total variation in the environment. I'll take each in turn.

A robust way to analyze coexistence in fluctuating environments is by invasion analysis. Invasion analysis in similar models reveals that any fluctuation-dependent mechanisms must act through nonlinear effects of competition or interactions between competition and the environment. (This argument is made by Peter Chesson and others, justified on the use of invasion analysis to define stochastic persistence, see Schreiber et al [2011] and citing articles.). Here, as in all Lotka-Volterra models, competition is linear and so we can ignore the effect of nonlinear competition. That leaves just interactions between competition (here species densities weighted by competition coefficients) and environmental effects (here $w(T)$). While it appears at first that such covariation is possible, it doesn't occur. Multiplying w through eqn (1) shows that species densities act independently of w in a species' per-capita growth rate ($N_i^{-1}dN_i/dt$). Hence, their effects do not interact and so there are no fluctuation-dependent effects in the model. (One example of this approach in a Lotka-Volterra model with discussion of the effects of variation at different scales that is relevant to the paper here is Li and Chesson [2016].)

Therefore, fluctuations can only affect species average performance, regardless of their densities. Based on eqns (3a) and (3b), this hierarchical model of T suggests that temperature is normally distributed with E[T] unaffected by the variances, and Var(T) = $\sigma^2_{short} + \sigma^2_{long}$. Hence, the total variance is sufficient to describe any changes in the distribution of T and therefore the distribution and means of w. All that is to say that I see no place where the timescale of variation per se is playing a role (there is a role for other moments of the normal distribution, but I don't understand how these other moments are affected by the time scales either). You can find the full invasion analysis of the model, which shows the mathematically the arguments I've given here, below in a section "Invasion Analysis."

Coexistence in the analysis I present is defined by mutual invasibility, which implies stochastic persistence. A question I have is, how did the authors determine persistence and coexistence in the model? I don't see it explained anywhere in the text. Only Figure 2 refers to "species coexistence occurs if both species sustain through 20,000 short-term variation…." The word "sustain" is doing a lot of work in this context, but it's not clear at all what it means. An explanation here might help resolve the issue.

I also wonder whether the time scales of variation are not equally well represented in the simulations. In other words, perhaps the effects in the figures are transient with respect to long time scales. To have equivalent coverage of the long-term variation as the short-term variation, one would need approximately δ times (=70x) more time steps. The authors state that they use 4million time steps. I wonder if even this number is sufficient given the extremely large variation in temperature investigated in these figures. For example, in figure 2c, any region at the top has Var(T) on the order of 100s with mean on the order of 10s, meaning the CV of at least 10. This is quite large variation to simulate. One way to check this is to see that the E[T] converges well under these parameters under such large variation.

But this brings up another issue. For each of the replicate runs and for each value of σ_{short}, σ_{long}, and T_{mean}, did the authors sample the environmental process independently? I don't mean independently over time, but rather independently across simulation runs. If the authors set a fixed random seed in their code, then they are not, and these effects are possibly transient. An explanation to clear this up would be helpful.

The other issue I have related to this analysis is that, as short-term and long-term variation are changed, they are changed, but so too is the variance in temperature because $\mathrm{Var}(T) = \sigma^2_{\mathrm{short}} + \sigma^2_{\mathrm{long}}$ [see Mean and Variance of Temperature section below]. Hence, these two effects are potentially confounded in the simulations. Increasing variances generally will make the species more equal on average in their performance, given the shapes of their performance curves.

An alternative that breaks this positive association is to keep $\mathrm{Var}(T) = \sigma^2_T$ fixed and changing the relative proportion of variation that is short and long term. One could simply write $\sigma^2_{short} = p\sigma^2_T$ and $\sigma^2_{\mathrm{long}} = (1-p)\sigma^2_T$, where p is the proportion of total temperature variation that is short-term. Varying p is probably a better way to look at timescales per se because the total variance also has lots of effects.

Finally, there is the potential that some of the areas where species don't coexist is due in part to the fact that one (or both) of the species are not viable given current parameters. If the species are going extinct, but not because of competitive interactions, that can greatly color the perspective on species coexistence. It would be valuable to know if certain environmental changes are unsuitable for the species to persist. But such an outcome should be differentiated from exclusion based on the presence of another species. In practical terms, this means outlining regions of parameter space, say in figures 2 and 5 (note figure 3 is missing), where species don't coexist because one of the species is not viable in that environment.

An alternative is to increase the value of r (alternatively decrease d) such that the viability condition is satisfied at the lowest possible performance value, w_{base}. Viability requires that $r\bar{w} - d(1 - \bar{w}) > 0$ for the time-average w. Since $\bar{w} \geq w_{\mathrm{base}}$, a sufficient condition for viability is that $w_{\mathrm{base}} > d/(r + d)$. With values $d = 0.01$ and $r = 0.5$, this means that the w_{base} needs to be larger than ≈ 0.02. But w_{base} is a full order of magnitude smaller than this value. I expect, especially for some combinations of means and variances, that some of the population simply cannot persist in these conditions.

I do think the results are interesting. But, at present, I have no way to explain them, and so I am suspicious. The article is a bit thin on this point. Addressing the points above could go a long way. The results would be quite interesting, if true. It's certainly possible, for example, that these results represent "transient" effects. Pointing that out in this case would be extremely valuable, considering that "transient" in the present context mean times much longer than expected periods of earth's history with relatively constant climate. Such transient effects would be valuable to know about. However, they would need to be discussed as such.

Mean and Variance of Temperature

$$E[T] = E[E[T|T_{\mathrm{smean}}]] = \int E[T|T_{\mathrm{smean}}]f_{Tsmean}\, dT_{smean} = \int T_{\mathrm{smean}}f_{Tsmean}\, dT_{smean} = E[T_{\mathrm{smean}}] = T_{\mathrm{mean}}.$$

$$\mathrm{Var}(T) = E[\mathrm{Var}(T|T_{\mathrm{smean}})] + \mathrm{Var}(E[T|T_{\mathrm{smean}}]) = E[\sigma^2_{short}] + \mathrm{Var}(T_{\mathrm{smean}}) = \sigma^2_{short} + \sigma^2_{long}$$

Invasion Analysis

Two species coexist in the sense of stochastic boundedness if both species have positive growth rates as invaders (see Schreiber et al 2011). Species i's growth rate as invader is

$$\lim_{N_i \to 0} \frac{1}{N_i}\frac{dN_i}{dt} = r_i\left(w_i(T) - \frac{aN_j}{K_i} \right) - d_i\left(1 - w_i(T)\right). \qquad (1)$$

It’s long-term invader growth rate is

$$E\left[\lim_{N_i \to 0} \frac{1}{N_i}\frac{dN_i}{dt} \right] = r_i\left(E\left[w_i(T)\right] - \frac{aE\left[N_j\right]}{K_i} \right) - d_i\left(1 - E\left[w_i(T)\right]\right). \qquad (2)$$

For a viable resident species (i.e., when growing alone), it’s growth rate satisfies

$$E\left[\frac{1}{N_j}\frac{dN_j}{dt}\bigg|_{N_i=0} \right] = r_j\left(E\left[w_j(T)\right] - \frac{E\left[N_j\right]}{K_j} \right) - d_j\left(1 - E\left[w_j(T)\right]\right) = 0, \qquad (3)$$

because intraspecific competition limits indefinite positive growth and viability precludes indefinite negative growth.

Equation (3) implies that

$$\frac{E\left[N_j\right]}{K} = E[w_j] - \frac{d_j}{r_j}\left(1 - E[w_j]\right). \qquad (4)$$

To simplify things, we can call the RHS $\kappa_j = E[w_j] – d_j(1–E[w_j])/r_j$, which represents how well a species grows in the absence of any density-dependence. In the parlance of Chesson, κ_j is species *j’s* average fitness.

Plugging (4) into (2) yields

$$\begin{aligned} r_i\left(\bar{w}_i - a\frac{\bar{N}_j}{K} \right) - d_i\left(1 - \bar{w}_i\right) &= r_i\left(\bar{w}_i - ak_j\right) - d_i\left(1 - \bar{w}_i\right) \\ &= r_i\left[\bar{w}_i - \frac{d_i}{r_i}(1 - \bar{w}_i) - ak_j \right]. \qquad (5) \\ &= r_i\left(k_i - ak_j\right) \end{aligned}$$

This invader growth rate only depends on the average performance of each species. The invader growth rate for species *i* is positive when $\kappa_i > \alpha\kappa_j$. Doing the same for species *j* as the invader means that species *j* can invade when $\kappa_j > \alpha\kappa_i$. Hence, both species can invade, and therefore stably coexist, when

$$\frac{1}{a} > \frac{k_i}{k_j} > a\,.$$

The outer bounds here are quite large when $\alpha \ll 1$ and are equal when $\alpha = 1$. (In fact, α plays the exact same role as niche overlap (ρ) in Chesson and Kuang (2008), which is also a Lotka-Volterra model.) Here, the *α*’s don’t depend on the environment; only the *κ’s* depend on temperature, which here are species average fitness (sensu Chesson). While environmental fluctuations have some effect in this context, they can only change relative fitness of each species, but not generate coexistence on their own. The fluctuations are almost immaterial if $\alpha \ll$

1 (and so almost any two viable species coexist) and when $\alpha = 1$, in which can no two viable species can coexist in any environment.

2) Conceptual issues brought up in the introduction
Definition of stationarity, equilibrium, and the effects of environmental fluctuations are not clear. Making matters worse is that the model does not deal with issues brought up in the introduction. The introduction stresses nonequilibrium situations in reference to nonstationary environmental change. However, the model is stationary in the long-term. The environment (temperature) is normally distributed, and so is fully characterized by the mean and variance. It can be shown that the mean and variance are constants and do not depend on time. I'd remove any discussion of nonstationary environments in the discussion, since you do not deal with it here. You might move the text to the discussion, since climate change is a nonstationary environmental process, yet models rarely include nonstationary fluctuations.

One way to characterize the effects of environmental fluctuations (in the realm of stationary environments) as having two general effects. The first are average environmental effects, which change the average performance of species. The analysis above suggests these are the environmental effects that are present in the model. The environment can only be equalizing (or unequalizing) (sensu Chesson). The other effects are those of the fluctuations themselves, which fall into the category of fluctuation-dependent mechanisms. These can be stabilizing or destabilizing. Many simple models can isolate one effect (say stabilizing) without affecting the other. However, any complex model will likely have both. One way to have both in your model is to remove w_i in the denominators of the competition terms in eqn (1). That way, there can be an interaction between the fluctuations and species densities (i.e., competition). While there is no direct dependence of $N(t)$ on $w(t)$ (only dN/dt on $w(t)$), an association can emerge with autocorrelated responses (see Roy et al (2008) and Schreiber (2020)).

Line 72: I'd suggest distinguishing an equilibrium from a stationary distribution of population fluctuations. For most readers of Proc B, I suspect that the term equilibrium brings about the concept of an equilibrium **point**. As I understand it, this is not what you are referring to here, but instead a stationary distribution of population fluctuations, which is a stochastic analogue to the equilibrium point. To clarify this difference, another term should be used here.

It is unclear what is meant by nonequilibrium systems. Equilibrium in the ecological literature often refers to an equilibrium point. Do the authors mean nonequilibrium in the sense that the populations do not settle down to a single value or do they mean that the population never settles down to any sort of equilibrium?

Line 75-77: I do not agree on this point. This statement implies the absence of fluctuation-dependent mechanisms, which by definition are those that promote coexistence only in the presence of fluctuations. Fluctuation-dependent mechanisms act in addition to any effects of mean environmental conditions. Simply substituting the mean into the dynamical equations does not yield the same effects.

Line 109-112: The first point—that stable coexistence is unlikely in fluctuation environments—seems theoretically untrue to me. Certainly, species can coexist indefinitely in many models in fluctuating environments. Chesson (1994) evaluates a large class of models for which this is true. There are cases where the fluctuations are responsible for coexistence but also cases where species coexist in spite of environmental fluctuations. Turelli and Gillespie (1980) [pg 177, section “Two-species competition” therein] gives a specific example with a Lotka-Volterra model with stochastic variation and Kremer and Klausmeier (2013) review similar concepts with deterministic variation (seasonal in their case). The point must be referring to something other than this large body of theoretical literature, correct? Please clarify.

Line 115-116: “which supplements previous models focusing on stable coexistence at equilibrium states [16] or fixed population sizes [36].” Reference [16] is Chesson (1994) and reference [34] is Ellner et al (2016). Surely these are mismarked. The models investigated in Chesson (1994) are nonequilibrium, in the authors terminology, and the models used in Ellner et al (2016) do not have fixed population size (the lottery model used therein has fixed community size, but not population size).

Minor comments/questions

There is no description of δ. I’ve inferred that it is the number of time-increments before the T_{smean} is resampled in the simulations. This should be stated in the methods section.

Line 198: Nonequilibrium coexistence is not the same as unstable. Unstable coexistence refers to an equilibrium (be it a point or a distribution of population fluctuations) for which the dynamics do not return when perturbed.

Eqn (2): Something is off with the quadratic tail of this function. As written, $w < 0$ for $T > T_{\text{max}}$. Perhaps the authors intended for this condition to apply to $T_{\text{opt},i} \leq T \leq T_{\text{max},i}$ and $w_i(T) = w_{\text{base}}$ for $T > T_{\text{max}}$. It’s fine to have $w < 0$, although based on Figure 1, this does not appear to be the intention. Also, for the degree of variation used in the simulations, this almost certainly leads to inviable populations for the vast majority of the parameter space investigated.

Lines 184-186: It’s unclear what is meant by continuous and discrete in this context. Can you clarify? Usually, continuous and discrete are used in reference to the time-dependence of the variation, with discrete reserved for a stochastic process with sampling at discrete time units. Continuous generally refers to stochasticity in the form of Brownian motion.

Figure 3 is missing. It’s referenced in the text, but I cannot find it.

In the population dynamics section, can you provide a brief biological description of the two species in terms of their temperature responses? For example,

> “these are two ectotherms with differing thermal preferences. Species 1 is a relative specialist on warm temperatures and species 2 is a relative specialist on cool temperatures (Topt,1 > Topt,2). While broadly similar in the shapes of their performance curves, we assume that species 1 performs well in a broader range of environments that species 2 ($\sigma_1 > \sigma_2$). Therefore, we expect from these curves that species 1 should generally perform

better in fluctuating environments than species 2 (although this would change if the mean temperature were cooler)."

Some statements that guide the reader about the kinds of species we are considering would be helpful. You could even define their thermal overlap if you felt so inclined.

Technical comment: This model is an ode and therefore the environmental stochastic process should be consistent with the continuous-time framework (e.g., Ornstein–Uhlenbeck process). To discuss the model that way, the environmental process would have to be defined in terms of the distribution of independent temperature increments (rather than temperature values), with all the associated technicalities of a continuous-time stochastic process. That said, simulating the process effectively puts the model back in discrete time for both the dynamics and the environmental process. Readers of Proc B probably have no interest in these technicalities. However, an appendix or supplement that adequately describes how the environment is modeled and the dynamics are simulated is necessary. As is, readers are left in the dark about how to perform the simulations.

Chesson, P. 1994. Multispecies Competition in Variable Environments. Theoretical Population Biology **45**:227-276.

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Kremer, C. T., and C. A. Klausmeier. 2013. Coexistence in a variable environment: eco-evolutionary perspectives. J Theor Biol **339**:14-25.

Li, L., and P. Chesson. 2016. The Effects of Dynamical Rates on Species Coexistence in a Variable Environment: The Paradox of the Plankton Revisited. Am Nat **188**:E46-58.

Roy, M., R. D. Holt, and M. Barfield. 2005. Temporal autocorrelation can enhance the persistence and abundance of metapopulations comprised of coupled sinks. Am Nat **166**:246-261.

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Schreiber, S. J., M. Benaim, and K. A. Atchade. 2011. Persistence in fluctuating environments. Journal of Mathematical Biology **62**:655-683.

Turelli, M., and J. H. Gillespie. 1980. Conditions for the Existence of Stationary Densities for Some Two-Dimensional Diffusion-Processes with Applications in Population Biology. Theoretical Population Biology **17**:167-189.

Appendix B

Editors' and reviewers' comment 1:

Dear Dr Shen:

I am writing to inform you that your manuscript RSPB-2020-2643 entitled "Antagonistic effects of long- and short-term environmental variation on species coexistence" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.
4) Data - please see our policies on data sharing to ensure that you are complying (https://royalsociety.org/journals/authors/author-guidelines/#data).

To upload a resubmitted manuscript, log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Sincerely,

Dr Sasha Dall
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
Two thorough and helpful reviews have been received. One comments on considerable lack of clarity and explanation in the submitted ms, leading to them being unable to follow important elements of the arguments being put forward. The other reviewer has provided detailed comments in a separate file, in which they also raise a number of important areas for clarification, and specifically from a modelling perspective provide a series of direct questions, and some theoretical information which, if they can be responded to and clarified in the ms, could lead to an ms that does contain novel value and advance the field. On that basis I feel that rejection allowing resubmission is appropriate.

Author response 1:
Thanks to the editor for giving us the opportunity to revise the manuscript. We have rewritten much of the introduction with input from the reviewers (especially reviewer 2), as well as reanalyzed the simulation results and provided an analytical model. As you can see, the main conclusions of the paper remain the same, but we now have a clearer understanding of the mechanisms that led to these results.

Editor and referee comment 2:
Reviewer(s)' Comments to Author:
Referee: 1
Comments to the Author(s)
The authors present an interesting analysis of the expected outcome of a two species competitive interaction under different thermal regimes. Two-species approaches are useful initially to explore an idea, but are perhaps best considered unusual. Many assemblages are characterised by multiple species in a given setting with interactions between all of them. An example are the transitive hierarchies found in ant assemblages, but other come to mind too. Thus, the case made here is for a situation that perhaps best reflects only certain circumstances (and especially some of this originally envisioned by experimentalists such as Park and ecologists such as

MacArthur.

The authors could spend some time making the argument clearer. For example, I could not follow the second sentence of the introduction. No comparison exists though two are expected given the ‘Although’ and the ‘greater’. Such an early difficulty compromises ease of following an argument that must be clearly laid out from the start.

I wondered too whether the authors had actually made good sense of the arguments by Chesson and others of how even variable environments could be considered stationary, and that nonstationarity can be overcome by consideration of an asymptotic environmentally determined trajectory. I am not a specialist in this field, but it seems to me that the arguments are not made sufficiently clear to distinguish how the current approach actually adds to work done by Chesson and others.

Author response 2:

Thanks to the reviewer's comments, we have rewritten the introduction to address these issues.

Editors’ and reviewers’ comment 3:

In this regard, I missed too consideration of the fact that the effect of environmental thermal variation is not independent of the generation time of the species in question because that determines the extent to which the variation occurs either within or among generations, which in turn affects niche breadth, or at least niche breadth in terms of thermal performance curves which is, of course, thermal performance breadth.

Author response 3:

We have now added the effect of generation time on population fluctuations in the methods section. The results show that population size changes in species with long generations are relatively insensitive to environmental fluctuations. However, the effect of generation time on species coexistence needs further study and we think it may be more appropriate to explore it in detail in a separate paper.

In addition, our model does not consider the effects of evolution. We have considered the effect of the time scale of environmental fluctuation on the evolution of the thermal performance curve in other papers (Chan *et al.* 2016; Liu *et al.* 2019). However, since models of species coexistence usually do not consider the effect of evolution, we do not consider this factor here either. Thanks to the reviewer's suggestion, we will try these eco-evolutionary dynamics in a future paper.

Editors' and reviewers' comment 4:

Moreover, while the application for thermal performance curves seems a reasonable assumption, these curves are quite unlike other survival curves. Thus, these curves tend to be very different for traits related to variation in precipitation which show a much more characteristic S-shape, than the asymmetric curve characteristic of thermal performance.

Author response 4:

We have added this point in the introduction, as follows (Line 137-139):
"*Although we focus on temperature, our approach can be applied to other climatic measures like precipitation (a different performance curve is needed to represent it).*"

Editors' and reviewers' comment 5:

In the explanations for the short- and long-term variation I found little consideration either of the changes that may occur to thermal performance curves over relatively short time scales or the fact that the authors have to consider ectotherms only and then assume that the temperatures equate to body temperature. The main reference they cite (Dillon et al. 2016 Integr. Comp. Biol.) makes all of this clear, yet the authors do not specify how they have treated these matters or whether they simply overlooked them.

Author response 5:

Integrating the comments of reviewer 1 and 2, we now provide a clearer description of the thermal performance curves applied to our model in the method section, as follows (Line 170-184):

"*Species 1 is a relative specialist on warm temperatures and species 2 is a relative specialist on cool temperatures ($T_{opt,1} > T_{opt,2}$). While broadly similar in the shapes of their performance curves, we assume that species 1 performs well in a broader range of environments that species 2 ($\sigma_1 > \sigma_2$). From a biological point of view, our model can be applied to a variety of species for which thermal performance can be measured; the performance component can be the survival of the species, reproduction or other fitness components. Although in the literature the thermal performance curve was earlier applied to the performance of ectotherms at different body temperatures (Huey & Stevenson 2015; Sinclair et al. 2016), the concept of* *thermal performance curve has been extended to the performance of different fitness components of organisms at different environmental or body temperatures (Deutsch et al. 2008; Tsai et al. 2020; Levesque & Marshall 2021). As a result, our model can be applied to both endotherms and ectotherms. For simplicity, we do not consider the possibility that the thermal performance curve may change over a relatively short time frame (Dillon et al., 2016). Instead, we assume that the thermal performance curve of a species is fixed.*"

Editors' and reviewers' comment 6:

What was also not clear to me is whether the authors maintained the autocorrelation structure of the data with the short-term variation and long-term variation or whether they changed it to a greater extent in one versus the other. It would seem to me that the autocorrelation structure of the original time-series was maintained for the short-term variation increase, but not for the long-term. It's not clear how this is likely to influence the outcomes independently of the actual variation in the time series. In other words, the authors are not very clear about what they mean by increased variation versus increased stochasticity.

Author response 6:

We have now modified Figure 1, which shows the autocorrelation structure under relatively stable environments, larger short-term variation, and larger long-term variation (Figure 1a, d, g; respectively). We find that increasing short-term variation removes autocorrelation, while increasing long-term variation enhances the positive autocorrelation of the temperature time series. We expect this analysis, together with the window averaging analysis and the original analysis (Figure S1), to better describe stochastic temperature fluctuations.

Editors' and reviewers' comment 7:

In considering the two model species, it appears that the performance breadths differ between the two species and no detail is given on the Topt. Thus, it's not clear to what extent the differences are simply a consequence of differences in these specific parameters of the models. Likewise, no information is given on whether K, r and d differed between species. One has to assume it's identical, but this seems unrealistic.

Author response 7:

Thanks for the suggestion, we have now listed all the parameters in Table 1.

Editors' and reviewers' comment 8:

In the results I could not fathom the statement ‘the proportion of species coexisting’. With two species either there is coexistence or there is not. Thus, the first paragraph was not at all clear to me. I also found the statements about continuous and discrete short-term and long-term variation poorly explained. This causes some difficulty in making a clear assessment of the outcomes. The pdf version I saw had no Figure 3, so I was not able to assess that outcome fully. In Figure 4, it seemed to me that a broader set of conditions would have revealed the fuller suite of outcomes and I wondered why the authors selected the various parameter values they did. This is never explained in the ms.

Author response 8:

Because we are discussing the coexistence of species that may randomly go extinct under transient coexistence, the results are presented as the proportion of species that coexist in the repeated simulation runs until the end of the simulation. We also present other results of the simulation (i.e., species 1 outcompetes species 2 and species 2 outcompetes species 1) in this revision, hoping to create a more complete picture of the results.

We understand that our previous results may not have been clear, so we have significantly modified the results section according to the comments of reviewers 1 and 2. We have made the following changes in Figure 2: In Figure 2, we have removed the confusing description of “discrete” time scales, as follows:

“*We first explore how combinations of temperature variation at different time scales and different mean temperatures affect species coexistence under (1) continuous short-term variations with different long-term variation (Fig. 2a-d) and (2) continuous long-term variations with different short-term variations (Fig. 2e-h).*” (L263-L266)

For the results in Figures 4 and 5, we only list the patterns of "environmental variability-species coexistence" that may arise when considering environmental fluctuations at different timescales. In this new analysis, we discuss the mechanisms by which different variation (Fig. 3) and different mean temperatures (Fig. 4) cause changes in species coexistence results. We hope that this change will help readers understand our model more easily.

Editors' and reviewers' comment 9:

As a consequence of these initial difficulties, evaluating the generality of the outcomes is problematic. As matters stand I wondered what the effect of generation time and spatial dynamics would be. Mike Angilletta has shown how important spatial dynamics are for competitive outcomes influence by temperature and I saw little of that considered here.

Author response 9:

We hope that our substantially revised paper has presented our results more clearly. As for the spatial structure, we think it can be easily incorporated into our model framework. However, since we already have a lot of results in the paper, we think it may be more appropriate to leave the spatial part to future papers.

Referee: 2
Comments to the authors

Editors' and reviewers' comment 10:

The authors investigate the effects of environmental fluctuations on different time scales on coexistence of two species in a Lotka-Volterra model. Special reference is made to nonstationary environmental change (e.g., climate change) and potential effects of this variation on species coexistence. The authors model differences in short- and long-term variation using a hierarchical model of the environment where the average of the distribution of temperature is also a random variable that changes on some time-scale. The authors conclude through simulations that short-term environmental fluctuations generally promote species coexistence and long-term fluctuations generally erode coexistence. They suggest that these results could be used to explain the varied effects of environmental fluctuations hypothesized in the literature, including references to Hutchinson's and May's thoughts, as well as the intermediate disturbance hypothesis.

I think these issues are very interesting to disentangle. There are a great many complexities in the study of environmental variability. As the authors can probably attest, one of the issues is that environmental variability can come in many forms (and be modeled in many ways), each of which may not have equivalent effects on some ecological outcome, such as species coexistence. The investigation of short- and long-term variation is a very interesting one. However, I could not understand how the model permits results that depend on the timescale of variation per se. Some of the modeling is not exactly clear, and needs to be clarified to better interpret and understand the results. I give an analytical treatment of the model to make clear the origin of my skepticism toward the disparate effects of timescales of variation. This is the major issue to be resolved.

There were some other conceptual and technical issues that I found concerning. The discussion of model types and the effects of environmental fluctuations in the introduction was not clear and seemed to include some errors. This was probably made confusing by the fact that terms like nonequilibrium were not defined, which is often used in disparate ways in the literature. I provide more detailed comments on the use of these terms in the introduction.

Major Issues:

1) Issue concerning the results I'm not convinced that the effects presented in the figures are due to the time scales of variation per se, rather than the magnitude of variation. This skepticism is motivated by two points, which I expand on in detail below. The detail is for no other reason than that I feel I owe you, the authors, sufficient justification for my hesitancy in accepting the results. In this way, any errors I have made in my argument are clear to you and so can be adequately scrutinized.

The first argument is that an analytical treatment of the model reveals that temperature can only have effects on species interactions through changes in the average performance of species, E[w], which should not depend on timescales of variation (asymptotically). The second is the fact that changes in variation at any particular timescale is confounded with changes in the total variation in the environment. I'll take each in turn.

Author response 10:

Thanks to the reviewer for the very clear and detailed comments. These comments made us rethink the mechanism that caused our simulation results. We found that the environment averages are different for different timescales in a stochastic environment (windowed average). Therefore, the concept of central limit theorem can be used to help explain our results. In addition, we have also collaborated with a physicist to provide analytical models in the electronic supplementary material (ESM) to demonstrate the generality of our results. As mentioned earlier, we have substantially revised the introduction, the results, and some of the discussion. Please see below for details of our response.

Editors’ and reviewers’ comment 11:

A robust way to analyze coexistence in fluctuating environments is by invasion analysis. Invasion analysis in similar models reveals that any fluctuation-dependent mechanisms must act through nonlinear effects of competition or interactions between competition and the environment. (This argument is made by Peter Chesson and others, justified on the use of invasion analysis to define stochastic persistence, see Schreiber et al [2011] and citing articles.). Here, as in all Lotka-Volterra models, competition is linear and so we can ignore the effect of nonlinear competition. That leaves just interactions between competition (here species densities weighted by competition coefficients) and environmental effects (here w(T)). While it appears at first that such covariation is possible, it doesn’t occur. Multiplying w through eqn (1) shows that species densities act independently of w in a species’ per-capita growth rate (Ni–1dNi/dt). Hence, their effects do not interact and so there are no fluctuation-dependent effects in the model. (One example of this approach in a Lotka-Volterra model with discussion of the effects of variation at different scales that is relevant to the paper here is Li and Chesson [2016].)

Therefore, fluctuations can only affect species average performance, regardless of their densities. Based on eqns (3a) and (3b), this hierarchical model of T suggests that temperature is normally distributed with E[T] unaffected by the variances, and Var(T) =$\sigma^2_{\text{short}} + \sigma^2_{\text{long}}$. Hence, the total variance is sufficient to describe any changes in the distribution of T and therefore the distribution and means of w. All that is to say that I see no place where the timescale of variation per se is playing a role (there is a role for other moments of the normal distribution, but I don’t understand how these other moments are affected by the time scales either). You can find the full invasion analysis of the model, which shows the mathematically the arguments I’ve given here, below in a section “Invasion Analysis.”

Author response 11:

Thanks to reviewer's analysis, this discussion makes the question very concrete. The reviewer's analysis shows that temperature can only affect species interactions through changes in the average performance of species E[w], so they believe that E[w(T)] is not affected by the time scale of environmental changes. However, a very delicate question is which time period should be taken to average the species performance? For example, suppose there are 10,000 years of continuous dry seasons and 10,000 years of continuous wet seasons. Compare this with a half-year dry season interspersed with a half-year wet season. From the perspective of indefinite coexistence, a wet season specialist must be able to invade a dry season specialist's population in a continuous 10,000-year dry season in order to meet the definition of indefinite coexistence. (Of course, a wet season specialist can also invade a dry season specialist's population in the dry season of a semi-annual dry season). However, as the reviewer correctly pointed out, our model explores transient coexistence, so our model results show that it is difficult for a wet season specialist to invade a dry season specialist population in a dry season of 10,000 consecutive years, but it is easier to invade a dry season specialist population in a semi-annual dry season.

Mathematically, E[w(T)] is indeed influenced by environmental variation at different timescales. The reason is that in the case of environmental variation at long time scales, the environmental state at a certain period of time will not be the same as the average distribution of environmental states. Therefore, species that happen to experience a series of environments that are less suitable for them have a higher chance of being outcompeted by competitors (the parameter space we explored is the range in which the species would survive in isolation, see response 16). We also performed a simplified version of the analytical model using windowed averaging to show that environmental variation at different timescales does indeed affect the pattern of species coexistence, a result that differs from previous studies of global averaging (ESM section 2-3).

Editors' and reviewers' comment 12:

Coexistence in the analysis I present is defined by mutual invasibility, which implies stochastic persistence. A question I have is, how did the authors determine persistence and coexistence in the model? I don't see it explained anywhere in the text. Only Figure 2 refers to "species coexistence occurs if both species sustain through 20,000 short-term variation...." The word "sustain" is doing a lot of work in this context, but it's not clear at all what it means. An explanation here might help resolve the issue.

Author response 12:

The timescale of coexistence is the key issue for our paper. Thanks to the reviewer for the reminder. Our paper is about the transient coexistence of species at finite time scales. Sd have now rewritten the whole introduction of our paper, and also provide the analytical model, and rearrange the methodological description and results to emphasize the importance of timescale for species coexistence. Also, we make it clear that our results are conceptually different from the discussion of indefinite coexistence in the modern coexistence theory.

Editors' and reviewers' comment 13:

I also wonder whether the time scales of variation are not equally well represented in the simulations. In other words, perhaps the effects in the figures are transient with respect to long time scales. To have equivalent coverage of the long-term variation as the short-term variation, one would need approximately δ times (=70x) more time steps. The authors state that they use 4million time steps. I wonder if even this number is sufficient given the extremely large variation in temperature investigated in these figures. For example, in figure 2c, any region at the top has Var(T) on the order of 100s with mean on the order of 10s, meaning the CV of at least 10. This is quite large variation to simulate. One way to check this is to see that the E[T] converges well under these parameters under such large variation.

Author response 13:

As suggested by the reviewer, we conducted simulations with 4-, 40-, and 400-million-time steps. The results of these simulations with different time steps are qualitatively similar (Fig. S2).

Editors' and reviewers' comment 14:

But this brings up another issue. For each of the replicate runs and for each value of σ_{short}, σ_{long}, and T_{mean}, did the authors sample the environmental process independently? I don't mean independently over time, but rather independently across simulation runs. If the authors set a fixed random seed in their code, then they are not, and these effects are possibly transient. An explanation to clear this up would be helpful.

Author response 14:

Thanks to the reviewer for pointing out this technical problem, our random numbers are generated by pseudorandom number generator, using one of the most widely used generators (Mersenne Twister; https://en.wikipedia.org/wiki/Mersenne _Twister). During initialization, we generated 2^19937-1 random numbers for the simulation, using the time when the execution is performed as the seed (https://www.tutorialspoint.com/c_standard_library/c_function_time.htm). Because the seeds used in each simulation are different, the random numbers are generated independently of each other, even though they are generated through the same algorithm.

Editors' and reviewers' comment 15:

The other issue I have related to this analysis is that, as short-term and long-term variation are changed, they are changed, but so too is the variance in temperature because $Var(T) = \sigma^2_{short} + \sigma^2_{long}$ [see Mean and Variance of Temperature section below]. Hence, these two effects are potentially confounded in the simulations. Increasing variances generally will make the species more equal on average in their performance, given the shapes of their performance curves.

An alternative that breaks this positive association is to keep $Var(T) = \sigma^2_T$ fixed and changing the relative proportion of variation that is short and long term. One could simply write $\sigma^2_{short} = p\sigma^2_T$ and $\sigma^2_{long} = (1–p)\sigma^2_T$, where p is the proportion of total temperature variation that is short-term. Varying p is probably a better way to look at timescales per se because the total variance also has lots of effects.

Author response 15:

We followed the suggestion of the reviewer to simulate $\sigma^2_{short} = p\sigma^2_T$ and $\sigma^2_{long} = (1–p)\sigma^2_T$, and the results are qualitatively similar to the original results: species coexistence does not occur when the long time scale change is the dominant environmental change; species are more likely to coexist when the short time scale change is the dominant environmental change (Fig. S2; $(\sigma_{short}-0.5)^2+(\sigma_{long}-0.5)^2= 400$).

Editors' and reviewers' comment 16:

Finally, there is the potential that some of the areas where species don't coexist is due in part to the fact that one (or both) of the species are not viable given current parameters. If the species are going extinct, but not because of competitive interactions, that can greatly color the perspective on species coexistence. It would be valuable to know if certain environmental changes are unsuitable for the species to persist. But such an outcome should be differentiated from exclusion based on the presence of another species. In practical terms, this means outlining regions of parameter space, say in figures 2 and 5 (note figure 3 is missing), where species don't coexist because one of the species is not viable in that environment.

An alternative is to increase the value of r (alternatively decrease d) such that the viability condition is satisfied at the lowest possible performance value, w_{base}. Viability requires that $r\overline{w} – d(1 – \overline{w}) > 0$ for the time-average w. Since $\overline{w} \geq w_{base}$, a sufficient condition for viability is that $w_{base} > d/(r + d)$. With values d = 0.01 and r = 0.5, this means that the w_{base} needs to be larger than ≈ 0.02. But w_{base} is a full order of magnitude smaller than this value. I expect, especially for some combinations of means and variances, that some of the population simply cannot persist in these conditions.

Author response 16:

We have followed the reviewer's suggestion to draw the parameter space where the inappropriate species can exist independently, showing that our results focus on the response of species competition to species coexistence in a parameter space where species can exist independently(Fig. S3; $(\sigma_{\mathrm{short}}-0.5)^2+(\sigma_{\mathrm{long}}-0.5)^2= 400$).

Editors' and reviewers' comment 17:

I do think the results are interesting. But, at present, I have no way to explain them, and so I am suspicious. The article is a bit thin on this point. Addressing the points above could go a long way. The results would be quite interesting, if true. It's certainly possible, for example, that these results represent "transient" effects. Pointing that out in this case would be extremely valuable, considering that "transient" in the present context mean times much longer than expected periods of earth's history with relatively constant climate. Such transient effects would be valuable to know about. However, they would need to be discussed as such.

Author response 17:

Thank you for pointing this out, as our paper is indeed about transient coexistence, and we have now emphasized this point in various parts of the paper. See also the response 12.

Editors' and reviewers' comment 18:

Mean and Variance of Temperature

$$E[T] = E[E[T|T_{\mathrm{smean}}]] = \int E[T|T_{\mathrm{smean}}]f_{Tsmean}\, dT_{smean} = \int T_{\mathrm{smean}}f_{Tsmean}\, dT_{smean} = E[T_{\mathrm{smean}}] = T_{\mathrm{mean}}.$$

$$\mathrm{Var}(T) = E[\mathrm{Var}(T|T_{\mathrm{smean}})] + \mathrm{Var}(E[T|T_{\mathrm{smean}}]) = E[\sigma^2{}_{short}] + \mathrm{Var}(T_{\mathrm{smean}}) = \sigma^2{}_{short} + \sigma^2{}_{long}$$

Invasion Analysis

Two species coexist in the sense of stochastic boundedness if both species have positive growth rates as invaders (see Schreiber et al 2011). Species i's growth rate as invader is

$$\lim_{N_i \to 0} \frac{1}{N_i}\frac{dN_i}{dt} = r_i\left(w_i(T) - \frac{\alpha N_j}{K_i}\right) - d_i\left(1 - w_i(T)\right). \qquad (1)$$

It's long-term invader growth rate is

$$E\left[\lim_{N_i \to 0} \frac{1}{N_i}\frac{dN_i}{dt}\right] = r_i\left(E[w_i(T)] - \frac{\alpha E[N_j]}{K_i}\right) - d_i\left(1 - E[w_i(T)]\right). \qquad (2)$$

For a viable resident species (i.e., when growing alone), it’s growth rate satisfies

$$E\left[\frac{1}{N_j}\frac{dN_j}{dt}\bigg|_{N_j=0}\right]=r_j\left(E\left[w_j(T)\right]-\frac{E\left[N_j\right]}{K_j}\right)-d_j\left(1-E\left[w_j(T)\right]\right)=0, \tag{3}$$

because intraspecific competition limits indefinite positive growth and viability precludes indefinite negative growth.

Equation (3) implies that

$$\frac{E\left[N_j\right]}{K}=E[w_j]-\frac{d_j}{r_j}\left(1-E[w_j]\right). \tag{4}$$

To simplify things, we can call the RHS κj= E[wj] – dj(1–E[wj])/rj, which represents how well a species grows in the absence of any density-dependence. In the parlance of Chesson, κj is species j’s average fitness.

Plugging (4) into (2) yields

$$\begin{aligned} r_i\left(\overline{w}_i-\alpha\frac{\overline{N}_j}{K}\right)-d_i\left(1-\overline{w}_i\right)&=r_i\left(\overline{w}_i-\alpha\kappa_j\right)-d_i\left(1-\overline{w}_i\right)\\ &=r_i\left[\overline{w}_i-\frac{d_i}{r_i}(1-\overline{w}_i)-\alpha\kappa_j\right].\\ &=r_i\left(\kappa_i-\alpha\kappa_j\right) \end{aligned} \tag{5}$$

This invader growth rate only depends on the average performance of each species. The invader growth rate for species i is positive when κi> ακj. Doing the same for species j as the invader means that species j can invade when κj> ακi. Hence, both species can invade, and therefore stably coexist, when

$$\frac{1}{\alpha}>\frac{\kappa_i}{\kappa_j}>\alpha\ .$$

The outer bounds here are quite large when α ≪ 1 and are equal when α = 1. (In fact, α plays the exact same role as niche overlap (ρ) in Chesson and Kuang (2008), which is also a Lotka-Volterra model.) Here, the α’s don’t depend on the environment; only the κ ’s depend on temperature, which here are species average fitness (sensu Chesson). While environmental fluctuations have some effect in this context, they can only change relative fitness of each species, but not generate coexistence on their own. The fluctuations are almost immaterial if α ≪ 1 (and so almost any two viable species coexist) and when α = 1, in which can no two viable species can coexist in any environment.

Author response 18:

This analysis is very helpful. Hopefully, our modifications and responses have made it clear how the timescale of environmental change affects the environmental average.

Editors' and reviewers' comment 19:

2) Conceptual issues brought up in the introduction

Definition of stationarity, equilibrium, and the effects of environmental fluctuations are not clear. Making matters worse is that the model does not deal with issues brought up in the introduction. The introduction stresses nonequilibrium situations in reference to nonstationary environmental change. However, the model is stationary in the long-term. The environment (temperature) is normally distributed, and so is fully characterized by the mean and variance. It can be shown that the mean and variance are constants and do not depend on time. I'd remove any discussion of nonstationary environments in the discussion, since you do not deal with it here. You might move the text to the discussion, since climate change is a nonstationary environmental process, yet models rarely include nonstationary fluctuations.

Author response 19:

As mentioned in the previous response, following the reviewer's suggestions and questions, we have now almost rewritten our entire introduction, as well as much of results. We have also provided additional analysis to show that our model is indeed non-equilibrium at finite timescales, and that the environmental mean, although sampled from the normal distribution, is not the same for the windowed mean at different timescales. In addition to providing an analytical model to prove this, we also invoke the central limit theorem to explain this result.

Editors' and reviewers' comment 20:

One way to characterize the effects of environmental fluctuations (in the realm of stationary environments) as having two general effects. The first are average environmental effects, which change the average performance of species. The analysis above suggests these are the environmental effects that are present in the model. The environment can only be equalizing (or unequalizing) (sensu Chesson). The other effects are those of the fluctuations themselves, which fall into the category of fluctuation-dependent mechanisms. These can be stabilizing or destabilizing. Many simple models can isolate one effect (say stabilizing) without affecting the other. However, any complex model will likely have both. One way to have both in your model is to remove wi in the denominators of the competition terms in eqn (1). That way, there can be an interaction between the fluctuations and species densities (i.e., competition).

While there is no direct dependence of N(t) on w(t) (only dN/dt on w(t)), an association can emerge with autocorrelated responses (see Roy et al (2008) and Schreiber (2020)).

Author response 20:
We now use a simulation and analysis model to show that the average environmental effect is affected by the timescale of environmental variation (windowed average). Thus, to keep things simple, we do not assume that the interspecific competition coefficient is directly affected by environmental variation; instead, our model describes the state in which the interspecific competitive intensity is affected by population size (Discussion: Line 415-423).

Editors' and reviewers' comment 21:
Line 72: I'd suggest distinguishing an equilibrium from a stationary distribution of population fluctuations. For most readers of Proc B, I suspect that the term equilibrium brings about the concept of an equilibrium point. As I understand it, this is not what you are referring to here, but instead a stationary distribution of population fluctuations, which is a stochastic analogue to the equilibrium point. To clarify this difference, another term should be used here.

It is unclear what is meant by nonequilibrium systems. Equilibrium in the ecological literature often refers to an equilibrium point. Do the authors mean nonequilibrium in the sense that the populations do not settle down to a single value or do they mean that the population never settles down to any sort of equilibrium?

Author response 21:
We have now defined equilibrium more clearly, and we do want to refer to whether the system has converged to an equilibrium point. However, on a finite timescale, our system does not converge to a point of equilibrium.

Editors' and reviewers' comment 22:
Line 75-77: I do not agree on this point. This statement implies the absence of fluctuation-dependent mechanisms, which by definition are those that promote coexistence only in the presence of fluctuations. Fluctuation-dependent mechanisms act in addition to any effects of mean environmental conditions. Simply substituting

the mean into the dynamical equations does not yield the same effects.

Author response 22:

We have rewritten the introduction and removed this sentence.

Editors' and reviewers' comment 23:

Line 109-112: The first point—that stable coexistence is unlikely in fluctuation environments—seems theoretically untrue to me. Certainly, species can coexist indefinitely in many models in fluctuating environments. Chesson (1994) evaluates a large class of models for which this is true. There are cases where the fluctuations are responsible for coexistence but also cases where species coexist in spite of environmental fluctuations. Turelli and Gillespie (1980) [pg 177, section "Two-species competition" therein] gives a specific example with a Lotka-Volterra model with stochastic variation and Kremer and Klausmeier (2013) review similar concepts with deterministic variation (seasonal in their case). The point must be referring to something other than this large body of theoretical literature, correct? Please clarify.

Author response 23:

Originally this text was about empirical evidence, and we cited empirical papers. We have now revised our introduction to make it clear that we are discussing transient coexistence at finite time scales.

Editors' and reviewers' comment 24:

Line 115-116: "which supplements previous models focusing on stable coexistence at equilibrium states [16] or fixed population sizes [36]." Reference [16] is Chesson (1994) and reference [34] is Ellner et al (2016). Surely these are mismarked. The models investigated in Chesson (1994) are nonequilibrium, in the authors terminology, and the models used in Ellner et al (2016) do not have fixed population size (the lottery model used therein has fixed community size, but not population size).

Author response 24:

We have removed the paragraph.

Minor comments/questions

Editors' and reviewers' comment 25:

There is no description of δ. I've inferred that it is the number of time-increments before the Tsmean is resampled in the simulations. This should be stated in the methods section.

Author response 25:

Added as suggested (Line 196-197).

Editors' and reviewers' comment 26:

Line 198: Nonequilibrium coexistence is not the same as unstable. Unstable coexistence refers to an equilibrium (be it a point or a distribution of population fluctuations) for which the dynamics do not return when perturbed.

Author response 26:

We think the reviewer was referring to line 108. We have used transient coexistence to represent it now.

Editors' and reviewers' comment 27:

Eqn (2): Something is off with the quadratic tail of this function. As written, $w < 0$ for $T > T_{max}$. Perhaps the authors intended for this condition to apply to $T_{opt,i} \leq T \leq T_{max,i}$ and $w_i(T) = w_{base}$ for $T > T_{max}$. It's fine to have $w < 0$, although based on Figure 1, this does not appear to be the intention. Also, for the degree of variation used in the simulations, this almost certainly leads to inviable populations for the vast majority of the parameter space investigated.

Author response 27:

Modified as suggested in equation 1.

Editors' and reviewers' comment 28:

Lines 184-186: It's unclear what is meant by continuous and discrete in this context.

Can you clarify? Usually, continuous and discrete are used in reference to the time-dependence of the variation, with discrete reserved for a stochastic process with sampling at discrete time units. Continuous generally refers to stochasticity in the form of Brownian motion.

Author response 28:

Thanks for the reminder. We changed the sentence to " *We first explore how combinations of temperature variation at different time scales and different mean temperatures affect species coexistence under (1) continuous short-term variations* *with different long-term variation (Fig. 2a-d) and (2) continuous long-term variations with different short-term variations (Fig. 2e-h).* " to avoid confusion (Line 253-256).

Editors' and reviewers' comment 29:

Figure 3 is missing. It's referenced in the text, but I cannot find it.

Author response 29:

Sorry for the inconvenience. We now have redone the analysis and uploaded the new version of the figures.

Editors' and reviewers' comment 30:

In the population dynamics section, can you provide a brief biological description of the two species in terms of their temperature responses? For example,

> "these are two ectotherms with differing thermal preferences. Species 1 is a relative specialist on warm temperatures and species 2 is a relative specialist on cool temperatures (Topt,1 > Topt,2). While broadly similar in the shapes of their performance curves, we assume that species 1 performs well in a broader range of environments that species 2 (σ1 > σ2). Therefore, we expect from these curves that species 1 should generally perform better in fluctuating environments than species 2 (although this would change if the mean temperature were cooler)."

Some statements that guide the reader about the kinds of species we are considering would be helpful. You could even define their thermal overlap if you felt so inclined.

Author response 30:

Added as suggested, as follows (Line 170-184):
"*Species 1 is a relative specialist on warm temperatures and species 2 is a relative specialist on cool temperatures* ($T_{opt,1} > T_{opt,2}$)*. While broadly similar in the shapes of their performance curves, we assume that species 1 performs well in a broader range of environments that species 2* ($\sigma_1 > \sigma_2$)*. From a biological point of view, our model can be applied to a variety of species for which thermal performance can be measured; the performance component can be the survival of the species, reproduction or other fitness components. Although in the literature the thermal performance curve was earlier applied to the performance of ectotherms at different body temperatures (Huey & Stevenson 2015; Sinclair et al. 2016), the concept of thermal performance curve has been extended to the performance of different fitness components of organisms at different environmental or body temperatures (Deutsch et*

al. 2008; Tsai et al. 2020; Levesque & Marshall 2021). As a result, our model can be applied to both endotherms and ectotherms. For simplicity, we do not consider the possibility that the thermal performance curve may change over a relatively short time frame (Dillon et al., 2016). Instead, we assume that the thermal performance curve of a species is fixed."

Editors' and reviewers' comment 31:

Technical comment: This model is an ode and therefore the environmental stochastic process should be consistent with the continuous-time framework (e.g., Ornstein–Uhlenbeck process). To discuss the model that way, the environmental process would have to be defined in terms of the distribution of independent temperature increments (rather than temperature values), with all the associated technicalities of a continuous-time stochastic process. That said, simulating the process effectively puts the model back in discrete time for both the dynamics and the environmental process. Readers of Proc B probably have no interest in these technicalities. However, an appendix or supplement that adequately describes how the environment is modeled and the dynamics are simulated is necessary. As is, readers are left in the dark about how to perform the simulations.

Author response 31:

We now use temporal autocorrection and windowed average analysis to present the characteristics of the environmental fluctuation that we modelled. We also added an analytic model in the ESM to describe how we deal with environmental variability at long- and short-time scales. We hope this is clearer now.

Appendix C

Thanks to the authors for putting a lot of time and effort into clarifying the manuscript. The overall objective and scope of the work is now much clearer, with I think a better treatment in the introduction of some of the conceptual issues related to species coexistence in fluctuating environments. In particular, I think the examples related to timescales of environmental change are quite helpful for readers (including myself!) to grasp the issue at hand. Timescales are a serious issue in nearly all ecological phenomena, with long-time equilibria taking precedent because of their concreteness. But the authors make a good point about some of the issues with taking a long-term equilibrium approach in models of fluctuating environments (the equilibrium here being the average over the distribution of environmental states). I am convinced these ideas are of practical importance. However, I am a bit worried about the treatment of the lessons about short- and long-term variation. In part, this is because of the aforementioned many ways that environmental fluctuations affect competitive outcomes. I also have a few lingering questions about the analysis and some suggestions to improve the clarity of the ideas and concepts.

Do short-term fluctuations always promote coexistence (and long-term fluctuations always promote exclusion)?

This was the dominant question lingering in my mind while reading the discussion. The results show as much for this model, and I would be okay if we stopped there. However, the discussion generally implies that short-term fluctuations always promote coexistence. For example, the second sentence of the discussion reads,

> "environmental variation can either promote or hinder species coexistence depending on the temporal scale of variation. This is because short-term environmental variation generally favors species coexistence, whereas long-term environmental variation promotes exclusion…"

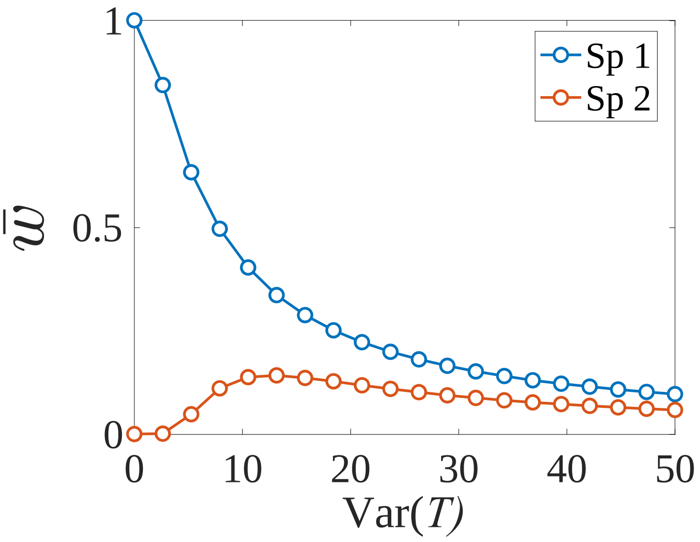
I'm worried about the perspective on environmental fluctuations generally presented in the paper, without any qualifiers. The model is quite specific—competitive effects are linear, the competitive effects are unaffected by the environment, the range of temperature variation averages over a largely concave fitness surface, and the species are identical except for their temperature responses—and so I suspect that the general discussion of short- and long-term variation does not apply. Do you have any other reason to suspect that short-term fluctuations always promote coexistence? If not, I would suggest that you limit the discussion of timescales to the conditions present in your model, and soften your stance on the effects of environmental fluctuations more generally.

What is the true effect of environmental fluctuations in determining competitive outcomes?

Some of the issue with timescales of variation can be cleared up by explaining to the reader the practical effect of environmental fluctuations on competitive outcomes. Here, the paper is most deficient, because the reader has to figure it out for themselves with little help from the manuscript. Environmental variation clearly has an effect. But what we know is that it does not affect the strength of the coexistence mechanism, which is proportional to $1–\alpha$. Indeed, α amounts to niche overlap in this model ($1–\alpha$ is what has been called "stabilizing niche differences," although I prefer nice overlap). Since α is constant across all temperatures, there is no effect of temperature fluctuations on the coexistence mechanism itself.

But there is clearly a role for the environment in determining whether this coexistence mechanism is sufficiently strong. Here is where the model can be valuable. The authors show that the mechanism is more often strong enough to allow coexistence when the environment varies on short time scales than on long time scales. And I think the authors appropriately attribute this to the range of variation that occurs on short time scales. However, environmental fluctuations have a very particular effect in their model, and they may not be shared in many other models. Because of the shapes of the temperature performance curves, the dominant effect of environmental variation is to equalize the average performance of the two species, i.e., to decrease the measure $|\bar{w}_1 - \bar{w}_2|$ (see example in the figure below). Stating as much would help the readers greatly and would increase their confidence in the particular results. In Chesson's terminology, environmental variation has a purely equalizing effect, making $\bar{w}$ more similar between species. And there is a greater likelihood that this happens on short timescales when the variation is dominated by short-term variation.

One could envision alternative models where environmental variation *increases* the differences in species average fitness (i.e., it is unequalizing), in which case short-term environmental fluctuations would not promote coexistence but rather undermine coexistence. This gets at the main point above about the generality of the results about the timescales of variation.



Values of $\bar{w}$ when sampling from 2,000,000 i.i.d. samples from $T \sim N(30, \mathrm{Var}(T))$.

Minor comments

I suggest taking a look at Li and Chesson (2016), which gives an updated perspective on timescales related to Hutchinson's hypothesis. The results here create an interesting contrast with those. Given the similarity in question, a discussion of its relevant results seem warranted.

As in my prior review, I still see no clear discussion of what is meant by coexistence. The main issue is one of transparency and reproducibility. We simply do not know how the authors are characterizing coexistence and so are unable to completely evaluate and reproduce the results. What exactly is the criterion to say that species coexist? In figure 2, it is stated that "species coexistence occurs if both species sustain…." This is a continuous-population density model, and so the populations always sustain, they just get infinitesimally small. Presumably there is some cutoff value in which the population is assumed extinct? Or is the condition not based on the values of *N*, but instead some other measure? Please provide the exact criteria. As with any ODE of this sort, *N* may approach zero but never actually reaches zero, meaning that sustain is an insufficient term in this context.

Issues in the supplement

I don't find the discussion of Ito calculus helpful or particularly relevant. It doesn't seem relevant because the variation occurs in discrete increments, i.e., the process describing *T* has a deterministic time delay before variation occurs. The authors perhaps felt compelled to include such an analysis because of my suggestion that the model was actually a stochastic differential equation. I had suggested as much because the underlying relationship between temperature variation and the ecological dynamics were not clearly discussed in the prior version of the manuscript. It seemed natural to me to assume that temperature varied continuously according to a continuous-time stochastic process. The current version makes clear that the model of temperature variation is continuous in time but with discrete increments in which condition are constant. Stochastic calculus here could be used, but a much simpler, and more commonly used calculus would do.

Given the highly technical nature of the Ito calculus and its lack of clear applicability to the model at hand, I'd suggest deleting all the supplementary material about stochastic calculus and refer the reader to more complete texts on the issue.

Other parts of the supplement are not helpful because they have a high likelihood of misleading the reader. The main culprit is the mean-field approximation to the dynamics, which is a poor approximation for the actual dynamics of species. Only in the case where the variance is negligible compared to the mean can one reasonably assume that $<N_i^2> = <N_i><N_i>$, as the authors have done in the supplement. Given the range of variation in *T* and the variance shown in the figures of the dynamics, these assumptions will not do.

But the question is not so much about the actual dynamics, but the qualitative nature of the dynamics over some time-horizon (do species coexist or not?). The qualitative outcome is predicted well by the mean-field approximation in the following sense. Over some time-period, a species will be bounded away from extinction if it's low density growth rate is positive in the presence of a competitor. The low-density growth rate really only depends on the average of *w*, as the authors use in the latter section of the dynamics. In the authors' notation this low density growth rate is

$$\lim_{N_i \to 0} \left\langle \frac{1}{N_i} \frac{dN_i}{dt} \right\rangle = r_i \left\langle w_i \right\rangle - \frac{a}{K_i} \left\langle N_j \right\rangle - d_i \left(1 - \left\langle w_i \right\rangle \right).$$

A similar expression for a resident shows that $<N_j>$ largely only depends on $<w_j>$ and so $<w_j>$ should be the focus of study.

Line-specific comments:

Throughout the authors use the term "environmental fluctuation." My thought here is that this should be the plural "environmental fluctuations" to represent the idea that you are describing a system beyond a single perturbation and to indicate the large number of qualitatively distinct regimes of conditions that change over time.

Line 65-67: “whereas increased fluctuation prevents species from reaching equilibrium and therefore prevents competing species from excluding others [4-18].” This particular hypothesis is a dubious one and doesn’t hold up to theoretical scrutiny. A paper that tackles this particular form of the intermediate disturbance hypothesis is Chesson and Huntly (1997). They show there that species still exclude others, although it may take longer. But some other mechanism is required to explain the sustained coexistence of species.

Lines 73-75: The definition of fitness differences here is not a real definition, as in a reader without knowledge of the concept could not reasonably be expected to understand it from this sentence. I recognize how difficult it can be to adequately define these terms. I suggest perhaps removing the definition and sticking with sufficient citations for others to look into. The most up-to-date definition of the concept is in Chesson (2018), in which the following quote begins a paragraph on the bottom of pg 1779:

> “The species average fitness, κ, is a summary ability of the species to succeed in the given environment relative to other species in the same guild.”

The paragraph concludes with

> “κ is rarely described as an average tolerance to competition and is not commonly derived that way, but as some approximation to an average tolerance of competition. Nevertheless, this is what it amounts to.”

There is lots of confusion in the literature about these terms. You could set an example by giving an appropriate definition.

Line 78-79: “by equalizing the effects that minimize average fitness differences between species.” As written, this sort of implies there are multiple factors minimizing fitness differences. I think more appropriate wording is “environmental fluctuations potentially promote species coexistence by minimizing average fitness differences (equalizing mechanism) or by creating different temporal niches (stabilizing mechanism).”

Lines 88-97: Clear example to illustrate where the timescales might matter. Thanks for this.

Line 168: You need to specify here that $w_{\text{base}} \geq 0$. Without this stipulation, the model takes a very strange interpretation if $w < 0$, in which the death rate acts like a birth rate.

Lines 212: I get this statement here, but there are other equilibria in the model in the sense that there are points to which the system tends, and returns to when perturbed. For example, in the single-species version of the model, the single-species equilibrium average population density is

$$\bar{N}_i^* = K_i[\bar{w}_i(r_i + d_i) - d_i],$$

where the overbar here means the expectation over the distribution of environmental states. (Once could similarly define shorter term equilibria, where the overbar would indicate an average over some shorter-term scale of variation.) The expression is, by definition, an equilibrium,; it is just not a point equilibrium as ecologists traditionally like to think of equilibria. You could do the readers a service by pointing out this fact, as it is not widely appreciated that there are alternative conceptions of equilibria that are useful to have in mind when studying environmental variability.

Lines 217-219: “remain constant over time” and “chance that the environment remains constant in time” are incorrect characterization. Perhaps “consistency over time” would suit your purposes better. Having a constant value certainly implies consistency, but consistency does not imply constancy.

Lines 257: I find the phrase “proportion of species coexisting” odd. It suggests that this is about a bunch of species, and only some fraction coexist. I suggest changing this to ensure it’s clear that you are running replicate experiments, and this is the fraction of experiments where species coexist.

Lines 276-277: “promotes competitive interactions…” You mean promotes exclusion, correct?

Figure 3: This equation keeps the total variance constant only *approximately.* By the law of total variance, $\mathrm{Var}(T) = \sigma^2_{\mathrm{long}} + \sigma^2_{\mathrm{short}}$ by the law of total variance. The expression given is $(\sigma_{\mathrm{long}} - 0.5)^2 + (\sigma_{\mathrm{short}} - 0.5)^2$ is fixed. One can rewrite this equation as $\mathrm{Var}(T) + 0.5 - (\sigma_{\mathrm{long}} + \sigma_{\mathrm{short}})$. For the parameters given, the difference is marginal. But it is worth pointing out that the variance is not actually constant. Using the extreme values on the y-axis of the figures, we have $\mathrm{Var}(T) = (20.5)^2 + (0.5)^2 = 420.5$ and $\mathrm{Var}(T) = (14.6)^2 + (14.6)^2 = 426.32$. Clearly, these are not the same.

From the supplement

Equations (a3)-(a4): The quadratic form on these equations differs from the main text equations.

References

Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. Am Nat **150**:519-553.

Chesson, P. 2018. Updates on mechanisms of maintenance of species diversity. Journal of Ecology **106**:1773-1794.

Li, L., and P. Chesson. 2016. The Effects of Dynamical Rates on Species Coexistence in a Variable Environment: The Paradox of the Plankton Revisited. Am Nat **188**:E46-58.

Appendix D

Reviewer comment 1:

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This was the dominant question lingering in my mind while reading the discussion. The results show as much for this model, and I would be okay if we stopped there. However, the discussion generally implies that short-term fluctuations always promote coexistence. For example, the second sentence of the discussion reads,

> “Environmental variation can either promote or hinder species coexistence depending on the temporal scale of variation. This is because short-term environmental variation generally favors species coexistence, whereas long-term environmental variation promotes exclusion…”

I’m worried about the perspective on environmental fluctuations generally presented in the paper, without any qualifiers. The model is quite specific—competitive effects are linear, the competitive effects are unaffected by the environment, the range of temperature variation averages over a largely concave fitness surface, and the species are identical except for their temperature responses—and so I suspect that the general discussion of short- and long-term variation does not apply. Do you have any other reason to suspect that short-term fluctuations always promote coexistence? If not, I would suggest that you limit the discussion of timescales to the conditions present in your model, and soften your stance on the effects of environmental fluctuations more generally.

Author response 1:

We have now restricted our discussion of the relationship between temporal scale and species coexistence to only the settings of our model, as suggested by the reviewer (Line 333-338).

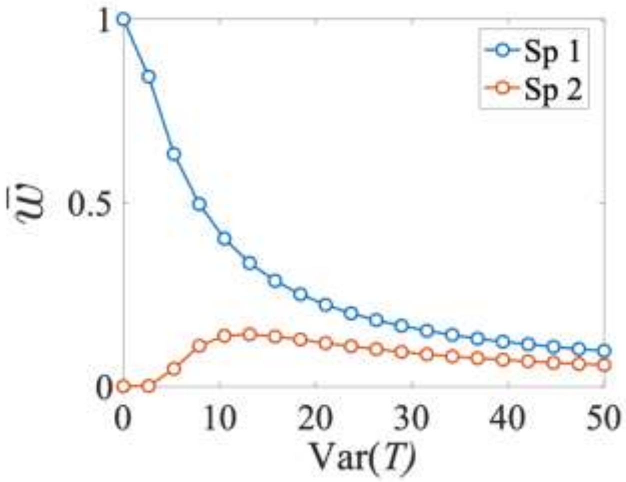
Reviewer comment 2:

What is the true effect of environmental fluctuations in determining competitive outcomes?

Some of the issue with timescales of variation can be cleared up by explaining to the reader the practical effect of environmental fluctuations on competitive outcomes. Here, the paper is most deficient, because the reader has to figure it out for themselves with little help from the manuscript. Environmental variation clearly has an effect. But what we know is that it does not affect the strength of the coexistence mechanism, which is proportional to $1–\alpha$. Indeed, α amounts to niche overlap in this model ($1–\alpha$ is what has been called "stabilizing niche differences," although I prefer nice overlap). Since α is constant across all temperatures, there is no effect of temperature fluctuations on the coexistence mechanism itself.

But there is clearly a role for the environment in determining whether this coexistence mechanism is sufficiently strong. Here is where the model can be valuable. The authors show that the mechanism is more often strong enough to allow coexistence when the environment varies on short time scales than on long time scales. And I think the authors appropriately attribute this to the range of variation that occurs on short time scales. However, environmental fluctuations have a very particular effect in their model, and they may not be shared in many other models. Because of the shapes of the temperature performance curves, the dominant effect of environmental variation is to equalize the average performance of the two species, i.e., to decrease the measure $|\overline{w}_1 - \overline{w}_2|$ (see example in the figure below). Stating as much would help the readers greatly and would increase their confidence in the particular results. In Chesson's terminology, environmental variation has a purely equalizing effect, making $\bar{w}$ more similar between species. And there is a greater likelihood that this happens on short timescales when the variation is dominated by short-term variation.

One could envision alternative models where environmental variation *increases* the differences in species average fitness (i.e., it is unequalizing), in which case short term environmental fluctuations would not promote coexistence but rather undermine coexistence. This gets at the main point above about the generality of the results about the timescales of variation.



Values of $\bar{w}$ when sampling from 2,000,000 i.i.d. samples from $T \sim N(30, \mathrm{Var}(T))$.

<u>Author response 2:</u>

We have now modified the discussion as suggested:

“*In the terminology of modern coexistence theory, we do not assume a stabilizing effect; our transient coexistence is due to environmental changes that equalize the average performance of the two species (i.e., equalizing effect).***”** (Line 420-423)

Reviewer comment 3:

Minor comments

I suggest taking a look at Li and Chesson (2016), which gives an updated perspective on timescales related to Hutchinson’s hypothesis. The results here create an interesting contrast with those. Given the similarity in question, a discussion of its relevant results seem warranted.

Author response 3:

We have now cited and added some discussion of Li and Chesson (2016) in the Discussion as suggested (Line 361-364).

Reviewer comment 4:

As in my prior review, I still see no clear discussion of what is meant by coexistence. The main issue is one of transparency and reproducibility. We simply do not know how the authors are characterizing coexistence and so are unable to completely evaluate and reproduce the results. What exactly is the criterion to say that species coexist? In figure 2, it is stated that "species coexistence occurs if both species sustain…." This is a continuous-population density model, and so the populations always sustain, they just get infinitesimally small. Presumably there is some cutoff value in which the population is assumed extinct? Or is the condition not based on the values of *N*, but instead some other measure? Please provide the exact criteria. As with any ODE of this sort, *N* may approach zero but never actually reaches zero, meaning that sustain is an insufficient term in this context.

Author response 4:

Yes, there is a cutoff value (i.e., $N_{ext} = 0.5$) to prevent the dynamics staying at very small positive values. We have now added a description for the cutoff value in the Methods (Line 159-161), the legend of Fig. 2, and Table 1.

Reviewer comment 5:

Issues in the supplement

> I don't find the discussion of Ito calculus helpful or particularly relevant. It doesn't seem relevant because the variation occurs in discrete increments, i.e., the process describing *T* has a deterministic time delay before variation occurs. The authors perhaps felt

compelled to include such an analysis because of my suggestion that the model was actually a stochastic differential equation. I had suggested as much because the underlying relationship between temperature variation and the ecological dynamics were not clearly discussed in the prior version of the manuscript. It seemed natural to me to assume that temperature varied continuously according to a continuous-time stochastic process. The current version makes clear that the model of temperature variation is continuous in time but with discrete increments in which condition are constant. Stochastic calculus here could be used, but a much simpler, and more commonly used calculus would do.

Given the highly technical nature of the Ito calculus and its lack of clear applicability to the model at hand, I'd suggest deleting all the supplementary material about stochastic calculus and refer the reader to more complete texts on the issue.

Other parts of the supplement are not helpful because they have a high likelihood of misleading the reader. The main culprit is the mean-field approximation to the dynamics, which is a poor approximation for the actual dynamics of species. Only in the case where the variance is negligible compared to the mean can one reasonably assume that $<N_i^2> = <N_i><N_i>$, as the authors have done in the supplement. Given the range of variation in T and the variance shown in the figures of the dynamics, these assumptions will not do.

But the question is not so much about the actual dynamics, but the qualitative nature of the dynamics over some time-horizon (do species coexist or not?). The qualitative outcome is predicted well by the mean-field approximation in the following sense. Over some time-period, a species will be bounded away from extinction if it's low density growth rate is positive in the presence of a competitor. The low-density growth rate really only depends on the average of w, as the authors use in the latter section of the dynamics. In the authors' notation this low density growth rate is.

$$\lim_{N_i \to 0}\left\langle \frac{1}{N_i}\frac{dN_i}{dt}\right\rangle = r_i\langle w_i\rangle - \frac{\alpha}{K_i}\langle N_j\rangle - d_i\left(1-\langle w_i\rangle\right)$$

A similar expression for a resident shows that $<N_j>$ largely only depends on $<w_j>$ and so $<w_j>$ should be the focus of study.

Author response 5:

Although we feel that it would be a pity to remove all of analytical models in the supplementary material, we agree with the reviewer's suggestion. These complex models may be misleading to readers. Therefore, we have decided to remove these supplements as suggested by the reviewer.

Reviewer comment 6:

Line-specific comments:

Throughout the authors use the term “environmental fluctuation.” My thought here is that this should be the plural “environmental fluctuations” to represent the idea that you are describing a system beyond a single perturbation and to indicate the large number of qualitatively distinct regimes of conditions that change over time.

Author response 6

Modified as suggested.

Reviewer comment 7:

Line 65-67: “whereas increased fluctuation prevents species from reaching equilibrium and therefore prevents competing species from excluding others [4-8].” This particular hypothesis is a dubious one and doesn’t hold up to theoretical scrutiny. A paper that tackles this particular form of the intermediate disturbance hypothesis is Chesson and Huntly (1997). They show there that species still exclude others, although it may take longer. But some other mechanism is required to explain the sustained coexistence of species.

Author response 7

We modified the text to add this citation (Line 67).

Reviewer comment 8:

Lines 73-75: The definition of fitness differences here is not a real definition, as in a reader without knowledge of the concept could not reasonably be expected to understand it from this sentence. I recognize how difficult it can be to adequately define these terms. I suggest perhaps removing the definition and sticking with sufficient citations for others to look into. The most up-to-date definition of the concept is in Chesson (2018), in which the following quote begins a paragraph on the bottom of pg 1779:

> "The species average fitness, κ, is a summary ability of the species to succeed in the given environment relative to other species in the same guild."

The paragraph concludes with

> "κ is rarely described as an average tolerance to competition and is not commonly derived that way, but as some approximation to an average tolerance of competition. Nevertheless, this is what it amounts to."

There is lots of confusion in the literature about these terms. You could set an example by giving an appropriate definition.

Author response 8

We removed the sentence and added citations as suggested (Line 73-74).

Reviewer comment 9:

Line 78-79: "by equalizing the effects that minimize average fitness differences between species." As written, this sort of implies there are multiple factors minimizing fitness differences. I think more appropriate wording is “environmental fluctuations potentially promote species coexistence by minimizing average fitness differences (equalizing mechanism) or by creating different temporal niches (stabilizing mechanism).”

Author response 9

Modified as suggested.

Reviewer comment 10:

Lines 88-97: Clear example to illustrate where the timescales might matter. Thanks for this.

Author response 10

Thank you for your previous suggestion.

Reviewer comment 11:

Line 168: You need to specify here that $w_{\text{base}} \geq 0$. Without this stipulation, the model takes a very strange interpretation if $w < 0$, in which the death rate acts like a birth rate.

Author response 11

Added as suggested (Line 169).

Reviewer comment 12:

Lines 212: I get this statement here, but there are other equilibria in the model in the sense that there are points to which the system tends, and returns to when perturbed. For example, in the single-species version of the model, the single-species equilibrium average population density is

$$\bar{N}_i^* = K_i[\bar{w}_i(r_i + d_i) - d_i],$$

where the overbar here means the expectation over the distribution of environmental states. (Once could similarly define shorter term equilibria, where the overbar would indicate an average over some shorter-term scale of variation.) The expression is, by definition, an equilibrium, it is just not a point equilibrium as ecologists traditionally like to think of equilibria. You could do the readers a service by pointing out this fact, as it is not widely appreciated that there are alternative conceptions of equilibria that are useful to have in mind when studying environmental variability.

Author response 12

We have added the concept in the model description section as follows: "*Note that equilibrium can be defined more broadly; for example, an equilibrium state describes having some system converge and return to those points on perturbation, not just the equilibrium points we define here*" (Line 213-216).

Reviewer comment 13:

Lines 217-219: "remain constant over time" and "chance that the environment remains constant in time" are incorrect characterization. Perhaps "consistency over time" would suit your purposes better. Having a constant value certainly implies consistency, but consistency does not imply constancy.

Author response 13

Modified as suggested.

Reviewer comment 14:

Lines 257: I find the phrase "proportion of species coexisting" odd. It suggests that this is about a bunch of species, and only some fraction coexist. I suggest changing this to ensure it's clear that you are running replicate experiments, and this is the fraction of experiments where species coexist.

Author response 14

We have modified the sentence to “*We found a uniform trend such that the proportion of replicate experiments with species coexistence increases with an increase in short-term variation*”, as suggested (Line 260-262).

Reviewer comment 15:

Lines 276-277: “promotes competitive interactions…” You mean promotes exclusion, correct?

Author response 15

Yes. We have corrected the wording.

Reviewer comment 16:

Figure 3: This equation keeps the total variance constant only *approximately*. By the law of total variance, $\mathrm{Var}(T) = \sigma^2_{\mathrm{long}} + \sigma^2_{\mathrm{short}}$ by the law of total variance. The expression given is $(\sigma_{\mathrm{long}} - 0.5)^2 + (\sigma_{\mathrm{short}} - 0.5)^2$ is fixed. One can rewrite this equation as $\mathrm{Var}(T) + 0.5 - (\sigma_{\mathrm{long}} + \sigma_{\mathrm{short}})$. For the parameters given, the difference is marginal. But it is worth pointing out that the variance is not actually constant. Using the extreme values on the y-axis of the figures, we have $\mathrm{Var}(T) = (20.5)^2 + (0.5)^2 = 420.5$ and $\mathrm{Var}(T) = (14.6)^2 + (14.6)^2 = 426.32$. Clearly, these are not the same.

Author response 16

We have added the clarification in the figure legend.

Reviewer comment 17:

From the supplement

Equations (a3)-(a4): The quadratic form on these equations differs from the main text equations.

Author response 17

We have removed the supplement as suggested.

References

Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. Am Nat **150**:519-553.

Chesson, P. 2018. Updates on mechanisms of maintenance of species diversity. Journal of Ecology **106**:1773-1794.

Li, L., and P. Chesson. 2016. The Effects of Dynamical Rates on Species Coexistence in a Variable Environment: The Paradox of the Plankton Revisited. Am Nat **188**:E46-58.