

Editor and reviewer comments (we provide below the full context of each review) are in *italics*, while our responses are in regular text.

Editor's comments:

As you can see from the comments of the expert reviewers below, both are broadly positive about the manuscript, but both have suggestions for further improvement. Referee 1, in particular, thinks that the submission would benefit from some fairly substantial rewriting in places, and I would tend to agree.

We thank the editor for the opportunity to revise our manuscript. We found the reviewers' comments very helpful, with many overlapping requests for clarity or a more careful message. We provide detailed point-by-point responses below.

Reviewer 1 comments:

The authors suggest that tracking individual species' phenological response to environmental change may be insufficient to meaningfully predict community response to future climate change due to the influence of species' interdependence beyond trophic interactions and other influences at the community level. In brief, whether or not a particular species will survive climate change is complex and depends on a range of external factors that affect fitness including the influence of other species in a dynamic system that cannot be predicted by simply tracking its phenology. The impact of climate change on species' interactions with the physical environment and other organisms is notoriously complex and difficult to disentangle. Overall, this is a very timely and important topic and I would support its publication after tightening up of the language and presenting a sharper, clearer message. As it stands this manuscript appears wordy and sometimes laboured in places which tends to mask the key message being conveyed. It would be useful to highlight how this manuscript contributes to advancing the field of predicting species' response to climate change and how this in turn may impact community assemblages.

Agree, could make the message clearer and make the writing easier on readers. We made XX changes.

Abstract

Consider replacing 'of' with 'for' in the first sentence. Consider removing 'us' in second last sentence.

Changed first sentence a little (but stuck with 'of'), removed the 'us.' Also, re-write the abstract some.

Briefly define 'stationary and non-stationary systems'. Consider conveying in this sentence that the proposed method will 'help' predict rather than definitively 'predict'. It would be useful to emphasize the key findings of the review.

Added a glossary; seems hard to define in the abstract!

Introduction

In the second sentence, consider mentioning phenology before space to be consistent with 'time

and space’ at the end of the first sentence.

Good catch! We altered the second sentence to make the connection to ‘time’ in the first sentence more clear.

P4L12 Consider adding ‘and locations’ after ‘..across species’.

Done.

P4L38 It would be useful to clarify what is meant by ‘...the underlying distribution of the environment.....’ is this related physical climatic parameters?

Done in the glossary.

P4L53/54 Consider replacing ‘measuring tracking in current environments and evaluating the fitness outcomes of tracking’ with ‘measuring tracking and evaluating its fitness outcomes, in current environments’.

Done. We also just removed ‘in current environments’ to make the sentence less wordy.

In Figure 1 it would be useful to know how many years before and after 1980 were included in the analysis.

It’s already said in the caption!

What is the specific aim of this review the authors mention what they are going to review but why is it necessary and what is this synthesis expected to reveal?

Great point, we have added this here (paragraph starting on line 33) and in the abstract.

Defining and measuring tracking

Consider sticking to vegetation or animal examples not a combination of both or explain the rationale for using both groups.

We have restructured this section slightly and now address this question in line 51-line 54.

L42 consider replacing ‘these’ with ‘the timing and/or intensity’.

We have removed this sentence (we believe, we’re not sure of page number).

Overall, I found section 2 very wordy and difficult to follow. P5L47 Consider the following sentence ‘Tracking is commonly used to describe how phenology responds to climate change, yet it is rarely defined’. This section could be clearer and ‘tighter’.

Agreed! Made lots of changes here, including the one suggested.

P6L25/26 consider replacing ‘...to be something that can be accurately modeled..’ with ‘to permit/allow accurate modeling’.

Done.

P6L33/34 remove ‘a’ before ‘interaction’.

We believe this text has been removed in the revision process.

Does environmental tracking include parameters other than climatic variables and photoperiod, such as, nutrient availability etc.? It might be useful to state this.

Environmental tracking is a product of an organism’s cue system, and we have worked to clarify this in the text, especially in the glossary. To date major cue systems have found evidence of photoperiod, temperature, moisture cues mainly. Environmental tracking is not directly related to nutrients, but it is correlated with it. Cue system is tuned to maximizing nutrient availability but its not responding directly to it.

Another possible reason that species may not appear to ‘track’ maybe that some species require a greater amount of change in the environmental cue i.e. a higher threshold, before they respond. It seems likely that there are more than 3 major reasons why tracking is not detectable. A clear rationale for selecting and focusing on these reasons would be useful.

We actually think these are the three major reasons.

P7L40/41 consider placing ‘briefly’ before ‘review’.

Done.

P9L18/19 replace ‘that’ with ‘the’.

Done.

P10L54/55 repetition of ‘fluctuations in the environment’ consider something like ‘mechanisms which are dependent on, or independent of, fluctuations in the environment.....

Done.

P11L9/10 Consider ‘In community ecological modeling, definitions of the environment generally fall into two broad categories’.

Done.

P13L5/6 consider removing ‘including the previous example’. L16-18 is it necessary to be so explicit? Throughout the MS I find much of the information presented within brackets distracting.

Removed and we agree! We have tried to remove these caveats and explicit additions throughout. We were trying to be exact and thorough, but it makes it hard to read and isn’t always very critical.

P13L21-25 if the resource is in limited supply this may provide an advantage to early arrivals but later arrivals will benefit from the same resource if it is not depleted by earlier arrivals and other conditions may be better such as less risk of late frost. It is well established that the environmental variables being monitored are not exactly what the organism is responding to as micro-climate varies considerably in even the simplest ecosystem, furthermore, do we even know if budburst for example is triggered to the temperature of the bud surface, some internal temperature or some interaction with root (or some other organ) temperature. Defining the specific environmental variable and the specific threshold each species and each phenophase is responding to appears overly complex there must be some trade-off between a researchers effort and the applicability of the results. I just wonder where we draw (or don't) the line. This is a very challenging and important topic that the authors are addressing.

Thanks?

Conclusions are more of a summary of the topics reviewed rather than a comprehensive synthesis of the literature to draw new and more advanced conclusions based on the collective information from the review. It might be useful to make some recommendations on what is needed and why. Therefore, perhaps point 5 could be expanded.

Definitely.

Reviewer 2 comments:

In this review the authors argue that phenological tracking data needs to be combined with co-existence theory to help make predictions about how climate change will affect communities, particularly in non-stationary environments. Generally, this was well-written, clear in its logic, and really laid out how phenological tracking vs. coexistence theory are currently divided but could be integrated. The one aspect that fell short was suggesting specific types of experimental data that might help us reach this integration of phenological cues and climate change in a multi-species framework. I also have a couple of clarifying questions throughout. But otherwise, this was a really interesting review proposing a novel combination of two research areas that would really strengthen predictions about the consequences of climate change.

1. The argument for phenological tracking combined with coexistence theory in stationary environments itself is something that needs more work, but it was kind of glossed over in favor of non-stationary environments. It might be worth laying out more about the gaps between tracking and coexistence in stationary environments in the intro (pg.4, between lines 33 and 34?).

Tried to this somewhat (lines line 14-line 19), but the literature is focused on climate change and thus non-stationarity.

2. Pg.4, L49: Can you be more specific about examples of the community-level processes here? At first I thought this meant phenological tracking as a process but that would be individual or population level.

Yes! We have added 'such as competition and priority effects' (see line line 31).

3. Pg.5, L31: Isn't number of offspring still measured at the individual level? What does "higher

levels” mean here? Perhaps an example like synchrony at the community level would fit better?

Good point, switched to population.

4. Pg.5, L35: I agree that the first event is not equivalent to the number of flowers (or a continuous phenological metric), but yes/no flowering is not the same as first event either these variables seem conflated in this section.

We have removed the sentence about first events.

5. Pg.6, L34-36: This section made me wonder if there are any examples where researchers know the exact cues and can measure phenological tracking more precisely in systems like Arabidopsis?

Great point! We have added mention of the photothermal model of flowering of *Arabidopsis thaliana* (see line line 101) and a couple more examples from this system elsewhere in the manuscript.

6. Pg.7, L49: This is somewhere where I thought empirical directions could be suggested (or using this, have a section on future research at the end) the heritability of phenological tracking made me think maybe we need more studies linking phenological plasticity to genetic variation and heritability (e.g., do more plastic populations harbor more genetic variation in phenological traits)?

Good point, we added this to line 481-line 489 in a new section ‘Building from cue systems to phenological tracking’ in our future directions section.

7. Pg.8, L23: This is the other spot where I wanted more background/discussion of gaps in the links between phenological tracking and stationary environments before moving on to non-stationary environments.

Good point, we have expanded on this, see lines line 161-line 168.

8. Pg.8, L24: Is “unpredictable” environments here different from non-stationary environments? In pg.9, L3, it sounds like non-stationary also means unreliable in this context, so I was a bit unclear on why unpredictability was introduced in 3.1 instead of 3.2 (I might have missed some key difference). A glossary box for some of these terms could also be helpful.

Good point, this rather inexact, we removed this word and are more specific now (see line line 169).

9. Pg.9, L18: What is the fundamental “model” here? Is this underlying fitness?

Good point, we meant the model of fundamental tracking which we now say explicitly (see line line 201).

10. Pg. 9, L33: The idea that phenological tracking might vary not only in stationary vs. non-stationary environments but also in environments transitioning from stationary/predictable to

non-stationary/non-predictable is cool (and brought up again later in the review), but it's introduced so late in this section and without any context! Definitely worth expanding on.

Good point, we introduced it late as it's setup for our next section, but it does seem a big point that we're making rather to easy to miss. We have expanded to a full paragraph (lines line 212-line 218).

11. Pg.9, L47: This statement felt short perhaps include some reasons why competition is critical. Additionally, this is another spot with some future directions implications because phenological shifts aren't often studied in the context of their effects on species interactions (although we often make assumptions based on biology, e.g. invasive-native comparisons). Perhaps a call to include phenological shifts across environments as part of per-capita competition experiments?

Good point, we changed to 'Yet decades of research show that competition drives the niche differences necessary for species to co-exist (Hutchinson, 1959; Chesson, 2000)' (line r2whycomp). Also, added this to section on future directions, see lines line 504-line 513.

12. Pg.10, first paragraph: I found this argument really interesting because although it made sense, it read as counterintuitive to invasive-native comparisons of phenology. The argument here is that more plastic species are probably inferior resource competitors. But studies that find that invasive species are more plastic also assume invasive species are the superior resource competitors. I wonder if this section needs some caveat in our assumptions for invasive species in these models? (Similarly in 4.2, but I think that the argument that "best-matched" species could drive the other extinct (Pg.12, L45) starts to help with this.)

NEED to DO.

13. Pg.12, L55: What if phenological tracking itself could be a stabilizing mechanism by affecting resource partitioning?

NEED to DO. Megan—help!

14. Pg.13, L5-12: The review draws on plasticity literature, but there are definitely studies linking plasticity (including phenological plasticity) to fitness that seem overlooked in this first paragraph. E.g., Lustenhouwer, N., et al. (2018). Global Change Biology 24(2): e534-e544.

Good point! We agree this literature is broad and deep.

15. Pg.13, L35: I'm unclear on whether phenology is explicitly in these models. Otherwise, how is phenology connected to studies of production that don't measure phenology?

NEED to DO.

16. Pg.13, L38: Figure 6 is your model, it doesn't show whether other studies model environmental distributions. Why referenced here?

NEED TO DO, just add refs to papers instead of our model.

17. Pg.14, L25: Could you expand on why the new communities would exist only as long as the environment remained non-stationary? Could plastic species that arrived in a non-stationary environment also stay if the environment was just consistently warmer, for example (i.e., stationary)?

18. Pg. 14, L48: I love this call to action great place to put the types of data we still need.

Thanks!

19. The figures are all great I found 2 and 5 particularly helpful for some of the complicated concepts in here. Figure 5a also made me think about whether we need more studies changing the timing of resource (or stress) pulses and how that affects tracking.

Thanks!

References

- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.
- Hutchinson, G.E. (1959). Homage to Santa-Rosalia or why are there so many kinds of animals. *American Naturalist*, 93, 145–159.