

Subject: Ecology Letters - ELE-01197-2019
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Dr. Elizabeth Wolkovich
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Wilhelmshaven, 03-Dec-2019

Dear Dr. Wolkovich,

Manuscript number: ELE-01197-2019

Title: How environmental tracking shapes communities in stationary & non-stationary systems

Author(s): Wolkovich, Elizabeth; Donahue, Megan

We have now received the Referees' reports on your manuscript, which accompany this letter.

Although based on these reports, I have decided to decline your manuscript for publication consideration in Ecology Letters, if you believe that you can fully address the points raised by the reviewers, then we would be prepared, in principle, to consider a revised and resubmitted manuscript. However, as detailed by the handling editor, such a resubmission would need a full reworking of the manuscript to overcome the critical comments of the very thorough reviewers.

Your resubmission should include a point-by-point list of replies to all of the reviewers' comments. We strongly suggest that you carefully lay-out your point-by-point replies (each referring to page and line numbers in the revised manuscript), since they will be provided verbatim to the ensemble of the Reviewers on your submission. Please note that if you should resubmit your study, then we may choose to seek additional reports if we feel that additional expert advice is needed, or if the original reviewers are unavailable.

To upload a resubmitted manuscript, log into <http://mc.manuscriptcentral.com/ele> and enter your Author Centre, where you will find the manuscript title listed under "Manuscripts with Decisions." Under "Actions" click "Create a Resubmission."

It is the policy of Ecology Letters that manuscripts be resubmitted within 3 months of the date of receipt of this letter. Please contact the Editorial Office if you are unable to submit your revision before the option expires.

Finally, it is important to note that this letter does not pre-judge the issue of whether your paper will be finally accepted: a consensus of novelty and generality must be obtained after reassessment if your revision is to be published in our journal.

Yours sincerely,

Helmut Hillebrand

Referees' comments to the author(s):

Referee: 1

Comments for the Authors

The authors present an interesting (I'd call it perspective not review) manuscript that is focused on what they call "environmental tracking". With that, they really mean the ability of species to shift their phenologies in response to changing environmental conditions. This is clearly an important and timely topic, and I was excited to see someone tackling this. This said, the title & abstract did not prepare me for the content, and I felt a bit let down. The focus is much narrower than both suggest, and does not provide clear insights into a community context. The main content of the paper is focused on why some species track long term changes (e.g. in temperature) and others don't, with some speculation of how this might affect competition. The literature is not reviewed comprehensively, and largely focused on a few systems and big reviews, without really digging into the available literature. I know there isn't as much out there on this topic, but there is more than is given here. For a review, that's not enough, for a perspective, it's still a bit short. The main part of the paper is a model, and that is where I had the most issues. I'll explain the details below, but it really appears to be a not well developed toy model (albeit I may have missed how exactly it worked, see below), and highly system, condition specific. As a consequence, much of what it shows we already know, or its unclear how we can generalize it to other systems and scenarios. There are no analytical solutions or comprehensive simulations & exploration of the parameter space. The authors also ignore much of the theory we already have on this type of model (it may not be called "phenology", but otherwise very similar). In the end, there are so many restrictions on the model that the outcome is known without any need of simulating the dynamics. There is even little to now discussion of existing models specifically on consequences on phenological shifts, which almost feels like intentional omission, but it's not clear why. While highly relevant (some could predict similar outcomes) none of them are discussed or but in context to current models, so we don't really know what's new or different. As a consequence, I don't think that this is a good fit for Ecology Letters. I would suggest the authors either focus on a more comprehensive literature review and drop the model component, or really dig into developing the model and focusing on the exciting new questions that could be addressed with it, but that deserves it's own paper. I know this is not an encouraging review, but I like the inherent idea and there is clearly a need for this topic to be emphasized, so I'd like to see more of this.

Overall, I faced some major confusion with the model and really got stuck on many aspects of it. So let me go more in detail:

- Resource in this system is specified to not be renewed and only gets depleted. This is a reasonable assumption for some systems, but not for others, so it should be clarified and emphasized to avoid confusion. Importantly, this sets the system up for positive priority effect, i.e. resources are always at maximum at start of the season, so early arriver will always have a benefit over later arrivers. Again, this is reasonable for certain systems, but not for others so it requires some more explanation and justification. It also prevents consumers from overshooting, i.e. there is not punishment for arriving too early (before the resource). Later on the authors confirm this expectation on early arrival advantage. It would be good to cite some literature on this (this is a common optimality problem and has been used in wide range of models). However, there should also be some detailed discussion on what systems match these specific conditions, and which don't (e.g. systems where resources don't start at max but build up over time, systems where later arrivers have an advantage etc.)
- It took me a bit to think through the model formulation to understand how "timing" is incorporated here, and I'm not sure I'm still totally clear on it. Part of it stems from confusion about the two time scales, within vs between years and the notation was confusing to me which one is which. For instance, is $g(t)$ the germination for year t , or for time t within a year? The latter would suggest that there is some sort of distribution of germination events within a given year, while the first would indicate a single event. From the wording, I assumed that it is indeed a single event per year. Furthermore, it appears that there is not difference in relative timing per se (say relative to the resource), but instead timing

effects with a given year are solely driven by how many germinate in a given year, out of the total. So it's not a question of "when", but "how many"

- Overall, this confusion makes it hard to evaluate what the model does. If we stick with the one germination event a year, let's assume both species are identical for sake of argument. In that case, both species appear at the same time, but at different initial abundances, creating solely numerical priority effects.

- It also assumes that per-capita effects are unchanged, which is a specific assumption that is reasonable for some systems, but not many others. In addition, it would ignore the temporal dynamics, i.e. temporal overlap of competitors should be different, but without an explicit start time, it's not. Again, all this is based on not having enough information to determine how the model really works, but based on the supplemental information I assume all populations start at same time within a given year just at different abundances.

This confusion is further increased by not providing information on how "non-stationary" is modeled in this system. If there is no real timing, does this mean it's modeled as move from environmental to biological timing? So "shift" results in decrease in number of individuals if biological timing doesn't shift but environmental timing shifts "earlier"?

So to summarize I took away these following assumptions:

(1) Simulations of within season population dynamics start at the same time, there is no temporal offset of population dynamics, and no "escape" from competition in time. So there is no explicit temporal niche modelled

(2) temporal differences only affect starting densities not temporal dynamics or per capita effects. In other words, this is a model where phenological shift only affect reproduction (and thus numerical), not interaction effects.

(3) There is always an early arriver advantage: which ever is closest to environment timing, has higher proportion of seeds emerging and will win (assuming all else equal)

(4) Season ends when resource is depleted to lowest R^* . So season is not ended by environmental conditions but resource availability, and just a function of competitor densities.

(5) Germination function with difference in environmental vs. biological timing is non-linear.

(6) Tracking parameter is difference between fixed vs. moving biological timing.

Given this set of assumption, the generality of the model is strongly limited to a few systems/scenarios (very specific plant system), limiting the general inference that can be obtained from it.

Overall, I gained very little from the model, and as far as I can tell nothing new emerged from the model that we did not already know from other systems (e.g. much of this reminds me of stage-specific multi-parasitoid competition systems where the life stage of the host resembles the environment here, or a simple inter-annual model where reproduction varies across years, and this may or may not be correlated across species). In addition, given the specific conditions, the conclusion that non-stationary environments will change coexistence outcome has to be true given the model formulation, and could be easily inferred from recent Rudolf 2019 model (which shows how phenological shifts alter coexistence conditions).

As far as I can tell, the only novel aspect here is the tracking aspect, which I quite liked. But, the way it's implemented, it's not dynamic but forced on the system and simply shifts the initial relative numerical abundance of species, so again the outcome could be inferred from a simple L-V type competition model. So I'm still struggling to understand why this model is necessary and what new insights we gained. Otherwise it just adds confusion, so maybe it would be best shown in a simple verbal or graphical model. In fact, I would strongly favor the graphical option, since that would be clearer, and outcome can easily be predicted without simulation the system from the many existing models we already have. I still think the tracking approach is very interesting, but hasn't been fully developed to ask more detailed question on how tracking will affect long-term dynamics, and rigorously explores when and how it influences long-term dynamics. I think this deserve its own fully developed manuscript, and sticking it in here is really selling it short of its potential. This would also allow the authors to examine how many of the unresolved questions they list later on influence the outcome, e.g. what are consequences of tracking if changes in environmental conditions alter multiple aspects (e.g germination & per-capita effect) etc.

Outside of the model, I generally liked the idea of getting a much better understanding of what species track environments, and which ones don't. I completely agree with the authors that we know way too little about this, and more research needs to be done. This said, the manuscript here did not feel like a review, but a "food for thought" short opinion paper. If this is truly supposed to be a review, I would expect a more thorough and quantitative analyses of the literature, since much literature was missed, and largely restricted to plant systems. So my main complaint here would be that it felt like it was just touching the surface and did not provide enough depth (i.e. go into existing studies). Finally, there was very little coverage over theory on phenological shift. The authors mention Rudolf 2019 in passing, without discussing any similarities, differences that are clearly there. Similarly, they never mention other phenology models, like Nakazawa & Doi, 2012, Revilla et al 2014 etc. Even the simple graphical temporal niche approach that the authors introduced themselves (Wolkovich & Cleland 2011) is not discussed (but brings up interesting question about "single" vs multiple resources approaches).

Specific comments:

P 3 L30ff: the notion that earlier spring should favor earlier phenologies relies on the assumption that the "niche" is empty i.e. no other species are earlier. So this applies to very specific systems (i.e. resources are not available before that time point, so temporary resources) and should be clarified.

L34-35, there are some studies (and should be cited here), e.g. Block et al 2019 Oikos. Showing that phenological plasticity is a poor predictor of performance.

L 50ff: there has been progress, e.g. Rudolf 2019 specifically incorporates non-stationary systems and variability to examine how it influences coexistence and communities (since it's focused on phenology it seems like a highly relevant citation here). In fact this citation would be great to support the claim that it matters, instead of simply stating that nobody looked at it (which is incorrect).

Equation 9: "n" is undefined. Along the same line, what determines the end of a growing season?

P13 L 9: this prediction hinges on the assumption of early arriver advantage and single resource competition etc. So as it stands, this is one of the predictions, not the only one.

P15 L10ff: what about species that are just very plastic, i.e. can adjust to cope with various environmental conditions, and thus take an alternative strategy to shifting. There has been increasing discussion of phenotypic plasticity vs let's call it "environmental " plasticity, i.e. species that can perform equally well at cold and warm temperatures. So environmental generalists.

Same page, next paragraph (sorry, having not continuous line numbers across pages makes this a bit frustrating). Good examples here would be species where phenologies are correlated across season/life stages. In some cases, phenologies in spring are determined by what happens in fall, or what happens later in summer may depend on how individuals perform during earlier life stages in spring (e.g. changed developmental rates alter later phenologies etc.) In same context, Yang & Cencer 2019 Ecology examine "seasonal windows of opportunity", which fits nicely in the context here. They took rigorous approach in finding what constraints those windows, which would also determine how shifts in them would change the optimal window.

P16 L 34-35: very cool, I'll have to look up change-point and hinge models, never heard of them!

P 16 L38ff: some recent approaches suggest using whole phenological distributions can strongly increase power as well (e.g. single species: Steer et al 2019 Methods E&E, or for species interactions Carter et al 2018 Ecol Letters)

Referee: 2

Comments for the Authors

1. Need clearer motivation in the introduction (section 1, "main text").
 - a. What is the specific definition of "tracking" applied here? Tracking a set of abiotic conditions? Does it extend to tracking biotic conditions? Is there a way to quantify the relevant set of conditions, and therefore an organism's ability to track them?

b. The second paragraph of the introduction suggests that “a shift toward earlier spring should favor earlier species, especially those that can environmentally track ever-earlier seasons” I’m not sure I follow the logic here; it seems like earlier spring conditions could just as easily limit the success of early spring species in particular. It’s not that the proposed hypothesis is never true, but it also doesn’t seem that it is likely to be necessarily or generally true, at least based on the argument presented. Is this intended as a straw hypothesis?

c. It seems like the assumption of stationarity has never been true, and ecological theory has always been a bit uneasy about this. Though maybe because so much of ecological theory is generally explanatory rather than specifically predictive, these deviations haven’t been too troublesome. Perhaps the question then is more about how much worse the situation is with rapid climate change.

2. Environmental variability and change (1.1)

a. L21–24: Is there good evidence of historical stationarity? The distinction between stationary vs. non-stationary environments seems to be scale-dependent, and thus somewhat subjective. Is that a problem?

3. Environmental tracking in time (1.2)

a. Chmura et al (2019) suggest that relatively little is actually known about the mechanistic/cueing bases of differences in phenological shifts, either because most studies don’t consider cues per se, or because they very rarely assess alternative mechanisms. If this is true, how does this affect the framework described in this section?

b. The trade-off between plasticity (“tracking”) and bet-hedging has been examined in studies by Chevin, Lande, Ghalambor and others. Do those studies provide a useful perspective here?

c. The long-term value of plasticity vs. bet-hedging may not be apparent in relatively short field studies, since the relevant measure of fitness could require more time to assess.

4. Interspecific variation in tracking (1.3)

a. I’m a little concerned about the slant of this first sentence, which seems to suggest that tracking is both universally important and positive. Modeling studies seem to suggest that under some circumstances, more plastic responses could be maladaptive. The section goes on to identify some very interesting potential trade-offs with competitive ability, but the broader point is that it doesn’t seem to be entirely clear that “tracking” per se is universally favored even absent a competition trade-off. Perhaps this goes back to our limited ability to quantify “tracking” ability, and the implicit assumption that we can assess an organism’s ability to find optimal conditions. In most systems, it seems like we don’t have enough data to quantify tracking ability. In the absence of this, we can assess plasticity to specific cues, but whereas “tracking” may implicitly imply adaptive plasticity, plasticity is not always adaptive.

b. L55–56. Because many climatic cues are correlated, and also correlated with other cues (photoperiod, biotic, etc), the observation that temperature models can explain more than 90% of variation in phenology probably shouldn’t be assumed as evidence of causation. Temperature in particular can be a very complex cue, and the determination of mechanistic causation is difficult, as described by Chmura et al (2019).

5. Model description and simulations (1.4.1)

a. This model conceptualizes “tracking” ability as a variable between 0 and 1 which describes an organism’s ability to adjust its biological start time to the (optimal?) environmental start time in a given year. This leaves aside some messy but potentially interesting issues of mechanism and constraint, including any explicit consideration of cues or environmental conditions. I’m not sure how I feel about this approach. This could be an effective way to focus on the issue of “tracking” per se, but also risks being too far abstracted from reality to provide a meaningfully realistic model. For example, how should we conceptualize “tracking” ability if the optimal start time becomes worse over time? Or if there is a disconnect between cues and conditions (i.e., an optimal tracking of cues leads to a poor tracking of conditions)?

6. Tracking in stationary environments (1.4.2)

a. If I’m understanding this model correctly, there is the assumption of some kind of intrinsic circannual rhythm (represented by the fixed biological start time) which is then modified by cues (abstractly represented as “tracking”) to yield an effective or realized

start time. This seems different than my understanding of circannual rhythms and *zietgebers* in a potentially important way, where the current model would assume that even in the absence of any cues (or with a tracking ability of 0), an organism would consistently start on the same calendar day each year. This seems like a modeling decision that should be explained and justified. Are there studies to indicate that this is a reasonable model?

7. Tracking in non-stationary environments (1.4.3)

a. I get that this is not intended to be a realistic climate change scenario, but wasn't able to understand the details of how the non-stationary environment was created without the SI. The key thing that seems clear is that the non-stationary environment favored earlier start times. It wasn't clear if the optimal start time was actually advancing gradually over time, or if it was just changed in a single step. If I understand it correctly, this model doesn't allow for any evolutionary responses.

8. Model conclusions (1.4.4)

a. The observation that tracking is favored seems to be almost an assumption of the model, rather than a conclusion. Could it be otherwise in this model?

b. The idea that "tracking" should be considered as a part of larger "trait syndrome" seems appealing, though I'm not entirely sure what it means. What are the other parts of this syndrome? My concern is that the idea of "tracking" ability per se is not sufficiently defined or justified to develop in this way, abstracted from cues and physiological mechanism.

c. Despite this, I actually like the idea of a trade-off between tracking ability and competitive ability; it seems intuitively appealing, if not clearly defined. I think I'd like some additional justification that the idea of "tracking ability" is a meaningful one in nature, and that there are empirical reasons (not just based on theory) to think that it trades off with competitive ability. As a counterpoint, it seems like phenological traits are just as likely to be used as a tool in competition, where an organism may benefit by showing an earlier phenology in the presence of competitors (due to pre-emption, or asymmetric competition, e.g. for light), even when it would do better to have a later start in the absence of competitors. This requires a more careful definition of "tracking" – is an organisms that deviates from its optimal timing in an abiotic-only context showing good tracking or poor tracking? What if a deviation from the abiotic optimum is favored under competition? What if competitive ability depends on the relatively phenological/ontogenetic stages of the competitors? Instead of thinking of ways in which phenological "tracking" and competitive ability trade-off, I'm left wondering more about the complex ways in which they could interact.

9. Future research (1.4.5)

a. While I agree that improved predictions of climate change would be valuable, it isn't clear how these improved (i.e., more complex) climate predictions would benefit this model in particular. This model already seems quite far abstracted from cues and mechanism. More generally, I actually get the feeling that climatic projections are constantly improving though improved climatological models (especially better local or regional scale models), but our ability to predict ecological outcomes (coexistence or otherwise) is not typically limited by the detail, complexity or resolution of these climatological projections.

b. I would also be interested to know more about potential trade-offs between "tracking" and other traits, but would want to know first whether "tracking" ability is a meaningful construct. In this model, tracking is mathematically defined as inversely correlated with the difference between the intrinsic timing and the (optimal?) "environmental (abiotic)" start time. My sense is that there are very few systems where either the intrinsic start time is a realistic concept, or where the (optimal?) environmental (abiotic) start time has been well-characterized. If there are good examples of systems that support these concepts, they should be described. If this model is intended to provide more of any abstract framework, I would suggest that these caveats of definition and characterization should be much more prominent, and assessing these issues would probably be valuable future directions.

c. Despite my concerns about the framework of this paper, I do think the question of how climate change will shape coexistence mechanisms is an interesting one. I'm not entirely convinced that this model sheds much light on this issue, but would be glad to be convinced otherwise.

10. Boxes

a. The three boxes in this manuscript touch upon some of the issues that concern me about this manuscript, albeit too briefly. It seems clear that the authors have thought about some of these issues. Why not examine some of these complexities more centrally in this manuscript?

Editor

Editors Comments for the Author(s):

Both reviewers and I really like the 'premise' of this article. Unfortunately, both reviewers were also quite critical of a number of aspects of the paper, including the background, the definitions, caveats, and model itself. Given these concerns, I am sorry to say that I cannot support publication of this paper in Ecology Letters. I see two options:

First, the authors could revise their manuscript as best as they can and seek publication elsewhere. Especially if they were to take on several of the reviewer comments, this might be a relatively straightforward task.

Second, if the authors feel that they can rather fundamentally alter the shape and structure of their manuscript, we might be willing to consider a reworked version. I should say, however, that given the nature of the reviews, and the detailed advice about the concerns and possible ways forward, that this would be a rather significant reworking bordering on a new submission. Such a revision would need to rework the model section, broaden the scope, and really tackle many of the caveats and issues brought up by the reviewers.

Of course, I completely understand if the authors choose the first pathway, as the second pathway would be a lot of work and there is no guarantee that it would satisfy the reviewers. Nevertheless, there is important potential for the authors and topic, and I wanted to leave the 'door open' should the authors be willing to take on this task.
