

Subject: Ecology Letters - ELE-00300-2020
From: Nathalie Espuno <onbehalf@manuscriptcentral.com>
Date: 5/10/20, 9:35 PM
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Dr. Elizabeth Wolkovich
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Leipzig, 11-May-2020

Dear Dr. Wolkovich,

UPDATE:

The coronavirus epidemic is impacting ecologists around the globe, with fieldwork, office work, and lab work all affected as people work from home and self-isolate. In addition, in some countries, schools are shut, which means many of us will be looking after children at home. We appreciate that this disruption can impact all aspects of work and home life. For that reason, we are pleased to provide extensions to manuscript revisions. If you miss a deadline to resubmit a manuscript, please do not worry – we will reopen the submission pipeline when you are ready to resubmit. Stay well. Best wishes, from all of us at Ecology Letters

Manuscript number: ELE-00300-2020 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. You will find them below. As you will see, the referees make a number of comments with the aim of improving the manuscript.

I invite you to revise and resubmit your contribution (see instructions below), and the subsequent publication decision will be based in part upon your point-by-point responses to the referees' comments. It is possible that in making this decision, we will refer back to the original referees or have additional referees examine the paper.

Your revision should include a point-by-point list of replies to all of the 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 reviewers on your submission.

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.

It is the policy of Ecology Letters that revised manuscripts be resubmitted within 6 weeks 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.

It is our expectation that revisions will not make the manuscript exceed the permitted maximum number of words: Letters and Methods should be no more than 5000 words in length and

contain no more than 6 figures or tables. Ideas and Perspectives and Reviews and Syntheses should be no more than 7500 words and contain no more than 10 figures or tables.

Authors should use concise writing, avoid giving several duplicate citations to support the same statement, and consider moving to Supplementary Information materials that are beyond the interest of most general readers who wish to understand what was done in general terms.

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Yours sincerely,

Dr. Jonathan Chase
Senior Editor
Ecology Letters

Referees' comments to the author(s):

Referee: 1

Comments for the Authors

General comments:

The authors present a manuscript that attempts to summarize our current knowledge about ecological tracking, i.e. the ability of an organism to track the phenological niche. This is particularly interesting in the context of climate change and earlier onset of seasons in the northern hemisphere. The topic of phenological shifts is interesting, and I found the manuscript overall very well written.

I have a few general concerns about the manuscript which I detail below, and some specific ones, which I will address later in a chronological order.

1) I am not familiar with the topic of ecological tracking, but I am very familiar with the literature regarding phenological shifts in response to climate change. In my opinion, ecological tracking appears to me as a rebranding of a phenomenon about which much has been written. I am aware that the authors will disagree with this view, but their manuscript did not convince me that ecological tracking is fundamentally different from the widely observed phenological shifts. Maybe it is a subset of those, but it is nothing new. Nevertheless, the effect of phenological changes on ecological communities is an interesting one.

2) After carefully reading the manuscript, I did not understand what this manuscript actually is about and what the authors want to achieve with it.

a) The authors claim it is a review, but many studies– and many reviews about them (e.g. by C. Parmesan or A. Menzel) – have described phenological shifts in response to climate change. Only very few of those are mentioned, and in the description of their narrow search criteria they end up with only a handful of studies, because it appears that the reviews and the studies therein were actively omitted.

b) It is also not clear to me why they reviewed these papers and not the theoretical

literature or the physiological literature. Both types of studies were discussed in detail in the manuscript but not reviewed – at least I would doubt that the lack of studies identified by the authors regarding theory or the physiology of the cues can be based on a handful of studies. There must be myriads of studies in animals and plants addressing the physiological basis of cueing for phenological events, e.g. flowering time in plants or breeding time or migration time in birds. I was particularly surprised that they also excluded theoretical studies in their search, while at the same time relying heavily on theoretical papers throughout the remaining manuscript to describe several aspects of ecological tracking and its consequences for populations and communities. If this was a review, why exclude theory?

c) It was unclear to me whether they were searching for studies that explicitly talk about 'ecological tracking' (which are, I believe few), or any study that has ever observed a shift in phenology due to warming. The latter is not achieved, but it is also maybe not needed given the many reviews we already have. The former is probably not needed, too, because ecological tracking is, in my opinion, largely a rebranding of (adaptive) phenological shifts.

d) If I accept it is not a review, then it is possibly an opinion paper or a perspective. I understood that the authors mention a whole suite of understudied aspects of ecological tracking and that they want to fuel a whole suite of new studies. However, for a perspective, the rationale for addressing some of the understudied aspects of ecological tracking is not always clear. For example, for studying mismatches between phenologies of coexisting species, it is not crucial to know the exact cue. Also, while the need for non-stationary models appears logical, I could not find anywhere clear predictions about why and how coexistence mechanisms would be changing differently in non-stationary systems compared to stationary (but fluctuating) ones. This is regrettable because I assumed that the interaction between tracking and coexistence mechanisms was a main focus of this manuscript – at least this would be an interesting topic.

In fact, I would not expect large differences between a classical storage effect model and a model where the environment changes gradually and directionally over time, especially as storage effect models also look at environments with different statistical properties. Specifically, if say, we have a storage effect model (or a model addressing priority effects) where the environment does not fluctuate strongly, species would probably not be selected for being able to track, simply because tracking is not needed when the environment is stable. However, if we model (as in a classical storage effect scenario, or in a priority effect model) the environment as highly variable and unpredictable in time (and space), then species inhabiting such an environment must be able to track, because they cannot know what the ideal timing would be in any given year, unless there is a good cue (in which case the environment would not be unpredictable). Thus, I would expect a similar change from non-tracking to tracking when comparing stable with fluctuating (stationary) environments as when comparing a stationary with a non-stationary one. In other words, species inhabiting highly variable environments should be tracking, which may equip them with an advantage also in a gradually changing world. This idea has been voiced before in models (e.g. Bonebrake, T. C. & Mastrandrea, M. D. 2010. *Proc. Natl. Acad. Sci. USA* 107: 12581–12586) but also in experimental studies conducted in fluctuating habitats, where no effect of experimentally induced climate change was found.

So maybe the lack of a prediction about why we should look at non-stationary models and how their outcome would be different from what we know may be explained: the outcome would not be much different. It is also possible that the authors had attempted to exactly derive such a prediction in their model in the previous version of this manuscript, but I understood that they did in fact not produce any surprising results.

3) I was also not sure what exactly the topic of this manuscript is. From the previous reviews and the author's replies I understood I that this manuscript aimed at coupling ecological tracking theory with coexistence theory, which would be an exciting topic.

However, only approx. 10% of the manuscript is devoted to this topic. The remaining 90% are spread across several different and partly unrelated aspects of ecological tracking. These are, to name a few, the lack of physiological evidence for cueing, definitions of ecological tracking and measuring it, description of bet hedging as opposed to tracking, a brief note about the equivalence of phenotypic plasticity and ecological tracking, trade-offs between tracking ability and competitive ability (why this trade-off and no other one?), and some more. Interestingly, none of these various topics is actually reviewed in detail, which brings me back to my initial question of whether or not this is a review.

In my opinion, the authors do themselves a disservice by evoking expectations about linking ecological tracking with coexistence theory, when in the end they spread sometimes thinly across several aspects of ecological tracking. The manuscript could thus really profit from being concise in the selection of aspects discussed and then discuss these aspects exhaustively.

4) It is not clear to me why out of all possible biotic interactions, competition is dealt with so prominently. I understand that competition is the other side of the coexistence coin, but since coexistence theory is not the core of the manuscript, other biotic interactions should have been discussed, too. There could be positive interactions that are decoupled by climate change and (as mentioned by the authors) decoupling of interactions among trophic levels.

The subsequent focus on trade-offs between tracking and competitive ability appears to me equally arbitrary. If we accept that plasticity comes at a cost, it can trade-off with any trait. For example, I would think that stress resistance (which in plants is assumed to trade-off with competitive effect ability) would trade-off with tracking, ability, too. Also, there could be trade-offs between phenological plasticity (i.e. tracking) and plasticity in other traits that enable fitness homeostasis even if no ecological tracking occurs. This relationship is not addressed. However, it could be fundamental if organisms are highly plastic in other traits, in which case they may not even need to track.

5) Ecological tracking is regarded exclusively as a plastic response. However, the (very few) solid studies on evolutionary change in response to climate change indicate that phenological traits could be among the first under real selection. I was asking myself why plasticity should be the main mechanism by which species can track, and whether we need this assumption for defining ecological tracking, or whether the definition could also embrace rapid evolutionary change.

Specific comments (chronological order, line numbers are references given):

Line 1-12: reference to the many studies and reviews about 'escape in time' is missing (e.g. Parmesan, Menzel, and many more). This leaves the impression that we know nothing about ecological tracking, which is, in my opinion, not true.

37ff: Do we need to show that tracking is related to fitness? Isn't that self-evident and if not, why?

74ff: Is it true that we know nothing about environmental cues? I did not take the time to dive deep into the literature but I would think that studies on birds and plants are plentiful. Maybe the mechanistic studies (i.e. experimental) are rarer than correlations (but they do exist, e.g. reciprocal transplant studies and not only Arabidopsis), but even evidence for correlations of e.g. flowering time with e.g. growing degree day units is abundant.

84ff: The advancement in phenology by certain numbers of days has been demonstrated by C. Parmesan or A. Menzel (and others) much earlier than what is cited here. I am puzzled why their work is not cited.

93ff: Why is it so crucial to know the exact physiological mechanism of tracking and why the cue? For example, if we are mostly interested in the same trophic level and competitive interactions, we may, as a first approximation, assume that the organisms use a similar set of cues. Also, if it is true that we know nothing about the relationship between physiology and the cue, this seems a rather bleak perspective and may lead to the conclusion that we will never understand ecological tracking. So why is this important?

192–194. Some variable environments do provide cues, e.g. in the Sonoran desert annual system (see Pake, C. E. and Venable, D. L. 1996. *Ecology* 77: 1427 – 1435), the amount of the first rainfall in a year seems to partly predict the rainfall of the season. Predictive germination has also been addressed from a theoretical perspective by Cohen (1967) and subsequent authors.

195ff: One important aspect of the cueing seems to me the reliability of the cue. Unfortunately, the authors do not mention this and only focus on benefits and costs. To me, this seems a key aspect which is tightly related to the costs (i.e. low reliability, high potential costs). The reliability is not touched upon in the cost-benefit discussion.

208ff: The discussion about bet hedging is too much black and white (i.e. between not germinating and germinating). There is also plasticity in germination rates and some of it is driven by cues (see literature about predictive germination). I would actually assume that in the 'classical' bet-hedging system (desert annuals), tracking ability would be selected for very strongly because in a fluctuating environment, plants need to respond very plastically to the ever-changing conditions. So the idea that there is either tracking or bet-hedging is not plausible for me.

217–229: This paragraph does not appear to contain much information, so it could be left out.

243ff: I am missing an in-depth discussion about plasticity, i.e. the ability to maintain fitness (fitness homeostasis) even when the environment fluctuates strongly. Plasticity is expected to evolve under unpredictably varying conditions, and tracking is only one aspect of that plasticity. There should be trade-offs among the different types of plasticity.

1.4: This paragraph is entirely devoted to tracking-competitive ability relationships. It seems logical that tracking ability should also trade-off with tolerance to stress (e.g. low temperatures if e.g. bud burst is early) which in turn may trade-off with competitive ability.

336ff: Isn't the storage effect the same as tracking only that it is about inter-annual variation and not variability in intra-annual timing? So what would then be the fundamental difference between stationary and non-stationary models when, e.g. we start with a storage effect model in a randomly fluctuating environment where species must already be able to track? I feel it would be crucial to provide clear predictions about what non-stationary models may predict in contrast to 'classical' models. Without these, the call for 'more and different models' is not very well justified. Here, the main justification is that 'it has not been done', but not 'this is why stationary models are entirely misleading'. Unfortunately, the Box remains vague about this.

1.5 I found this section somewhat – if not completely– redundant with the sections before and was not sure why it is needed. Much of the discussion here remains somewhat vague. The conclusions are that we need more interdisciplinarity, more understanding and measuring of tracking, more looking at trade-offs with selected traits, and more models that are different from the current ones. Overall, this is not the strongest section of the manuscript. It could be merged with the previous sections and made much more concise.

1.6. I feel that this section could be removed from the manuscript because it is very speculative.

Box

578–581: Could the finding of early species tracking more simply be due to the fact that response to environmental variables (e.g. higher temperatures) follow a logistic curve where the late species attain high fitness because they are always in their climatic comfort zone? Whereas the early species experience, during their life or evolutionary history a much larger range of temperatures, some of which are clearly decreasing fitness?

600ff: Many models and data have been published about within-season timing of (germination) events. They could make a valuable contribution to this section (e.g. Simons, A. M. 2009. Proc. R. Soc. B 276: 1987 – 1992. Simons, A. M. 2011. Proc. R. Soc. B 278: 1601 – 1609).

607ff: I believe that a similar storyline could be created with stress tolerance instead of competitive ability.

Referee: 2

Comments for the Authors

The resubmitted paper “How environmental tracking shapes species and communities in stationary and non-stationary systems” by Wolkovich and Donahue deals with environmental tracking, specifically how environmental tracking can be measured and analyzed, how it may influence species co-existence and species responses to climate change. I think the topic of the paper is novel and highly relevant, and overall the authors did a very good job in reviewing the literature on the topic. I specifically like the part about how tracking may trade-off with other traits (e.g. those related with competition) and thereby shape the co-existence among species in ecological communities.

I only have one point to criticize: although the authors highlight that “researchers are increasingly recognizing the need to consider multiple climate variables” (L 14) this review is mainly focused on environmental tracking in response to temperature changes. I am aware that there is much more known about phenological responses to temperature change compared to precipitation change, which is also supported by the result of the literature search in the Supplement. However, as this review deals with climate change and not only climate warming and we know that climate change is complex and multivariate, I would love to see more examples in the text about environmental tracking and precipitation change. Are there any studies about how temperature and precipitation change may interactively affect environmental tracking (e.g. via changes in snow cover)? If not, I think this could be highlighted in the future directions paragraph more explicitly. Just out of curiosity, would it be possible to include such interactive effects of multiple resources in the model?

L 502 Not only temperature is rising but we already and will face non-homogeneous but fundamental differences in the precipitation regime around the globe

Referee: 3

Comments for the Authors

In a review piece, Wolkovich & Donahue comprehensively present the idea of environmental tracking by species in stationary and non-stationary environments. This review is loaded with information and touches on several fundamental ecological ideas in relation to environmental tracking by species. The effort therefore is commendable with a potential to motivate new research avenues for climate change ecology—particularly the phenology research. Having said that, I also struggled at various places to grasp the core idea authors were intending to communicate. I outline them below.

I definitely agree with phenology as a trait and tracking as a plasticity of this trait (lines 244–246). I also liked how authors relate the idea of subsequent trade-offs in traits owing to costs associated with plasticity. I, however, missed examples of which traits and plasticity of them are going to trade-off the most with tracking, and how these may differ in

stationary and non-stationary environment. Can we also say something whether the strength of trade-offs may differ in these two environments?

Difference in species' ability to track environmental changes as something similar to competition-colonization trade-off is further a stimulating idea (lines 273–280). I was, however, left guessing if authors modelled this at all in their theoretical frameworks. My initial impression was that figure 3 gets at this, but I am not really sure if two species scenarios in figure 3 relate one species as a competitor (lower cue) and the other as colonizer (higher cue). Can this be clarified or if possible implemented?

Some other comments

Line 5 (Abstract): species responses

Line 12 (Abstract): through the lens of which ecological theory? Later, you mention community ecology theory. Perhaps, use the latter to be consistent.

Line 2: Perhaps, use more recent IPCC citation.

Lines 10–12: The "indirect effects of climate change" is not very clear. Why could it not be a direct effect of climate change? Please clarify.

Line 21: Can you elaborate which foundational ecological theory is meant here?

Line 43: Which basic community ecology theory? Please be specific when mentioning a theory as you did in lines 23–26.

Lines 237–240: Would not this be a trophic mismatch case still predictable from the stationary environment? Or does this imply that trophic mismatch will not occur in the non-stationary environment? Please clarify.

Lines 254–256: But what about the benefit side of the tracking? And which other traits those be where trade-off with tracking will be higher?

Line 309: two "the"s

Lines 386–388: Please use this example as a separate sentence.

Lines 408: Please provide more example studies when you suggest "many studies".

Line 416: Here one or two examples will help the readers.

Referee: 4

Comments for the Authors

There are some very interesting ideas in this review on phenological responses to environmental change and I can see it making a stimulating contribution. However, there are a lot of aspects that require attention, including the structure. In general I found the ms rather imprecise in its use of terminology and quite verbose. I hope the comments below are useful in revising the ms. I have not really commented on the coexistence theory aspect as I am not sufficiently familiar with this literature.

My biggest criticism of the ms is that the term "environmental tracking", which is central to the ideas being developed is not clearly defined, despite having a section devoted to its definition. A clear definition is provided for "fundamental tracking", but then the text switches to environmental tracking without providing a definition (except in fig 2). This

term seems to be applied more loosely to any case of phenological change, but initially without any discussion of what the yardstick is (Visser and Both 2005), meaning that it's unclear that "tracking" is taking place – for instance the response could be maladaptive. The yardstick for tracking could (from hardest to quantify to easiest) be the rate at which (i) the optimum is changing (as in Chevin's B or the author's fundamental tracking); (ii) a resource is shifting or (iii) the environment is changing (Amano et al. 2014). Related ideas are introduced from line 100, but you might consider introducing them sooner. Overall I found sections 1.1 and 1.2 quite muddled. I think "environmental tracking" as used in these sections is synonymous with how the existing literature would refer to "phenological responses" to cues (line 109), and I don't see that introducing new terminology brings something useful to the table unless there is also some discussion of how much the environment is shifting, i.e. we need to know something about what is being tracked. Another concern is that introducing new poorly defined terms will just generate greater confusion in the field.

The section 1.3 on "understanding variation in environmental tracking" is rather long and doesn't offer up novel perspectives. I think it could be greatly reduced by briefly summarising some of the theoretical literature on the evolution of plasticity in response to environmental cues.

I was surprised to see plasticity really only mentioned half way through the review (around line 245), given that along with any shifts in the environmental cues, this is the most important determinant of the phenological response at least in the short/medium term. I suggest that this could be mentioned earlier when you define "environmental tracking". For instance, you could briefly outline the processes that can allow tracking, which I think are plasticity at the individual level, adaptation at the population level and species sorting at the community level. In lines 65–66 the mechanism underpinning a plastic response is defined and you might draw attention to that.

I like the section on Tracking in Multi-Species Environments, as this is the first part of the ms that introduces some novel perspectives. I think the ms would be improved if the preceding components were edited down, so that you get to this point much sooner. In general I thought the second half of the ms was more stimulating and well-explained than the first.

Minor Comments

Environmental tracking: Where this idea is introduced (line 45) I think it might help to begin at the population level with a clear evolutionary definition of environmental tracking, where $|B-b|$ is small following the equation in Chevin et al. 2010.

Line 6. What proportion? The cited paper by Cook et al. is just about phenology so doesn't support the general point. A paper by Amano et al. 2014 finds that UK plant species that shift less in terms of phenology have a greater tendency to range shift. I think this finding has been replicated in other systems but can't remember the reference.

Line 14. And evolutionary theory, particularly Chevin et al. 2010 PLOS Biol.

Line 15. I think the terminology in this sentence is confusing. From an evolutionary biology perspective plasticity has a clear meaning (a change in genotype's phenotype in response to the environment), but here I think it is being used to more vaguely imply flexibility, and I think "flexibility" would be a less loaded term. Also note that tracking can involve evolution.

Line 17. Please cite an evolutionary theory paper to support this statement. Perhaps Norberg, J., Urban, M. C., Vellend, M., Klausmeier, C. A., & Loeuille, N. (2012). Eco-evolutionary responses of biodiversity to climate change. *Nature Climate Change*, 2(10), 747–751. Or some of Russ Lande's work.

Line 29–36. I agree that climate change has greatly exacerbated the non-stationary aspect of climate, but looking at historical records it seems as though climate is often somewhat non-stationary.

Line 56. I think a more precise/mathematical definition of cue quality could be helpful, e.g., something based on the sum of squares between optimum and actual event timing (RMSE?). Also note that the literature on the evolution of plasticity uses the term “cue reliability” to refer to the correlation between the environment of development and the environment of selection.

Line 62. Do you simply mean that in different locations if the individuals have the same reaction norms but environment differs then the outcome will differ? This could be explained in clearer language. Also there is a large literature by the likes of Scheiner, Lande, Chevin, Tufto, Hadfield on the evolution of cues and plasticity that goes uncited here.

Line 64–67. Here the definition of tracking seems to be at odds with the evolutionary literature. The mechanism described is a plastic response to a cue, whereas in evolutionary biology tracking is usually with respect to a fitness optimum. This also seems to be at odds with your definition of “fundamental tracking” (line 48–49).

Line 67. The organism is only expected to track the optimum proportional to the correlation between the environment of development and environment of selection.

Line 84. Here you outline a series of papers that present information on phenological responses to temperature. However there is an absence of information on what the “fundamental tracking” or shifts in the optimum are doing. I think various methods exist for generating a yardstick (Visser and Both 2005) for fundamental tracking. One option is to use the response of resources. Alternatively, the estimation of the “environmental sensitivity of selection” (Chevin 2010) and use of this in prediction is an informative avenue (Vedder et al. 2013, Gienapp et al. 2013). We also use a space for time approach to estimate tracking of the optimum in plants (Tansey et al. 2017). In terms of environmental tracking another interesting perspective is that presented in the Amano et al. paper I mention above.

Line 90–92. With respect to consumers tracking prey is this just the phenological shift shown? Here I think there is an opportunity to quantify whether tracking is adaptive (based on Ghalambour et al’s 2007 definitions of adaptive plasticity).

Line 174. See also Reed, T. E., Jenouvrier, S., & Visser, M. E. (2013). Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology*, 82(1), 131–144.

Line 201. See Chevin et al. 2015.

Line 250. Is there a theory reference for this? I would have thought that the plastic response to each multivariate cue would be lower than the response to a single reliable cue.

Line 253. Evidence that the most plastic species have fared best – Willis et al.

Line 420. This recommendation is a bit vague. Is there something quantitative that researchers should do?

Box. 2. An additional challenge for observational studies is teasing apart the influence of photoperiod. This may only be possible for spatiotemporal or experimental studies.

Signed,

Ally Phillimore [I sign all of my reviews]

Literature cited

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Editor's comments to the author(s):

Editor

Editors Comments for the Author(s):

reviewers were quite critical of a number of aspects of the article. In the end, I think the biggest issue is one of communication. The authors need to focus their arguments much more clearly and deliberately.

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