

2 August 2019

Dear Dr. Alyssa Findlay:

We propose a Review Article in *Nature Climate Change* entitled ‘Trophic phenological mismatch: Disconnects between underlying theory and climate change responses’. As requested, we provide below a full synopsis of our manuscript here, beginning with the background of the topic, followed by the basic structure of the article.

**Background**

Climate change is causing phenological shifts—changes in the timing of life history events—that vary across species as well as between functional groups and trophic levels. Such species-specific variation in response to climate change has led to changes in phenological synchrony—the relative timing of key activities among interacting species. These changes in synchrony can have fitness consequences (e.g., Post and Forchhammer 2007)—often termed ‘phenological mismatch’—with cascading effects on ecosystem-level properties in some contexts. However, these effects on fitness are not consistent across all systems (e.g., Burthe et al. 2012) and do not always scale up to the population level.

Recent theoretical and empirical studies based in single systems have aimed to improve predictions and address these diverse findings. Moreover, recent work has aided our understanding about when and where mismatches are likely to occur. Yet—while there is general agreement that predicting phenological mismatches is critical for determining the extent to which pair-wise species interactions, communities, and ecosystem function (e.g. pollination) will be affected by climate change—we still have no substantive ability to predict the outcomes of shifts in phenological synchrony due to climate change.

Here, we argue that much of the difficulty in predicting the consequences of climate change-driven shifts in synchrony is due to a disconnect between ecological theory and current empirical approaches used in studies of phenological mismatch. We argue that current methodological inconsistencies across studies and intrinsic differences across systems make it difficult to test the relevant underlying ecological theory in the context of climate change. Without better evidence, we cannot attribute variation in findings of phenological match vs. mismatch across studies to species, site, or more specific mechanisms. Further, without an understanding of the mechanisms underlying the well-documented patterns in phenological shifts, our ability to make accurate predictions about species’ responses, and species’ interactions, to climate change remains limited.

We focus on the widely-cited Cushing match-mismatch, or trophic mismatch, hypothesis, the most commonly applied hypothesis concerning consumer-resource interactions in this literature. We show how advances could come from direct tests of the hypothesis and clear definitions of baselines, when possible. Our aim is not to put forward additional hypotheses about the context in which phenological mismatch will occur, which has been reviewed extensively elsewhere (e.g., Miller-Rushing et al. 2010; Renner and Zohner 2018, Visser and Gienapp 2019), but rather to guide the study of phenological mismatch by outlining the path forward to developing robust climate change predictions that can scale up to inference across sites and systems.

**Structure**

Although the Cushing hypothesis has been applied to other types of interactions (e.g. mutualism), we limit our discussion to antagonistic interactions between consumers and their food resources, which are the most well-studied empirically and theoretically.

1. *Overview of the main ecological theory*- We define the Cushing hypothesis, and its associated predictions and assumptions.
2. *Disconnect between theory and empirical studies-* Weoutline the divide between the hypothesis and the empirical studies using a systematic literature review of phenological mismatch. From this search, we examine 43 observational studies.
   1. *Testing the Cushing hypothesis-* We review the array of potential mechanisms underlying the match-mismatch hypothesis (e.g., life history trade-offs, bet-hedging strategies, food web theory).
      1. *Data requirements-* We discuss the type of data required to robustly test the hypothesis (e.g., per capita estimates of fitness, equivalent data for consumer and resource).
      2. *Current state of the literature*- We show how the type of data currently collected by researchers testing or applying the mismatch hypothesis in the context of climate change rarely provides a strong test of the hypothesis.
   2. *Testing pre-climate change conditions*- We show how baselines—which are rarely defined—are critical to mechanistic understanding and robust predictions.
      1. *Identifying pre-climate change baselines*- We define the concept of pre-climate change baseline and show from our systematic review how few studies consider or define a pre-climate change baseline.
      2. *Implications of not identifying pre-climate change baselines-* We show that without a defined baseline, studies assume conditions of stationarity, and thus may incorrectly attribute the cause of synchrony changes to climate change over other drivers, and make inaccurate predictions.
      3. *Identifying proximate cues-* We discuss the importance of identifying the proximate phenological cues of consumer and resource in order to accurately predict whether climate change will lead to a mismatch.
3. *Towards robust forecasting of phenological mismatch*- We discuss how changes to research methodologies could rapidly advance our understanding and help forecast of the impacts of climate change on ecological communities—the ultimate goal of most of the phenological mismatch literature.
   1. *Testing fundamental theory*- We discuss how different approaches (e.g., long-term data, experimental studies) can be used to test multiple mechanisms and define key baselines.
   2. *Defining baselines-* We discuss different approaches to defining a baseline (e.g., using inter-annual variation in abiotic conditions, hindcasting etc.).
   3. *Final thoughts on forecasting*- We briefly discuss how the field could move beyond forecasting a specific system and towards diverse systems, as well as forecasting longer-term demographic responses due to mismatch with continued climate change.

**Novelty**

The context in which phenological mismatch will occur has been reviewed extensively elsewhere, most recently by Visser and Gienapp (2019). Their review outlines a conceptual framework about the eco-evolutionary consequences of phenological mismatch, but does not consider these consequences in the context of climate change, provide a systematic review of the literature, or a guide for forecasting.

Our manuscript is the first to highlight the data-theory discrepancy on the topic of phenological mismatch. By doing so, we believe our paper will help shape the future path of the field and help improve forecasts of the impacts of climate change on ecological communities—the ultimate goal of most of the phenological mismatch literature. Forecasting the ecological impacts of climate change has implications for a diverse audience—from land managers to climate scientists. It will also provide the framework for building the required depth in evidence across studies to determine general quantitative patterns and their underlying mechanisms, an approach not currently possible given the current state of the field.

Finally, we believe this article will have broad interest to readers of *Nature Climate Change* as the consequences of phenological mismatch could influence varying levels of biological organization (e.g., populations to ecosystems) with potential impacts on important global feedbacks (e.g. climate-carbon cycles). Moreover, given the possible effects on plant and herbivore life cycles, this article will have relevance for growers, breeders, forest and fishery managers etc.

This paper is authored by experts on phenological synchrony and phenological methods who bring a combined 20 years of experience in this area.

I hope that you will find it suitable to submit to *Nature Climate Change*, and look forward to hearing from you.

Sincerely,



Heather Kharouba (First author)

References:

Burthe, S., Daunt, F., Butler, A., Elston, D. A., Frederiksen, M., Johns, D., Newell, M., Thackeray, S. J. and Wanless, S. 2012. *Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web.* Marine Ecology Progress Series, 454: 119-133.

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W. and Post, E. 2010. *The effects of phenological mismatches on demography*. Philosophical Transactions of the Royal Society B: Biological Sciences, 365: 3177-3186.

Post, E. and Forchhammer, M. C. 2007. *Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch*. Philosophical Transactions of the Royal Society B: Biological Sciences, 63: 2367-2373.

Renner, S. S. and Zohner, C. M. 2018. *Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates*. Annual Review of Ecology, Evolution, and Systematics, 49:165-182.

Visser, M. E., and Gienapp, P. 2019. Evolutionary and demographic consequences of phenological mismatches. *Nature ecology & evolution*, 1.