

7 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 this article is unsolicited, we provide 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 (Ovaskainen et al. 2013; CaraDonna et al. 2014; Thackeray et al. 2016). Such species-specific variation in response to climate change has led to changes in the relative timing of key activities (phenological synchrony) among interacting species (Kharouba et al. 2018). These changes have caused fitness consequences (Post and Forchhammer 2008; Plard et al. 2014; Doiron et al. 2015)—often termed ‘phenological mismatch’ (Box 1)—and have influenced ecosystem-level properties in some contexts (Burkle et al. 2013), but not influenced fitness in other circumstances (Vatka et al. 2011; Burthe et al. 2012) or had consistent effects at a demographic-level (e.g. Reed et al. 2013). Recent theoretical (Johansson et al. 2015; Bewick et al. 2016) and empirical studies (e.g. Samplonius et al. 2016) based in single systems have worked to improve predictions and address diverse findings. Moreover, recent work has improved our understanding about when and where mismatches are likely to occur (e.g., Gienapp et al. 2014; Thackeray et al. 2016). 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 (O’Connor et al. 2012; Chmura et al. 2018).

Here we focus on the widely-cited Cushing match-mismatch, or trophic mismatch, hypothesis (1974), 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 2010; Renner and Zohner 2018, Visser and Gienapp 2019), but rather to help guide the study of phenological mismatch by outlining a path forward to develop 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 (Kudo and Ida 2013)), we limit our discussion to antagonistic interactions between consumers and their food resources.

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.
   1. *Testing the Cushing hypothesis-* We review the diverse 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 systematically reviewed the phenological mismatch literature and examined 43 observational studies. 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 are assuming conditions of stationarity, potentially wrongly attributing the cause of synchrony changes to climate change over other drivers and predicting climate change will necessarily lead to a decline in consumer’s fitness.
      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).
   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 (11). Their review outlines a conceptual framework about the eco-evolutionary consequences of phenological mismatch. Their review does not thoroughly consider these consequences in the context of climate change nor did the authors conduct a systematic review of the literature.

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. 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). This paper is authored by experts on phenological synchrony and phenological methods who bring a combined 20 years of experience in this area (8, 12-14).

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

Sincerely,