

**Title:** Trophic phenological mismatch: Disconnects between underlying ecological theory and climate change responses

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## **Abstract**

Many researchers hypothesize that climate change will lead to phenological mismatches—where the timing of critical life history events between interacting species becomes desynchronized with potential negative consequences for those interacting species and their ecological communities. Yet, evidence documenting negative impacts on fitness is mixed. The most common ecological theory that underlies these studies is the Cushing match-mismatch hypothesis. It offers a testable hypothesis that—when combined with a system’s pre-climate change baseline—can predict the consequences of desynchronized phenology due to climate change. However, a review of the current literature shows that no study has collected the data required to provide strong tests of this major hypothesis, making it difficult to assess support for it. Further, 74% of studies fail to define pre-climate change baselines in their study system, making predictions about climate change impacts on consumer fitness difficult. Moving the field of phenological mismatch forward—from documentation of mismatch towards forecasting mismatches due to climate change—requires higher quality data (e.g., long-term data, experiments that clearly link timing to fitness and test extremes). Such data must critically enable the testing of fundamental hypotheses and defining of key baselines. We highlight how improved approaches could rapidly advance our mechanistic understanding and thus allow robust predictions of shifts with continuing climate change.

## **Introduction**

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). These shifts have led to fitness consequences in some cases but not in all or at all levels (e.g., Ramula et al. 2015). Such species-specific variation in response to climate change has led to changes in the relative timing of key activities among interacting species (phenological synchrony, Kharouba et al.

2018). These changes can have fitness consequences (Post and Forchhammer 2008; Plard et al. 2014; Doiron et al. 2015)—termed ‘phenological mismatch’ (Box 1)—and influence ecosystem-level properties in some contexts (Burkle et al. 2013). However, these changes do not always influence fitness (Vatka et al. 2011; Burthe et al. 2012) or have consistent demographic effects (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 mismatch 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 general framework 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 in much of the literature currently. We show below how 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).

We focus on the widely-cited Cushing match-mismatch, or trophic mismatch, hypothesis (Hjort 1914, Cushing 1969, 1974, 1990), 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), 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.

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. Below, we provide an overview of the Cushing hypothesis then outline the divide between the hypothesis and the empirical studies using a systematic literature review of phenological mismatch. We next discuss how current approaches are impeding greater progress in the field, and 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.

### ***Overview of the main ecological theory***

The Cushing match-mismatch hypothesis is the most common ecological theory underlying phenological mismatch studies. This hypothesis predicts the often-shown concave-down curve between a component of consumer fitness and relative timing between the consumer and its resource (Hjort 1914, Cushing 1969, 1974, 1990; Figure 1). While this curve has been applied across many ecosystems (e.g. Winder and Schindler 2004; Vatka et al. 2011; Arula et al. 2014), the theory originally emerged from the marine fisheries literature as a way to explain the variation in population recruitment of fish stocks.

Based on life-history theory, the Cushing match-mismatch hypothesis implicitly suggests that selective pressure should cause the consumer to temporally ‘match’ the peak of its most

energetically demanding period with the peak of resource availability (Figure 1), and thus has the highest fitness. **Given this strong selective pressure**, if there is any change to the relative timing of the interaction, there will be a decrease in fitness associated with this period for the consumer (i.e., a mismatch), thus producing a concave-down curve (Figure 1). For example, if a consumer (e.g. adult bird) reproduces too early in the spring (Figure 1b) and the resource has not yet emerged, the offspring will risk starvation. At the curve's limits, this component of consumer fitness should fall to zero when the change in relative timing is sufficiently large (Figure 1). For example, the early offspring (Figure 1b) can only survive so many days without food.

This hypothesis is based on two important assumptions. First, the resource is the major controller on consumer fitness (i.e., strong interaction strength, bottom-up control; Cury et al, 2003). Second, the consumer and resource must present a certain degree of seasonality (e.g., resource is only available for part of the year; Durant et al. 2005; Durant et al. 2007), limiting the optimal period for growth and reproduction for the consumer. If neither of these assumptions is met, then fitness consequences due to changes in the relative timing of the interaction will be either weak or non-existent.

We make two other clarifications related to the way we apply the hypothesis here. First, Cushing's (1990) use of the term 'mismatch' is focused on the 'match' having the highest fitness. In other words, a fitness component of the focal species is maximized at phenological synchrony. While other terminology has been suggested (Visser and Gienapp 2019), we follow Cushing's definition of mismatch and its connections with fitness, which is in line with numerous other studies (e.g., Durant et al. 2007; Kerby et al. 2012; Johansson et al. 2015). Second, we discuss the hypothesis following Cushing, as if it considers a narrow definition of fitness, whereby it is defined by a single component, for example reproductive success, and where trade-offs between reproduction and other components are likely.

## ***Disconnect between theory and empirical studies***

In its original state, the hypothesis has been debated, contested and criticized, particularly in the marine literature (Leggett and DeBlois 1994; Durant et al. 2007). In part because, although a relatively simple hypothesis, it is inherently difficult to test in the field, an assertion even Cushing himself made. Indeed, the shape and strength of the relationship of the curve varies greatly across observational studies (e.g., Philippart et al. 2013; Reed et al. 2013; Plard et al. 2014; Atkinson et al. 2015). While some have suggested that this is because of data limitations and the model's implication of complex multitrophic dynamics (Durant et al. 2007; Kerby et al. 2012), we argue that there are two key theoretical areas that make it difficult to determine whether this hypothesis is widely supported in the context of climate change: studies often fail to rigorously test the Cushing hypothesis and/or test pre-climate change conditions (Figure 2). Below, we introduce the current objectives of the phenological mismatch literature and then discuss these two areas.

To put our argument in context, we systematically reviewed the phenological mismatch literature. From this search, we examined 43 observational studies that met our criteria (see Appendix for details) for evaluating the effects of a change in relative timing on the fitness or performance (hereafter referred to as performance) of the consumer. The majority of the studies (27/43) focused on: i) documenting how climate change is affecting the timing of a trophic interaction and how those changes have affected the consumer's performance; and ii) evaluating the roles of abiotic and biotic factors in influencing synchrony. The ultimate goal of these studies was to predict the impacts of climate change on ecological communities (hereafter called 'climate change' studies). Our database also included studies (16/43) whose aim was to understand the underlying processes related to timing (e.g., coevolution, life history trade offs, food web dynamics) that drive consumer or resource dynamics (hereafter called 'fundamental studies'), independently of climate change. Another divide across studies were those that measured performance of the consumer at the individual level (28/46 interactions; hereafter

referred to as ‘life history studies’) vs. those at the population or community level (18/46 interactions; hereafter referred to as ‘population/community studies’) (see Table 1).

#### i) Testing the Cushing hypothesis

The Cushing hypothesis offers testable predictions of the magnitude and direction of fitness changes in response to climate-change driven shifts in synchrony. To date, much research in the biological impacts of climate change literature has focused on the direct relationships between organisms and the abiotic environment (e.g., Menzel et al. 2006, Chen et al. 2011) rather than testing predictions about the outcomes of species’ responses to changes in abiotic factors (Lavergne et al. 2010; O’Connor et al. 2012; Mouquet et al. 2015; Barner et al. 2018). However, progress on the Cushing hypothesis requires rigorously testing the assumptions and ultimate mechanisms from a diversity of ecological and evolutionary theory (Figure 2). This represents the major challenge of the hypothesis and—we argue—may be why support for it has been so mixed.

Many mechanisms can produce the Cushing curve, and they vary across systems, space and time. Here we focus on the ultimate mechanisms related to life history theory and food web theory. Mechanisms predicted by life-history theory (Box 1), for example, trade-offs between fecundity and mortality, breeding and bet-hedging strategies (Figure 2), can produce the Cushing curve—as consumers maximize their fitness through ideal timing with their primary resource—this forms the theoretical basis for the original hypothesis. A species’ breeding strategy (e.g., whether a consumer provisions its offspring with resources acquired prior to reproduction or during the breeding period) influences how well-timed a consumer will be with its resource (Kerby and Post 2013). Similarly, bet-hedging, a strategy that has evolved to allow organisms to cope with temporal and spatial environmental heterogeneity (Levins 1968), has often been suggested to be involved in the evolution of phenological traits and can influence how ‘matched’ interacting species are (Lof et al. 2012). The Cushing hypothesis, however, is

also connected to food web theory which focuses on predator prey dynamics (Box 1) and is related to the timing of a consumer to its food resource.

Identifying the ultimate mechanisms (e.g., a specific life history trade-off) relates to the likelihood that the key assumptions of the Cushing hypothesis are met (Figure 2; Johansson et al. 2015). For example, if mechanisms such as density dependence or top-down population regulation are thought to be at play, then the first assumption of the hypothesis is unlikely to be met (Durant et al. 2013; Johansson et al. 2015). Even when both of the assumptions of the Cushing hypothesis have been met, identifying the ultimate mechanism is critical to predicting how interactions will respond to climate change (discussed in more detail in the next section; Figure 2). Given the diversity of theory related to the Cushing hypothesis and therefore potential diversity in the outcomes in consumer performance (e.g., magnitude, direction) due to phenological shifts in synchrony, the better our mechanistic understanding is of these patterns, the more robust our predictions will be (e.g., steepness of the Cushing curve).

Studies deviate in what forces they hypothesize control the peak in the food resource (a critical component of the Cushing curve and a key assumption, see Figure 1 and 2). For example, in aquatic systems—where top-down forces are generally more influential compared to terrestrial systems (Shurin et al. 2005)—many studies suggest that the resource peak is controlled by release from, or predation by, a consumer (Carpenter and Kitchell 1996; Shurin and Seabloom 2005; Borer et al. 2006). If the resource peak is controlled by release from a predator rather than abiotic factors, then the first assumption of the hypothesis is unlikely to be met and the subsequent predictions from the Cushing hypothesis are unlikely to hold. This is a very different hypothesis from others that suggest seasonality in the environment produces the resource peak (Hampton et al. 2006). In terrestrial systems, the relative contribution of direct vs. indirect effects on consumer dynamics remains poorly understood (e.g. Boggs and Inouye 2012) and these two hypotheses can result in different types of effects on population dynamics.



220 a) *Data requirements*

221 The diversity of ecological theory that can produce the basic shape of the Cushing curve  
222 means that different researchers may collect very different data depending on what mechanism  
223 they suspect underlies the curve in their particular system or what their main objective is.  
224 Researchers studying the hypothesis from the lens of life history theory require per capita  
225 estimates of fitness, including measurements of fecundity and mortality, and how they vary  
226 across ontogeny; such measurements allow researchers to assess fitness consequences at the  
227 level of selection (i.e., the individual) and to directly link any fitness changes to timing. Studies  
228 addressing the Cushing hypothesis from the perspective of food web theory require equivalent  
229 data on the consumer and resource but do not require per capita fitness consequences for the  
230 consumer.

231 Strong tests of the Cushing hypothesis include clear tests of the assumptions alongside  
232 tests of multiple potential mechanisms underlying relationships between phenological synchrony  
233 and consumer performance. To accomplish this, equivalent data would ideally be assessed for  
234 both the consumer and resource—at the level of the individual when possible. Equivalent data  
235 for the consumer and resource facilitate testing assumptions and multiple mechanisms related  
236 to the Cushing hypothesis at once. Without at least population-level data on the resource, it is  
237 difficult to test the second assumption of the hypothesis; for example, resource abundance can  
238 be used to determine the likelihood that consumers will encounter enough resource at the tails  
239 of their temporal distributions, thus defining the degree of seasonality in the resource. Per-capita  
240 data on the resource, when available, also extend our mechanistic understanding beyond the  
241 consumer, thus improving our ability to make predictions of climate change-driven phenological  
242 mismatches for the consumer-resource interaction in its entirety. For example, fine-scale data  
243 on the resource are needed to fully incorporate feedbacks between the consumer and resource  
244 (e.g., Thackeray 2012; Durant et al. 2013), measure interaction strength (which informs a key  
245 assumption of the hypothesis, Miller-Rushing et al. 2010), and accurately predict changes in

resource abundance due to climate change. Together, these data help to determine the wider implications of phenological mismatches for the community (e.g., Nakazawa and Doi 2012; Revilla et al. 2014).

*b) Current state of the literature*

Currently such data are non-existent in this literature (i.e. none of the pair-wise interactions we found had individual-level data for both the consumer and resource). Of the interactions we examined with per-capita performance data on the consumer (i.e. life history; n=28 interactions), none had equivalent measures of performance on the resource (Table 1). For the majority of these interactions (18/28), the researchers measured performance at the community level for the resource (e.g. biomass; Table 1) and many had no measure at all for the resource (6/28 interactions; Table 1). As expected, researchers that measured population- or community-level data on the consumer (n=18 interactions) collected equivalent data on the resource and consumer (e.g. abundance). For the majority of these interactions, researchers also collected population-level (7/18) or community level data for the resource (7/18) (Table 1). Across all life history and population/community interactions, researchers measured per-capita performance on the resource for only one interaction (Philippart et al. 2003).

Part of these discrepancies may stem from differing generation times—studies that can easily observe a resource curve shaped by predation often focus on organisms with generation times on the scale of days to week. For example, aquatic studies that focus on phytoplankton as the resource may observe many generations in one summer while a terrestrial study focused on caterpillars in temperate areas would generally observe a comparably smaller number generations (e.g. 1-2, depending on latitude and species for caterpillars). When populations turn over too quickly to track individuals, researchers struggle to collect robust data on per capita fitness. The fundamental difference in the scale of generation times pervades aquatic/terrestrial comparisons, particularly at lower trophic levels (Borer et al. 2005; Shurin et al. 2005; Gruner et

al. 2008), and may drive the difference in the objectives of aquatic vs. terrestrial studies in the phenological mismatch literature. Indeed, the majority of researchers studying aquatic-based interactions in our review approached the Cushing hypothesis from the perspective of populations or communities (15/20 interactions), whereas researchers approached terrestrial-based interactions from life-history theory (23/26; Table 2).

A further divide across studies may come from the size, and population size, of the consumer, properties correlated with generation time: it can be difficult to collect per capita fitness data when consumers are too small and numerous, ultimately making it difficult to track the fate of individuals. In cases where individuals can be distinguished, marked and monitored, it is possible to gather per-capita data; otherwise data are more likely to be aggregated at the population or community-level. In these cases, we may be unlikely to overcome the discrepancy between studies conducted at the individual level and those at the population level. Of the life history interactions, the majority of consumers were birds (19/28) and mammals (6/25; Table 2). Comparatively, invertebrates were measured at the population or community level and the vast majority were aquatic (11/12) (Table 2). Therefore, only certain classes of organisms are tested for each category of mechanisms and in one type of biome, further limiting generalizations across systems.

This places the phenological mismatch studies on a continuum: at one end, aquatic studies focus generally on food web mechanisms, collect equivalent data on the consumer and resource but no per-capita fitness data and at the other end, terrestrial studies focus on life history theory from the lens of the consumer, collect individual-level data on the timing and fitness of the consumer, with much less information on the resource. The fundamental problem with these approaches is that researchers test only one piece of the much larger field of mechanisms that could underlie the Cushing curve. Though it is highly possible that both food web and life history theory together explain many of the consumer-resource systems studied, data limitations make it hard to assess mechanisms related to both theories at once.

Consequently, most studies do not actually provide strong tests of the Cushing hypothesis, making it difficult to refute the hypothesis if no evidence is found, a prevalent issue in ecology and evolution (Betini et al. 2017). If researchers find their proposed mechanisms explain little of the variation they observe, they rarely have the data to test alternative hypotheses.

Without strong support for the Cushing hypothesis (i.e., relative timing explains substantial variation in consumer fitness and clear patterns that align with predictions), the mechanisms underlying it will likely be uncertain. This uncertainty can be caused by two reasons: (1) hypotheses that are not mutually exclusive (i.e. different mechanisms yield the same predictions). For example, the relative timing of an interaction will change in the same direction regardless of whether temperature (or some other abiotic factor) directly or indirectly affects a resource's peak; or (2) considering multiple mechanisms yields different predictions than considering only a single mechanism. For example, researchers have pointed out how a broader perspective on life history, such as including other sources of mortality beyond those related to resource access or alternative resource types (Samplonius et al. 2016), can lead to alternative predictions than the synchrony predicted by the Cushing curve (Singer and Parmesan 2010; Johannsson & Jonzen 2012).

#### ii) Testing pre-climate change conditions

Applying the Cushing hypothesis to understanding—and ideally predicting—the consequences of climate change for interacting species requires more than testing the assumptions and underlying mechanisms of the hypothesis (Figure 2). Meeting the assumptions of the Cushing hypothesis and understanding the mechanisms driving it are just the first step for predictions. Researchers still need an understanding of the system dynamics before climate change and the phenological cues that affect the timing of consumer and resource levels to predict what shifts in the climate have—and will—do to the timing and fitness of the players

(Figure 2). Below we discuss these steps in more detail.

*(a) Identifying pre-climate change baselines*

The concept of a pre-climate change baseline (i.e., defining the range of natural variation) is rarely, if ever, considered by phenological mismatch studies; yet, establishing a baseline in a system has important implications for the Cushing hypothesis in both climate change and fundamental studies. Of the studies we considered, only 26% (11/43) of the studies began before the early 1980s, the same time that pronounced recent climate change began (Solomon et al. 2007). Even in this subset of studies, not all studies had more than three years of data (2/11 had only one or two years of data for inference). This is also an issue with the phenological synchrony literature, which does not necessarily consider the ecological consequences of shifts in synchrony (Kharouba et al. 2018). Even those studies with time-series that extend into decades before the 1980s do not explicitly define a pre-climate change baseline in synchrony (but see Philippart et al. 2003; Adrian et al. 2006; Arula et al. 2014).

*(b) Implications of not identifying pre-climate change baselines*

There are several major implications of not establishing a pre-climate change baseline (Figure 3). First, studies without a baseline are implicitly assuming conditions of stationarity (i.e., a constant underlying probability distribution) before climate change occurred (Figure 3a; Wolkovich et al. 2014). This is problematic when climate change has led to non-stationarity to different extents in different systems (Figure 3a). Without a defined pre-climate change baseline in the system, we do not know whether, and to what magnitude, we should predict a divergence in synchrony due to climate change (Figure 3a). It is then further difficult to determine how much of the observed change in the interaction can be attributed to climate change or some other driver, for example nitrogen deposition (Edmondson 1994), land use change (Sala et al. 2000), species introductions (e.g., Ricciardi et al. 1998; Fritts and Rodda 1998; Verschuren et al.

2002;), or natural variation. Thus, knowledge of the pre-climate change baseline may rule out climate change and identify other drivers, which is key for conservation management decisions for threatened species.

Second, these studies confound a pre-climate change baseline with the peak of the Cushing curve: that is, they assume that fitness was highest before climate change began because the consumer's timing was well matched to the resource's (i.e. the synchrony baseline; Box 1; Figure 3b; Singer and Parmesan 2010). The resulting prediction is that climate change will necessarily change the relative timing of the interaction (i.e. non-stationarity) leading to a decline in the consumer's fitness (Figure 2, Figure 3b). However, without knowledge of the pre-climate change baseline, it is difficult to predict the direction and magnitude of fitness consequences due to climate change-driven shifts in synchrony, especially when alternative conditions could be the baseline (Figure 3b,c).

An alternative hypothesis put forward by Visser et al. (2012) suggests that in some contexts, 'adaptive mismatch' (i.e. when the most energetically demanding period of the consumer is not lined up with the peak resource availability for many individuals in the population; Box 1; Figure 3b) could be occurring. They postulate that in some systems, asynchrony for many individuals in a population might be adaptive due to life-history tradeoffs, where lifetime fitness is maximized but not necessarily individual components of fitness (e.g., Singer and Parmesan 2010; Visser et al. 2012) or due to a combination of life-history trade-offs and competitive advantage from intra-specific competition (Iwasa et al. 1983; Wiklund et al. 1977; Johansson et al. 2014). This could happen when a consumer cannot measure the timing of its resource well (Singer and Parmesan 2010), for example; in this scenario, some individuals would appear mismatched, while others would appear matched. This scenario may persist most often when fitness consequences of mismatch are not extremely high; otherwise it could lead to population extirpation (Figure 3b). However, whether a synchrony vs. asynchrony is considered to be adaptive for the consumer, and thus whether fitness decreases are predicted with climate

change, will depend on which fitness components have been measured in the study (e.g. reproductive success vs. lifetime fitness) and whether asynchrony is adaptive at the individual or population-level (Visser et al. 2012; Johansson et al. 2014; Visser and Gienapp 2019). For example, fitness may increase or decrease with climate change in bird species where there is a competitive advantage of hatching early, depending on whether short-term or long-term populations responses are considered (Johansson et al. 2014).

In either hypothesis (i.e. synchrony vs. adaptive mismatch; Figure 3b), a pre-climate change baseline of asynchrony (Box 1; Figure 3c) could occur through several mechanisms. Shifts in the drivers of phenology for the consumer or resource (e.g., nutrient enrichment) could have pushed the system away from synchrony before climate change. An asynchronous baseline would also be predicted—at times—by a co-evolutionary arms race (Thompson 1994): when the resource is ahead in the arms-race, asynchrony would be the predicted baseline (Figure 3c), this would then shift back towards synchrony when the consumer is winning the arms race. In systems where asynchrony or some type of transient conditions might be the baseline state, our ability to anticipate the effects of climate change will be even more challenging as these transient conditions could lead to vastly different predictions under climate change (Figure 3c). For example, interactions might become less (i.e. fitness increases) or even more mismatched (i.e. fitness decreases) with climate change (Figure 3b-c).

The pre-climate change baseline is also dependent on the ultimate mechanism(s) generating the Cushing curve (Figure 2). For example, a species that provisions its offspring with resources acquired during the breeding period (i.e., an income breeder; e.g., West Greenland caribou: *Rangifer tarandus*) is predicted to have a pre-climate change baseline of synchrony, whereas a species that provisions its offspring with resources gained prior to reproduction (i.e., a capital breeder; e.g., muskoxen: *Ovibos moschatus*) is more likely to have a baseline of asynchrony (Kerby and Post 2013). Therefore, researchers need an understanding of the system dynamics before climate change began.

Establishing a pre-climate change baseline also has implications for fundamental studies that aim to understand the underlying processes of consumer-resource dynamics. A pre-climate change baseline would determine whether the system is most probably in equilibrium or in transient dynamics. For example, life-history trade-offs, including those that can cause patterns predicted by the Cushing hypothesis, predict some form of equilibrium conditions, but if climate change has pushed the system away from a previous baseline, then the system might likely be in a transient phase rather than at equilibrium (Figure 3). To this end, an understanding of the system's pre-climate change baseline state is important for providing context and even designing fundamental studies.

#### *(c) Identifying proximate cues*

For climate change to lead to phenological mismatch, the underlying assumption is that changes in climate will drive changes in the relative timing of species interactions. Therefore, predicting how climate change will affect the relative timing of a consumer and resource, and potentially the fitness of the consumer, will also depend on the identification of the proximate phenological cues of the consumer and resource (Figure 2). For example, climate change is likely to lead to fitness declines for a consumer that has a pre-climate change baseline of synchrony and that shares different environmental cues with its resource (Figure 2). Currently, relatively little is known about the similarity of cues for interacting species across trophic levels (Chmura et al. 2018). Finally, predictions will also depend on how phenological cues will change under climate change scenarios (Chmura et al. 2018).

#### **Towards robust forecasting of phenological mismatch**

While the Cushing hypothesis provides testable predictions regarding the consequences of phenological mismatch in response to climate change, it is uncertain how much support there



is for it. Here we have suggested two major reasons for this, both of which provide a clear path forward for progress in the field (Figure 2). First, most studies do not actually provide strong tests of the Cushing hypothesis because (a) studies do not collect equivalent fitness and population data on the consumer and resource, and (b) multiple mechanisms are not evaluated. This makes it difficult to refute the Cushing hypothesis if no evidence is found. Unless researchers are extremely clear about the mechanistic hypotheses they are testing, progress will continue to be slow. Second, pre-climate change baselines are not defined in the majority of studies in this literature. Lack of a relevant baseline makes it difficult to determine whether recent phenological mismatch can be attributed to climate change and limits our ability to understand and predict the direction and magnitude of phenological mismatch due to climate change.

Moving the field of phenological mismatch forward (i.e., from documentation towards forecasting) requires higher quality data that enables the testing of fundamental hypotheses and defining of key baselines. Below, we highlight how new approaches can improve testing of the Cushing hypothesis. These approaches will also provide the framework for building the required depth in evidence across studies to determine general quantitative patterns in phenological mismatch and their underlying mechanisms, an approach not currently possible given the state of the field.

#### (i) Testing assumptions and mechanisms of the Cushing hypothesis

By having the potential to test multiple mechanisms and define key baselines, the integration of long-term data (i.e. that start before the 1980s) and an experimental approach in a single system represents the 'gold standard' to move the field of phenological mismatch forward. However, in the absence of long-term data, the integration of observational data across a spatial gradient in climatic conditions, and thus variation in the relative timing of the interaction, with an experimental study can provide a powerful approach to test multiple

hypotheses. For example, Samplonius et al. (2016) combine descriptive and experimental data to test many confounding factors and key assumptions of the Cushing hypothesis in their system (e.g., ontogenetic dietary shifts, habitat quality). Consequently, they advanced the field by providing a strong test of the Cushing hypothesis, demonstrating that this hypothesis is pertinent in their system, and ruling out competing hypotheses related to habitat quality.

Independent of whether observational data is available, experiments can be used to test and disentangle multiple mechanisms, for example they can disentangle direct from indirect effects or abiotic mismatches from phenological ones (e.g., Bauerfeind and Fischer 2013; Rudolf and Singh 2013). Experiments provide a high degree of inference about mechanisms that descriptive data alone cannot provide. For example, Berger et al. (2014) manipulated water temperature, stratification depth and the presence/absence of zooplankton in lake mesocosms to separate the direct effects of light and temperature on spring plankton dynamics from effects mediated through the consumer. They showed that temperature had little effect on zooplankton phenology and performance suggesting that climate change is unlikely to result in phenological mismatch in this system. The extrapolation of their results to the lake ecosystem are uncertain, however, given the lack of long-term data in the system and the uncertainty about phenological cues for *Daphnia* in the field (Berger et al. 2014).

Baselines themselves can also be used to test multiple mechanisms (see next section for discussion about defining baselines). Researchers with long-term data in systems where multiple attributes of the environment have changed at different points can leverage this variation to test which driver is most closely associated with shifts in phenological mismatch through time. For example, many lakes experienced large changes in nutrient inputs in the 1960s and 1970s (e.g., George 2012; Lake Washington (Edmondson 1994)), before the onset of recent climate change in the early 1980s. Researchers can test different breakpoints with their long-term data to determine where the non-linearity or non-stationarity most likely began (Figure 3a), thus providing evidence for which factor is likely to be the major driver of changes in

phenological synchrony. For example, studies have shown that changes in nutrient inputs have had larger impacts on plankton dynamics in Lake Washington than warming over the past three decades (Law et al. 2009; Francis et al. 2014).

Higher temporal resolution data in some systems may help with teasing apart different mechanisms and testing the assumptions of the Cushing hypothesis. Regardless of aim, ideally, sampling frequency should be relative to the life history of the species of interest. For example, testing any mechanism related to life history theory requires data about ontogeny. In the great tit-winter moth system, caterpillar biomass sampling is usually conducted a few times a week (e.g., Votka et al. 2014). Given that the larval stage of the winter moth life cycle is typically 4-6 weeks (Holliday 1977; Tikkanen et al. 2000), this sampling frequency allows researchers to obtain an accurate estimate of growth and development for this life cycle stage. In the lower trophic levels of aquatic systems, where there is often quick turnaround between producers and consumers, it can be difficult to determine how strong of an influence producers have on consumers and vice versa (Carpenter and Kitchell 1996). Without higher temporal resolution data, it is difficult to assess whether this key assumption of the Cushing hypothesis (i.e., the dependence of the consumer on the producer) is supported. In cases where there are multiple short, potentially overlapping, generations, determining the seasonal order of the consumer vs. producer is necessary to assess the degree of dependence of the consumer on the producer.

Higher temporal resolution data will also help determine the seasonal availability of the consumer and resource, the other key assumption of the Cushing hypothesis (Figure 1b-d). For example, temperate aquatic and terrestrial systems differ in how most organisms survive the winter. While many terrestrial plants and herbivores have dormancy phases during the winter, in aquatic systems some zooplankton are never in complete dormancy (i.e., they remain at low densities), and thus do not fully meet the assumption of the hypothesis. Without more frequent data, accurately estimating the seasonal distribution of the lower trophic levels of some aquatic systems will be difficult. Nevertheless, some aquatic studies have been successful in achieving

daily sampling frequency of lower trophic levels (e.g., Wiltshire et al. 2008), suggesting that—though more challenging—critical assumptions of the Cushing hypothesis can be tested in aquatic systems.

## ii) Defining baselines

Researchers with long-term data have the potential to test whether synchrony vs. asynchrony was the pre-climate change baseline (Figure 2; Figure 3). By testing for a clear peak in fitness across years in relation to the relative timing of the interaction (i.e. evidence for the synchrony baseline) in the pre-climate change data, researchers can place their system on the Cushing curve (Figure 3). Whenever possible, incorporating the most energetically expensive part of the consumer's annual cycle or estimating when the measured phenological phase occurs relative to the most expensive part (e.g., food demands of the great tit, *Parus major*, chicks are highest 9 days after hatching, the phenological phase most commonly monitored; Gebhardt-Henrich 1990; Keller and van Noordwijk 1994; Visser et al. 2006) will help define a peak in consumer fitness. If there is no clear peak in fitness, then well-designed experiments (in systems where possible) that have the ability to reveal the limits of the curve (i.e. where consumer fitness reaches zero) can be used to reject the hypothesis of an asynchrony baseline. Knowledge of when/if different resources are available (e.g. Samplonius et al. 2016) and whether the interaction type changes throughout the season (Borcherding et al. 2010) can also help describe the limits of the curve.

Where long-term data are not available, there is no perfect solution to the challenge of defining a baseline. Researchers with multiple years of data may be able to use inter-annual variation in abiotic conditions (e.g., temperature) to define a baseline, where closer-to mean conditions represent a proxy for a historical baseline and, for example, cooler vs. warmer years act as alternatives to pre- and post- climate change, respectively (e.g., Gullett et al. 2013; Francis et al. 2014). However, extrapolation from short-term datasets only work if the species

responses' to varying climate themselves are not in flux, a criterion difficult to meet in many systems already (Visser et al. 2006; Singer and Parmesan 2010). Null modeling to simulate historical data may be another alternative (e.g., Dornelas et al. 2014; Sgardeli et al. 2016; Kharouba et al. 2018). Null models can help put the magnitude of observed changes in phenology and performance since significant climate change began into context and to quantify how much variation may be due to noise (i.e., factors other than climate change; Kharouba et al. 2018).

When not all required data are available across a long time period, the integration of experimental and observational data for a single system could again be a useful approach (Figure 4). For example, in one study the performance data for an insect herbivore (winter moth; *Operophtera brumata*), and its main host plant (common oak; *Quercus robur*) are not available for more than 10 years from a single location (van Asch and Visser 2007); however, different researchers manipulated the timing of larval emergence relative to bud break to test for support for the Cushing hypothesis (Tikkanen and Julkunen-Tiitto 2003; Figure 4). Although the strength of the relationship may vary across populations (e.g., Visser et al. 1998; Charmantier et al. 2008), a synthesis of the findings from the two approaches (i.e. observational and experimental) can shed light on the state of our knowledge of the system and can guide future research. Here, for this system, we learned where the interaction is currently placed along the curve, how little of the curve is sampled with a 10 year post-climate change time-series, and that—without a clear baseline—it is difficult to predict how the performance of *O. brumata* will be affected by changes in phenological synchrony. Given the knowledge about the Cushing curve for this interaction, modelling pre-climate change baselines based on knowledge of phenological cues using a hindcasting approach (Senner et al. 2016; Deacy et al. 2017), process-based phenological models (Chuine and Régnière 2017), and/or phenologically explicit consumer-resource models (Bewick et al. 2016) could help to fill in information about the interaction before climate change began. Experiments could help define the parameters of a process-based model that could then

elucidate that mechanisms may—or may not—appear feasible for the interaction (Chuine and Régnière 2017).

### iii) Final thoughts on forecasting

Given the complexity involved, accurately forecasting phenological mismatch in response to climate change is a major test of ecological theory and methods. It requires a mechanistic understanding of the processes involved to ensure robust predictions of changes in consumer performance (e.g., steepness of the Cushing curve). Previous work has identified factors that will help predict **when** a mismatch is more likely to lead to a population decline but this work is largely theoretical. While we have outlined how to work around data limitations, the best tests of mismatch theory will come from data-rich systems where the energetic links between consumer and resource species are well understood. With such information in hand, researchers can then begin to consider forecasting longer-term demographic responses due to mismatch with continued climate change. Forecasting of phenological synchrony can be built off climate projection forecasts whenever phenological cues for both species (Chuine and Régnière 2017; Chmura et al. 2018) are well known. Forecasting longer-term demographic responses to phenological mismatch will require data about lifetime fitness for the consumer and comprehensive data on the resource, a standard that, to our knowledge, has yet to be met by any empirical study to date.

As more information is gathered across habitats and diverse consumer-resource interactions, forecasting should eventually move beyond a system-specific approach and towards forecasting diverse systems through a multi-level modeling approach based on our mechanistic understanding of what drives mismatch. Such a model would be built on mechanistic studies of the mismatch hypothesis that carefully measure the fitness, phenologies, interactions and other still-unknown important attributes of systems. The model would then allow researchers to measure currently unknown but critical attributes of species, sites, and

ecosystems that control the shape, strength and uncertainty surrounding the Cushing curve. But progress towards such an approach requires the ability to combine knowledge from across diverse systems into one complex but well-defined mechanistic model. As we have outlined above, most current data in the field make it hard or impossible to compare across systems. Given intrinsic differences between aquatic and terrestrial systems, progress may be accelerated if these systems are considered separately before being combined. Nevertheless, without improved methods – to test multiple mechanisms and define pre-climate change baselines – the goal of general predictions of the ecological consequences of shifts in phenological synchrony will remain well out of reach.

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## Box 1. Glossary

**Cushing match-mismatch hypothesis-** this hypothesis postulates that the consumer should temporally 'match' the peak of its most energetically demanding period (i.e. reaching maximum fitness) with the peak of resource availability and if there is any change to the relative timing of the interaction, there will be a decrease in fitness for the consumer (i.e., a mismatch). At the curve's limits, consumer fitness should fall to zero when the change in relative timing is sufficiently large. (Figure 1)

**Phenological synchrony-** is based on the phenological differences between pair-wise interacting species and is a measure of the overlap between two events, each of which has a temporal distribution. Synchrony implies that the peak of the most energetically demanding period of the consumer with the peak of resource availability completely overlaps. Importantly, this term does not incorporate fitness consequences for either species.

**Phenological mismatch** - decreases in consumer fitness associated with changes in the relative timing of key life history activities among interacting species. Importantly, this mismatch occurs between interacting species; it does not occur with the abiotic environment. It also considers a narrow definition of fitness, whereby it is defined by a single component, for example reproductive success, rather than total fitness.

**Baseline-** a representative or benchmark time series of conditions that describes the species interaction. A baseline incorporates the historical range of variability in the relative timing of the interaction.

**Synchrony baseline-** a hypothesis that before climate change, the most energetically demanding period of the consumer was at the same time of peak resource availability, and thus consumer fitness was at its maximum (i.e. a match).

**Asynchrony baseline** - a hypothesis put forward by Singer and Parmesan (2010) that before climate change, the most energetically demanding period of the consumer was not timed to the peak resource availability, and thus consumer fitness was not at its maximum. This could occur for various reasons (e.g., co-evolutionary arms race, other transient dynamics).

**Adaptive mismatch hypothesis-** a hypothesis put forward by Visser et al. (2012) that postulates that, in some systems, life-history trade-offs will promote asynchrony for many or most individuals in a population.

**Stationarity-** any stochastic process with a constant underlying probability distribution

**Life-history theory-** the study of the causes and consequences of the diversity of life history strategies based on evolutionary theory.

**Food web theory-** the study of the patterns, causes and consequences of food-web structure.

953 **Tables**

954 Table 1. A comparison across studies of the type of performance data collected for consumer  
955 and resource. We define a life-history study as one that collected data at the individual level and  
956 a population/community study as one that collected data at the population or community (i.e.,  
957 across species) level. Counts in the table are numbers of individual pair-wise interactions  
958 (n=46).  
959

			Resource performance				
			Life-history		Population/Community		
			None	Individual	Population	Community	Totals
Consumer performance	Life-history	Individual	6	0	4	18	28
	Population/	Population	1	1	7	7	16
	Community	Community	0	0	1	1	2
Total			7	1	12	26	46

960

961 Table 2. A comparison across studies of the type of performance data collected for the  
 962 consumer across systems and taxonomic group. Counts in the table are numbers of individual  
 963 pair-wise interactions (n=46).  
 964

		System		Taxonomic group			
		Aquatic	Terrestrial	Invertebrate	Vertebrate		
Level of consumer performance	Individual	5	23	1	2	19	6
	Population	14	2	9	4	2	1
	Community	1	1	2	0	0	0
	<b>Sub-totals</b>	<b>20</b>	<b>26</b>	<b>12</b>	<b>6</b>	<b>21</b>	<b>7</b>
	<b>Totals</b>		<b>46</b>				<b>46</b>

965



## Figures

Figure 1. Conceptualization of the Cushing match-mismatch hypothesis represented by the curve in panel (a). The hypothesis postulates that a consumer should temporally ‘match’ the peak of its most energetically demanding period with the peak of resource availability and thus have the highest fitness (a,c); if there is any change to the relative timing of the interaction (e.g., because the consumer shifts its phenology earlier (b) or later (d) relative to the resource), there will be a decrease in the consumer’s fitness (i.e., a mismatch) (a). At the curve’s limits, consumer fitness should fall to zero when the change in relative timing is sufficiently large (a). Curves in panels b-d represent the seasonal changes in the abundance of the consumer (black) and resource (red) where during some part of the year abundance declines to zero.

Figure 2. A simplified flow diagram for forecasting climate change effects on consumer fitness as predicted by the Cushing hypothesis. First, both major assumptions must be met; if, for example, consumer density is the major controller on its own fitness, then no further work is warranted. If both assumptions are met, forecasting requires both knowledge of the ultimate mechanisms (which often relate to testing the first assumption) and the pre-climate change baseline. In some cases, the mechanism predicts the pre-climate change baseline (i.e., in both our examples); we colour mechanisms in whether they predict both pre-climate change synchrony and asynchrony depending on specifics (purple), synchrony (blue) or asynchrony (red). Note that multiple mechanisms may operate in many systems, and that this figure is in no way exhaustive, but rather serves to highlight a pathway that researchers can take.

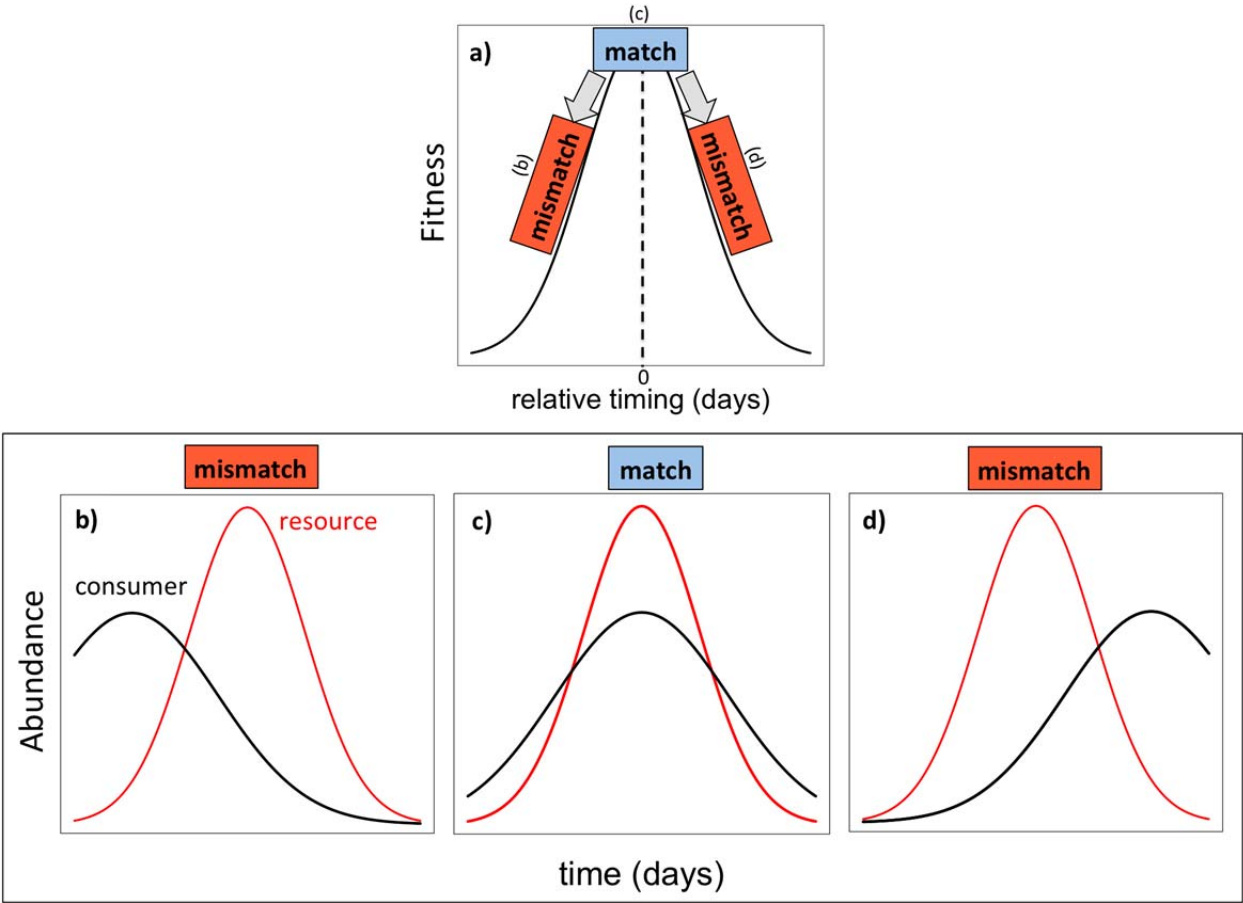
Figure 3. Conceptualization of key assumptions, and resulting implications for climate change predictions, often made about the Cushing hypothesis when pre-climate change baselines are not defined. (a) Differences in the phenological time-series of a consumer-resource interaction, where red represents the resource and black represents the consumer, during conditions of

stationarity; when the environment becomes non-stationary (shown here just after 1980) the consumer and resource each can shift in varying directions, representing the range of recent documented phenological shifts (e.g. Thackeray et al. 2016), leading potentially to shifts in synchrony. (b) Most studies in the current literature assume that consumer fitness was highest before climate change (i.e., a match) leading to a 'synchrony baseline'. However, an alternative hypothesis put forward by Visser et al. 2012 (i.e., what they term as the 'adaptive mismatch' hypothesis) postulates that that, in some systems, life-history trade-offs will promote asynchrony for many or most individuals in a population. This hypothesis may lead to asynchrony as a pre-climate change baseline (see c; 'asynchrony baseline' (Singer and Parmesan 2010)) or a population where few individuals are matched; we show this latter possibility here (i.e. 'adaptive mismatch hypothesis with synchrony baseline'; our representation of this hypothesis is at the population level). The implications for climate change predictions for the two hypotheses are illustrated: If the synchrony baseline is supported, then climate change will necessarily lead to declines in consumer fitness. If the 'adaptive mismatch hypothesis' with a synchrony baseline is supported, climate change may not lead to large declines in consumer fitness. (c) Without establishing a pre-climate change baseline and defining where an interaction falls along a curve, it is difficult to predict how climate change-driven changes to the relative timing of the interaction may affect consumer fitness. For example, with an asynchrony baseline, climate change could lead to an increase or decrease, or to varying magnitudes, in consumer fitness depending on how the relative timing of the interaction changes. For panels b and c, blue boxes represent the range of conditions detected in the system over a long time period.

Figure 4. Case study illustrating how the integration of experimental (a) and observational data (b) in a single system (the winter moth, *Operophtera brumata*, and common oak, *Quercus robur*) can provide evidence for the Cushing hypothesis and highlight weakness in our predictions. (a) The results from two related experiments (green and red points) where the authors manipulated

the number of days that neonates (i.e. early instar larvae) spent without food (green points; first experiment) and the emergence times of larvae relative to budburst (red points; second experiment). These experimental results provide strong support that the first assumption of the Cushing hypothesis (i.e., the resource is the major controller on consumer fitness) is met in this system, much stronger support than observational data provide (b), which show inter-annual variation in relative timing between median egg hatch date of *O. brumata* and the median bud opening date of *Q. robur* from 1996-2005 in the Netherlands. Horizontal error bars represent the lower and upper quartiles of the data. Further, these observational data cover only 10 years, all post-climate change, (b) include only a small portion of the x-axis of the Cushing curve, and do not include any performance data of *O. brumata*. This makes it difficult to define the pre-climate change baseline and thus accurately predict how the performance of *O. brumata* will be affected by changes in phenological synchrony due to climate change (Figure 3). Nevertheless, long-term data such as these can be used to test the underlying assumption that changes in climate will drive changes in the relative timing of species interactions by identifying the proximate phenological cues of the consumer and resource. In this case the inter-annual variation provides evidence that the herbivore and host plant differ in some cues (Figure 2). For both panels, negative values along the x-axis denote where egg hatching occurred before bud opening (i.e. time without food), whereas positive values indicate egg hatching occurred after bud opening (i.e. time with food). Raw data for (a) was obtained from Tikkanen and Julkunen-Tiitto (2003; Figure 3), while for (b), data was retrieved from Van Asch and Visser 2007 Figure 2. Consequently, data are from different populations. See Appendix for more details.

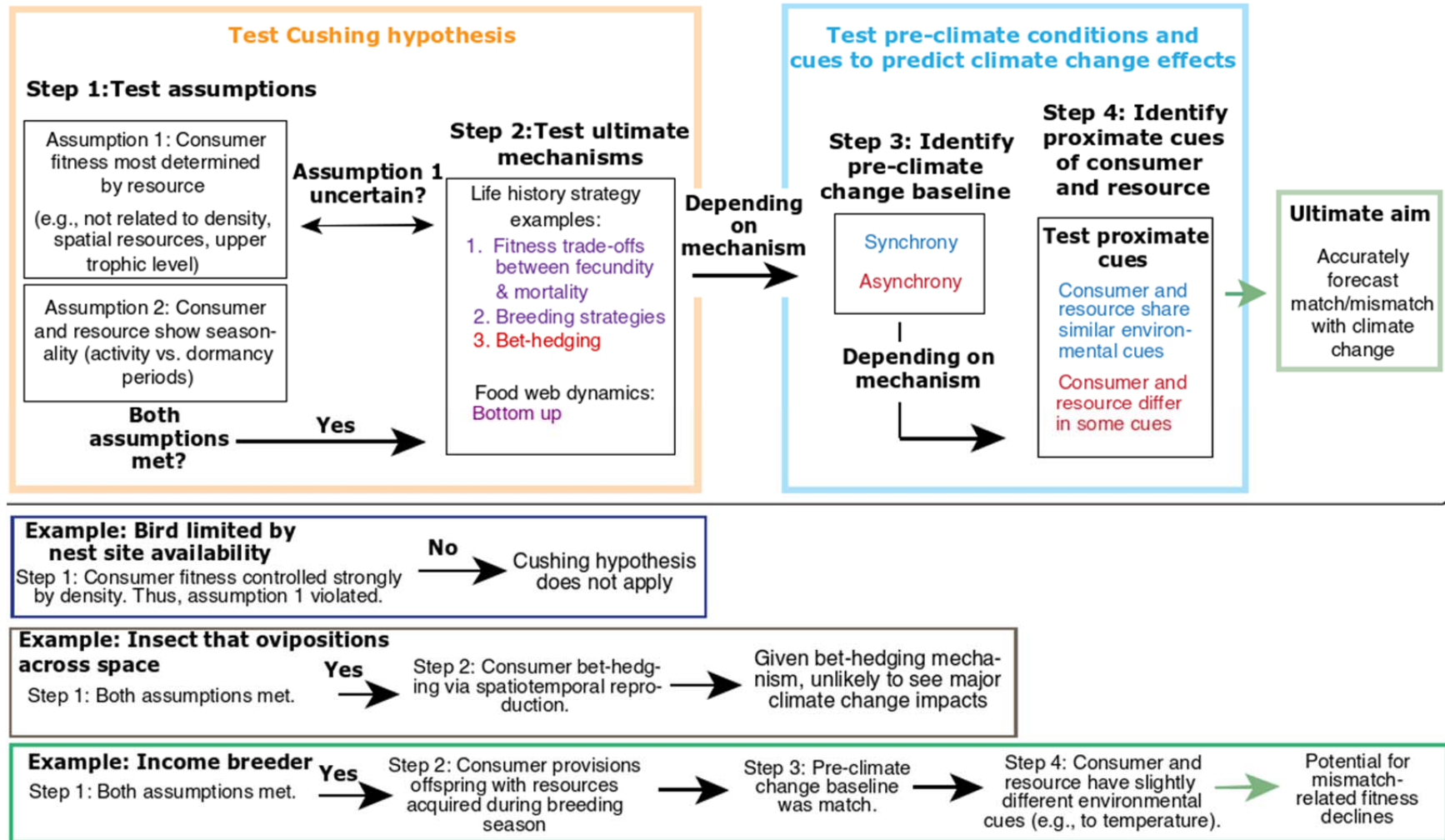
1040     Figure 1.



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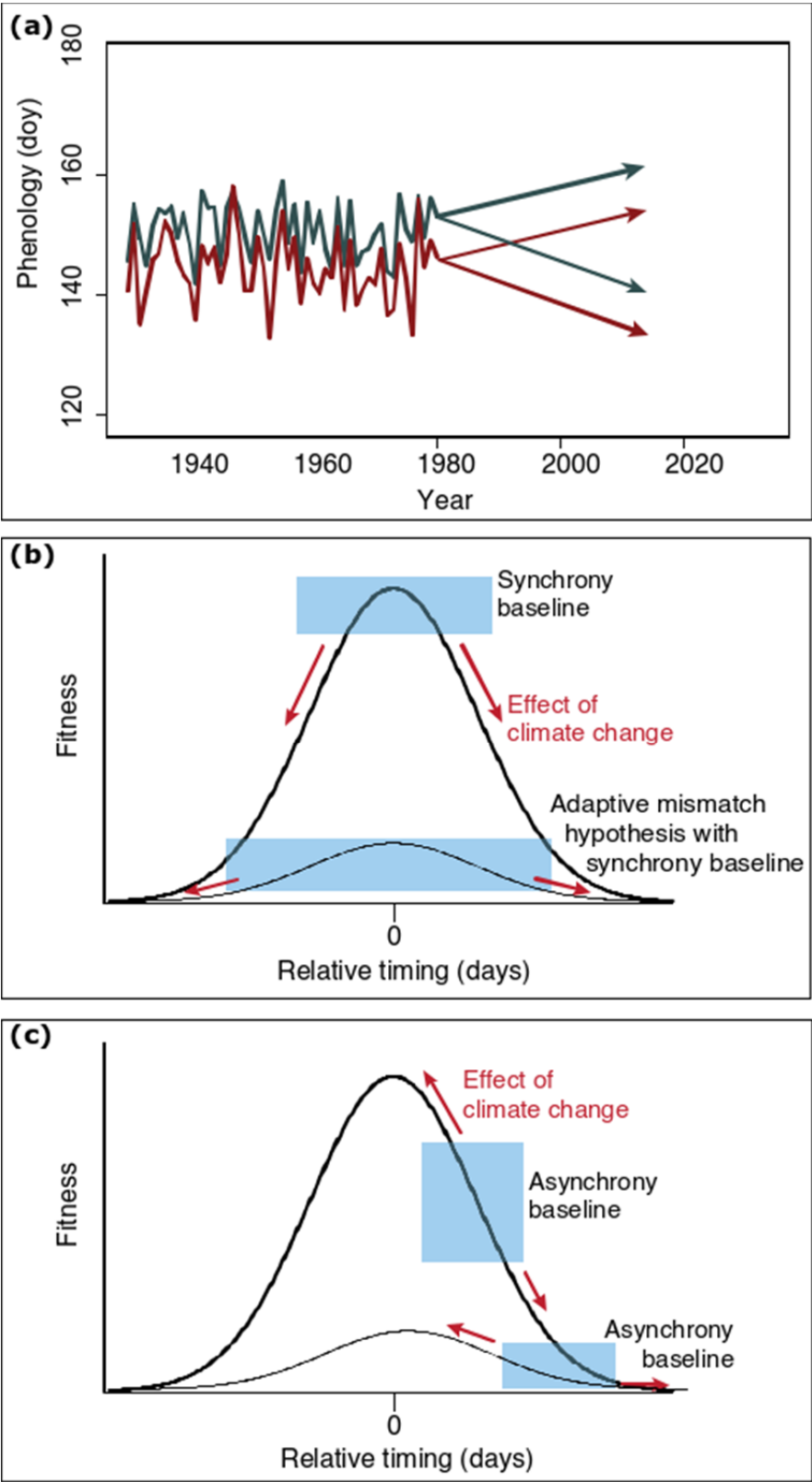
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## Using the Cushing hypothesis to predict and forecast consumer fitness with climate change



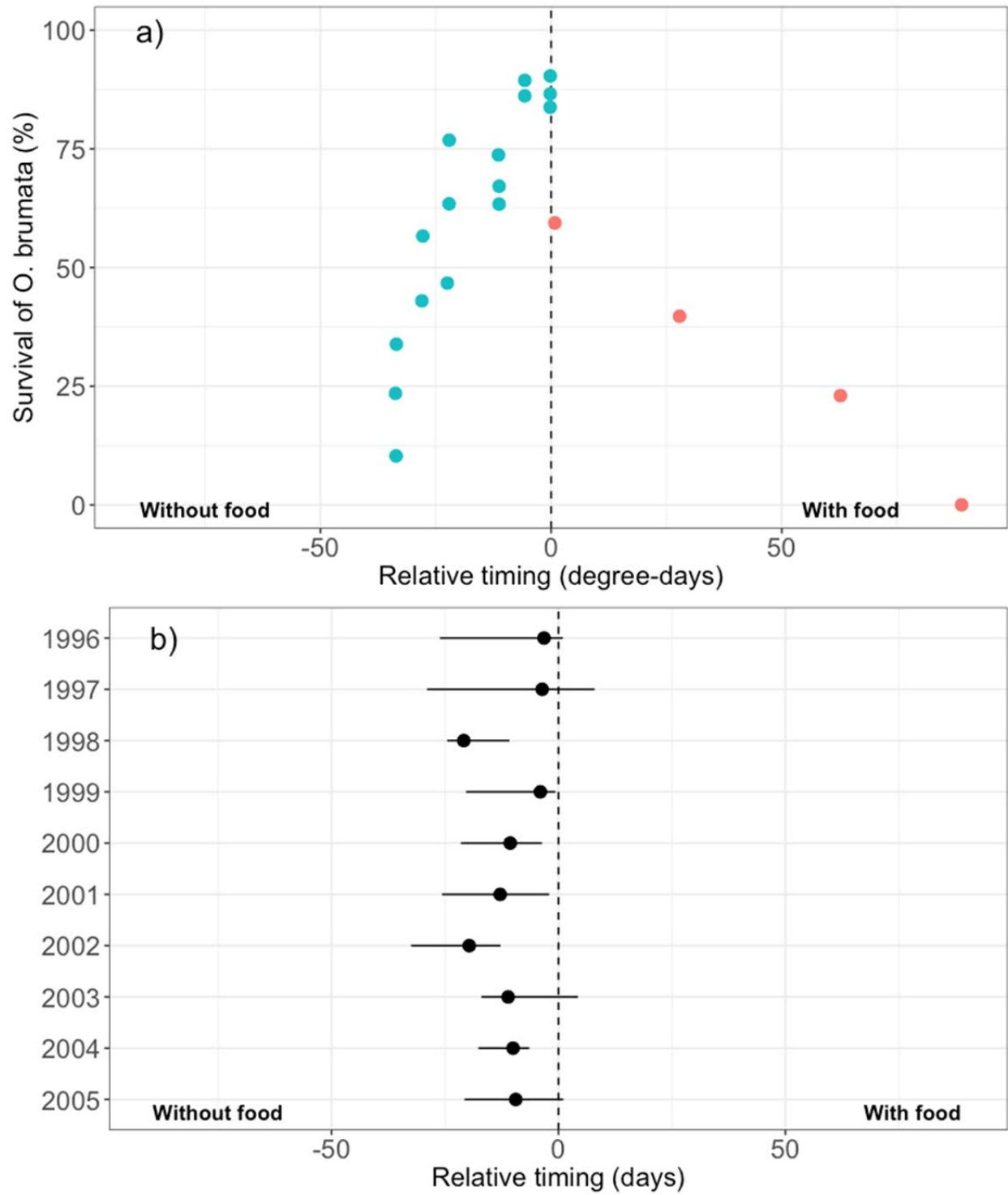
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1045 Figure 3.



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1047 Figure 4.



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## **Appendix**

### *Literature search*

We located papers relating phenological data from trophic interactions to fitness and/or performance of the consumer and/or the resource by conducting keyword searches in ISI Web of Science published up to June 2017. Keywords included phenolog\* AND mismatch\* OR synchron\* AND interact\* AND (fitness\* OR performance\*). Our initial search netted 2906 papers so we further refined our search by excluding categories that included engineering and computer science. This resulted in 393 papers. From these, we focused on observational studies and excluded studies if they did not: (1) measure phenology directly (e.g. used derived measures of phenology, such as NDVI or spring temperature); (2) measure phenology of at least one of the species; (3) quantitatively link consumer fitness or performance to the relative timing between consumer and resource; and (4) explicitly state that the two species interacted (e.g. specifying type of interaction). Estimates of consumer fitness or performance (i.e., growth or development) had to be direct estimates (e.g. we did not include studies that used diet proportions to measure consumer performance) and included a range of proxies, for example, growth, survival, abundance. To ensure a reasonable sample size and to include studies across different major biomes, we included interactions that were resolved to the family-level and below. To reduce redundancy within systems, we only kept studies that were unique across pairs-location-year combinations. If more than one measure of phenology was included, we chose the one used by the authors to calculate mismatch and examine its impact on performance.

Our final review included 43 studies with 46 pair-wise species interactions (3 studies had 2 interactions). These studies encompassed terrestrial, marine and freshwater ecosystems as well as a large latitudinal gradient.

### *Summary of studies and interactions*



We classified studies as 'climate change' or 'fundamental' depending on whether they mentioned climate change in the abstract or in the introduction of the paper. Based on the type of data collected for the consumer and resource, we classified these studies as life history (i.e. one that collected data at the individual level) or food web-based (i.e. one that collected data at the population or community (i.e., across species)). To determine whether studies had the potential to define pre-climate change baselines, we measured the study's time span and years of data based on the years where phenology data was available for both the consumer and resource, and consumer performance data was available.

#### *Additional details for Figure 4*

Raw data for panel (a) was obtained from Figure 3 in Tikkanen and Julkunen-Tiitto (2003). The data come from two related experiments where the authors manipulated the number of days that neonates (i.e. early instar larvae) spent without food (first experiment) and the emergence times of larvae relative to budburst (second experiment). In the first experiment, there were six groups of 30 larvae that spent 0, 5.5, 11, 22, 27.5 and 33 degree-days without food. In the second experiment, there were four cohorts, each separated by intervals of 3-5 days. All *O. brumata* eggs and larvae originated from laboratory stock originally from Turku, Finland whereas the foliage originated from trees near Banchory, NW Scotland.

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