Strengthening the evidence base for temperature-mediated phenological asynchrony and its impacts

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Climate warming has caused the seasonal timing of many components of ecological food chains to advance. In the context of trophic interactions the match-mismatch hypothesis (MMH) postulates that differential shifts can lead to phenological asynchrony with negative impacts for consumers. However, at present there has been no consistent analysis of the links between temperature change, phenological asynchrony, and individual-to-population level impacts across taxa, trophic levels and biomes at a global scale. Here, we propose five criteria that all need to be met to demonstrate that temperature-mediated trophic asynchrony poses a growing risk to consumers. We conduct a literature review of 109 papers studying 132 taxa, and find that all five criteria are assessed for only two taxa, with the majority of taxa only having one or two criteria assessed. Crucially, nearly every study was conducted in Europe or North America, and most studies were on terrestrial secondary consumers. We thus lack a robust evidence base from which to draw general conclusions about the risk that climate-mediated trophic asynchrony may pose to populations worldwide.

The shifting seasonal timing of key life history events, such as the budburst of trees, emergence of insects or the migration and breeding times of vertebrates, is one of the three universal ecological responses to climate warming[1,2] alongside range shifts and reductions in organismal body size[3,4]. Such shifts in phenology have provided some of the earliest and strongest evidence that rising temperatures have left a discernible imprint on the planet's ecosystems[5–8]. For many consumer species, phenological events are timed to coincide with peak abundance of a predictable food resource. However, the strength and direction of the phenological response to temperature frequently differs among species occupying different trophic levels, leading to asynchrony between resource and consumer (box 1). The consequences of such asynchrony were first studied in the early 1900s in the context of trophic interactions between fish larvae and their zooplankton resource. This generated the classic match-mismatch hypothesis[9]. Fish larvae were found to spawn at a relatively fixed date, but zooplankton phenology was more variable across years, causing annual variation in asynchrony between consumer and resource. The degree of asynchrony (referred to as mismatch by Cushing) was proposed to account for annual fluctuations in fish recruitment to the population[9]. In recent years, the hypothesis that changing temperatures might increase the frequency of costly trophic asynchrony between consumers and their resources has been increasingly discussed[10–13]. The impact of asynchronous phenological interactions on the fates of consumer species was identified as a key uncertainty in the fifth assessment report of the IPCC[14].

Phenological asynchrony and mismatch are often used interchangeably in the ecological literature, but the meaning of the term "mismatch" is more ambiguous, as it is in some cases used to imply only dissimilar responses of adjacent trophic levels[13], and in other cases implying negative impacts on the consumer[15]. In this paper we refer to "trophic asynchrony" when the consumer demand does not coincide with the phenology of the resource, and to the match-mismatch hypothesis (MMH) when asynchrony has negative impacts on fitness or populations (box 1). We note that the MMH is normally conceptualised from a unidirectional, bottom-up perspective (i.e., asynchrony leading to detrimental effects on consumers), rather than potential top-down effects upon prey and resources[16].

Asynchrony has been detected in many study systems[7,17,18], but to demonstrate negative consequences of asynchrony on the consumer (i.e., the MMH), several conditions need to be met. For trophic asynchrony to be identified as detrimental, the consumer must depend on a short, seasonally-pulsed or ephemeral resource[19–25], and it should be established whether asynchrony might be an adaptive baseline state[26–28]. Moreover, there should be negative effects of asynchrony on consumer fitness[29–34]. Ultimately, asynchrony becomes of conservation concern when it affects mean demographic parameters and leads to population declines[13,35–38]. Although components of the MMH and consequences for population trends can be identified, these are based on very few and specific study systems.

We therefore lack a general overview of how often trophic asynchrony leads to population declines.

Box 1: Glossary of terms widely used in the study of trophic asynchrony

Phenology: the study of cyclically recurring biological events, such as the seasonal timing of tree leafing, insect hatching, or animal migration and reproduction. In this work, we also use it to refer to the events themselves, as has become the norm in the literature.

Trophic level: the position that an organism occupies in the food chain. Primary consumers are herbivores (e.g., winter moth, caribou), and secondary consumers are omnivores or carnivores (e.g., great tit, herring)

Phenological sensitivity/response: the interannual variation in phenology that relates to interannual variation in a biotic or abiotic cue, for example an advance in breeding in response to temperature.

Phenological/trophic asynchrony: when the seasonal peak in consumer demand for a resource does not coincide with the seasonal peak in availability of that resource.

The match-mismatch hypothesis (MMH): poses that trophic asynchrony has negative consequences for consumer fitness or population size. This is also sometimes referred to as trophic mistiming.

Five criteria for demonstrating risks of temperature-mediated asynchrony

Here, based on ideas that have been widely discussed in the literature and which we outline above, we propose five criteria that must all be met for temperature-mediated phenological asynchrony to be both present, and causing population declines (Table 1): (1) the consumer is highly reliant on a seasonally ephemeral resource; (2) the degree of trophic asynchrony between consumer and resource phenology is increasing over the years (evidenced by time series); (3) increasing trophic asynchrony is due to differing temperature responses of consumer and resource; (4) trophic asynchrony impacts negatively on consumer fitness, and (5) asynchrony impacts negatively on population growth[37]. In Table 1 we identify some of the methods that can be used to test each of these criteria. In the next section we summarise the existing biological evidence for these criteria, with a particular focus on general insights that have emerged from multi-species studies and formal meta-analyses on questions that are pertinent to the study of the MMH. The five criteria can be seen as a best-practice framework, but we realize that each study system poses unique challenges for studying these criteria. We do not intend for their application to oversimplify the complex study of phenology, nor do we claim that they cover everything that phenological studies need to focus on.

Evidence for phenological asynchrony

Large-scale comparative analyses of phenological responses and formal meta-analyses provide ample evidence that on average spring timings are advancing at mid-high latitudes, and that species vary in their response to temperature[8,17,39]. In two large multi-species analyses based on phenological data from the UK, the phenology of secondary consumers advanced less than primary producers and consumers over the years (criterion 2)[17] and secondary consumers have a lower phenological sensitivity to temperature (criterion 3)[7]. For marine taxa, the magnitude of phenological advance varied among trophic groups, with phytoplankton, zooplankton and bony fish all more responsive than seabirds[40,41]. However, while large-scale multi-species and multi-population studies provide valuable insights into general trends and patterns of inter- and intra-specific variation in phenological responses, they do not estimate *in situ* responses for specific trophic interactions, nor do they reveal anything about fitness or population consequences. Of those studies that focus on trophic interactions known to be important to the consumer for a short period (criterion 1) most focus on a single interaction. Such studies have reported increasing asynchrony over the years (criterion 2), for example in great tits, *Parus major,* and winter moth, *Operophtera brumata*[5,42]. However, a recent analysis of the phenological time series underpinning 27 species interactions (including but not limited to trophic interactions) found that whilst the degree of asynchrony has changed over the years, the number of cases where asynchrony had increased was roughly balanced by the number of cases where asynchrony had decreased[18]. The same study also found that whilst phenology was responding to temperature in the ecological systems considered, it was not possible to attribute temporal trends in asynchrony to long-term increases in temperature (criterion 3).

Potential consequences of trophic asynchrony

The most prominent evidence for the MMH comes from intensively-studied wild systems, such as that of the reliance of great tits on winter moth caterpillars to feed their young. For these birds, asynchrony between the timing of peak nestling demand and peak caterpillar biomass has negative consequences for individual fitness and annual mean fitness[30,31]. Meta-analyses of selection estimates in the wild report consistent selection pressures for earlier phenology[43,44], but directional selection has not become stronger over time[44]. However, meta-analyses addressing selection on phenology have considered only absolute timing, rather than the timing of a consumer relative to its resource[10], so it is unclear from these studies whether selection on consumers is being driven by asynchrony with resources.

Trophic asynchrony becomes a matter of conservation concern if it impacts negatively on population size (criterion 5)[37]. Two long-term studies of great tits found no evidence of an effect of asynchrony on population size[31,45], whereas a study of several populations of pied flycatchers *Ficedula hypoleuca* in the Netherlands reported stronger population declines where caterpillar phenology was earlier[36]. The only multi-species studies on this theme that we are aware of are for birds. One of these studies found that migrant passerines breeding in European forests had declined more than resident and marsh inhabiting species, which the authors attributed to the MMH[46]. The other study found that, across 21 UK bird species, population declines were more pronounced for species that had advanced their breeding phenology least and in species whose annual productivity was most reduced by asynchrony with general insect and plant phenology.[47] However, support for the MMH was weak and not reflected by declines in breeding success of those species.

Table 1. Criteria of evidence that climate change induced trophic asynchrony is increasing and deleterious for the consumer (the MMH), with a consideration of the data and methods that can be used.

Criterion	Evidence required	Data and Methods
1. An ephemeral resource contributes a large proportion of the consumer's diet	A large proportion of the diet is typically composed of a species or food type that shows a pulsed seasonal distribution	A variety of methods for quantifying diet composition exist, including direct observation of feeding, gut content dissection, faecal/regurgitate dissection, metabarcoding and stable isotope analysis. Requires that relevant aspects (e.g., biomass, abundance) of the favoured resource are measured over time within at least one season and analysis reveals a pulsed intra-year relationship.
2. Asynchrony between consumer and resource phenology is increasing over time	Analysis of time-series of consumer and resource phenology, with a test of whether trends in timing differ and whether this leads to an increase or decrease in asynchrony	Requires a time series that covers a period of temperature change. A large number of phenological time series exist, as recorded by researchers, citizens, herbaria, etc. Statistical analysis of increasing asynchrony is easily achieved by including an interaction between year and species. Inference of whether asynchrony is increasing or decreasing requires inspection of predictions based on estimated elevations and slopes of the modelled relationships for each species[18].
3. Variation in asynchrony is driven by interannual variation in temperature	Identification of the time period(s) over which consumer and resource is sensitive to temperature. Evidence that differential temperature sensitivity is the driver	A variety of methods exist for identifying the time period over which phenology of each species responds to temperature[48–51]. Confidence in attribution can be increased by experiments[26] or by including year as a term in the model[41], thereby de-trending the phenology data[52]. Estimating temporal trends in temperature variables is also worthwhile, as differing trends may generate asynchrony[53,54].
4. Asynchrony impacts negatively on consumer fitness	A suitable measure of consumer fitness decreases with increasing asynchrony	Can be assessed within years (relative fitness) or among years (mean fitness) or both[30,31]. Depending on how asynchrony varies across individuals or years, the relationship between fitness and asynchrony may be a linear decline or a humped relationship. If the former, care may need to be taken to establish causation[55]. Ideally, models should take into account both asynchrony with peak resource and phenological distribution of the resource[56,57]. Studies of impacts on relative fitness are informative regarding selection and opportunities for adaptation, whereas studies on mean fitness may be informative regarding demographic rates[13]

5. Asynchrony impacts negatively on consumer population size, density, or growth	Negative effects of asynchrony on fitness (4) that have a negative effect on population size/growth, as assessed over multiple years	Requires long-term data on asynchrony and population size or density. The impact of asynchrony on demographic rates can be incorporated into a population model[58] or the causal pathways between asynchrony and population growth can be assessed in a structural equation model[59]. It is important to rule out a causal effect of other variables (e.g., land-use, resource availability, sea ice, range shifts) that could cause populations to change over time[24]. Such confounding effects can partially be accounted for by including year as a term to detrend the analysis[41,52]. An alternative approach involves modelling a population's ability to persist on the basis of demographic and quantitative genetic parameters[45,60].

Literature survey

We conducted a broad survey (n=109) of published work on the match-mismatch hypothesis (MMH) across terrestrial, marine and freshwater systems with the aim of: (i) examining the evidence for temperature-mediated trophic asynchrony and its impacts and (ii) identifying gaps in the evidence base, thereby allowing us to (iii) make recommendations for priority areas for future work. To this end, we extracted data from published, peer-reviewed original research in which a trophic interaction was studied in relation to any of the five criteria we proposed as vital to the MMH (Table 1). Only original studies, where the specific interaction between consumer and resource could clearly be identified were included (see supplementary information for methodological details).

Taxonomic and geographical bias in the data

The search identified 772 papers, of which the full text was found for 760. Of these, 571 were not relevant (e.g., no trophic interactions were reported, or none of the five criteria were extractable), and 80 had no extractable data, resulting in a total of 109 papers that had relevant data on 132 consumer taxa (Fig. S2). All but six of the 109 trophic interaction studies were in Europe or North America (Fig. 1). The majority of trophic interactions were terrestrial (81.5% of the data), with marine (14%) and freshwater interactions (4.5%) being scarcer. For most interactions the consumer was a secondary consumer (58%), with studies of primary (36.5%) or higher than secondary (5.5%) consumers less common. Birds made up the majority of the consumer taxa studied (53%), while 29.5% of taxa were insects, 8% were fish, 5% were mammals and 4% were crustaceans.

Testing the five criteria

The most tested criterion was criterion 1 (97% of interactions, n=128/132) - relating to dependence on a seasonally pulsed resource (Fig. 2, top panels). However, rather than conducting direct tests on the seasonal distribution of resources, 72% (n=92/128) of these included only a statement based on *a priori* knowledge of the natural history of the system that the resource was both ephemeral and important to the consumer.

Of the study systems that were tested for dependence on a seasonally pulsed resource (i.e., where the resource was ephemeral and the consumer was a specialist), 42% (n=15/36) showed such dependence. Excluding the cases where criterion 1 was not explicitly tested, criterion 2 was the most frequently tested (72% of interactions, n=95/132), relating to whether phenological asynchrony was increasing over time (Fig. 2, top panels). The remaining criteria were all tested substantially less frequently, with criterion 5 (population consequences) being tested least often (7.6% of interactions, n=10/132). Surprisingly few studies report data for criterion 3 (Fig. 2, top panels), which relates temperature to asynchrony, and this was almost never reported for marine and freshwater taxa. The distributions of criteria tested were broadly similar across consumer levels and biomes, with the exception of primary consumers for which criteria 3 and 4 appear slightly more common.

Our analysis could identify only two out of 132 consumer taxa for which all five of our criteria have been tested at least once: both of these are forest-breeding passerine birds studied in Europe - the great tit and the pied flycatcher. In a further 13 taxa, four out of five criteria were assessed. In the remaining 117 taxa, three or fewer criteria were studied, with the majority (58%, n=77/132) of consumer taxa having only two of the five criteria known (Fig. 2, bottom panels). Breaking this same analysis down to the per study level, no single study explicitly tested all five criteria (Fig. S3). This is generally due to a tendency for studies to focus on either phenology slopes (criteria 2 & 3), or the consequences of asynchrony (criteria 4 & 5). Only a handful of studies detail temporal slopes, temperature slopes, and consequences of asynchrony in one study[61–63].

Phenology slopes over time and temperature

Consumer and resource responses appear to be positively correlated across studies, with consumers showing a slight tendency to advance their phenology by less than their resource (Fig. 3). In 61% (n=58/95) of the cases, the phenology slope over time was greater for the resource than for the consumer (Fig 3a,b). For the phenological response to temperature, the consumer slope was greater than the resource slope in 59% (n=13/22) of cases (Fig 3c,d). The degree to which these patterns differ across biomes and trophic levels could not be tested with this dataset, since the number of slope estimates is too low for non-terrestrial and non-secondary consumers. Based on visual inspection, it appears that especially terrestrial secondary consumers tend to be slower-advancing than their resource. However, more data on underrepresented groups would be required to reach robust conclusions about these patterns.

Fitness and demographic consequences

Fitness consequences in relation to trophic asynchrony (criterion 4) are studied in 36% (48/132) of the consumers (Fig. 2, top panels). Consequences of asynchrony for offspring (n=44) are studied over three times as often as consequences for adults (n=14, Fig. 4), though it is possible that this reflects a research bias to study fitness components that are more sensitive to asynchrony. In 29% of consumer taxa (n=14/48), no negative effect of asynchrony on fitness was reported (Fig. 4). The least studied consequence of trophic asynchrony is its effects on population demography (criterion 5, Fig. 2, 4). In half of these interactions (n=5/10), no effect of asynchrony was reported.

Discussion

Our literature survey on the ecological impacts of temperature-mediated trophic asynchrony reveals that the full causal chain from temperature change, to temperature-driven shifts in seasonal timing, consumer-resource synchrony, and individual-to-population level impact has rarely been studied. Only two out of 132 taxa were studied for all criteria, and for the majority of study systems, only one or two out of five criteria were met. The available studies were strongly biased toward terrestrial secondary consumers (especially birds) in the Northern Hemisphere (largely Europe and North America). Notably, the effects of climate warming on trophic asynchrony in aquatic systems and in the Southern Hemisphere are understudied[64], although this could be reflective of the small amount of temperate land mass in the Southern hemisphere. Tropical studies are also under-represented, but this may partly indicate a reduced importance of temperature as a phenological cue in tropical ecosystems[8]. Crucially, demographic consequences of trophic asynchrony are the least studied of the five criteria, despite this knowledge being the most important to conservation.

Bias in the Match-Mismatch Hypothesis evidence base across biomes

Terrestrial systems were by far the most represented of the three environments that we considered, presumably by virtue of the comparative ease of collecting data on both phenology and fitness in these systems. This ease of data collection is evident in the great contribution that citizen science data collectors have made to the study of terrestrial phenology[47,65–68], which is rare for aquatic systems. Monitoring phenology of many aquatic organisms is hampered by their wide ranges and underwater habitats[69], and compounded by the logistic and financial challenges encountered during offshore research. As a result, relatively few multi-decadal phenological time series have been collected at sufficient resolution to capture seasonal changes[70,71]. Moreover, separate sampling programmes are often needed for consumer and resource (e.g., piscivorous birds and their prey)[72], and even if resources can be quantified, many aquatic organisms are generalist feeders, further adding to the difficulties in quantifying the MMH. Citizen scientists can, however, collect valuable data on the terrestrial stages of aquatic organisms (e.g., dragonflies), or aquatic seasonal events that can be observed from shore (e.g., amphibian spawning, floating algal blooms). Furthermore, with ongoing technological innovation in data collection methodologies, it may become possible to widen the aquatic evidence base for some taxa. For example, radar can be used to quantify aquatic-terrestrial subsidies based on insect emergence, providing detailed measures of the timing and size of resource pulses[73], and satellite-based observation tools are providing a wide-scale perspective on phytoplankton phenology changes[74]. It would therefore be valuable to consider how diverse data sources, and lines of evidence, can be fruitfully combined to advance our knowledge of the importance of the MMH in aquatic systems.

Despite their overrepresentation in MMH research, even in terrestrial systems there are biases and gaps in the evidence-base that extend beyond the aforementioned geographic biases (Fig 1). Of the terrestrial studies, temperate forest taxa and birds in particular predominate, which is likely due to the fact that seasonality increases with latitude. Temperate forests experience a pronounced seasonal temperature-mediated pulse in resources[46], and they present particularly suitable study systems to study individual fitness in the wild (e.g., cavity nesting birds). In aquatic systems, individual marking of philopatric seabirds and pinnipeds permits some components of fitness to be monitored[75], but this is much harder for underwater organisms[76]. Likewise, for many widely-distributed groups such as fish, invertebrates, and plankton, individuals cannot be sampled repeatedly, and populations can rarely be sampled to the extent that demographic implications of asynchrony can be assessed. On the other hand, invertebrates are more amenable to experimental study[32], and numerous national surveys of population sizes exist[77,78] that could be used to infer demographic consequences of trophic asynchrony. Another key research gap in aquatic systems involves the specific role of cross system consumer-resource interactions in mediating trophic asynchrony. For example, some freshwater consumers feed upon terrestrial resources, which represents a substantial source of nutrients[79]. The delivery of at least some of this material is strongly seasonal. Leaf fall, for example, is triggered by photoperiod in conjunction with drought and temperature[80]. Aquatic phenology research would greatly benefit from increased consideration of the synchrony between freshwater consumers and terrestrial resources.

Further challenges in studying the MMH

We recognise that studying these five criteria and improving the evidence base regarding the risks posed by the MMH will not be straightforward and we have already discussed how aquatic environments present particular challenges, but other complexities remain. While criteria 2 and 3 are perhaps the easiest to satisfy, even here challenges exist in attributing a change in phenology/asynchrony to temperature, as sensitivity estimates can be obscured by non-climate drivers or compensatory mechanisms[62,81]. For example, changing nutrient availability and light conditions can influence the seasonal timing of phytoplankton blooms[82,83], but would not be expected to affect consumer organisms in the same way. In this article we have simplified the interaction between resource and consumer to a single metric, the asynchrony between the peak demand of consumer and availability of the resource. However, as the MMH predicts that consumer fitness relates to resource availability during a particular window[9], consumers might in addition to asynchrony be sensitive to the height and width of the resource[11,37], either of which could be sensitive to temperature and exacerbate or ameliorate effects on fitness. Although the potential for resource abundance to influence fitness is widely acknowledged, it is unusual for studies on the MMH in relation to fitness (criterion 4) or population size (criterion 5) to include its effect[56,57]. We realize that especially criterion 4 may be hard to satisfy for study systems where individuals cannot be studied, which should not discourage people from working on such systems. Whilst fulfilling all the other criteria would allow one to infer whether the mismatch is causing population declines, there are clear advantages of studying individuals within populations. Apart from the fact that such data helps demonstrate causative effects of asynchrony on fitness, it can tell us whether seasonal timing will be under directional selection.

Where the resource is in fact a guild (caterpillars, phytoplankton) rather than a species, temperature-mediated shifts in the aggregate phenology may arise from a variety of processes, from similar plastic responses of different species, to changes in the relative abundance of early- and late-blooming constituent species, even when these species independently might show no or weak phenological shifts[84]. While the effect of asynchrony on the consumer may not be sensitive to these two scenarios, if we want to project phenological changes into the future we need to understand the processes that underpin community phenological responses. An obvious solution to this problem is to improve the species level resolution of sampling[85], but this can be costly and impractical in the short term, and might require new sampling approaches such as eDNA[86].

Is trophic asynchrony of conservation concern?

This review reveals a lack of robust evidence for the MMH, and even the two best studied taxa in terrestrial systems present a mixed message. In great tits, matching with the caterpillar peak has fitness impacts at both the individual and population level[30,31], but trophic asynchrony currently poses no threat to their population persistence[31,45]. Pied flycatchers also perform worse when poorly matched with the caterpillar peak[22,87], but, in contrast to great tits, declines in asynchronous flycatcher populations have been recorded in the Netherlands[36]. Nevertheless, those pied flycatcher populations have been increasing again since 2002[88]. Interestingly, pied flycatchers breed about two weeks later than tits[89], the average nest is rarely matched with the caterpillar peak[90], and a long-term study in the Netherlands found no correlation between annual mean asynchrony with the caterpillar peak and the strength of the seasonal decline in the number of recruits[91]. Moreover, pied flycatchers are more generalist than tits in the nestling diet[92], so it remains uncertain to what extent these flycatcher populations will be negatively affected by trophic asynchrony compared to specialists.

It would nevertheless be premature to conclude from this that a relative shortage of evidence for demographic consequences of trophic asynchrony constitutes evidence of absence of an effect. Even in species for which negative population consequences are not yet apparent, such as great tits, it is possible that continued increases in temperature will be problematic. Application of an integral projection model to a UK population of great tits suggested that under a high emission scenario, more rapid responses of the prey species (the winter moth caterpillar) coupled with limits to plasticity in great tit hatch date being reached, lead to an acceleration in directional selection. An increase in evolution of hatch date timing was to an insufficient degree to prevent negative consequences of trophic asynchrony, and the population in that scenario is projected to have an increased risk of extinction[93]. Such demographic approaches should be greatly expanded upon, and provide a unique way to understand which life stages will likely matter from the perspective of pathways leading to shifts in population growth rate and density[58].

Research Priorities

Based on our five criteria and our review of the literature we identify six priorities for future work to properly test the match-mismatch hypothesis and its impacts.

1. **From cause to effect - focusing on population consequences:** There is an urgent need for studies that consider the full causal chain, from climate driver to seasonal timing, synchrony, and individual-to-population level impact. In particular, we need many more tests of the impact of asynchrony on population change (criterion 5), across taxa and habitat types. This most important criterion from the perspective of conservation and policy[13,37] and yet has received the least attention. Furthermore, given that the population impacts of trophic asynchrony at one location may be buffered by matching at another location[90], we strongly advocate expanding the spatial scale of current research to include multi-population studies. This will allow the consequences of phenological shifts to be interpreted in the context of other universal climate warming responses such as range shifts.
2. **Balancing the evidence - data collection and synthesis for aquatic systems**: Despite the marine origin of the MMH, current monitoring and research has so far led to a limited understanding of the MMH in marine and freshwater systems, compared to terrestrial habitats. It is imperative for funders to continue to support time series, since with each passing year the statistical power of these to reveal patterns improves. We further recommend for underused historic records, including museum collections and naturalist observations, to be coupled with new work on these systems to create well documented long time series within a matter of years. However, we must also ask how additional monitoring approaches (e.g., eDNA, radar) might be usefully combined with “traditional” monitoring approaches, to expand the species representation, monitoring of individual states and fitness consequences, and spatial coverage of aquatic ecosystem studies, and support a broader understanding of changes in phenological asynchrony (criterion 2) and the role of temperature as a driver (criterion 3) in these systems.

3. **Environmental drivers of phenology - beyond temperature**: Here, we have addressed phenological asynchrony in relation to temperature (criterion 3), the best-studied driver. However, the environmental drivers of phenology vary geographically. For instance, at lower latitudes seasonally pulsed precipitation is a more important driver of phenology[8], and at higher latitudes the timing of snow melt is a key mechanism[94–99]. In order to gain a global perspective on the risks posed by climate-mediated phenological asynchrony poses there is an urgent need to apply our framework to alternative environmental drivers of phenology.
4. **Assessing the risks - global predictions and species traits:** We need more studies on trophic asynchrony and its drivers at different latitudes and many more to be conducted outside of Europe and North America (see Fig. 1). As data on the MMH accumulate, a fruitful approach would be to conduct comparative analyses to identify the taxonomic groups, trophic levels, environments and regions where fitness or population impacts of phenological asynchrony (criterion 4 and 5) are most likely. Based on first principles we may expect temperature-mediated asynchrony to be more frequent and deleterious when the consumers are endotherms rather than ectotherms[8], income rather than capital breeders[24,37], and at higher latitude regions experiencing the most seasonal climates and the most rapid climate change[8]. However, empirical validation of these predictions is lacking.
5. **Observing interactions - enhancing the role of citizen science**: Mass participation citizen science has resulted in millions of phenological records that underpin many of the studies quantifying phenological shifts[7,17,65,100] and can even be used to project weather records into the past[101]. A strength of these schemes is their spatial as well as temporal coverage. In some instances it is possible to identify the phenology of consumer species and their resources from existing datasets[102], but this requires the assumption that co-occurring species are actually interacting. While using data amassed over larger spatial scales (e.g., via citizen science or remote sensing) is attractive as a means to examining geographic variation in temporal

trends in asynchrony (criterion 2) and temperature sensitivity (criterion 3) or fitness consequences (criteria 4&5), care is required in matching data at a resolution that is pertinent to the trophic interaction[103,104]. Moreover, we are not aware of any study combining citizen science-derived datasets to study the impacts of asynchrony of specific trophic interactions on population change (criterion 5). Therefore an opportunity exists for development or extensions of citizen science schemes to collect data on the phenology of species interactions across trophic levels and on the fitness and/or population sizes of the consumer.

6. **Clarifying the concept - "asynchrony" or "mismatch"**: There exists a degree of terminological inconsistency in relation to the MMH, which may confuse attempts at achieving a common understanding of the potential importance of this phenomenon. Many studies that claim to address "mismatch" identify the conditions that could lead to greater asynchrony, but stop short of explicitly testing whether asynchrony leads to any negative consequences for the consumer. Where no evidence for negative repercussions is presented we encourage authors to use the term "asynchrony", rather than "mismatch", which implies a negative consequence.

Concluding remarks

Temperature-mediated trophic asynchrony and its consequences are widely discussed in global change research and have been intensively studied over the past two decades. In this study we have presented five criteria that together provide a causal chain to explicitly demonstrate the risk that temperature-mediated asynchrony poses to populations, which we hope will strengthen future work. In an extensive review of the literature we found that no single study and only two study systems have tested all five criteria, with a clear deficit of studies considering the impact of asynchrony on population size, which is the most important criterion from a conservation perspective[37]. This means that at present we cannot state from the literature that temperature-mediated trophic asynchrony will have a widespread negative impact on consumer population size or growth. We identify six research priorities, which need to be tackled to get a comprehensive understanding of the frequency and magnitude of trophic asynchrony and its impacts on consumers. A more consistent approach to the study of the match-mismatch hypothesis and its population consequences at the global scale will allow us to better target conservation efforts and provide much needed evidence for possible consequences of one of the most intriguing impacts of climate change on global biota: phenological change.

Figure legends

Figure 1. Locations of studies on phenological asynchrony identified by our analysis, subdivided by biome (light blue = freshwater, dark blue = marine, orange = terrestrial) and consumer trophic level (triangles = primary, squares = secondary, circles = >secondary). There is a clear geographical bias of studies, with a considerable overrepresentation of Europe and North America.

Figure 2. Individual criteria tested across taxa (a,b), and the total number of criteria tested per taxon (c,d). The most tested criteria (a,b) were 1 “ephemeral resource” and 2 “phenological change over the years”. The total number of criteria tested (c,d) was two out of five for most taxa, and all five criteria were tested for only two out of 132 taxa (c,d). The left panels (a, c) are divided by trophic level, and the right panels by biome (b, d).

Figure 3. Consumer versus resource slopes in relation to year and temperature. Symbol shapes represent consumer trophic level (triangles = primary, squares = secondary, circles = >secondary), colour represents biome (light blue = freshwater, dark blue = marine, orange = terrestrial) and larger symbols are from longer time series (average 21 years, range 6 to 119 years). The solid diagonal line represents an equal rate of change by consumer and resource. Where the resource slope < 0, points above the line represent systems where resource phenology is advancing by more than that of the consumer, whereas points below the line represent systems where consumer phenology is advancing more rapidly than resource phenology. Where resource slope > 0, points below the line represent systems where resource phenology is delaying by more than that of the consumer, whereas points above the line represent systems where consumer phenology is delaying more rapidly than resource phenology.

Figure 4. Number of taxa in which consequences of trophic asynchrony were studied, divided into those where the effect reported was negative or neutral (statistically non-significant, no positive effect of trophic asynchrony was ever reported for this taxon). Results are clearly biased toward juvenile rather than adult life stages.

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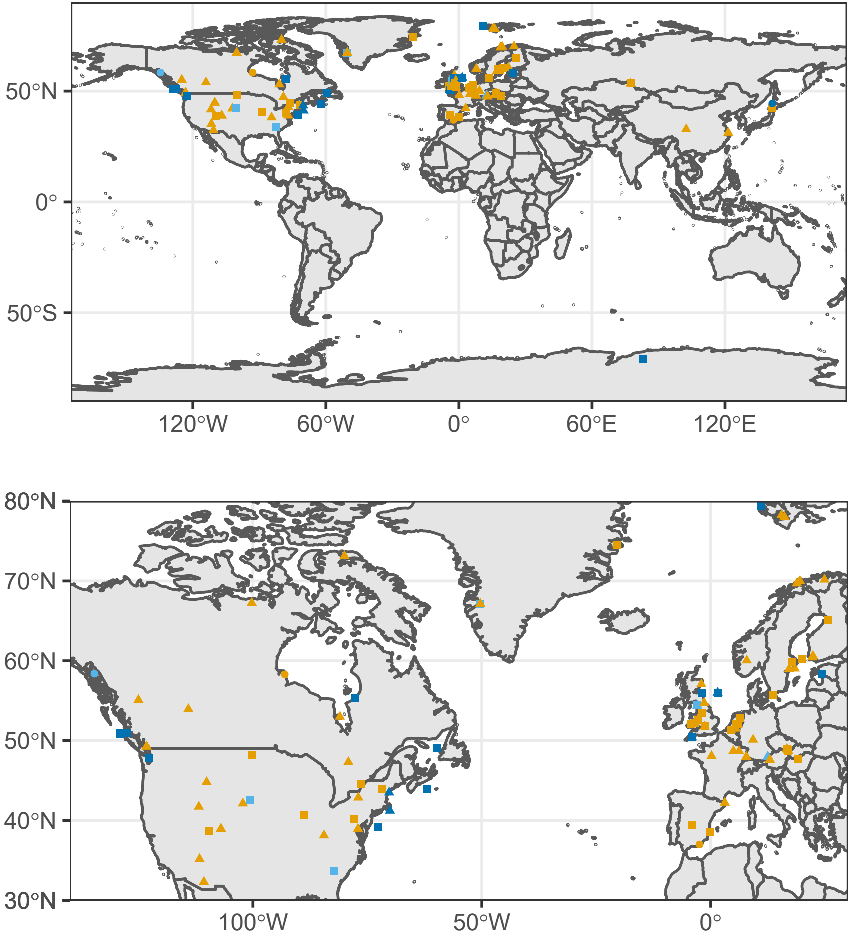
Author contributions

JMS, ABP, AA, CH, KK, SJT, JJA, MDB, JJ, KHM, JWPH, EGS, ØV, JCW, DZC, EFC, FD, TH, OWL, NP, and BCS contributed to conceiving ideas. All authors contributed to editing the manuscript. JMS, ABP, AA, CH, KK, SJT, JJA, MDB, JJ, KHM, JWPH, EGS, ØV, and JCW extracted data for the analyses. JMS, ABP, AA, CH, KK, and SJT contributed to writing the manuscript. JMS and ABP expanded on the initial ideas to determine the structure and content of the manuscript and wrote most of it. JMS conducted the analyses.

Competing Interests

The authors declare no competing interest.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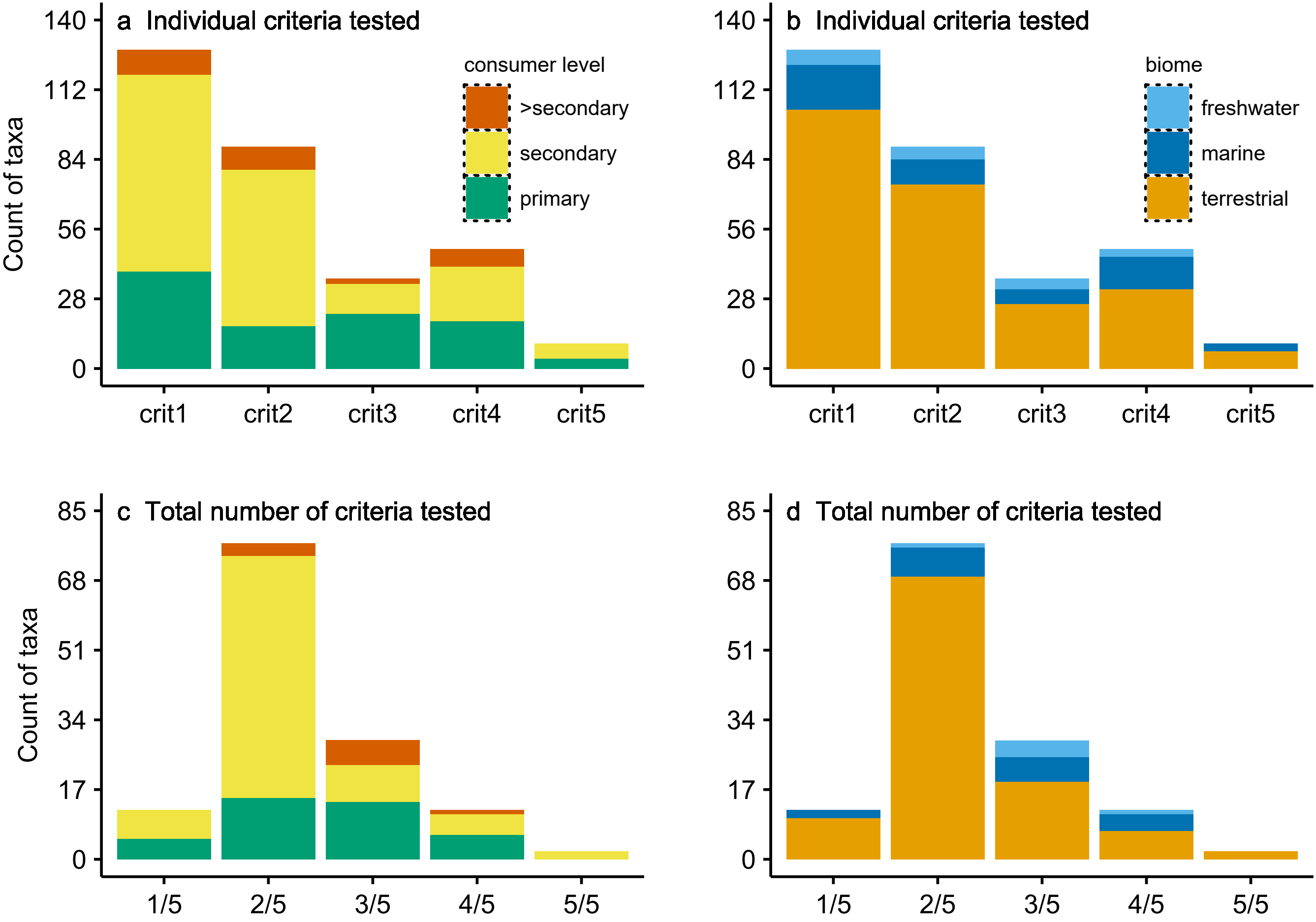
a Individual criteria tested
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c Total number of criteria tested
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140
112
84
56
28
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85
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17
crit1
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1/5
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consumer level
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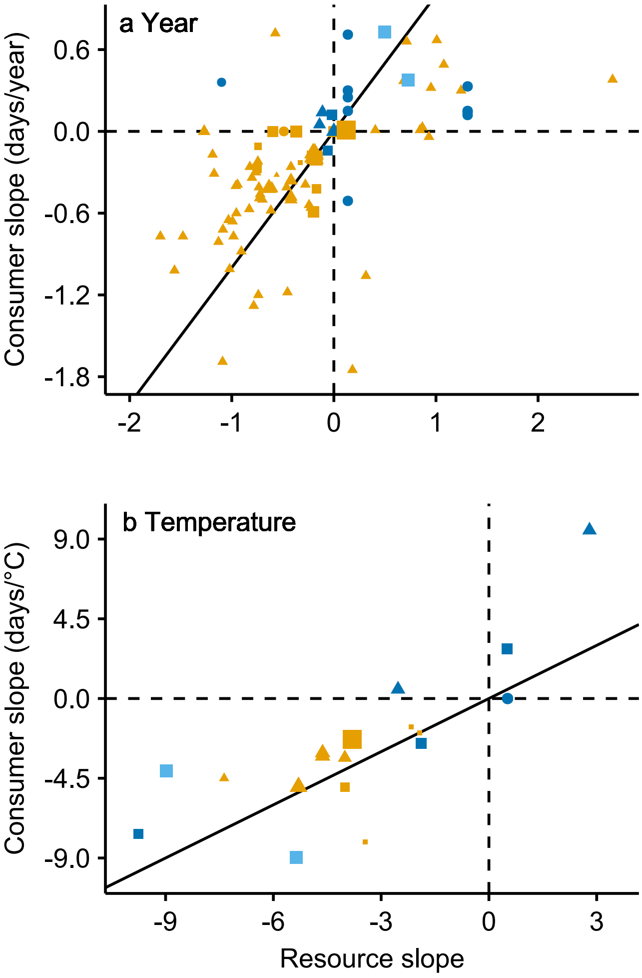
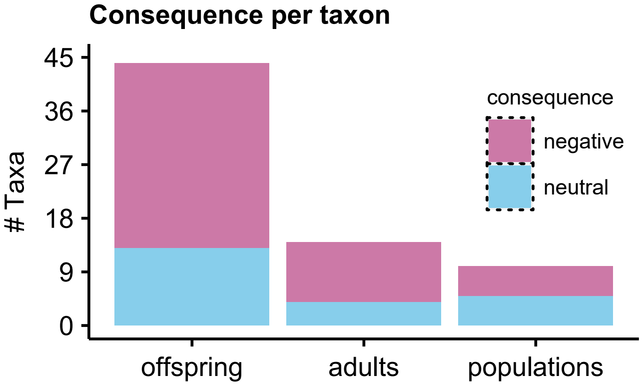
secondary
primary
biome
freshwater
marine
terrestrial


a Year
Consumer slope (days/year)
0.6
0.0
-0.6
-1.2
-1.8
-2
-1
0
1
2
b Temperature
Consumer slope (days/°C)
9.0
4.5
0.0
-4.5
-9.0
-9
-6
-3
0
3
Resource slope


Consequence per taxon
Taxa
45
36
27
18
9
0
offspring
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negative
neutral