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31 **Climate warming has caused the seasonal timing of many components of ecological**

32 **food chains to advance. In the context of trophic interactions the match-mismatch**

33 **hypothesis (MMH) postulates that differential shifts can lead to phenological**

34 **asynchrony with negative impacts for consumers. However, at present there has been**

35 **no consistent analysis of the links between temperature change, phenological**

36 **asynchrony, and individual-to-population level impacts across taxa, trophic levels and**

37 **biomes at a global scale. Here, we propose five criteria that all need to be met to**

38 **demonstrate that temperature-mediated trophic asynchrony poses a growing risk to**

39 **consumers. We conduct a literature review of 109 papers studying 132 taxa, and find**

40 **that all five criteria are assessed for only two taxa, with the majority of taxa only**

41 **having one or two criteria assessed. Crucially, nearly every study was conducted in**

42 **Europe or North America, and most studies were on terrestrial secondary consumers.**

43 **We thus lack a robust evidence base from which to draw general conclusions about**

44 **the risk that climate-mediated trophic asynchrony may pose to populations**

45 **worldwide.**

46

47 The shifting seasonal timing of key life history events, such as the budburst of trees,

48 emergence of insects or the migration and breeding times of vertebrates, is one of the three

49 universal ecological responses to climate warming[1,2] alongside range shifts and reductions in

50 organismal body size[3,4]. Such shifts in phenology have provided some of the earliest and

51 strongest evidence that rising temperatures have left a discernible imprint on the planet's

52 ecosystems[5–8]. For many consumer species, phenological events are timed to coincide with

53 peak abundance of a predictable food resource. However, the strength and direction of the

54 phenological response to temperature frequently differs among species occupying different

55 trophic levels, leading to asynchrony between resource and consumer (box 1). The

56 consequences of such asynchrony were first studied in the early 1900s in the context of

57 trophic interactions between fish larvae and their zooplankton resource. This generated the

58   classic match-mismatch hypothesis[9]. Fish larvae were found to spawn at a relatively fixed

59   date, but zooplankton phenology was more variable across years, causing annual variation

60   in asynchrony between consumer and resource. The degree of asynchrony (referred to as

61   mismatch by Cushing) was proposed to account for annual fluctuations in fish recruitment to

62   the population[9]. In recent years, the hypothesis that changing temperatures might increase

63   the frequency of costly trophic asynchrony between consumers and their resources has

64   been increasingly discussed[10–13]. The impact of asynchronous phenological interactions on

65   the fates of consumer species was identified as a key uncertainty in the fifth assessment

66   report of the IPCC[14].

67   Phenological asynchrony and mismatch are often used interchangeably in the

68   ecological literature, but the meaning of the term "mismatch" is more ambiguous, as it is in

69   some cases used to imply only dissimilar responses of adjacent trophic levels[13], and in other

70   cases implying negative impacts on the consumer[15]. In this paper we refer to "trophic

71   asynchrony" when the consumer demand does not coincide with the phenology of the

72   resource, and to the match-mismatch hypothesis (MMH) when asynchrony has negative

73   impacts on fitness or populations (box 1). We note that the MMH is normally conceptualised

74   from a unidirectional, bottom-up perspective (i.e., asynchrony leading to detrimental effects

75   on consumers), rather than potential top-down effects upon prey and resources[16].

76   Asynchrony has been detected in many study systems[7,17,18], but to demonstrate

77   negative consequences of asynchrony on the consumer (i.e., the MMH), several conditions

78   need to be met. For trophic asynchrony to be identified as detrimental, the consumer must

79   depend on a short, seasonally-pulsed or ephemeral resource[19–25], and it should be

80   established whether asynchrony might be an adaptive baseline state[26–28]. Moreover, there

81   should be negative effects of asynchrony on consumer fitness[29–34]. Ultimately, asynchrony

82   becomes of conservation concern when it affects mean demographic parameters and leads

83   to population declines[13,35–38]. Although components of the MMH and consequences for

84   population trends can be identified, these are based on very few and specific study systems.

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

108   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.

109

110

111   **Five criteria for demonstrating risks of temperature-mediated asynchrony**

112   Here, based on ideas that have been widely discussed in the literature and which we outline

113   above, we propose five criteria that must all be met for temperature-mediated phenological

114   asynchrony to be both present, and causing population declines (Table 1): (1) the consumer

115   is highly reliant on a seasonally ephemeral resource; (2) the degree of trophic asynchrony

116   between consumer and resource phenology is increasing over the years (evidenced by time

117   series); (3) increasing trophic asynchrony is due to differing temperature responses of

118   consumer and resource; (4) trophic asynchrony impacts negatively on consumer fitness, and

119   (5) asynchrony impacts negatively on population growth[37]. In Table 1 we identify some of the

120   methods that can be used to test each of these criteria. In the next section we summarise

121   the existing biological evidence for these criteria, with a particular focus on general insights

122   that have emerged from multi-species studies and formal meta-analyses on questions that

123   are pertinent to the study of the MMH. The five criteria can be seen as a best-practice

124   framework, but we realize that each study system poses unique challenges for studying

125   these criteria. We do not intend for their application to oversimplify the complex study of

126   phenology, nor do we claim that they cover everything that phenological studies need to

127   focus on.

128

129   *Evidence for phenological asynchrony*

130   Large-scale comparative analyses of phenological responses and formal meta-analyses

131   provide ample evidence that on average spring timings are advancing at mid-high latitudes,

132   and that species vary in their response to temperature[8,17,39]. In two large multi-species

133   analyses based on phenological data from the UK, the phenology of secondary consumers

134   advanced less than primary producers and consumers over the years (criterion 2)[17] and

135   secondary consumers have a lower phenological sensitivity to temperature (criterion 3)[7]. For

136   marine taxa, the magnitude of phenological advance varied among trophic groups, with

137   phytoplankton, zooplankton and bony fish all more responsive than seabirds[40,41]. However,

138   while large-scale multi-species and multi-population studies provide valuable insights into

139   general trends and patterns of inter- and intra-specific variation in phenological responses,

140   they do not estimate *in situ* responses for specific trophic interactions, nor do they reveal

141   anything about fitness or population consequences. Of those studies that focus on trophic

142   interactions known to be important to the consumer for a short period (criterion 1) most focus

143   on a single interaction. Such studies have reported increasing asynchrony over the years

144   (criterion 2), for example in great tits, *Parus major,* and winter moth, *Operophtera*

145   *brumata*[5,42]. However, a recent analysis of the phenological time series underpinning 27

146   species interactions (including but not limited to trophic interactions) found that whilst the

147   degree of asynchrony has changed over the years, the number of cases where asynchrony

148   had increased was roughly balanced by the number of cases where asynchrony had

149   decreased[18]. The same study also found that whilst phenology was responding to

150   temperature in the ecological systems considered, it was not possible to attribute temporal

151   trends in asynchrony to long-term increases in temperature (criterion 3).

152

153   *Potential consequences of trophic asynchrony*

154   The most prominent evidence for the MMH comes from intensively-studied wild systems,

155   such as that of the reliance of great tits on winter moth caterpillars to feed their young. For

156   these birds, asynchrony between the timing of peak nestling demand and peak caterpillar

157   biomass has negative consequences for individual fitness and annual mean fitness[30,31].

158   Meta-analyses of selection estimates in the wild report consistent selection pressures for

159   earlier phenology[43,44], but directional selection has not become stronger over time[44].

160   However, meta-analyses addressing selection on phenology have considered only absolute

161   timing, rather than the timing of a consumer relative to its resource[10], so it is unclear from

162   these studies whether selection on consumers is being driven by asynchrony with resources.

163   Trophic asynchrony becomes a matter of conservation concern if it impacts

164   negatively on population size (criterion 5)[37]. Two long-term studies of great tits found no

165   evidence of an effect of asynchrony on population size[31,45], whereas a study of several

166   populations of pied flycatchers *Ficedula hypoleuca* in the Netherlands reported stronger

167   population declines where caterpillar phenology was earlier[36]. The only multi-species studies

168   on this theme that we are aware of are for birds. One of these studies found that migrant

169   passerines breeding in European forests had declined more than resident and marsh

170   inhabiting species, which the authors attributed to the MMH[46]. The other study found that,

171   across 21 UK bird species, population declines were more pronounced for species that had

172   advanced their breeding phenology least and in species whose annual productivity was most

173   reduced by asynchrony with general insect and plant phenology.[47] However, support for the

174   MMH was weak and not reflected by declines in breeding success of those species.

175

176 Table 1. Criteria of evidence that climate change induced trophic asynchrony is increasing and
177 deleterious for the consumer (the MMH), with a consideration of the data and methods that can be
178 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].

179

180

181   **Literature survey**

182   We conducted a broad survey (n=109) of published work on the match-mismatch hypothesis

183   (MMH) across terrestrial, marine and freshwater systems with the aim of: (i) examining the

184   evidence for temperature-mediated trophic asynchrony and its impacts and (ii) identifying

185   gaps in the evidence base, thereby allowing us to (iii) make recommendations for priority

186   areas for future work. To this end, we extracted data from published, peer-reviewed original

187   research in which a trophic interaction was studied in relation to any of the five criteria we

188   proposed as vital to the MMH (Table 1). Only original studies, where the specific interaction

189   between consumer and resource could clearly be identified were included (see

190   supplementary information for methodological details).

191

192   *Taxonomic and geographical bias in the data*

193   The search identified 772 papers, of which the full text was found for 760. Of these, 571

194   were not relevant (e.g., no trophic interactions were reported, or none of the five criteria were

195   extractable), and 80 had no extractable data, resulting in a total of 109 papers that had

196   relevant data on 132 consumer taxa (Fig. S2). All but six of the 109 trophic interaction

197 studies were in Europe or North America (Fig. 1). The majority of trophic interactions were

198 terrestrial (81.5% of the data), with marine (14%) and freshwater interactions (4.5%) being

199 scarcer. For most interactions the consumer was a secondary consumer (58%), with studies

200 of primary (36.5%) or higher than secondary (5.5%) consumers less common. Birds made

201 up the majority of the consumer taxa studied (53%), while 29.5% of taxa were insects, 8%

202 were fish, 5% were mammals and 4% were crustaceans.

203

204 *Testing the five criteria*

205 The most tested criterion was criterion 1 (97% of interactions, n=128/132) - relating to

206 dependence on a seasonally pulsed resource (Fig. 2, top panels). However, rather than

207 conducting direct tests on the seasonal distribution of resources, 72% (n=92/128) of these

208 included only a statement based on *a priori* knowledge of the natural history of the system

209 that the resource was both ephemeral and important to the consumer.

210   Of the study systems that were tested for dependence on a seasonally pulsed

211 resource (i.e., where the resource was ephemeral and the consumer was a specialist), 42%

212 (n=15/36) showed such dependence. Excluding the cases where criterion 1 was not

213 explicitly tested, criterion 2 was the most frequently tested (72% of interactions, n=95/132),

214 relating to whether phenological asynchrony was increasing over time (Fig. 2, top panels).

215 The remaining criteria were all tested substantially less frequently, with criterion 5

216 (population consequences) being tested least often (7.6% of interactions, n=10/132).

217 Surprisingly few studies report data for criterion 3 (Fig. 2, top panels), which relates

218 temperature to asynchrony, and this was almost never reported for marine and freshwater

219 taxa. The distributions of criteria tested were broadly similar across consumer levels and

220 biomes, with the exception of primary consumers for which criteria 3 and 4 appear slightly

221 more common.

222   Our analysis could identify only two out of 132 consumer taxa for which all five of our

223   criteria have been tested at least once: both of these are forest-breeding passerine birds

224   studied in Europe - the great tit and the pied flycatcher. In a further 13 taxa, four out of five

225   criteria were assessed. In the remaining 117 taxa, three or fewer criteria were studied, with

226   the majority (58%, n=77/132) of consumer taxa having only two of the five criteria known

227   (Fig. 2, bottom panels). Breaking this same analysis down to the per study level, no single

228   study explicitly tested all five criteria (Fig. S3). This is generally due to a tendency for studies

229   to focus on either phenology slopes (criteria 2 & 3), or the consequences of asynchrony

230   (criteria 4 & 5). Only a handful of studies detail temporal slopes, temperature slopes, and

231   consequences of asynchrony in one study[61–63].

232

233   *Phenology slopes over time and temperature*

234   Consumer and resource responses appear to be positively correlated across studies, with

235   consumers showing a slight tendency to advance their phenology by less than their resource

236   (Fig. 3). In 61% (n=58/95) of the cases, the phenology slope over time was greater for the

237   resource than for the consumer (Fig 3a,b). For the phenological response to temperature,

238   the consumer slope was greater than the resource slope in 59% (n=13/22) of cases (Fig

239   3c,d). The degree to which these patterns differ across biomes and trophic levels could not

240   be tested with this dataset, since the number of slope estimates is too low for non-terrestrial

241   and non-secondary consumers. Based on visual inspection, it appears that especially

242   terrestrial secondary consumers tend to be slower-advancing than their resource. However,

243   more data on underrepresented groups would be required to reach robust conclusions about

244   these patterns.

245

246   *Fitness and demographic consequences*

247   Fitness consequences in relation to trophic asynchrony (criterion 4) are studied in 36%

248   (48/132) of the consumers (Fig. 2, top panels). Consequences of asynchrony for offspring

249 (n=44) are studied over three times as often as consequences for adults (n=14, Fig. 4),

250 though it is possible that this reflects a research bias to study fitness components that are

251 more sensitive to asynchrony. In 29% of consumer taxa (n=14/48), no negative effect of

252 asynchrony on fitness was reported (Fig. 4). The least studied consequence of trophic

253 asynchrony is its effects on population demography (criterion 5, Fig. 2, 4). In half of these

254 interactions (n=5/10), no effect of asynchrony was reported.

255

256 **Discussion**

257 Our literature survey on the ecological impacts of temperature-mediated trophic asynchrony

258 reveals that the full causal chain from temperature change, to temperature-driven shifts in

259 seasonal timing, consumer-resource synchrony, and individual-to-population level impact

260 has rarely been studied. Only two out of 132 taxa were studied for all criteria, and for the

261 majority of study systems, only one or two out of five criteria were met. The available studies

262 were strongly biased toward terrestrial secondary consumers (especially birds) in the

263 Northern Hemisphere (largely Europe and North America). Notably, the effects of climate

264 warming on trophic asynchrony in aquatic systems and in the Southern Hemisphere are

265 understudied[64], although this could be reflective of the small amount of temperate land mass

266 in the Southern hemisphere. Tropical studies are also under-represented, but this may partly

267 indicate a reduced importance of temperature as a phenological cue in tropical ecosystems[8].

268 Crucially, demographic consequences of trophic asynchrony are the least studied of the five

269 criteria, despite this knowledge being the most important to conservation.

270

271 *Bias in the Match-Mismatch Hypothesis evidence base across biomes*

272 Terrestrial systems were by far the most represented of the three environments that we

273 considered, presumably by virtue of the comparative ease of collecting data on both

274 phenology and fitness in these systems. This ease of data collection is evident in the great

275   contribution that citizen science data collectors have made to the study of terrestrial

276   phenology[47,65–68], which is rare for aquatic systems. Monitoring phenology of many aquatic

277   organisms is hampered by their wide ranges and underwater habitats[69], and compounded by

278   the logistic and financial challenges encountered during offshore research. As a result,

279   relatively few multi-decadal phenological time series have been collected at sufficient

280   resolution to capture seasonal changes[70,71]. Moreover, separate sampling programmes are

281   often needed for consumer and resource (e.g., piscivorous birds and their prey)[72], and even

282   if resources can be quantified, many aquatic organisms are generalist feeders, further

283   adding to the difficulties in quantifying the MMH. Citizen scientists can, however, collect

284   valuable data on the terrestrial stages of aquatic organisms (e.g., dragonflies), or aquatic

285   seasonal events that can be observed from shore (e.g., amphibian spawning, floating algal

286   blooms). Furthermore, with ongoing technological innovation in data collection

287   methodologies, it may become possible to widen the aquatic evidence base for some taxa.

288   For example, radar can be used to quantify aquatic-terrestrial subsidies based on insect

289   emergence, providing detailed measures of the timing and size of resource pulses[73], and

290   satellite-based observation tools are providing a wide-scale perspective on phytoplankton

291   phenology changes[74]. It would therefore be valuable to consider how diverse data sources,

292   and lines of evidence, can be fruitfully combined to advance our knowledge of the

293   importance of the MMH in aquatic systems.

294   Despite their overrepresentation in MMH research, even in terrestrial systems there

295   are biases and gaps in the evidence-base that extend beyond the aforementioned

296   geographic biases (Fig 1). Of the terrestrial studies, temperate forest taxa and birds in

297   particular predominate, which is likely due to the fact that seasonality increases with latitude.

298   Temperate forests experience a pronounced seasonal temperature-mediated pulse in

299   resources[46], and they present particularly suitable study systems to study individual fitness in

300   the wild (e.g., cavity nesting birds). In aquatic systems, individual marking of philopatric

301   seabirds and pinnipeds permits some components of fitness to be monitored[75], but this is

302 much harder for underwater organisms[76]. Likewise, for many widely-distributed groups such

303 as fish, invertebrates, and plankton, individuals cannot be sampled repeatedly, and

304 populations can rarely be sampled to the extent that demographic implications of asynchrony

305 can be assessed. On the other hand, invertebrates are more amenable to experimental

306 study[32], and numerous national surveys of population sizes exist[77,78] that could be used to

307 infer demographic consequences of trophic asynchrony. Another key research gap in

308 aquatic systems involves the specific role of cross system consumer-resource interactions in

309 mediating trophic asynchrony. For example, some freshwater consumers feed upon

310 terrestrial resources, which represents a substantial source of nutrients[79]. The delivery of at

311 least some of this material is strongly seasonal. Leaf fall, for example, is triggered by

312 photoperiod in conjunction with drought and temperature[80]. Aquatic phenology research

313 would greatly benefit from increased consideration of the synchrony between freshwater

314 consumers and terrestrial resources.

315

316 *Further challenges in studying the MMH*

317 We recognise that studying these five criteria and improving the evidence base regarding the

318 risks posed by the MMH will not be straightforward and we have already discussed how

319 aquatic environments present particular challenges, but other complexities remain. While

320 criteria 2 and 3 are perhaps the easiest to satisfy, even here challenges exist in attributing a

321 change in phenology/asynchrony to temperature, as sensitivity estimates can be obscured

322 by non-climate drivers or compensatory mechanisms[62,81]. For example, changing nutrient

323 availability and light conditions can influence the seasonal timing of phytoplankton

324 blooms[82,83], but would not be expected to affect consumer organisms in the same way. In

325 this article we have simplified the interaction between resource and consumer to a single

326 metric, the asynchrony between the peak demand of consumer and availability of the

327 resource. However, as the MMH predicts that consumer fitness relates to resource

328 availability during a particular window[9], consumers might in addition to asynchrony be

329   sensitive to the height and width of the resource[11,37], either of which could be sensitive to

330   temperature and exacerbate or ameliorate effects on fitness. Although the potential for

331   resource abundance to influence fitness is widely acknowledged, it is unusual for studies on

332   the MMH in relation to fitness (criterion 4) or population size (criterion 5) to include its

333   effect[56,57]. We realize that especially criterion 4 may be hard to satisfy for study systems

334   where individuals cannot be studied, which should not discourage people from working on

335   such systems. Whilst fulfilling all the other criteria would allow one to infer whether the

336   mismatch is causing population declines, there are clear advantages of studying individuals

337   within populations. Apart from the fact that such data helps demonstrate causative effects of

338   asynchrony on fitness, it can tell us whether seasonal timing will be under directional

339   selection.

340   Where the resource is in fact a guild (caterpillars, phytoplankton) rather than a

341   species, temperature-mediated shifts in the aggregate phenology may arise from a variety of

342   processes, from similar plastic responses of different species, to changes in the relative

343   abundance of early- and late-blooming constituent species, even when these species

344   independently might show no or weak phenological shifts[84]. While the effect of asynchrony

345   on the consumer may not be sensitive to these two scenarios, if we want to project

346   phenological changes into the future we need to understand the processes that underpin

347   community phenological responses. An obvious solution to this problem is to improve the

348   species level resolution of sampling[85], but this can be costly and impractical in the short

349   term, and might require new sampling approaches such as eDNA[86].

350

351   *Is trophic asynchrony of conservation concern?*

352   This review reveals a lack of robust evidence for the MMH, and even the two best studied

353   taxa in terrestrial systems present a mixed message. In great tits, matching with the

354   caterpillar peak has fitness impacts at both the individual and population level[30,31], but trophic

355   asynchrony currently poses no threat to their population persistence[31,45]. Pied flycatchers

356   also perform worse when poorly matched with the caterpillar peak[22,87], but, in contrast to

357   great tits, declines in asynchronous flycatcher populations have been recorded in the

358   Netherlands[36]. Nevertheless, those pied flycatcher populations have been increasing again

359   since 2002[88]. Interestingly, pied flycatchers breed about two weeks later than tits[89], the

360   average nest is rarely matched with the caterpillar peak[90], and a long-term study in the

361   Netherlands found no correlation between annual mean asynchrony with the caterpillar peak

362   and the strength of the seasonal decline in the number of recruits[91]. Moreover, pied

363   flycatchers are more generalist than tits in the nestling diet[92], so it remains uncertain to what

364   extent these flycatcher populations will be negatively affected by trophic asynchrony

365   compared to specialists.

366   It would nevertheless be premature to conclude from this that a relative shortage of

367   evidence for demographic consequences of trophic asynchrony constitutes evidence of

368   absence of an effect. Even in species for which negative population consequences are not

369   yet apparent, such as great tits, it is possible that continued increases in temperature will be

370   problematic. Application of an integral projection model to a UK population of great tits

371   suggested that under a high emission scenario, more rapid responses of the prey species

372   (the winter moth caterpillar) coupled with limits to plasticity in great tit hatch date being

373   reached, lead to an acceleration in directional selection. An increase in evolution of hatch

374   date timing was to an insufficient degree to prevent negative consequences of trophic

375   asynchrony, and the population in that scenario is projected to have an increased risk of

376   extinction[93]. Such demographic approaches should be greatly expanded upon, and provide a

377   unique way to understand which life stages will likely matter from the perspective of

378   pathways leading to shifts in population growth rate and density[58].

379

380   **Research Priorities**

381 Based on our five criteria and our review of the literature we identify six priorities for future

382 work to properly test the match-mismatch hypothesis and its impacts.

383 1. **From cause to effect - focusing on population consequences:** There is an urgent

384   need for studies that consider the full causal chain, from climate driver to seasonal

385   timing, synchrony, and individual-to-population level impact. In particular, we need

386   many more tests of the impact of asynchrony on population change (criterion 5),

387   across taxa and habitat types. This most important criterion from the perspective of

388   conservation and policy[13,37] and yet has received the least attention. Furthermore,

389   given that the population impacts of trophic asynchrony at one location may be

390   buffered by matching at another location[90], we strongly advocate expanding the

391   spatial scale of current research to include multi-population studies. This will allow

392   the consequences of phenological shifts to be interpreted in the context of other

393   universal climate warming responses such as range shifts.

394 2. **Balancing the evidence - data collection and synthesis for aquatic systems**:

395   Despite the marine origin of the MMH, current monitoring and research has so far led

396   to a limited understanding of the MMH in marine and freshwater systems, compared

397   to terrestrial habitats. It is imperative for funders to continue to support time series,

398   since with each passing year the statistical power of these to reveal patterns

399   improves. We further recommend for underused historic records, including museum

400   collections and naturalist observations, to be coupled with new work on these

401   systems to create well documented long time series within a matter of years.

402   However, we must also ask how additional monitoring approaches (e.g., eDNA,

403   radar) might be usefully combined with "traditional" monitoring approaches, to

404   expand the species representation, monitoring of individual states and fitness

405   consequences, and spatial coverage of aquatic ecosystem studies, and support a

406   broader understanding of changes in phenological asynchrony (criterion 2) and the

407   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

436   trends in asynchrony (criterion 2) and temperature sensitivity (criterion 3) or fitness

437   consequences (criteria 4&5), care is required in matching data at a resolution that is

438   pertinent to the trophic interaction[103,104]. Moreover, we are not aware of any study

439   combining citizen science-derived datasets to study the impacts of asynchrony of

440   specific trophic interactions on population change (criterion 5). Therefore an

441   opportunity exists for development or extensions of citizen science schemes to

442   collect data on the phenology of species interactions across trophic levels and on the

443   fitness and/or population sizes of the consumer.

444   6. **Clarifying the concept - "asynchrony" or "mismatch"**: There exists a degree of

445   terminological inconsistency in relation to the MMH, which may confuse attempts at

446   achieving a common understanding of the potential importance of this phenomenon.

447   Many studies that claim to address "mismatch" identify the conditions that could lead

448   to greater asynchrony, but stop short of explicitly testing whether asynchrony leads to

449   any negative consequences for the consumer. Where no evidence for negative

450   repercussions is presented we encourage authors to use the term "asynchrony",

451   rather than "mismatch", which implies a negative consequence.

452

453   **Concluding remarks**

454   Temperature-mediated trophic asynchrony and its consequences are widely discussed in

455   global change research and have been intensively studied over the past two decades. In this

456   study we have presented five criteria that together provide a causal chain to explicitly

457   demonstrate the risk that temperature-mediated asynchrony poses to populations, which we

458   hope will strengthen future work. In an extensive review of the literature we found that no

459   single study and only two study systems have tested all five criteria, with a clear deficit of

460   studies considering the impact of asynchrony on population size, which is the most important

461   criterion from a conservation perspective[37]. This means that at present we cannot state from

462   the literature that temperature-mediated trophic asynchrony will have a widespread negative

463   impact on consumer population size or growth. We identify six research priorities, which

464   need to be tackled to get a comprehensive understanding of the frequency and magnitude of

465   trophic asynchrony and its impacts on consumers. A more consistent approach to the study

466   of the match-mismatch hypothesis and its population consequences at the global scale will

467   allow us to better target conservation efforts and provide much needed evidence for possible

468   consequences of one of the most intriguing impacts of climate change on global biota:

469   phenological change.

470

Figure legends

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

477

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

483

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

496

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

501

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502

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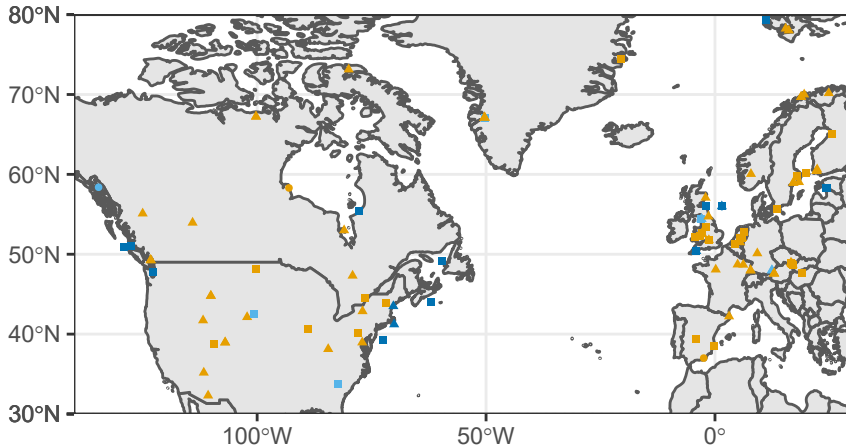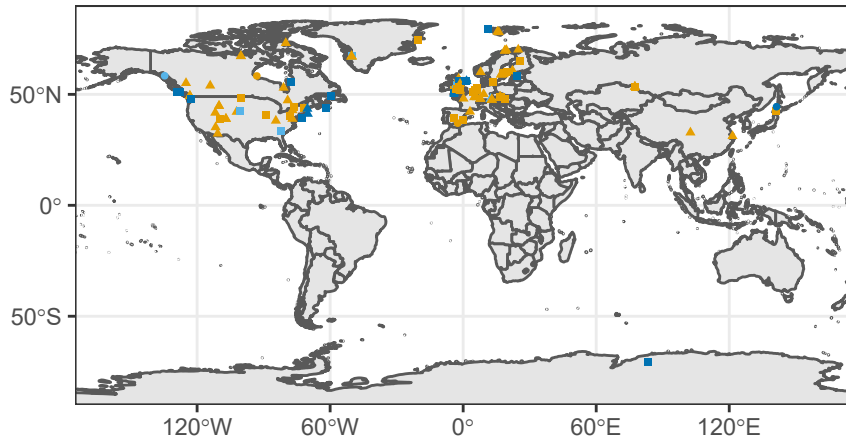
773 **Correspondence**

774   Correspondence should be addressed to JMS.
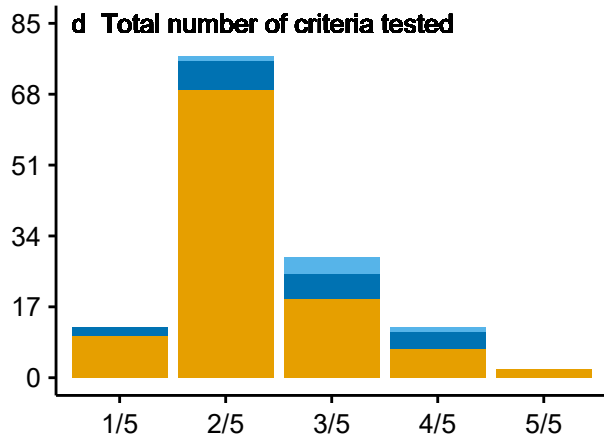
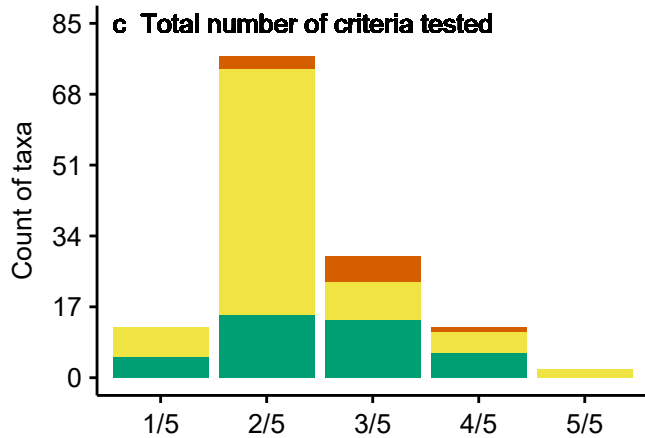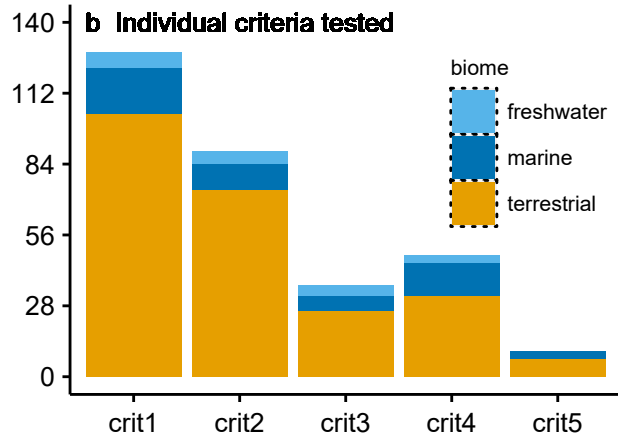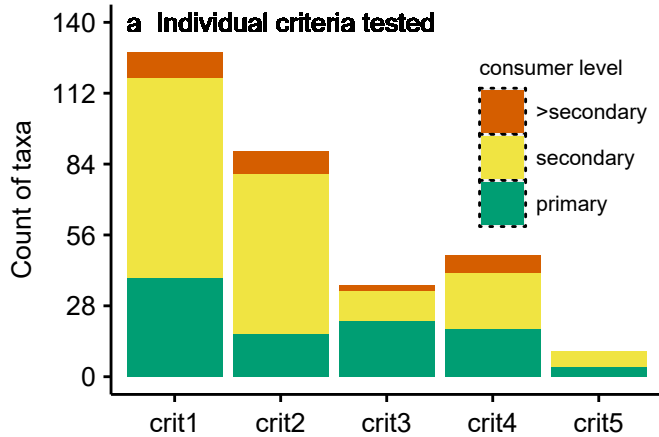779   **Author contributions**

780   JMS, ABP, AA, CH, KK, SJT, JJA, MDB, JJ, KHM, JWPH, EGS, ØV, JCW, DZC, EFC, FD,

781   TH, OWL, NP, and BCS contributed to conceiving ideas. All authors contributed to editing

782   the manuscript. JMS, ABP, AA, CH, KK, SJT, JJA, MDB, JJ, KHM, JWPH, EGS, ØV, and

783   JCW extracted data for the analyses. JMS, ABP, AA, CH, KK, and SJT contributed to writing

784   the manuscript. JMS and ABP expanded on the initial ideas to determine the structure and

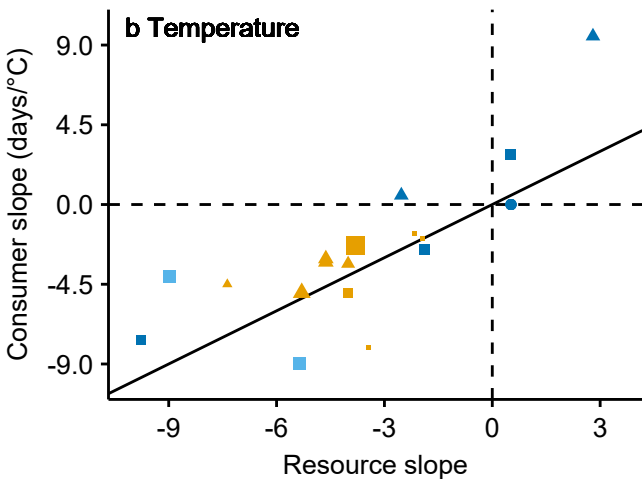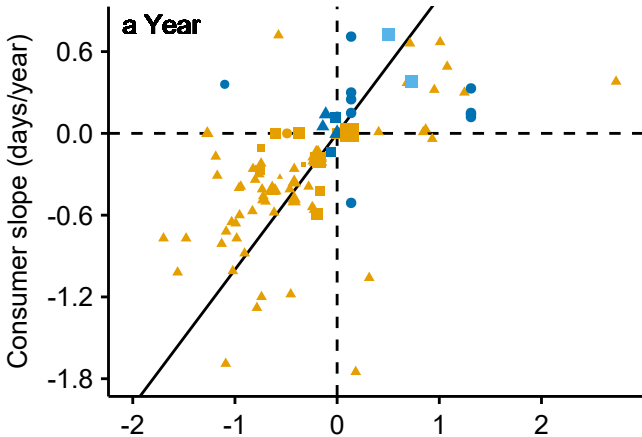785   content of the manuscript and wrote most of it. JMS conducted the analyses.

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787   **Competing Interests**

788   The authors declare no competing interest.

Consequence per taxon