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Evolutionary and demographic consequences of phenological mismatches

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1 **Review paper for Nature Ecology & Evolution**

2 *Evolutionary and demographic consequences of phenological*
3 *mismatches*

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9

10 **Abstract**

11 Climate change has often led to unequal shifts in the seasonal timing (phenology) of interacting
12 species, such as consumers and their resource, leading to phenological ‘mismatches’. Mismatches
13 occur when the time where resource demands of the consumer species are high does not match with
14 the period when this resource is abundant. Here, we review the evolutionary and population
15 consequences of such mismatches and how these depend on other ecological factors, as, for
16 example, additional drivers of selection or density-dependent recruitment. This review puts the
17 research on phenological mismatches into a conceptual framework, applies this framework beyond
18 consumer-resource interactions, and illustrates this framework using examples drawn from the vast
19 body of literature on mismatches. Finally, we point out priority questions for research on this key
20 impact of climate change.

21 **Introduction**

22 Phenology, the seasonal timing of life-cycle events, is generally important for individual fitness
23 because for each of these events a period exists during which environmental conditions are most
24 advantageous, i.e. an 'optimal time window'. For many species and phenological events this 'optimal
25 time window' is set by the phenology of other species. Many species have shifted their phenology in
26 response to global climate change, but species often do not shift at the same rate¹⁻⁴. For example,
27 terrestrial invertebrates shifted faster (4.1 days per decade) than terrestrial vertebrates (2.6 days per
28 decade)⁵. When the phenologies of interacting species, such as consumers and their resource, shift at
29 different rates³, this may lead to a mismatch in phenology⁴.

30 Mismatches between the phenology of resource and consumer should affect demographic rates of
31 the consumer due to reduced reproductive success or survival. They can also lead to selection on
32 seasonal timing of the consumer because individuals that are better matched to the phenology of the
33 resource will have a higher fitness than individuals that are less well matched. To address the
34 consequences of mismatches from both a population and evolutionary perspective, we will discuss a
35 conceptual framework of mismatch that goes beyond the often studied consumer-resource
36 interactions, and that clearly outlines evolutionary and population consequences of mismatches. We
37 will illustrate this framework with examples from the vast literature on consume-resource
38 mismatches and end by presenting priority questions for further research.

39 **Conceptual framework**

40 Mismatched phenology

41 The mismatch concept was introduced as a 'critical period' by Hjort⁶ and extended by Cushing⁷, who
42 termed it the 'match-mismatch hypothesis' in his study on the annual variation in recruitment in fish
43 populations in marine ecosystems. In this usage of the term, mismatches are said to occur when the
44 time in the annual cycle when resource demands of the consumer species (*i.e.* predators, herbivores)
45 are highest does not match with the period when its resource (*i.e.* prey, plants) is most abundant⁸⁻¹²

46 (Fig. 1A). Instead of using mismatch, other authors have used the terms “synchrony” and
47 “asynchrony”¹³⁻¹⁶.

48 Much of the research on the match-mismatch hypothesis focused on the timing of the consumer
49 peak resource demands, which has to match the timing of the peak resource availability. A more
50 precise measurement of mismatches than this difference in peak phenology would be to measure
51 the temporal overlap between the distributions of demands and availability^{11,13}, but see¹⁷. The height
52 of the resource peak will also be of relevance: in years or areas where resources are plentiful it is
53 likely that a (mild) mismatch will not have any negative effects on the consumer.

54 More recently, the match-mismatch framework has also been applied to species interactions other
55 than consumer and resource, for example, pollinators and plants (e.g. ¹⁸) or host and parasites (e.g.
56 ¹⁹) but also competing species (e.g. ²⁰). In the following, we will, however, focus on mismatches
57 between consumers and their resource because this kind of mismatch has been most frequently
58 studied. We will discuss these other kind of mismatches in the Outlook.

59 Why mismatches occur

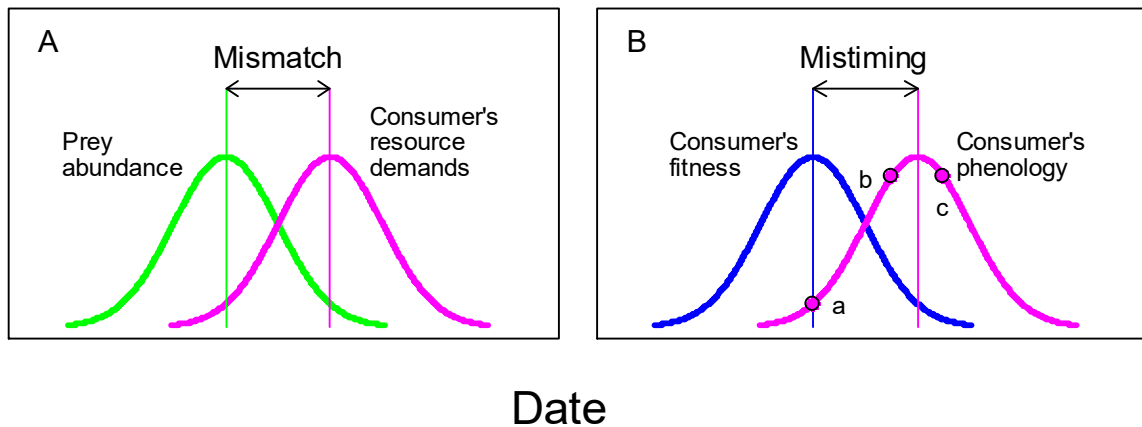
60 A key issue of seasonal timing is that in many biological systems the optimal time for phenological
61 events varies from year to year depending on environmental conditions. To track this inter-annual
62 variation, seasonal timing is often phenotypically plastic^{21,22}. Individuals are either directly
63 constrained by environmental variables, for example, due to their ectothermic physiology or use
64 environmental variables (termed ‘cues’) that are predictive of the ‘optimal time window’ to adjust
65 their phenology²³. The two cues most relevant for phenology are photoperiod and temperature²⁴ but
66 also rainfall²⁵ and development of vegetation²⁶ have been shown to play a role.

67

68

69

70 Figure 1



71

72 *Fig. 1* Definitions of mismatch and mistiming. (A) Mismatch occurs when the time in the annual cycle
73 where resource demands of the consumer species are highest does not match with the period where
74 this resource is most abundant. (B) Mistiming occurs when the phenology (of either the individual
75 (dots) or the population (vertical line)) deviates from the date at which fitness peaks, which will then
76 lead to directional selection for either earlier (as depicted here) or later consumer phenology.
77 Individual (a) is well-timed with the fitness optimum, while individuals (b) and (c) are too late and
78 hence mistimed.

79

80 Species differ in the relative importance of the different variables that affect their phenology, and in
81 the ways they respond to them. Mismatches between trophic levels can thus occur because the cue
82 used by one trophic level has changed at a different rate than the cue used by the other trophic level
83 e.g. ^{5,27,28,29}. Even if two species both rely on temperature, these cues are often temperatures during
84 different periods in the year. Climate change has not led to a uniform increase in temperatures over
85 the entire year (e.g. ³⁰) and these unequal increases in temperature can thus easily lead to
86 differential phenological shifts, and thereby to mismatches³¹⁻³³.

87 Another reason why mismatches may occur due to climate change is that the predictability of the
88 phenology of the interacting species is limited. The cues used by consumers are predictive for the
89 annual timing of their resource peak, but this predictability is not perfect as in almost all cases the
90 environment that affects the decision-making on the phenology of a life-cycle stage is not the same
91 as the environment that determines resource phenology, i.e. the environment of the selective drivers
92 on this stage³². This imperfect cue reliability leads to the selection on consumers to being less
93 sensitive to the cue than their resource. Thus, the phenotypic plasticity of phenology relative to
94 temperature is predicted to be weaker in consumers than in their resource and hence climate change
95 will lead to a weaker phenological advancement of predators than the advancement of their prey,
96 leading to mismatches^{8,31,34-38}.

97 Evolutionary consequences of mismatches at the individual level

98 Mismatches can lead to selection on phenology if better-matched individuals have a higher fitness
99 than less well-matched individuals. If consumer phenology is heritable, this selection should lead to
100 an evolutionary response. In the following we will discuss the difference between mismatch and
101 'mistiming' and whether mismatch will necessarily lead to mistiming³⁹.

102 For most traits there is an optimal phenotype and an individual's fitness will decline the more their
103 phenology deviates from the optimal phenotype. Mistiming (rather than mismatch) is then defined
104 as the deviation between the actual (either of the individual or the population) and the optimal
105 phenotype (Fig. 1B). Depending on the phenological event, different fitness components can be
106 affected, for example, reproductive success in case of breeding or survival in case of migration
107 phenology. When the fitness of the consumers depends solely or very strongly on the consumer
108 mismatch with resource phenology, as for example in many bird species reproductive success
109 depends on food phenology^{8,34-38}, mismatches lead to selection on phenology³⁷ and thus mismatch
110 equals mistiming.

111 However, if fitness depends (additionally) on other ecological variables, there may be no relationship
112 between mismatches and mistiming. For example, pre-breeding survival of long-distance migrants
113 may be affected by temperatures upon arrival⁴⁰ and this additional fitness component may alter the
114 optimal breeding time to a later date as inferred from mismatch only. Since selection on a trait
115 depends on whether total fitness, i.e. the net effect of all fitness components, co-varies with the
116 trait, true mistiming may also depend on environmental variables other than only mismatch, as, for
117 example, the cost of egg-production under potentially still adverse conditions in early spring^{39,41}. In
118 that case, animals may be optimally mismatched, *i.e.* fitness of the consumer is maximized at some
119 degree of mismatch with the peak in resource availability (Fig. 2a)³⁹.

120 Optimal mismatches can also be caused by a non-symmetrical fitness curve for consumer phenology
121 relative to the timing of peak abundance of its resource because the consumers' phenology will have
122 evolved to be away from the 'fitness cliff'⁴¹⁻⁴³. Such asymmetric 'fitness landscapes' can arise through
123 the combination of different fitness components (Fig. 2b). In the Edith's checkerspot butterfly
124 (*Euphydryas editha*) there may be life-history trade-offs between fecundity and mortality that can
125 lead to optimal mismatches¹⁴. In migratory birds, frequency-dependent competition for breeding
126 territories can result in asymmetric relationships between reproductive success and arrival date to
127 the breeding grounds, even though the fitness landscape determined by breeding resources might
128 have a symmetrical distribution^{44,45}. A similar argument can be made when the costs of egg
129 production are dependent on timing^{46,47} and thus a better match between offspring needs and
130 resource availability will reduce fitness due to the fitness costs of producing eggs early in the season
131 when conditions are still harsh³⁹ (see also Johansson⁴⁸ for an overview about such complex
132 evolutionary consequences of mistiming).

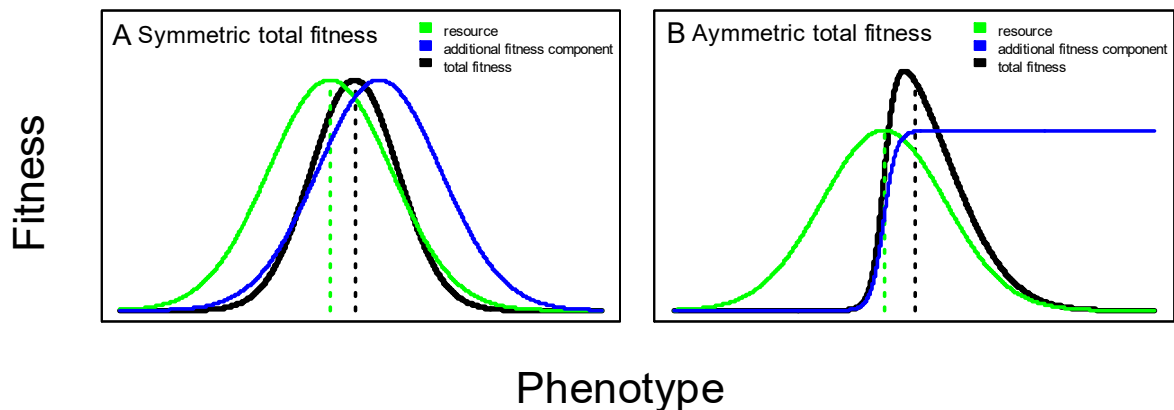
133 While many studies reported potential mismatches between trophic levels (e.g. ^{1,15}), the number of
134 studies showing that these mismatches lead to selection, i.e. that individuals were truly mistimed, is
135 more limited^{8,34-38}. These studies generally reported increasing selection with increasing mismatch

136 but some studies lack data on resource phenology and only used temperature as a proxy for
137 mismatch^{34,35,38}. This limited evidence for mismatch driving selection on phenology can be explained
138 by the logistical challenges of obtaining individual-level data on mismatch and fitness in wild
139 populations, which also limited such studies to mainly birds and mammals.

140 Evolutionary consequences of mismatches at the population level

141 At the population level, mismatches can lead to directional selection on phenology. If the optimal
142 time window for consumer phenology is narrow (compared to population-level variation in
143 phenology), fitness will increase and decrease sharply with increasing and decreasing synchrony
144 between individual phenotypes and the optimal phenotype leading to (strong) stabilising selection. If
145 the optimal time window is shifted relative to the consumer phenology and the majority of individual
146 phenotypes occur earlier (or later) than the optimal phenotype, there is directional selection for
147 earlier (or later) phenology.

148 When a population is mistimed, the resulting directional selection on timing may lead to genetic
149 changes, i.e. to micro-evolution, but due to the difficulties of detecting genetic change in wild
150 populations the number of studies on this is even more limited⁴⁹. One well documented example
151 comes from egg hatching in winter moths where climate change has led to a too early hatch date
152 relative to the timing of bud burst of the host plants¹⁶. Over a decade selection has now led to
153 genetic adaptation and hatching date has shifted to later dates⁵⁰.



155

156 *Fig. 2* Optimal mismatches caused by multiple fitness components of phenology. Total fitness (black
 157 solid line) is the product of fitness determined by resource phenology (green solid line) and another
 158 fitness component (blue solid line). In (A) the later fitness optima of the blue fitness component, e.g.
 159 fledgling survival probability due to predation, leads to a later optimal fitness and hence an optimal
 160 mismatch (difference between green and black dashed vertical lines). In (B) also the shape of the blue
 161 fitness component, e.g. adult pre-breeding survival, leads not only to a later peak of total fitness but
 162 also to an asymmetric total fitness curve, which will shift the optimal phenotype to an even later date
 163 when the environment varies through time (black dotted line). The overall outcome is an optimal
 164 mismatch (difference between green and black dashed vertical lines).

165

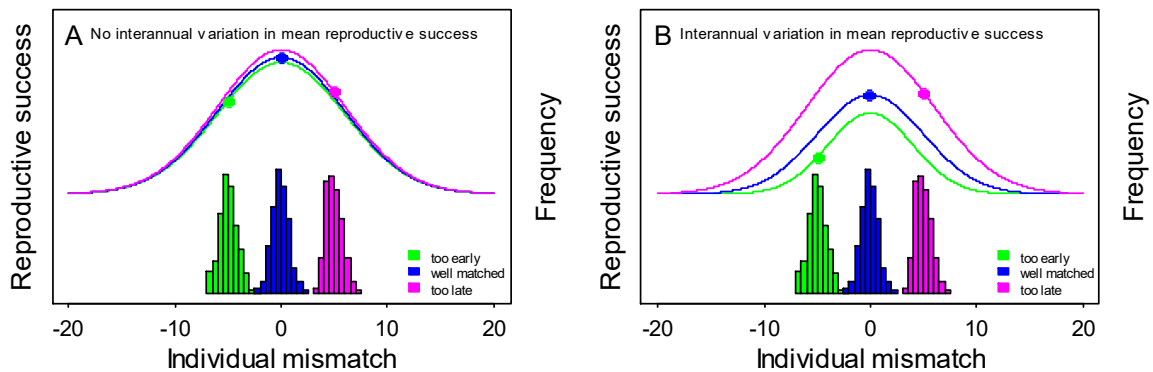
166 Population consequences of mismatches

167 To analyse the effects of mismatch on demography, the demographic rate of interest is often
 168 regressed against 'population mismatch': the difference between the mean population phenology
 169 and the resource phenology (i.e. the overall mean of individual mismatches)³⁷ (Fig. 3a,b). When
 170 individual mismatch is an important driver of selection, i.e. when mismatch has a strong effect on
 171 fitness, population mismatch will affect demographic rates, such as population offspring production
 172 or mean adult survival. This link between population mismatch and demographic rates can, however,

173 be complicated by the fact that the 'height' of fitness landscape may differ among years (Fig. 3b).
174 Theoretically, variation in resource height could correlate with (population) mismatch, which would
175 lead to complex relationships between mismatch and demographic rates.

176 Even when population mismatch affects demographic rates, there may not be a clear effect on
177 population numbers. Density dependence can buffer these effects when for instance recruitment
178 rates of offspring decrease with the number of offspring produced. This has been shown in great tits
179 where population mismatch led to lower number of fledged offspring, but where recruitment of
180 these offspring was higher in years with low offspring production (because density-dependent winter
181 survival increased juvenile recruitment) and hence there was no detectable effect of population
182 mismatch on population growth rate⁵¹. This shows that inferring negative effects of mismatch on
183 population dynamics without demonstrating this link in the data (e.g. ^{35,52,53-55}) may be problematic.

184 A number of studies found negative effects of mismatched phenology on demographic rates, mostly
185 reproductive success, in terrestrial^{34,56-58}, freshwater²⁸ or marine systems^{59,60}. For example, in caribou
186 (*Rangifer tarandus*), roe deer (*Capreolus capreolus*) and arctic breeding geese increased
187 temperatures led to a phenological mismatch between timing of reproduction and plant growth
188 phenology, which reduced reproductive success⁵⁶⁻⁵⁸. Similarly, increasing mismatch between
189 breeding time in common murre (*Uria aalge*) and the timing of inshore migration of their main prey,
190 the capelin (*Mallotus villosus*), reduced reproductive success despite increased adult foraging
191 effort⁶⁰.



193

194 *Fig. 3 Relationships between mismatch and reproductive success at the individual and population*
 195 *level. The coloured lines depict fitness curves in relation to individual mismatch for three different*
 196 *scenarios of mismatch (green: too early, blue: well matched, red: too late) indicated by the three*
 197 *frequency distributions of individual mismatch. The dots on the fitness functions indicate population*
 198 *mean fitness for each scenario. In (A) the height of the fitness curves of three scenarios is similar. This*
 199 *means that population mean reproductive success is only a function of population mean mismatch: If*
 200 *the population is on average too early (frequency distribution of phenology in green) or too late (red)*
 201 *it has a reduced population mean reproductive success (cf. dots on fitness curves). In (B) the height of*
 202 *the fitness curves differ: It is lowest when the population is too early (green curve and green*
 203 *frequency distribution) and highest when the population is too late (red curve and red frequency*
 204 *distribution). This leads to an increase of population mean reproductive success with mismatch (cf.*
 205 *dots on fitness curves), because mean mismatch covaries positively with the height of the resource*
 206 *peak. Note that the units of mismatch and the relationship between population mean mismatch and*
 207 *the height of the fitness curve have been chosen arbitrarily (this works the other way around too, i.e.*
 208 *a negative covariance between mean mismatch and the height of the resource peak).*

209

210 Unfortunately, the number of studies that analysed the effect of mismatch on both demographic
211 rates and natural selection on the trait is even more limited (e.g. ^{34,36,51}), which limits our ability to
212 reliably predict eco-evolutionary consequences of mismatch and hence the likelihood of successful
213 adaptation to climate change. Interestingly, none of these studies found demographic consequences
214 of selection for various reasons. In one case, mismatch increased selection on breeding time in great
215 tits and expectedly reduced reproductive success but population growth was unaffected due to
216 density-dependent winter survival ⁵¹. In another case, demographic rates of wheatears (*Oenanthe*
217 *oenanthe*) declined markedly simultaneously with a reduction in 'thermal matching', which is a proxy
218 for phenological match between the consumer and its resource³⁴. Selection, however, did not
219 increase and even changed from directional to more or less absent. This counterintuitive finding
220 could be explained by relaxed selection on arrival time, mediated by reduced competition for high-
221 quality territories, due to low population sizes⁶¹.

222

223 **Priority questions for the field**

224 Below, we outline four priority research questions in the field of phenological mismatches.

225 1. Eco-evolutionary interactions of mismatches

226 As highlighted above, mismatches can have evolutionary (through selection) and ecological effects
227 (through demography). These effects can even interact if, for example, reduced population density
228 relaxes selection^{34,61}, which would reduce the need for evolutionary responses. Such eco-
229 evolutionary interactions may be more common than previously thought because it is now
230 increasingly realised that evolutionary and ecological processes can happen at similar time-scales
231 (e.g. ⁶²). The evidence for such eco-evolutionary interactions is, however, likely limited by the need
232 for individual level fitness data to quantify selection, which requires linking parent and offspring.
233 Furthermore, it would also be desirable to explore the (quantitative) genetics of phenological traits
234 to assess whether they could respond fast enough to selection. Studies quantifying selection and

235 (quantitative) genetics have been mostly limited to mammal and bird species for logistical reasons
236 but the increasing availability of genomic tools for 'non model' species could potentially overcome
237 these hurdles^{63,64}.

238

239 2. Experimental approach to fitness consequences of mismatches

240 Key to the match-mismatch hypothesis is that there are negative fitness effects of being mismatched.

241 To assess fitness consequences of mismatch most often correlative data are used (e.g. ^{8,34-37}).

242 However, there is a large body of literature from life-history theory that shows that to establish the

243 true, causal link between a trait, here phenology, and fitness, experimental work is needed where

244 individuals are shifted on the timing (mismatch) axis and their fitness is measured (see ⁶⁵ for a

245 review). Such experimental work that assessed whether mismatches are indeed mistiming is

246 extremely rare. One example is where flowering time of plants was experimentally manipulated in

247 the green house and then visitation rates, as a proxy for pollination, measured⁶⁶. To determine how

248 often mismatches indeed lead to selection as opposed to reflecting pre-existing adaptive

249 mismatches, or adaptive responses to environmental change (i.e. individuals maximize their fitness

250 even when they are mismatched with the phenology of their resource), more experimental work is

251 needed.

252

253 3. Mismatches in interactions other than consumer-resource

254 Most of the reported instances of mismatches concern mismatches between consumers and their

255 resource but obviously other types of species interactions, such as predation risk, competition and

256 mutualism, can also become mismatched. Another potential area where mistiming can occur is

257 between life-cycle stages 'within' a species (see Box 1).

258 Studies on mismatches between consumers and resource typically studied demographic or
259 evolutionary consequences for the consumer but ignored consequences of altered phenological
260 match for the resource⁶⁷. For example, in the UK, newts (*Triturus spp.*) now enter ponds earlier,
261 whereas frogs (*Rana temporaria*) did not advance their breeding phenology. As a consequence, the
262 larvae of the frogs are exposed to higher levels of newt predation⁶⁸. Increasing temperatures
263 increased the overlap in autumn migration times of long-distance migratory birds and one of their
264 avian predators, the sparrowhawk (*Accipiter nisus*), while they decreased the overlap between short-
265 distance migrants and sparrowhawks, but population consequences remained unclear⁶⁹. However,
266 the consequences of mismatches do not need to be of similar importance for the different trophic
267 levels⁷⁰. For instance, while for the predator it may be important to be matched with the phenology
268 of its prey, predation may not be an important selection pressure on the phenology of the prey, as in
269 the case of the great tit and their caterpillar prey. As these temporal distributions of predation risks
270 are much harder to measure, more studies on predation risk phenology are needed.

271 Mismatches may also play a role in competition. For example, increasing temperatures altered the
272 competitive interactions between bird species or plankton species and thereby equilibrium
273 population densities or community structures^{20,71}. In the case of mutualisms, for example between
274 plants and pollinators, species are also likely to become mismatched with each other since climate
275 change affects different trophic levels at different rates¹⁸. However, whether such mismatches will
276 have consequences depends on the degree of specialisation and the asymmetry of the mutualism.
277 For example, certain plant species can only be fertilised by a single insect species, such as the early
278 spider orchid (*Ophrys sphegodes*) that depends almost exclusively on a solitary bee species (*Andrena*
279 *nigroaenea*) for pollination. Differential shifts in the phenology of these species would have negative
280 effects for the plant but not for the bee⁷². More generalist plant species are, however, less likely to
281 entirely miss out on being pollinated⁶⁶ but generally mismatches between plants and pollinators and
282 potential demographic effects are not well studied¹⁸.

283 Parasites obviously depend on their hosts being present or vulnerable, which generally varies
284 seasonally⁷³. Differential shifts in parasite and host phenology can hence also lead to mismatches.
285 For example, migration time of common cuckoos (*Cuculus canorus*) and some of their host species
286 have advanced at different rates⁵⁵, while (experimental) temperature increases led to a strong
287 mismatch between the phenologies of a trematode (*Ribeiroia ondatrae*) and its amphibian hosts¹⁹.
288 Such mismatches could have strong consequences for parasite or host population dynamics,
289 potentially leading to local extinction of the parasite⁷⁴.

290 Increasing temperatures do not only affect biological processes but also agricultural practices. For
291 example, in Finland sowing or mowing dates have shifted, which can lead to mismatches between
292 these practices and breeding time of farmland or meadow birds, possibly negatively affecting their
293 reproductive success and population numbers⁷⁵. Mismatches may also have consequences for
294 biochemical processes but these are hardly explored. For instance, a mismatch between the geese
295 grazing and plant growing season in arctic coastal wetlands affected the greenhouse gas fluxes⁷⁶.

296

297 4. Community ecological effects and ecosystem consequences

298 Most research on the match-mismatch hypothesis focuses on pairwise predator–prey, plant–
299 herbivore or plant– pollinator interactions. However, the selection on phenology of a focal species
300 depends on the (mis)matched phenology with the many species it interacts with. For example, a
301 plant that is pollinated by many different insect species will not suffer from mismatch with a single
302 species (e.g. ⁶⁶). The challenge is to scale up from pairwise interactions to more complex food webs.
303 Only via a better understanding of entire food web phenology we can understand community⁷⁷ and
304 possibly ecosystem-level consequences of climate change induced shifts in phenology⁷⁸. Some
305 pioneering work has been done in this area, in food web models that involve phenological shifts^{79,80}
306 and in plant – pollinator communities ⁸¹⁻⁸⁴. The way forward is to assess the strength of the
307 connections between the different species in the food web, and then determine how these change

308 due to the differential shifts in phenology of the different species. Then using network theory, the
309 properties of the networks prior to the shifts in phenology and after the shifts in phenology can be
310 assessed, to evaluate for instance whether the network has become less stable. For this, detailed
311 experimental work is needed for instance in simplified food webs where the phenology of the species
312 can be manipulated. This is, however, not a trivial challenge.

313 Concluding remarks

314 Phenological mismatches are one of the clearest consequences of climate change and over the past
315 two decades an impressive body of literature has been build up. We have outlined a conceptual
316 frame-work and illustrated this with key-examples from this body of literature. Challenges for the
317 next decade are to further study the population and evolutionary consequences of mismatches, for
318 which long-term studies are essential, and from there move on to community ecological effects and
319 ecosystem consequences. Ultimately, what is needed is to link climate change predictions to the
320 predicted degree of mismatch in species interactions and networks, taking evolutionary changes into
321 account, and from there assess the consequences for biodiversity and ecosystem functioning. Such
322 information is essential to link climate predictions to consequences for nature, which is needed for
323 such consequences to play a role in the debate on the acceptable rate of global climate change⁸⁵.

324

325

326 Box 1

327 Mistiming in annual life-cycles

328 Differential shifts in phenological events may not only happen between species but also between
329 different life-cycle stages within an individual as these life-cycles stages may respond differently to a
330 cue^{48,86}. Some life cycle events will be more sensitive to photoperiod (as, for example, moult in birds⁸⁷)
331 while others are more sensitive to temperature (such as reproduction⁵). Such different sensitivities can
332 lead to differential shifts in the phenology of these life-stages due to climate change^{12,88,89} provided
333 that there are no strong effects of one life-cycle stage on the phenology of the next stage. Examples
334 of differential shifts in the phenologies of coupled life-history traits are arrival date and breeding date
335 in migratory birds, where a lack of the shift in arrival date could potentially constrain shifts in breeding
336 phenology^{90,91}. However, changes in temperature can also lead to differential shifts in reproduction
337 and moult. For example, in pied flycatchers (*Ficedula hypoleuca*) moult is comparatively less sensitive
338 than reproduction⁸⁶. In red deer (*Cervus elaphus*) the phenologies of six traits were measured over a
339 28-year period⁹², and in female deer, parturition dates advanced almost twice as fast as date of first
340 oestrus. In males, antler casting and cleaning advanced at a similar rate but the end of the rut shifted
341 twice as fast as its start dates. Clearly, mistiming within the annual life-cycle could be very common.

342

343

344 'Inset'



345



346

347 Examples for mismatch affecting reproductive success: In common murrens (*Uria aalge*, top left),
348 great tits (*Parus major*, top right), caribou (*Rangifer tarandus*, bottom left) and roe deer (*Capreolus*
349 *capreolus*, bottom right) mean breeding success is reduced in years with an increased population-
350 level mismatch between breeding phenology and the phenology of the main food resource. Picture
351 credits and licenses: Melissa McMasters CC-BY, Luc Viatour CC-BY-SA, Andreas Eichler CC-BY-SA,
352 Alexandre Buisse CC-BY-SA (clockwise from top left).

353

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359 **Author contributions**

360 M.E.V. & P.G. contributed to the conception of, and wrote, the manuscript. P.G. generated the
361 figures.

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