Evolutionary and demographic consequences of phenological mismatches

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

Phenology, the seasonal timing of life-cycle events, is generally important for individual fitness because, for each of these events, a period exists during which environmental conditions are most advantageous — an 'optimal time window'. For many species and phenological events, this optimal time window is set by the phenology of other species. The phenologies of many species have shifted in response to global climate change, but often the shift is not at the same rate among species[1–4]. For example, terrestrial invertebrates shifted their phenology faster (4.1 days per decade) than terrestrial vertebrates (2.6 days per decade)[5]. When the phenologies of interacting species, such as a consumer and its resource, shift at different rates[3], this may lead to a mismatch in phenology[4].

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

Conceptual framework

Mismatched phenology. The mismatch concept was introduced as a 'critical period' by Hjort[6] and extended by Cushing[7], who termed it the 'match–mismatch hypothesis' in his study on annual variation of recruitment in fish populations in marine ecosystems. In this usage of the term, mismatches are said to occur when the time in the annual cycle when resource demands of the consumer species (predators, herbivores) are highest does not match with the time when its resource (prey, plants) is most abundant[8–12] (Fig. 1a). Instead of using mismatch as a descriptor, other authors have used the terms 'synchrony' and 'asynchrony'[13–16].

Much of the research on the match–mismatch hypothesis has focused on the timing of peak resource demands of consumers, which has to match the timing of the peak resource availability. A more precise measurement of mismatches than this difference in peak phenology is temporal overlap between the distributions of demands and availability[11,13] (but unpublished data from J. J. C Ramakers, P.G. and M.E.V. points out methodological problems with calculating this overlap). The height of the resource peak is also of relevance: in years or areas where resources are plentiful, it is likely that a (mild) mismatch will not have any negative effects on the consumer.

More recently, the match–mismatch framework has also been applied to species interactions other than consumer and resource, such as pollinator and plant[17], host and parasite[18], and species competing for a resource[19]. In the following, we will, however, focus on mismatches between consumers and their resources because this kind of mismatch has been the most frequently studied. We will discuss other kinds of mismatches in 'Priority questions for the field'.

Why mismatches occur. A key issue of seasonal timing is that, in many biological systems, the optimal time for phenological events varies from year to year depending on environmental conditions. To track this interannual variation, seasonal timing is often phenotypically plastic[20,21]. Individuals are either directly constrained by environmental variables because of, for example, their ectothermic physiology, or they use environmental variables (termed 'cues') that are predictive of the optimal time window to adjust their phenology[22]. The two cues most relevant for phenology are photoperiod and temperature[23], but also rainfall[24] and development of vegetation[25] have been shown to play a role.

The relative importance of the different variables that affect phenology varies among different species, as does the ways they respond to these variables. Mismatches between trophic levels can thus occur because the cue used by one trophic level has changed at a different rate than the cue used by the other trophic level[5,26–28]. Even if two species both rely on temperature, these cues are often temperatures during different periods in the year. Climate change has not led to
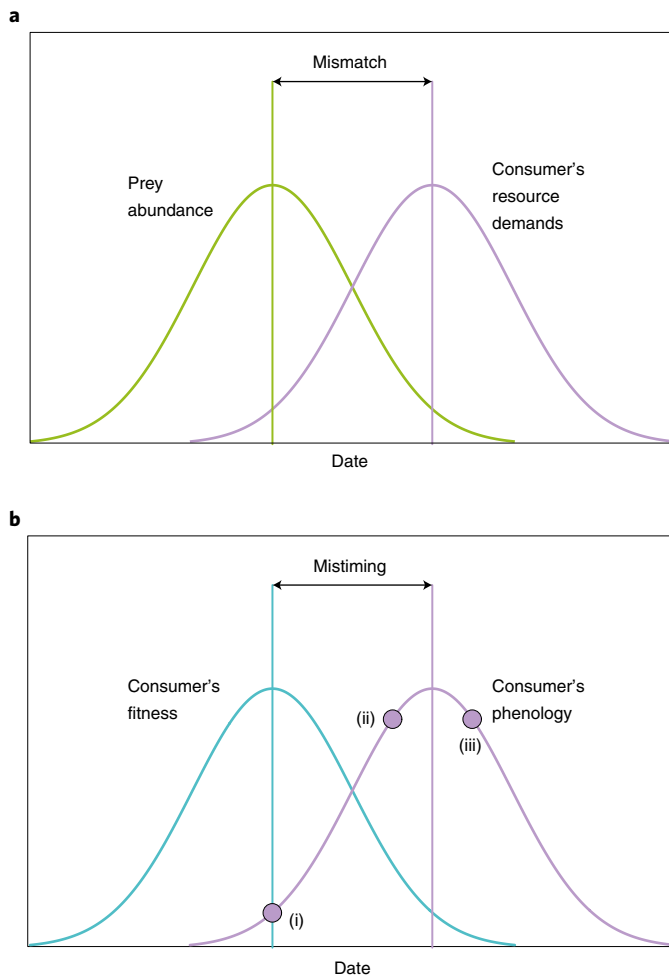
Fig. 1 | Definitions of mismatch and mistiming. a, Mismatch occurs when the time in the annual cycle at which a consumer species's demands for a resource are highest does not match with the period during which this resource is most abundant. **b**, Mistiming occurs when the phenology (of either the individual (dots) or the population (vertical lines)) deviates from the time at which fitness peaks, which will then lead to directional selection for either earlier (as depicted here) or later consumer phenology. Individual (i) is well-timed with the fitness optimum, while individuals (ii) and (iii) are too late and hence are mistimed.

a uniform increase in temperatures over the entire year[29], and these unequal increases in temperature can thus easily lead to differential phenological shifts and thereby to mismatches[30–32].

Another reason why mismatches due to climate change may occur is that the predictability of the phenology of the interacting species is limited. Consumers use cues that predict the phenology of their resources, but this prediction is not perfect, as in almost all cases the environment that affects a consumer's phenology is not the same as the environment that determines the phenology of its resource — that is, the environment of the drivers of natural selection on the consumer's phenology[31]. This imperfect cue reliability leads to the selection on consumers for a lower sensitivity to the cue than the effect the cue has on the phenology of their resources. Thus, the phenotypic plasticity of phenology in relation to temperature is predicted to be weaker in consumers than in their resources; hence, climate change will lead to a weaker phenological advancement of the phenology of the consumers than the advancement of the phenology of their resources, leading to mismatches[8,30,33–37].

Evolutionary consequences of mismatches at the individual level. Mismatches can lead to selection on phenology if better-matched individuals have a higher fitness than individuals who are not as well matched. If consumer phenology is heritable, this selection should lead to an evolutionary response. In this section, we will discuss the difference between mismatch and 'mistiming' and whether mismatch necessarily leads to mistiming[38].

For most traits, there is an optimal phenotype, and an individual's fitness will decline the more their phenology deviates from the optimal phenotype. Mistiming (rather than mismatch) is then defined as the deviation between the actual (either of the individual or the population) and the optimal phenotype (Fig. 1b). Depending on the phenological event, different fitness components can be affected — for example, reproductive success in the case of breeding or survival in the case of migration phenology. When the fitness of a consumer depends solely or very strongly on mismatch with their resource's phenology, as is the case in many bird species, reproductive success depends on food phenology[8,33–37], mismatches lead to selection on phenology[36] and thus mismatch equals mistiming.

However, if fitness depends (additionally) on other ecological variables, there may be no relationship between mismatches and mistiming. For example, prebreeding survival of long-distance migrants may be affected by temperatures upon arrival at their breeding grounds[39], and this additional fitness component may shift the optimal breeding time to a later date compared to the date where there would be a match with the phenology of their resources. Since selection on a trait depends on whether total fitness, the net effect of all fitness components, co-varies with the trait, true mistiming may also depend on environmental variables other than only mismatch, such as the cost of egg production under conditions in early spring that are potentially still adverse[38,40]. In that case, animals may be optimally mismatched — the fitness of the consumer is maximized at some degree of mismatch with the peak in resource availability (Fig. 2a)[38].

Optimal mismatches can also be caused by a non-symmetrical fitness curve for consumer phenology relative to the timing of peak abundance of its resource because consumer phenology will have evolved away from the 'fitness cliff', the range of phenologies where fitness strongly declines[40–42]. Such asymmetric 'fitness landscapes' can arise through the combination of different fitness components (Fig. 2b). In the Edith's checkerspot butterfly (*Euphydryas editha*), there may be life-history trade-offs between fecundity and mortality that can lead to optimal mismatches[14]. In migratory birds, frequency-dependent competition for breeding territories can result in asymmetric relationships between reproductive success and date of arrival at breeding grounds, even though the fitness landscape determined by breeding resources might have a symmetrical distribution[43,44]. A similar argument can be made when the costs of egg production are dependent on timing[45,46]; thus, a better match between offspring needs and resource availability will reduce fitness because of the fitness costs of producing eggs early in the season when conditions are still harsh[38] (see ref. [47] for an overview of such complex evolutionary consequences of mistiming).

While many studies have reported potential mismatches between trophic levels[1,15], the number of studies showing that these mismatches led to selection, that is, that the phenologies of individuals were truly mistimed, is more limited[8,33–37]. These studies generally reported increasing selection with increasing mismatch, but some studies lack data on resource phenology and only used temperature as a proxy for mismatch[33,34,37]. This limited evidence for mismatch driving selection on phenology can be explained by the logistical challenges of obtaining individual-level data on mismatch and fitness in wild populations, which have also limited such studies to mainly birds and mammals.
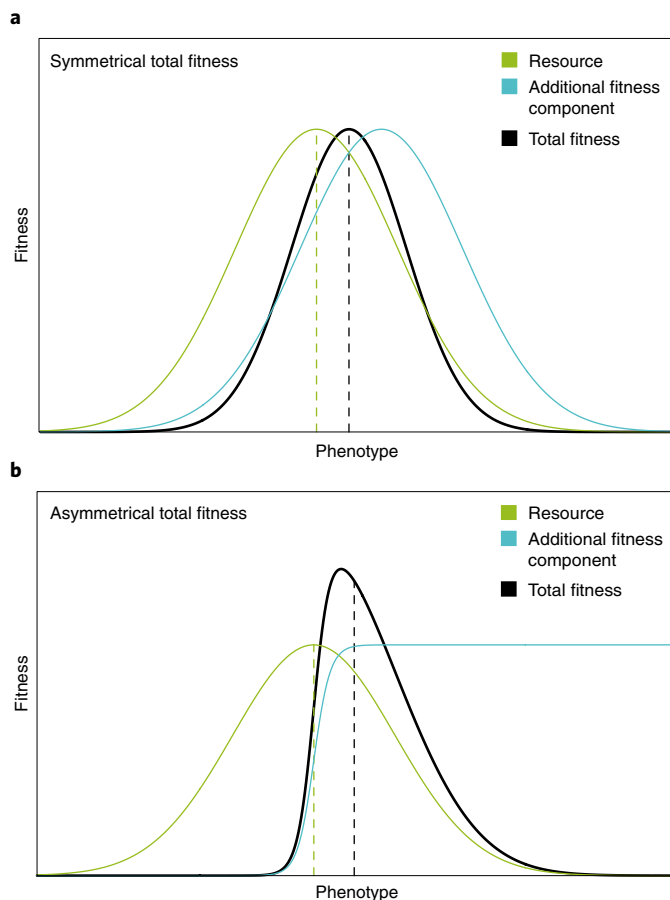
Fig. 2 | Optimal mismatches are caused by multiple fitness components of phenology. Total fitness (black solid line) is the product of fitness determined by resource phenology (green solid line) and another fitness component (blue solid line). **a**, The later fitness optimum of the blue fitness component, for example, low fledgling survival probability due to predation early in the season, leads to a later optimal fitness and hence an optimal mismatch (difference between green and black dashed vertical lines). **b**, The shape of the blue fitness component, for example, low adult pre-breeding survival early in the season, leads not only to a later peak of total fitness, but also to an asymmetric total fitness curve, which will shift the optimal phenotype to an even later date when the environment varies through time (black dashed line). The overall outcome is an optimal mismatch (difference between green and black dashed vertical lines).

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

When a population is mistimed, the resulting directional selection on timing may lead to genetic changes (or micro-evolution), but, due to the difficulties of detecting genetic change in wild populations, the number of studies on this phenomenon is even more limited[48]. One well-documented example is egg hatching in winter moths (*Operophtera brumata*). Climate change has led to

a too-early hatch date relative to the timing of their food: the bud burst of the Oak (*Quercus robur*)[16]. Over a decade of selection has now led to genetic adaptation in the moths, and the egg hatching date has shifted to later dates[49].

Population-level consequences of mismatches. To analyse the effects of mismatch on demography, the demographic rate of interest is often regressed against 'population mismatch': the difference between the mean population phenology and the resource phenology (the overall mean of individual mismatches)[36] (Fig. 3a,b). When individual mismatch is an important driver of selection, that is, has a strong effect on fitness, population mismatch will affect demographic rates, such as population offspring production or mean adult survival. This link between population mismatch and demographic rates can, however, be complicated by the fact that the 'height' of fitness landscape may differ among years (Fig. 3b). Theoretically, variation in resource height could correlate with (population) mismatch, which would lead to complex relationships between mismatch and demographic rates.

Even when population mismatch affects demographic rates, there may not be a clear effect on population numbers. Density dependence can buffer these effects when, for instance, recruitment rates of offspring decrease with the number of offspring produced. This has been shown in great tits (*Parus major*), where population mismatch led to lower number of fledged offspring, but recruitment of these offspring was higher in years with low offspring production (because density-dependent winter survival increased juvenile recruitment); hence, there was no detectable effect of population mismatch on population growth rate[50]. This shows that inferring negative effects of mismatch on population dynamics without demonstrating this link in the data (for example, refs. [34,51–54]) may be problematic.

A number of studies have found negative effects, mostly in reproductive success, of mismatched phenology that impact demographic rates in terrestrial[33,55–57], freshwater[27] and marine systems[58,59]. For example, among caribou (*Rangifer tarandus*), roe deer (*Capreolus capreolus*) and the arctic breeding Ross's geese (*Chen rossii*) and lesser snow geese (*Chen caerulescens caerulescens*), increased temperatures have led to a phenological mismatch between timing of reproduction and plant growth phenology, which has reduced reproductive success[55–57]. Similarly, increasing mismatch between breeding time in common murres (*Uria aalge*) and the timing of inshore migration of their main prey, the capelin (*Mallotus villosus*), has reduced reproductive success despite increased adult foraging effort[59].

Unfortunately, there is an even more limited number of studies that have analysed the effects of mismatch on both demographic rates and natural selection on a trait[33,35,50], which limits our ability to reliably predict eco-evolutionary consequences of mismatch and hence the likelihood of successful adaptation to climate change. Interestingly, for various reasons, none of these studies found demographic consequences of selection. In one case, mismatch increased selection on breeding time in great tits and expectedly reduced reproductive success, but population growth was unaffected owing to density-dependent winter survival[50]. In another case, demographic rates of wheatears (*Oenanthe oenanthe*) markedly declined simultaneously with a reduction in 'thermal matching', which is a proxy for phenological match between the consumer and its resource[33]. Selection, however, did not increase and even changed from directional to more or less absent. This counterintuitive finding could be explained by relaxed selection on arrival time, mediated by reduced competition for high-quality territories due to small population sizes[60].

Priority questions for the field

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

1. Eco-evolutionary interactions of mismatches
As highlighted above, mismatches can have evolutionary (through selection) and ecological (through demography) effects. These effects can even interact if, for example, reduced population density relaxes selection[33,60], which would reduce the need for evolutionary responses. Such eco-evolutionary interactions may be more common than previously thought: it is now increasingly realized that evolutionary and ecological processes can happen at similar timescales[61]. The evidence for such eco-evolutionary interactions is, however, likely limited by the need for individual-level fitness data to quantify selection, which requires linking parent and offspring. Furthermore, it would also be desirable to explore the (quantitative) genetics of phenological traits to assess whether they could respond fast enough to selection. Studies quantifying selection and (quantitative) genetics have been mostly limited to mammal and bird species for logistical reasons, but the increasing availability of genomic tools for 'non-model' species could potentially overcome these hurdles[62,63].

2. Experimental approach to fitness consequences of mismatches
Key to the match–mismatch hypothesis is that there are negative fitness effects of being mismatched. To assess fitness consequences of mismatch, correlative data are most often used[8,33–36]. However, there is a large body of literature from life-history theory that shows that to establish the true, causal link between a trait, here phenology, and fitness, experimental work is needed in which the phenology of individuals are shifted and their fitness is measured (see ref. [64] for a review). Such experimental work that has assessed whether mismatches are indeed mistiming is extremely rare. In one example, flowering time of plants was experimentally manipulated in the green house, and then visitation rates by pollinators, as a proxy for pollination, were measured[65]. To determine how often mismatches indeed lead to selection as opposed to reflecting pre-existing adaptive mismatches, or adaptive responses to environmental change (when individuals maximize their fitness, even when they are mismatched, with the phenology of their resource), more experimental work is needed.

3. Mismatches in interactions other than consumer–resource
Most of the reported instances of mismatches concern mismatches between consumers and their resource, but obviously other types of species interactions, such as predation risk, competition and mutualism, can also become mismatched. Another potential area where mistiming can occur is between life-cycle stages 'within' a species (see Box 1).
Studies on mismatches between consumer and resource have typically studied demographic or evolutionary consequences for the consumer, but ignored consequences of altered phenological match for the resource[66]. For example, in the United Kingdom, newts (*Triturus* spp.) now enter ponds earlier in the year, whereas frogs (*Rana temporaria*) have not advanced their breeding phenology. As a consequence, the frog larvae are subjected to higher levels of newt predation[67]. Also, increasing temperatures have increased the overlap in autumn migration times of long-distance migratory birds and one of their avian predators, the sparrowhawk (*Accipiter nisus*), while they have decreased the overlap between short-distance migrants and sparrowhawks, but consequences on these populations remain unclear[68]. However, the consequences of mismatches do not need to be of similar importance for the different trophic levels[66]. For instance, while it may be important for the predator to be matched with the phenology of its prey, predation may not be an important selection pressure on the phenology of the prey, as in the case of the great tit and their caterpillar prey. As these temporal distributions of predation risks are much harder to measure, more studies on predation risk phenology are needed.
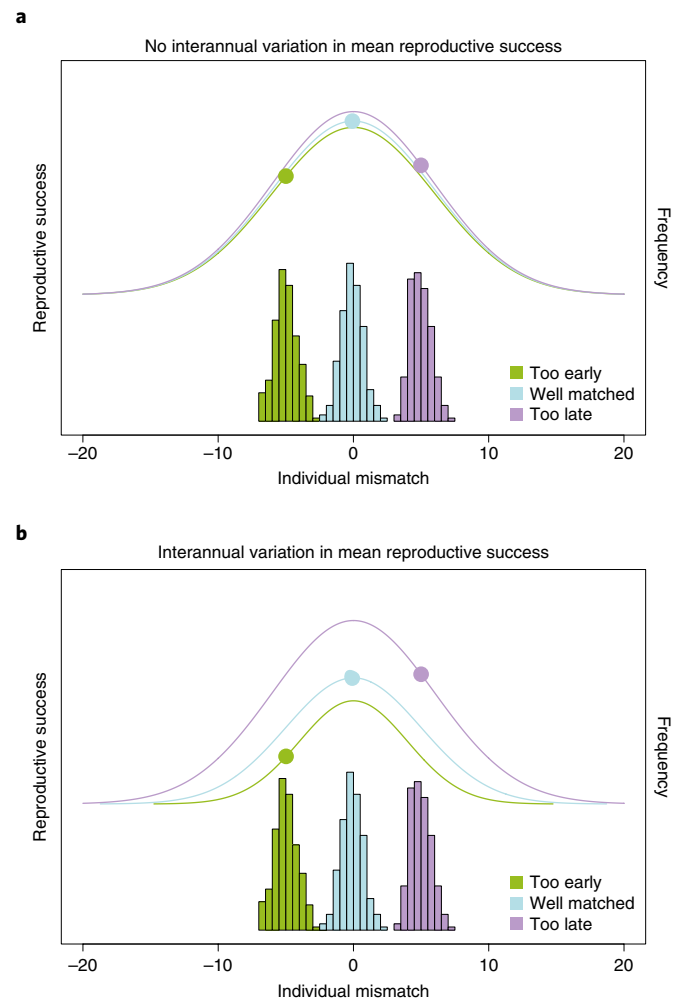
Fig. 3 | Relationships between mismatch and reproductive success at the individual and population level. The coloured lines depict fitness curves in relation to individual mismatch for three different scenarios of mismatch (green, too early; blue, well matched; purple, too late), indicated by the three frequency distributions of individual mismatch. The dots on the fitness functions indicate population mean fitness for each scenario. **a**, The height of the fitness curves of three scenarios is similar. This means that population mean reproductive success is only a function of population mean mismatch; if the population is, on average, too early (frequency distribution of phenology in green) or too late (purple), it has a reduced population mean reproductive success (cf. dots on fitness curves). **b**, The height of the fitness curves differ. The difference is lowest when the population is too early (green curve and green frequency distribution) and highest when the population is too late (red curve and red frequency distribution). This leads to an increase of population mean reproductive success with mismatch (cf. dots on fitness curves), because mean mismatch co-varies positively with the height of the resource peak. Note that the units of mismatch and the relationship between population mean mismatch and the height of the fitness curve have been chosen arbitrarily (this also works the other way around — a negative covariance between mean mismatch and the height of the resource peak).

Mismatches may also play a role in competition. For example, increasing temperatures have altered the competitive interactions between bird species and between plankton species and thereby equilibrium population densities and community structures[19,69]. In the case of mutualisms, for example, between plants and pollinators, species are also likely to become

Box 1 | Mistiming in annual life-cycles

Differential shifts in phenological events may happen not only between species, but also between different life-cycle stages within an individual, as these life-cycles stages may respond differently to a cue[47,84]. Some life-cycle events will be more sensitive to photoperiod (for example, moult in birds[85]), while others are more sensitive to temperature (such as reproduction[5]). Such differing sensitivities can lead to differential shifts in the phenology of these life-stages owing to climate change[12,86,87], provided that there are no strong effects of one life-cycle stage on the phenology of the next stage. Examples of differential shifts in the phenologies of coupled life-history traits are arrival date and breeding date in migratory birds, in which an arrival date that does not shift could potentially constrain shifts in breeding phenology[88,89]. However, changes in temperature can also lead to differential shifts in reproduction and moult. For example, in pied flycatchers (*Ficedula hypoleuca*), moult is comparatively less sensitive than reproduction[84]. In red deer (*Cervus elaphus*) the phenologies of 6 traits were measured over a 28-year period[90], and, in female deer, parturition dates advanced almost twice as fast as date of first oestrus. In males, antler casting and cleaning advanced at a similar rate, but the end of the rut shifted twice as fast as its start dates. Clearly, mistiming within the annual life-cycle could be very common.

Examples of mismatch affecting reproductive success. In common murres (*U. aalge*, top left), great tits (*P. major*, top right), caribou (*R. tarandus*, bottom left) and roe deer (*C. capreolus*, bottom right), mean breeding success is reduced in years with an increased population-level mismatch between breeding phenology and the phenology of the main food resource. Credit: Simon Litten/Alamy Stock Photo (top left); imageBROKER/Alamy Stock Photo (top right); Ron Niebrugge/Alamy Stock Photo (bottom left); Pim Leijen/Alamy Stock Photo (bottom right)

mismatched with each other since climate change affects different trophic levels at different rates[17]. However, whether such mismatches will have consequences depends on the degree of specialization and the asymmetry of the mutualism. For example, certain plant species can only be fertilised by a single insect species, such as the early spider orchid (*Ophrys sphegodes*), which depends almost exclusively on a solitary bee species (*Andrena nigroaenea*) for pollination. Differential shifts in the phenology of these species would have negative effects for the plant but not for the bee[70]. More generalist plant species are, however, less likely to entirely miss out on being pollinated[65], but generally mismatches between plants and pollinators and potential demographic effects are not well studied[17].

Parasites obviously depend on their hosts being present or vulnerable, which generally varies seasonally[71]. Differential shifts in parasite and host phenology can hence also lead to mismatches. For example, migration time of common cuckoos (*Cuculus canorus*) and some of their host species have advanced at different rates[54], while (experimental) temperature increases led to a strong mismatch between the phenologies of a trematode (*Ribeiroia ondatrae*) and its amphibian hosts[18]. Such mismatches could have strong consequences for parasite or host population dynamics, potentially leading to local extinction of the parasite[72].

Increasing temperatures affect not only biological processes, but also agricultural practices. For example, sowing or mowing

dates have shifted in Finland, which can lead to mismatches between these practices and breeding time of farmland or meadow birds, possibly negatively affecting their reproductive success and population numbers[73]. Mismatches may also have consequences for biochemical processes, but these are hardly explored. For instance, a mismatch between the geese grazing and plant growing season in arctic coastal wetlands affected the greenhouse gas fluxes[74].

4. Community ecological effects and ecosystem consequences
   Most research on the match–mismatch hypothesis focuses on pairwise predator–prey, plant–herbivore or plant–pollinator interactions. However, the selection on phenology of a focal species depends on the (mis)matched phenology with the many species it interacts with. For example, a plant that is pollinated by many different insect species will not suffer from mismatch with a single species[65]. The challenge is scaling up from pairwise interactions to more complex food webs. Only via a better understanding of entire food web phenology can we understand community-[75] and possibly ecosystem-level consequences of climate change-induced shifts in phenology[76]. Some pioneering work has been done in this area using food web models that involve phenological shifts[77,78] and in plant–pollinator communities[79–82]. The way forward is to assess the strength of the connections between different species in a food web and then to determine how these change because of the differential shifts in phenology of the different species. Following that, the properties of the networks before the shifts in phenology and after the shifts in phenology can be assessed using network theory to evaluate, for instance, whether the network has become less stable. For this, detailed experimental work is needed, for instance in simplified food webs where the phenology of the species can be manipulated. This is, however, not a trivial challenge.

Concluding remarks

Phenological mismatches are one of the clearest consequences of climate change, and, over the past two decades, an impressive body of literature in this area has been built up. We have outlined a conceptual framework and illustrated it with key examples from the body of literature. Challenges for the next decade are further study of the population-level and evolutionary consequences of mismatches, for which long-term studies are essential, and, from there, examination of ecological effects on communities and ecosystem consequences. Ultimately, what is needed is a link between climate change predictions and the predicted degree of mismatch in species interactions and networks, taking evolutionary changes into account. From there, the consequences for biodiversity and ecosystem functioning may be assessed. Such information is essential to link climate predictions to consequences for nature, which is needed for such consequences to be considered in the debate on the acceptable rate of global climate change[83].

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Acknowledgements

Author contributions

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

Additional information