



The eco-evolutionary consequences of interspecific phenological asynchrony – a theoretical perspective

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The timing of biological events (phenology) is an important aspect of both a species' life cycle and how it interacts with other species and its environment. Patterns of phenological change have been given much scientific attention, particularly recently in relation to climate change. For pairs of interacting species, if their rates of phenological change differ, then this may lead to asynchrony between them and disruption of their ecological interactions. However it is often difficult to interpret differential rates of phenological change and to predict their ecological and evolutionary consequences. We review theoretical results regarding this topic, with special emphasis on those arising from life history theory, evolutionary game theory and population dynamic models. Much ecological research on phenological change builds upon the concept of match/mismatch, so we start by putting forward a simple but general model that captures essential elements of this concept. We then systematically compare the predictions of this baseline model with expectations from theory in which additional ecological mechanisms and features of species life cycles are taken into account. We discuss the ways in which the fitness consequences of interspecific phenological asynchrony may be weak, strong, or idiosyncratic. We discuss theory showing that synchrony is not necessarily an expected evolutionary outcome, and how population densities are not necessarily maximized by adaptation, and the implications of these findings. By bringing together theoretical developments regarding the eco-evolutionary consequences of phenological asynchrony, we provide an overview of available alternative hypotheses for interpreting empirical patterns as well as the starting point for the next generation of theory in this field.

Global warming has caused phenological changes in all major ecosystems and taxa (Peñuelas and Filella 2001, Fitter and Fitter 2002, Sparks and Menzel 2002, Parmesan and Yohe 2003). Many spring and summer events have advanced but there is also a considerable variation in the rate of phenological change among species and phenophases (Schwartz et al. 2006, Thackeray et al. 2010). Such variation may reflect differential effects of warming on development rates of different organisms, and on cues that affect the seasonal scheduling of species activities (Yang and Rudolf 2010). It may also reflect variation in either genetic variance affecting the rate of adaptation through microevolution, or constraints on phenotypic plasticity (Gienapp et al. 2007).

Many interspecific ecological interactions are dependent upon the temporal coordination of the seasonal activities of the interacting species. For example, Thomson (2010) has shown that pollen limitation in a subalpine lily (*Erythronium grandiflorum*) has increased over a period of 17 years, and the suggested mechanism is that climate change has decreased the temporal match between plants and pollinators. Spawning phenology in the marine intertidal bivalve *Macoma balthica* is under selection by temporal variation in both its food resources (phytoplankton), and predation risk (shrimps) (Philippart et al. 2003, Visser and Both 2005). Hence, unequal rates of phenological change among interact-

ing species may alter the strength of ecological interactions or disrupt them altogether. The observation of phenological decoupling in many systems (Visser et al. 1998, Winder and Schindler 2004) accompanied by population declines (Both et al. 2006) is a cause for concern. As demonstrated by Donnelly et al. (2011), however, both winners and losers can be identified among species involved in documented cases of differential phenological shifts in various ecological systems.

Relatively few studies have quantified the demographic effects of unequal phenological shifts and subsequently there is still large uncertainty regarding their long-term consequences for species and ecosystems (Miller-Rushing et al. 2010, Bennett et al. 2015). In order to better understand patterns of phenological change and to guide our intuition about their consequences, development and application of appropriate theory has been demanded. As an example, Forrest and Miller-Rushing (2010) highlight that studies of interspecific variation in phenological shifts rarely take into account life-history theory and central trade-offs such as the one between optimal age and size at reproduction. Donnelly et al. (2011) point out that much modeling regarding phenological change mainly has considered single species and argue that future modeling should consider the functioning of the ecosystem as a whole and accommodate interactions among species as well as variation in temperature responses

of the timing of different seasonal activities. At the same time, much theory with relevance for differential phenological shifts has been developed relatively recently (Jonzén et al. 2007, McNamara et al. 2011, Visser et al. 2011, Lof et al. 2012, Nakazawa and Doi 2012, Johansson and Jonzén 2012a, Revilla et al. 2014) and there is a need to synthesize the various attempts to develop models for unequal phenological shifts into a coherent and useful theory for a more complete and general understanding of the problem. As stressed by Carpenter et al. (2009) the synthesis of diverse knowledge is a central part of all sciences, and climate ecology is no exception since it draws information from many disciplines.

The purpose of this article is to give a synthetic overview of key theoretical results regarding the consequences of unequal phenological shifts for fitness and microevolutionary adaptation. We will mainly focus on findings that relate to life history theory, population dynamic models and evolutionary game theory. We will also mainly consider phenological changes that influence biotic interactions, as opposed to phenological changes that affect species adaptation to seasonally varying abiotic conditions. Readers may in this context note that existing reviews cover empirical aspects of differential phenological shifts among interacting species (Visser and Both 2005, Donnelly et al. 2011, Forrest 2015) as well as genetic, physiological and behavioral aspects of phenological adaptation (Visser 2010, Wilczek et al. 2010).

The article is structured as follows. We will start by introducing a baseline model for phenological mismatch that we will use as a reference case throughout the paper. Then we will discuss how the intuitive predictions from this model can be influenced by various mechanisms that have been highlighted in the literature. Finally we will identify emerging, general patterns among these results and discuss their implications.

A baseline model for phenological mismatch

Assumptions and predictions

The model considers two species that interact with each other. The focal species is assumed to benefit from the interaction, for example as a predator, parasite or mutualistic partner of the other species. The non-focal species is furthermore assumed to be the main resource of the focal species at least during a part of the life cycle and in this sense the focal species can be considered to be a specialist. The benefit of the interaction to the focal species is assumed to depend on the relationship between the seasonal timing of a key life-cycle phase of the focal species and the seasonal timing of a life-cycle phase of the non-focal species. The reader may for example think of the focal species as a bird for which the reproductive output (the benefit) depends critically on the timing of its nestling stage in relation to the timing of the larval stage of an abundant insect species (cf. Lack 1954). As another example, one may consider a plant species for which the amount of flowers pollinated (the benefit) depends on the temporal overlap between its flowering phase and the activity period of a pollinating insect (cf. Memmott et al. 2007, Forrest 2015).

We consider a single population of each of the interacting species and focus on the timing of a single life-cycle

phase of each species. The temporal relationship between the life-cycle phases is assumed to primarily affect the strength of the interspecific interaction in terms of e.g. the amount of pollinated flowers or consumed resources per year. We let phenological synchrony denote a situation in which the life-cycle phases of the respective species occur simultaneously during the season (point *a* or *c* in Fig. 1, left panels). Note that synchrony in our context thus refers to an interspecific temporal relationship (in line with the use in e.g. van Asch and Visser 2007) and not the variability of individual phenology within a population or species, sometimes referred to as ‘population synchrony’ (Sweeney and Vannote 1982).

We assume that the interaction strength has a maximum at phenological synchrony (point *a* in Fig. 1). For the examples above we thus assume that the maximum occurs when there is full overlap between the nestling stage of the bird and the insect larval stage or between the flowering phase of the plant and the activity period of the pollinator. We then assume that the strength of the interaction has a positive influence on reproduction, survival or some other fitness component of the focal species (Fig. 1, right panel). For simplicity, we disregard any other effects on fitness of timing of the life-cycle phases, e.g. those resulting from life-history tradeoffs (cf. Singer and Parmesan 2010, Ehrlén 2015), and assume that the total fitness of the focal species increases with the interaction strength as well. We furthermore assume that increasing fitness results in a larger population density (Fig. 1, right panel). Thus, we assume that the interaction strength, the immediately affected fitness components of the focal species, its total fitness as well as its population density show qualitatively similar responses to changes in the temporal overlap of the life-cycle phases in question. In particular they all have a maximum at phenological synchrony.

Given the assumptions above, phenological synchrony (point *a* in Fig. 1) is an expected evolutionary endpoint for the focal species. We envision a scenario in which synchrony has evolved in some historical environment and consider changes in the environment which cause the interacting species to change their phenologies in relation to each other. The reader may for example envision situations in which climate change has differential effects on development rate of the interacting species, or on cues that affect the timing of biological events (Yang and Rudolf 2010). If, for example, the non-focal species advances its phenology in relation to the focal species, this gives rise to phenological asynchrony and a fitness decline of the focal species (point *b* in Fig. 1). According to the baseline model, the adaptive response of the focal species is now to adjust its timing of the key life-cycle phase to fit the corresponding life-cycle phase of the non-focal species. Thereby it would again reach phenological synchrony and the interaction strength would again be maximized (point *c* in Fig. 1). A similar reasoning holds for any unequal phenological shift, i.e. regardless of whether the phenological changes on an absolute calendar time scale occur in the focal species, in the non-focal species with which it interacts, or in both. Three key predictions of the model are thus that 1) phenological synchrony is favored by natural selection and that unequal phenological shifts 2) lead to asynchrony and 3) reduce the fitness of the focal species.

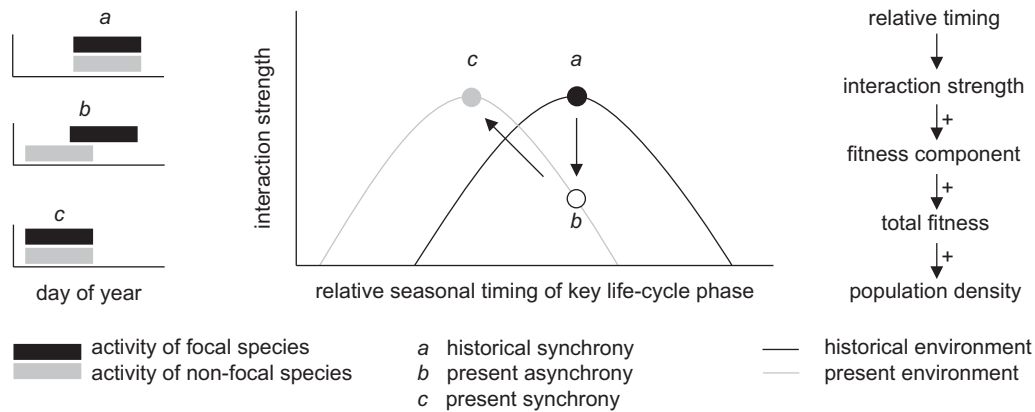


Figure 1. The baseline model of phenological mismatch used here for comparison with more complex scenarios. The model considers variation in that the strength of an ecological interaction, such as predation, depends on the temporal overlap between two life-cycle phases of two interacting species. It assumes that timing of the key life-cycle phase of the focal species has evolved to maximize the interaction strength by being synchronized (point *a*) to a life-cycle phase of the other species in some historical environment. When the environment changes and the timing of the life cycles change in relation to each other, the historical strategy becomes asynchronous and thus suboptimal (point *b*). An adaptive response is to restore synchrony (point *c*). As illustrated to the right, increasing the interaction strength has a positive influence of a fitness component of the focal species, as well as on its total fitness and population density.

Relationship to the previous research and comparable concepts

The baseline model is inspired by the match/mismatch hypothesis (MMH) by Cushing (1969). Originally, the MMH was developed for marine systems and related recruitment rates of fish species with temporal relationships between cod larval stages and stages of zooplankton that comprise their main food resource (Cushing 1990, see also Hjort 1914). The concept has since been applied to various marine and terrestrial systems (reviewed by Durant et al. 2007) and the terms match and mismatch are extensively used in research about unequal phenological shifts among interacting species (Miller-Rushing et al. 2010, Donnelly et al. 2011). MMH postulates that the recruitment rate of a predator species is maximized when the most energy-demanding stage of the predator overlaps with the highest availability of its prey species. This corresponds to the assumption of the baseline model that a fitness component of the focal species is maximized at phenological synchrony. Specifically, this assumption is equivalent to MMH when the focal/non-focal species are predator/prey species, the fitness component is recruitment rate and the life-cycle phases considered are stages of high energy demand of the predator and high availability of the prey.

While MMH is thus embedded in the baseline model, there are some noticeable differences between the concepts. Regarding terminology, match and mismatch in MMH corresponds to synchrony and asynchrony in the baseline model. Both pairs of terms are commonly used and they are also often used synonymously (Miller-Rushing et al. 2010, Donnelly et al. 2011). However, we have chosen synchrony/asynchrony since they reflect a more neutral description of temporal overlap. In contrast the terms match/mismatch may suggest that one state – mismatch – is inferior to the other – match – from the particular perspective of one of the involved species (e.g. the predator).

Another difference is that while MMH, at least in the original version, describes a trophic interaction, the baseline model has a slightly more general formulation

that encompasses also other types of interactions, such as mutualisms or host-parasite interactions. This was made to reflect the fact that the concept of match/mismatch is being applied to a large range of systems and situations (cf. Miller-Rushing et al. 2010, Donnelly et al. 2011). However it should be noted that the baseline model is still restricted to cases in which the focal species benefit from the interaction. For example it does not consider the fitness consequences of the prey or host, which instead can be expected to benefit from increased asynchrony with their predator or parasite (see Donnelly et al. 2011 for related empirical examples). It should also be noted that while spatial versions of MMH sometimes are discussed (Durant et al. 2007) we are here only concerned with the mismatch or asynchrony in the temporal sense.

The baseline model also contains some additional assumptions and some more far-reaching predictions compared to MMH. These extensions provide explicit links between unequal phenological shifts and changes in population densities and evolutionary equilibria. This is useful in the context of this review because it helps to identify mechanisms that are responsible for modifications of the predictions when we consider more complex scenarios.

Furthermore, the extensions provide links to common approaches to the problem of interpreting unequal phenological shifts in current research. In line with prediction 1) of the baseline model, phenological synchrony is commonly conceived of as a result of evolution through natural selection or as a historical state before recent climate change (Stenseth and Mysterud 2002, Visser et al. 2004, Durant et al. 2007, Both et al. 2009, Donnelly et al. 2011). The statement that natural selection in response to unequal phenological shifts, unless constrained, may “restore synchrony” (van Asch and Visser 2007) is also compatible with this prediction. The prediction 2) of the baseline model that unequal phenological shifts lead to asynchrony corresponds to the yardstick principle suggested by Visser and Both (2005). They suggested that the adaptive phenological response of a consumer – at least as a first approximation – is to change its phenology

at the same rate as that of its food distribution, which in this sense would serve as a yardstick. Should the consumer change its phenology at some other rate than they interpreted this as mistiming which corresponds to asynchrony in our framework. The third prediction of the baseline model, that increased asynchrony reduces fitness is also a common expectation (Visser et al. 2004, Durant et al. 2005) not least owing to empirical support of negative fitness consequences (Thomson 2010) or population declines (Both et al. 2006) associated with increasing asynchrony.

Factors that influence eco-evolutionary consequences to phenological asynchrony

We will now give examples of ecological mechanisms and life history characteristics that influence the eco-evolutionary responses to unequal phenological shifts (Fig. 2), focusing upon how they modify the key predictions the baseline model. The first factor (A), illustrates variation within the baseline model framework. The remaining factors (B to I) represent additional components of fitness or of the environment that are not part of the baseline model. The last three factors (G–I) furthermore require that we explicitly consider the life cycle of the focal species, in particular the fact that individuals undergo different life stages.

Although the scenarios we consider below thus may contain additional elements compared to the baseline model our focus remains on a pairwise interaction within that scenario, on the species that benefit from it and on the temporal relationship of two life cycle phases that influence its strength. We use the same definitions to the extent possible and also here consider unequal phenological shifts, i.e. changes of the phenologies of two species in relation to each other, which may result from environmental changes such as climate change.

(A) The sensitivity of the interaction strength to phenological asynchrony

The strength of an ecological interaction may be more or less strongly affected by increased phenological asynchrony. As an example, the consumption rate of a predator species can be expected to be more affected by phenological asynchrony if the availability of its prey species has a narrow temporal distribution (Fig. 2A, top panel) than if it has a wide temporal distribution (Fig. 2A, bottom panel). If unequal phenological shifts of a certain magnitude would occur in these two scenarios, the reduction in interaction strength (i.e. the difference between the black solid and black open circles) would be largest in the scenario with the narrow temporal resource distribution (Fig. 2A, top panel). A higher

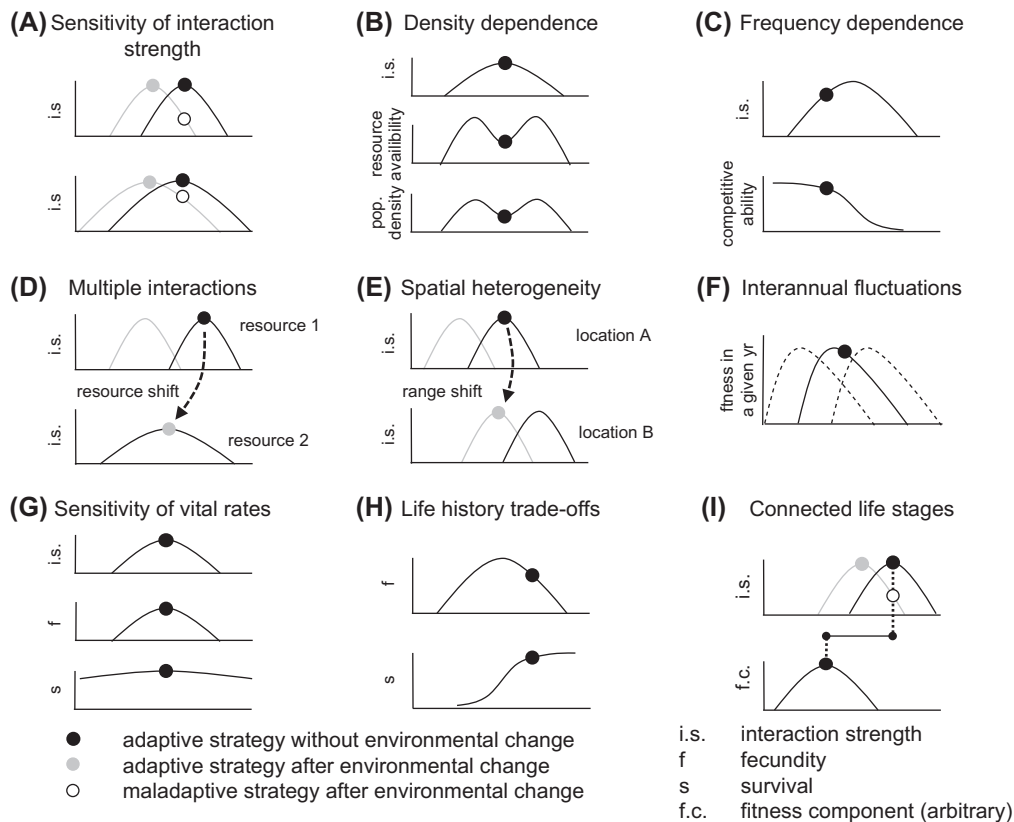


Figure 2. Factors that are expected to influence eco-evolutionary responses to unequal phenological shifts. Each panel illustrates at least one outcome that differs from the baseline model of phenological mismatch as illustrated in Fig. 1. Following the convention in Fig. 1, shaded curves indicate a situation after an environmental change. In (A) and (G) deviation from phenological synchrony causes only a small fitness decline. In (B) population density has a minimum at phenological synchrony. In (C), (F) and (H) phenological asynchrony is adaptive. In (D) and (E) unequal phenological shifts cause a different adaptive response than tracking the historical resource. In (I) phenological adaptation of a life stage to a temporal shift in the focal pairwise interaction fails because its timing is connected to the timing of an earlier life stage. More details are provided in the main text where each example is described and discussed in the sections for the respective factors.

sensitivity of the interaction can thus be expected to exacerbate negative fitness consequences of unequal phenological shifts at least provided that a weaker ecological interaction is translated into a lower fitness (as in the baseline model). For this reason, the sensitivity of bird reproductive output to temporal shifts in the availability of food resources may for example be predicted to be high when food is available only during a short period of time but low when food availability is relatively constant over the breeding season (Dunn et al. 2011). Similarly, pollination services to plants can be predicted to be relatively strongly affected by unequal phenological shifts when pollinators are active only during a short period (Memmott et al. 2007, Rafferty et al. 2015). Abiotic factors such as temperature may also influence how much the strength of an interspecific interaction is affected by unequal phenological shifts as shown by Rudolf and Singh (2013) in a study of two competing amphibian species.

While this type of sensitivity does not necessarily influence the timing of the optimal strategy (the adaptive strategy, synchrony, is unaffected by variation in the width of the curves in Fig. 2A top and bottom panels), it may influence microevolutionary responses to unequal phenological shifts (i.e. the rate of adaptation from point *a* to *c* in Fig. 1). When fitness is proportional to interaction strength (as in the baseline model) high sensitivity to unequal phenological shifts corresponds strong stabilizing selection (cf. Reed et al. 2015). Strong stabilizing selection will on the one hand increase the rate of microevolutionary change but may on the other hand also lead to a sharper population decline should the microevolutionary change not be sufficient to restore synchrony (Reed et al. 2015, see also Maynard Smith 1989, Lynch and Lande 1993). For illustration, the narrow curve in the top panel of Fig. 2A would result in a more rapid gradient of return to synchrony (from open circle to gray circle) compared to the wider curve in the bottom panel, but on the other hand be associated with a larger initial drop (from solid to open circle) in interaction strength and fitness as discussed above. Thus the net effect of increased sensitivity for long-term adaptation, and for the likelihood of evolutionary rescue, is not easily predicted.

(B) Density dependence

The baseline model predicts that fitness will be negatively affected by phenological asynchrony. However, when fitness depends on the density of the population (e.g. via competition for resources or via the probability to find mating partners), the direct effect of unequal phenological shifts can be counteracted or enhanced by subsequent changes in the population density. Compensatory effects can occur under negative density dependence (i.e. per capita growth rate decreases with population density), which in turn is expected under intraspecific competitive interactions. For example, the size of a population of great tits subjected to a shifted resource distribution was buffered against negative fitness effects from reductions in reproductive output by a concomitant increase in survival owing to reduced competition (Reed et al. 2013). Because negative density dependence may result in a relatively constant population size it can be seen as a stabilizing force. In contrast, positive density dependence (per capita growth rate increases with population density) can be seen as a destabilizing force. An example is an Allee effect (Allee

1931), where positive growth rates require a minimum population density. Thus if increased phenological asynchrony causes a population to decline below that minimum, the population will continue to decline. Positive density dependence is expected in mutualistic partner species since the presence of one enhances the fitness of the other. Thus it may play a role in enhancing detrimental fitness effects of differential phenological shifts among plants and pollinators (Gilman et al. 2012). Especially vulnerable to these negative effects are seasonal mutualistic interactions of short duration among short-lived partners (Rafferty et al. 2015).

Density dependence can also have the counterintuitive effect that the population density of a consumer species is at a minimum at synchrony (Fig. 2B) as demonstrated theoretically by Revilla et al. (2014). According to their analysis of a population dynamic model, increased synchrony with the resource and thus increased per capita consumption rates (Fig. 2B, top) reduced the abundance of available resources (Fig. 2B, middle). This in turn resulted in stronger intraspecific competition and in the long run a lower equilibrium size of the consumer population (Fig. 2C, bottom).

(C) Frequency dependence

Frequency dependence means that the outcome of an evolutionary scenario depends on the strategy used by the focal player as well as on the strategy of others. In the context of phenology, there are many reasons where fitness can be expected to depend upon the phenology of other individuals or species. In Marsh tits *Parus palustris*, parents that reproduce early relative to the other individuals in the population, gives an advantage in social competition for territories among their offspring (Nilsson and Smith 1988). In many animal taxa, early arrival to breeding grounds yields high success in contests for mating opportunities or territories (Fig. 2C, Kokko et al. 2006). For plants, germinating early relative to other species can convey a competitive advantage (Cleland et al. 2015).

Situations where fitness is frequency dependent can be considered as evolutionary games, which broaden the possible outcomes beyond the optimization principle suggested by the baseline model (Fig. 1). Sometimes, we can expect natural selection to favor phenologies that deviate from synchrony in Fig. 1 because of advantages to individuals that deviate from the group optimum – a kind of “tragedy of the commons” (Hardin 1968, Rankin et al. 2007). As an example, priority effects in territory acquisition will favor earlier-than-optimal phenology (Ketterson and Nolan 1976). This is illustrated in Fig. 2C where the cost of deviating from synchrony (Fig. 2C, top) is traded for the benefit of an increased competitive ability of an early phenology (Fig. 2C, bottom) due to the associated priority effects. The deviation can also occur in the opposite direction. For example, a later-than-optimal phenology is favored by a strategy wherein flowering is delayed in order to prioritize growing high and shading out other plants (Gadgil and Gadgil 1975). Since the competitive advantages lead to an evolutionary race towards phenologies that are suboptimal, adaptive responses may well be accompanied by decreasing population sizes (Kokko 2011, Johansson and Jonzén 2012b, Day and Kokko 2015, Schmidt et al. 2015). This is in contrast to the baseline model in which the maximum population density and the

evolutionary endpoint coincide (both represented by point a or c in Fig. 1) and adaptation thus is accompanied by population growth.

Evolutionary games can furthermore lead to the stable coexistence of two or more strategies (Maynard Smith and Parker 1976), instead of the single optimal strategy depicted in Fig. 1 by point a . This occurs when the fitness of a strategy increases when it is rare (negative frequency-dependence). One example of this in the context of phenology is the arrival times of migratory birds which can show a bimodal pattern with an early, competitive strategy coexisting with a later, risk-averse strategy (Sirot and Touzalin 2014). Similarly, a continuous distribution of breeding dates (i.e. a period over which individuals start breeding with some probability) has been suggested to evolve due to competitive advantages in a metacommunity under certain disturbance regimes (Iwasa and Levin 1995). It follows that the adaptive response to environmental change is not necessarily a temporal shift of a single life stage, but may involve more complex changes in how timing of individual life stages are structured within a population (see also (I) below).

(D) Interactions with several species

The eco-evolutionary response of a species to a phenological shift in relation to another species can be influenced by additional interspecific interactions, either buffering or exacerbating the detrimental effects. If the main resource of a species becomes less available due to an unequal phenological shift, negative consequences will be ameliorated if it can employ an alternative resource (Fig. 2D). Negative fitness consequences of a relative phenological shift of a single resource can also be expected to be lower for a generalist species that use multiple resources and interacts weakly with each of them than for a specialist species that is dependent on a single resource with which it has a strong interaction. For example, reproductive timing in bird species that can utilize multiple resources across the nestling period will be less sensitive to a shift in one of them (Cholewa and Wesolowski 2011). In this way alternative resources can be thought of as a buffer against severe negative fitness effects of temporal shifts in relation to a single resource. In contrast, Gilman et al. (2012) presented a model that showed that an alternative flower resource can also become an evolutionary trap that impedes adaptation of a pollinator's emergence to changes in the phenology of the focal flowering plant, again showing that the single peak in Fig. 1 may be an over-simplification.

Multiple interactions can also be a reason for the evolution of asynchrony in a given pair-wise interaction. For example, the optimal timing for flowering may deviate from synchrony with pollinators and instead be a compromise between maximizing pollination and avoiding seed predation (Ehrlén 2015).

Unequal phenological shifts across a pair of species may also have consequences for species in the surrounding food web, i.e. beyond the focal species pair. As an example, a phenological shift of a top species in a food chain can cause a cascade of changes in population densities down the trophic levels (Nakazawa and Doi 2012). Since we are here mainly concerned with the consequences for a single species of a phenological shift in relation to one other species, such

additional effects are beyond the scope of this paper. However, we note that such indirect effects may eventually feed back on the focal species pair (Revilla et al. 2014). For example, for a species in the middle of a tritrophic-level food chain, the benefit of phenological asynchrony with the top predator may be offset by a reduction in the abundance of its own prey owing to a trophic cascade.

(E) Spatial heterogeneity

The eco-evolutionary response to unequal phenological shifts occurs in a spatial context, often within heterogeneous landscapes. Consequently a population can be exposed to patches with quite different optimal schedules and timings depending upon the location in space as well as on the mobility of different life stages of the focal species. For example, mixed forests of deciduous and coniferous stands have different caterpillar-peak timings (Veen et al. 2010), and individuals that find themselves in the 'wrong' habitat may suffer fitness consequences (Lambrechts et al. 1997). At the same time, individuals may buffer against negative fitness effects by optimal habitat choice or engaging in range-shifts as an alternative to changing their own phenology to cope with unequal phenological shifts (Fig. 2E). As an example, male pied flycatchers that were mismatched to the caterpillar peak as nestlings and/or arrived late from migration the following year moved from their natal site to a site with later caterpillar phenology (Hušek et al. 2014).

Furthermore, spatial heterogeneity may force a species to compromise between the different environments it experiences rather than evolving to match a single local resource maximum. This follows from theoretical work on adaptation to heterogeneous environments, where the fitness of a passively dispersing organism depends on the matching between an (unspecified) ecological trait and an underlying resource distribution (Brown and Pavlovic 1992, Kisdi 2002). A generalist strategy, corresponding to an intermediate timing, is expected from natural selection when heterogeneous landscapes are fine-grained or when dispersal rates are high. Furthermore, the potential negative fitness consequences of a mismatch might be reinforced by fragmentation due to habitat destruction, which will reduce dispersal rates (Revilla et al. 2015). Deviation from a locally optimal strategy can also occur at ecological boundaries, particularly amongst plants and insects, as a reinforcement mechanism to avoid maladapted hybrids (Hendry et al. 2007).

(F) Inter-annual environmental fluctuations

Variation in the timing of seasonal events between years depends on fluctuations in e.g. temperature and precipitation. We here point out three ways by which such fluctuations may lead to eco-evolutionary consequences that deviate from those predicted by the baseline model. Firstly, inter-annual variability by itself can have negative fitness consequences because the best timing of an action is hard to predict, as cues used by organism such as photoperiod or a temperature threshold may only give partial information about the best timing (McNamara et al. 2011). Thus in a variable environment, changes in fitness may be caused by changes in the average phenology or by changes in the variability of phenology, e.g. due to increased variance of temperatures, assuming that vital rates are indeed affected

by phenology. This question is particularly relevant in the context of climate change (Boyce et al. 2006) since abiotic conditions such as temperature are believed to become more variable (Easterling et al. 2000).

Secondly, environmental fluctuations themselves may cause natural selection to favor phenologies that systematically deviate from the resource maximizing strategy (corresponding to point *a* in Fig. 1), as shown by Lof et al. (2012) in the context of bird reproduction. Specifically, they used an optimization model to study reaction norms, i.e. timing of reproduction as a function of the environmental state. In a constant environment, or with a symmetric fitness landscape, the average laying date given by the optimal reaction norm coincided with the nestling resource maximum (corresponding to point *a* in Fig. 1). However, when the seasonal environment varied between years and when fitness was an asymmetric function of timing, the average laying date occurred on the less steep side of the maximum (e.g. to the right of the solid curve in Fig. 2F). This is because, with an asymmetric fitness landscape, the fitness penalty for deviations from the maximum in one direction is larger than in the other and therefore deviation from the maximum is a way to avoid risk. Thus, inter-annual fluctuations in the temporal position of the fitness curve (illustrated by the dotted lines in Fig. 2F) correspond to an adaptive phenology somewhat after the maximum (i.e. on the less steep side of the fitness curve in Fig. 2F). Asymmetries in fitness functions should be common because the costs of deviating from the optimum often involve different mechanisms. For example for long-lived species of migratory birds, adult mortality may be a higher fitness cost to early arrival than missing out on a high quality nesting site by arriving late.

Thirdly, in temporally variable environments, fitness is taken from the geometric, as opposed to the arithmetic mean growth rate (Gillespie 1974), permitting the evolution of bet-hedging strategies (Simons 2011). These are strategies that reduce the temporal variances in fitness at the expense of reduced arithmetic mean fitness (Ripa et al. 2010). A common phenologically related bet-hedging strategy reported for many taxa, including plants (Childs et al. 2010), rotifers (García-Roger et al. 2014), and insects (Hopper 1999), is a variable dormancy period. For example, annual killifish can enter a reversible metabolic and developmental arrest at three divergent stages in their life history, a bet-hedging strategy against the unpredictable desiccation and refilling of the ephemeral pools they inhabit (Podrabsky et al. 2010, Poláčik et al. 2014). Consequently, individuals pursuing phenological bet-hedging strategies may be asynchronous to current resource conditions and thus appear maladapted in any given year, when in fact they are maximizing fitness over the long run.

(G) Sensitivity of fitness to vital rates

Phenology can influence population growth rates by affecting different vital rates like survival, growth and fecundity. However, population growth rate is typically more sensitive to changes in some vital rates than in others (Caswell 2001). Among mammals, for example, species with early maturity, large reproductive output and short life spans exhibit a relatively large sensitivity to effects on fecundity, whereas species with late maturity and fewer offspring per

reproductive event have a relatively large sensitivity to variation in survival rates (Heppel et al. 2000). Vital rates can also be differently strongly affected by phenology. As an example, the sensitivity of mortality to changes in flowering time (via seed predation) varies between plant species (Ehrlén 2015). Such variation may influence how severe negative fitness consequences of unequal phenological change might be. Consider for example a scenario in which phenological asynchrony influences two vital rates in a population such as fecundity and survival (Fig. 2G). Assume then that the sensitivities of the respective vital rates to changes to increased phenological asynchrony are different (fecundity is more sensitive than survival in Fig. 2G). Under such circumstances it is unclear how strong the net effect on total fitness will be, based on the degree of phenological shifts alone. In line with the results by Heppel et al. 2000 above, one may for example predict larger negative fitness consequences for a species with early maturity than for species with late maturity.

Owing to variation in the sensitivity of fitness among different vital rates, unequal phenological shifts may thus not automatically translate into a significant change in fitness even if it has significant effects on a particular vital rate. It also follows that studying the change of a single vital rate may be insufficient or even misleading when considering the effects of unequal phenological shifts on population sizes. As an example, advanced flowering has been showed to be associated with an increased population size in spite of reduced survival (Hutchings 2010).

(H) Life history tradeoffs

The timing of a single life stage may have opposing effects on different aspects of an individual's performance (Fig. 2H). While reproducing early in the season may yield a higher reproductive output because of a better temporal match with resources, it may also convey physiological costs or mortality risks for the mother (Lack 1950). Similarly, an annual organism that delays the age of maturation will prolong the growth phase resulting in larger size at the expense of a shorter phase of investing into reproduction (Cohen 1971, Iwasa 2000). When an unequal phenological change has a positive influence on some fitness components but a negative influence on others, the response to the shift will depend on the balance between these different effects. Thus the adaptive value of change in these situations is harder to evaluate compared to situations similar to the baseline model where phenology influences a single fitness component.

Life history tradeoffs may furthermore be a reason for the evolution of asynchrony across trophic levels. Singer and Parmesan (2010) put forward empirical evidence that trophic synchrony was not the historical state in two plant-insect interactions. In this case, when tradeoffs between fecundity and mortality are taken into account, the asynchronous phenology between the insects and their host plants was nevertheless adaptive. Such 'superficially maladaptive' historical phenologies emphasize that trophic asynchrony can be part of a strategy that increases overall fitness (Singer and Parmesan 2010). As another example, Visser et al. (2011) studied a model in which the reproductive value of the offspring was maximized when reproduction was synchronized with a food peak (corresponding to the maximum in Fig. 2H, top),

but where total fitness also depended on the probability of survival of the mother (as illustrated by Fig. 2H bottom). If this survival increased with later timing of reproduction, it would be optimal – an ‘adaptive mismatch’ – to reproduce somewhat after the food peak (i.e. to the right of the maximum as illustrated in Fig. 2H, top).

(I) Connected life stages

While the natural starting point to understand the eco-evolutionary consequences of unequal phenological shifts is to consider a single phenological event and its direct fitness consequences, in many cases several phenological events are interdependent (McNamara and Houston 2008, Ehrlén 2015). In the simplest case, the timing of the focal life stage may be directly influenced by the timing of an earlier event. In migratory birds, the arrival date to breeding grounds puts an absolute lower bound on subsequent phenological events like laying and hatching date (Both and Visser 2001). Similarly, in *Daphnia*, emergence time from diapausing eggs in the sediment constrains the timing of spring daphnia blooms (Winder and Schindler 2004). In both examples, inflexibility in an earlier phenological event is implicated as the cause of the mismatch of the second. This is illustrated in Fig. 2I where a late life stage suffers from phenological asynchrony (top panel). If an earlier life stage is still in synchrony and if the temporal connection between the life stages is inflexible, then the late life stage may remain in asynchrony (i.e. stay at open circle in top panel).

A more complex case is when the change in the timing of the connected event has fitness consequences of its own. For example, black-tailed godwits *Limosa limosa islandica* breeding on Iceland that hatch early in relation to the rest of the population acquire better quality wintering locations and consequently return earlier the following spring (Gill et al. 2014). Furthermore, resident birds that get delayed during breeding will be time-constrained during the ensuing molt, resulting in the production of insulating feathers of low quality. These birds will have to pay high energetic costs for thermoregulation during the start of the breeding season, constraining their potential for breeding early enough to match the food peak (Nilsson and Svensson 1996). Similarly, based on annual routine modeling approaches (McNamara and Houston 2008), Hedenström et al. (2007) predicted that the departure of migratory birds from the wintering site should only advance with the advancement of food resources in the spring for species with summer molt, but not for species with winter molt.

More complex again are cases where temporal connection of between life stages involves not only mere shifts in timing but fundamental changes to the structure of the life cycle. As an example, many insect species have responded to an advanced emergence with an increase in voltinism, i.e. the number of generations that are produced each year (Roy and Sparks 2000, Gomi et al. 2007, Altermatt 2010). Increased voltinism can furthermore modify eco-evolutionary responses to unequal phenological shifts by leading to stronger population growth rates or faster rates of evolutionary adaptation (Altermatt 2010). Taking into account such structural changes to life cycles requires a more complex approach than the baseline model of Fig. 1.

Summary and conclusions

Our survey highlights a number of ways in which taking into account various ecological mechanisms and life history characteristics will modify the predictions of a simple fitness optimization model (Fig. 1) that extends the match/mismatch hypothesis (MMH). Among these we distinguish four major themes that we discuss below.

Firstly, even in cases where synchrony is the historical state, a number of factors can modify the fitness consequences of unequal phenological shifts among interacting species. Population responses are for example expected to be relatively weak if the sensitivity of an interaction to differential phenological shifts is weak (factor A), when a species use multiple resources (factor D), when sensitivity of fitness to the vital rate influenced by the unequal phenological shift is weak (factor G), or under negative density dependence (factor B, Reed et al. 2013). Due to density dependence it is also possible that a phenological shift away from full synchrony can have a positive effect on population growth (factor B, Revilla et al. 2014). It follows that the development of asynchronies across species pairs should not necessarily be interpreted as a phenomenon with strong negative fitness consequences. This reinforces the observation that it is often unclear what the demographic effects of asynchrony would be (Miller-Rushing et al. 2010, Ehrlén 2015).

Secondly, there are several reasons why full synchrony in species interactions need not be expected from evolution in the first place. This may occur because the timing of the focal life stage has implications for other factors, beyond the focal interaction, that influence fitness. Such factors may include the phenology of competitors (factor C), avoidance of risk in stochastic environments (factor F), and life-history tradeoffs (factor H). It follows that phenological asynchrony can in principle be part of an adaptive response, in which the focal species is tracking an optimum that not only depends on the phenology of its focal resource species but on a range of other factors as well. Furthermore, if the historical starting point was a deviation from full synchrony, unequal phenological shifts may well lead to increased synchrony. For example, both coal tits *Periparus ater* and willow tits *Poecile montanus* have historically bred before the resource peak optimum, thus recent warming, shifting the peak towards earlier dates, has decreased their mismatch to the peak (as shown for coal tits by Both et al. 2009 and willow tits by Vátka et al. 2011).

Thirdly, in some cases the strategy that is expected to evolve does not coincide with the maximum of the population density. This occurs when the timing of an event has different implications for the success of an individual and for the growth rate of the population as a whole. Such a situation can arise because of density dependency (factor B, see also Fig. 2B) or because of frequency dependency (factor C) as discussed above. Regardless of the cause, the counter-intuitive implication is that an unequal phenological shift can cause a population to increase, and that the subsequent adaptive response can cause population to decline.

The final and fourth theme is that phenological adaptation may yield a structurally different outcome than a change in the timing of a single life stage. An adaptive response may for example include an increase in the number of generations

per year (factor I), range shifts (factor E), or the evolution of a bet-hedging strategy that expresses intraspecific phenological variation (factor F). In these cases, understanding phenological response will require us to move outside the scope of the baseline model and its derivatives described above.

These overarching themes represent general ways in which added complexity can alter the predictions of the baseline model and, at least in principle, can trigger a fundamentally different response than predicted by MMH. Additional complexity in eco-evolutionary responses can be expected due to interactions between these different factors. As an example, under territory competition with priority effects, density dependent population growth (factor B) may interact with frequency dependent selection (factor C) since competitive pressure can increase with population density. In theoretical studies of migratory birds it has been demonstrated that this interaction may weaken selection for advanced arrival to breeding grounds (Day and Kokko 2015), select for a later arrival date (Johansson et al. 2012), or select for later settlement in territories after arrival to the breeding grounds (Schmidt et al. 2015). Theoretical research can help to systematically map out possible interactive effects such as these, for example by using models that already integrate several of the factors discussed above (Barta et al. 2008, Lof et al. 2012) as a starting point.

The focus of this review has been on how unequal rates of phenological shifts influence population densities and selective responses of a single phenological trait. Theoretical research has however also been applied to study responses at other levels of biological organization related to the factors discussed above. For example, while we here have discussed how a pair-wise interaction can be influenced by interactions with further species (factor D), several studies have explored the effects of phenological shifts at the community level. This research includes population dynamic models of food webs (Nakazawa and Doi 2012, Revilla et al. 2014) and network theory applied to plant–pollinator communities (Memmott et al. 2007, Burkle et al. 2013, Revilla et al. 2015). It has also been argued that phenology is a key adaptive trait in shaping species geographic distributions (cf. point E above) and process-based species distribution models show that, at least in trees, the ability to fit the annual cycle to seasonal conditions shapes their distribution (Chaine 2010).

In sum, our review shows that various ecological mechanisms and life history characteristics may influence how species are affected by and respond to environmentally driven phenological shifts that influence ecological interactions. The idea that differential phenological shifts tend to cause deviation from synchrony in ecological interactions, form the conceptual basis in much recent research (Durant et al. 2005, Visser and Both 2005, Thackeray et al. 2010). The importance attached to this mechanism is reflected by the fact that it was the only ecological consequence of phenological changes mentioned in the first assessment report by IPCC (1990, p. 295), which stated that “complex synchronies are found in communities in which the life cycles of plants and pollinating and seed-dispersing animals must be closely linked. Changes in climate could disrupt these synchronies.”

In this light, the match/mismatch hypothesis is also a natural reference point to which we can compare theoretical results and alternative hypotheses. As shown here, there are a variety of ways in which the predictions based on MMH can be modified or violated altogether. However, we have also shown that by exploring different extensions of MMH along with related alternative approaches, theoretical research has resulted in a range of testable hypotheses to explain apparent idiosyncrasies in eco-evolutionary responses to unequal rates of phenological shifts. Thereby we hope this review will help to identify the missing or complicating factors that need to be invoked to help understanding recent observations regarding phenological changes and their implications for future population sizes and biodiversity in general.

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