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Prey–predator phenological mismatch under climate change

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Insect phenology is affected by climate change and main responses are driven by phenotypic plasticity and evolutionary changes. Any modification in seasonal activity in one species can have consequences on interacting species, within and among trophic levels. In this overview, we focus on synchronisation mismatches that can occur between tightly interacting species such as hosts and parasitoids or preys and predators. Asynchronies happen because species from different trophic levels can have different response rates to climate change. We show that insect species alter their seasonal activities by modifying their life-cycle through change in voltinism or by altering their development rate. We expect strong bottom–up effects for phenology adjustments rather than top–down effects within food-webs. Extremely complex outcomes arise from such trophic mismatches, which make consequences at the community or ecosystem levels tricky to predict in a climate change context. We explore a set of potential consequences on population dynamics, conservation of species interactions, with a particular focus on the provision of ecosystem services by predators and parasitoids, such as biological pest control.

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Introduction

Modifications of climatic conditions driven by human activities are now well established. Current climate change is characterised by an overall increase in mean temperatures of 0.85°C since 1880 mostly due to increasing greenhouse gases concentrations [1], and models predict up to 4°C of increase by the end of the century, as well as modifications in the frequency of extreme climatic events such as drought or rainfall episodes [2,3]. Changes in abiotic conditions are affecting life histories of all living organisms across all trophic levels [4], ultimately altering biotic interactions, community stability and ecosystem functioning [5,6]. As poikilothermic organisms, insects are particularly vulnerable to changes in temperature conditions. Their main documented responses to climate change are shifts in their distribution range, local shifts in thermal tolerance capacities, shifts in body size [7] and in phenology [6]. Considering the relative importance of these shifts across ecological organisation levels and disentangling plastic from evolutionary responses are keys to understand insect long-term adaptation to climate change.

However, rapid shifts in abiotic parameters due to climate change are not affecting all species from different trophic levels at the same rate, with for instance a lag in spring activity recovery dates between trophic levels [8–10] or asynchronous modifications of winter chilling or overwintering strategies [11,12]. In this context, we stress the importance of focusing on responses of biotic interactions, such as between hosts and parasites or preys and predators [13,14,15•]. First, because asymmetric changes in spatial or temporal range due to climate change may disrupt the synchronisation of their life cycles and thereby alter the strength of their interaction. Then, because the trophic-rank hypothesis predicts that organisms from high trophic levels are more strongly affected by environmental disturbances than organisms from lower trophic levels [16]. Therefore, predicting the consequences of climate change on these relationships is challenging because it affects both organisms separately as well as their interactions [17••].

Phenology

Organism phenology, defined as the seasonal timing of biological activities and life-cycle events, is widely put in focus to illustrate a major facet of the consequences of climate change on plant and animal ecology [13,18,19]. Insects have developed complex mechanisms to measure the relative duration of day and night, thus regulating their seasonal rhythms [20]. Most particularly in climatic areas subject to seasonal variations, phenology is under strong selective pressure and results from long-term adaptation of insects to seasonal changes in both their biotic and abiotic environments. This fluctuation in environmental conditions among seasons has shaped insect life-cycles by acting on the number of generation that populations can produce during a favourable climatic window within a year (i.e. voltinism) and on development rates [21]. Although tempered by evolutionary trade-offs or genetic drifts, each insect population tends to have locally adapted phenology that allows susceptible life stages avoiding unfavourable environmental conditions and that favours synchrony with resources that they exploit, ultimately allowing the persistence of insect communities [22–24]. In temperate climatic areas, insect phenology is characterised by the annual alternation of active period under favourable abiotic conditions and the reduced or non-activity period under less favourable periods of the year, often set apart by the onset of dormancy strategies such as diapause. Cues acting on insect phenology are diverse and their effect varies among species, but photoperiod is overall a reliable signal of seasonal change and is undoubtedly the main cue acting on phenology. Temperature, maternal effects, diet, resource availability, and other biotic (e.g. species interactions) and abiotic factors can also mediate photoperiodic control.

Additionally, insect phenology has been strongly shaped by interactions occurring within trophic networks. Indeed, organisms from a given trophic level are dependent on the lower level they exploit and have to adjust their phenology to match those of their prey or host which is a selective pressure for the predator's or parasitoid's phenology [25]. Species from lower trophic levels however have to avoid being active at the same period as their predators or parasites, which may exert an opposite selective pressure on phenology as they will benefit from asynchrony. It explains why we expect more bottom–up effects than top–down effects on insect phenology shifts in the context of climate-change [26]. For instance, from a nine years survey of host–parasitoid populations, it has been demonstrated how phenological synchrony was determinant for the population size of *Cotesia melitaearum* parasitoids contrary to the lack of direct effect on *Melitaea cinxia* hosts [27]. The existence of such arms race among trophic levels for phenology and thermal optima matches/mismatches [28] is central to consider for understanding both the maintenance of species synchrony and their adaptations to new climatic conditions. One can argue that asymmetric changes in the seasonal activities of closely interacting sympatric species, such as pollinators and plants, predators and prey, or parasites and hosts, would likely disrupt the synchronisation of their life cycles through feed-back effects [23,29••,30].

How do phenological asynchronies occur?

Plasticity and genetic evolution of seasonal rhythms

Seasonal rhythms of biological activities and life-cycle events are controlled by genetic factors [31,32], and are also showing plasticity allowing organisms to face environmental variability and unpredictability [24,33,34]. One of the best-known examples is the induction of insect facultative diapause before the onset of winter, which is a plastic response (polyphenism) to both biotic and abiotic environmental conditions that predict the arrival of detrimental conditions. So far, most of phenotypic changes in response to climate change, such as phenology, seem to be related to phenotypic plasticity more than to genetic adaptations, excepted in scarcely studied systems [35,36] such as in *Drosophilia* genus [37], making it hard to predict directions taken by shifts for a given organism and its interactions. Indeed, plasticity is not always adaptive and may simply be a response to provisional environmental constraints [38], potentially leading to temporary mismatches between a species' life-cycle and its biotic and abiotic environments [26].

Because of complex determinism of insect phenology by several abiotic parameters and their combination, variations of phenological responses to climate change occur at both intra-specific and inter-specific levels [39], across trophic levels, and across latitudes [40•]. Therefore, the relative phenological sensitivity of interacting organisms to shared abiotic parameters is likely to determine the synchrony or asynchrony of their phenology under climate change, independently of the plastic or adaptive origin of phenological changes.

For instance, the overall increase in mean temperatures and extreme sporadic events may favour the synchrony between primary consumers and bud burst of their host plants or alternative ones, when phenological shifts converge among trophic levels with temperatures modifications in new areas of their geographical range [41]. Reversely, asynchrony between early plant leaf, bud burst or flowering time and primary consumers hatching time is also now well documented for organisms that experienced divergent phenological shifts or at different rates following changes in the abiotic environment [42–44].

However, such an expectation is less obvious for less tightly interactive systems such as preys and predators and to date it has mostly been described in a nutritional ecology context showing qualitative mismatches resulting from asynchronies between developmental stages of interacting organisms [45,46]. Nevertheless, some examples on the disruption of trophic interactions due to phenological asynchrony between primary and secondary consumers have been documented, such as among birds and insects [9,47] or host–parasitoid systems [48]. When asymmetric shifts in developmental rate or voltinism create asynchrony, new environmental constraints appear that can in turn drive the plastic response or the evolution of interacting species phenology towards resynchronisation.

Change in development rates and population dynamics

Overall increase of mean temperatures and sporadic extreme climatic events are known as main drivers of insect phenology shifts, but also of several other life history trait modifications related to their development rates [19,49–51]. Modifications of these life history traits are associated with an overall acceleration of reproduction and population dynamics that may favour outbreak events as for instance in the moth *Helicoverpa armigera* [52] or in aphids that benefit from short mild period occurring during extreme heat events [53]. Inversely, changes in abiotic conditions such as higher temperatures during extreme heat events may have negative impacts and decrease population dynamics and reproduction rates [54,55]. Finally, population dynamics of top trophic level species can be accelerated or slowed down not only through changes in abiotic conditions, but also through bottom–up effects resulting from phenology modifications occurring at lower trophic levels [56]. Tightly interacting organisms such as in host–parasitoid systems may benefit from shared abiotic drivers on phenological shifts and from co-evolution pressures to maintain the synchronisation of their life-cycle (e.g. through bottom–up pressures). In other systems, depending on the rates of life-cycle changes, climate change is most likely to result in phenological matches with new organisms and in mismatches with current ones present in their phenological window. In both cases, the strength of their ecological links, as well as their sensitivity to mutual abiotic parameters will most likely determine the maintenance or not of their phenological synchronisation. For example, interactions resulting from opportunistic strategies such as between generalist predators and their preys are expected to be more prone to experience phenological mismatches and shifts in their interactions, especially if they do not share the same sensitivity to environmental changes. Phenological mismatches induced by developmental rate modifications have been already observed for plant-insect interactions with insects having faster hatching time compared to plant leaf sprouting [42,57,58]; however, it still remains less obvious among trophic interactions from higher trophic levels.

Change in voltinism

Resulting from the change in developmental rates and allowed by both developmental plasticity and short time generations, some insects species may experience increasing numbers of generations they can produce under given favourable climatic windows in a given year (i.e. votltinism) [59–61]. Small modifications in temperature can result in large shifts in voltinism [62] but the adaptive value of shifts in voltinism in response to climate change remains to be determined because physiological and ecological costs may arise from such developmental responses [63]. Similarly, to developmental rate modifications as described above, differential shifts in voltinism among interactive organisms may modify phenological synchrony. Indeed, increasing numbers of generations may create new overlapping period of activity between species from different trophic levels, favouring the synchronisation of a new interactive system, or at the opposite, decoupling generation timing between trophic levels and resulting in phenological mismatches [64]. Thus, the result of concomitant phenological shifts between trophic levels is again expected to depend on the strength of ecological links between species and on the relative sensitivity of each species to environmental stimuli. In addition, change in voltinism can be associated with modifications of life history traits involved in trophic interactions. For instance, additional generations of the orthopteran *Polionemobius mikado* have been demonstrated to result in smaller body size for the insect [65]. Such a situation may contribute to lower fitness gain in high trophic levels and thus may favour phenological mismatches and interactions shifts, especially in the most opportunistic prey–predator systems [45,61].

Multi-scale consequences of phenological asynchrony

Consequences on prey–predator or host–parasitoid interactions, conceptual framework

Although an increasing number of studies have demonstrated phenological shifts in response to climate change in invertebrates across ecosystems, there is little empirical evidence about directions taken by biotic interactions such as predation or parasitism [17••]. Mostly, modifications of such trophic interactions because of phenological asynchronies are expected to be specific to each interaction systems depending on several considerations. Firstly, as previously presented, it will be specific not only to individual species' responses to the modification of different abiotic parameters [66], but also to the phenological sensitivity of all species involved to common abiotic parameters and to their ability to shift in the same direction or not. Indeed, interacting species that do not rely on the same environmental cues to trigger phenological events may be more harshly impacted by climate-change, as, for example, photoperiod changes over the year will remain stable but not temperature changes. Parasitoids that enter and maintain diapause under the strict control of their host will likely remain synchronised following climate change. For example, some parasitoids can enter and terminate prolonged diapause when their hosts adopt the same strategy, indicating that they both are timed by the same external cues, potentially due to strong coevolution [67]. Predictions are more challenging for parasitoid and host species that rely on multiple diapause-inducing cues [68]. Secondly, it will depend on the response of consumer-resource interaction as a whole [69••] and on the degree of intimacy among resources and consumers between trophic levels and the strength of their ecological link. Indeed, tightly interactive systems such as host–parasitoid networks which are sharing long-term co-evolution history are expected to use similar environmental stimulus and to be less likely desynchronised by climate change [70]. However, it is important to take into account that within these strong coevolved systems, top levels of the trophic cascade will be highly susceptible to sudden phenological shifts occurring in lower levels. At the opposite, prey–predators' systems could be expected to be more prone to experience phenological asynchronies, still depending on the degree of specialisation.

In regard to climate change consequences on each species from different trophic levels, as well as feedback effects expected on the way they interact, it may be assumed that these new environmental conditions will lead to modifications of interaction occurrence and strength within trophic networks [71]. Either considered under the conceptual framework of mistiming of life-cycle events between trophic levels [29••], or under the framework of mismatched nutritional ecology [45], phenological asynchronies are notably expected to conduct to the modification of the realised niche of secondary consumers [16]. For instance, determinism of diet breadth as functional trait involved in phenological shifts appeared in recent meta-analyses output and support such expectations [72] as it has also been observed between plants and primary consumers [42,73]. Then, the consequences of phenological asynchronies induced by climate change on trophic interactions are expected to depend on population densities and microevolution events in organisms involved in interaction systems [74,75].

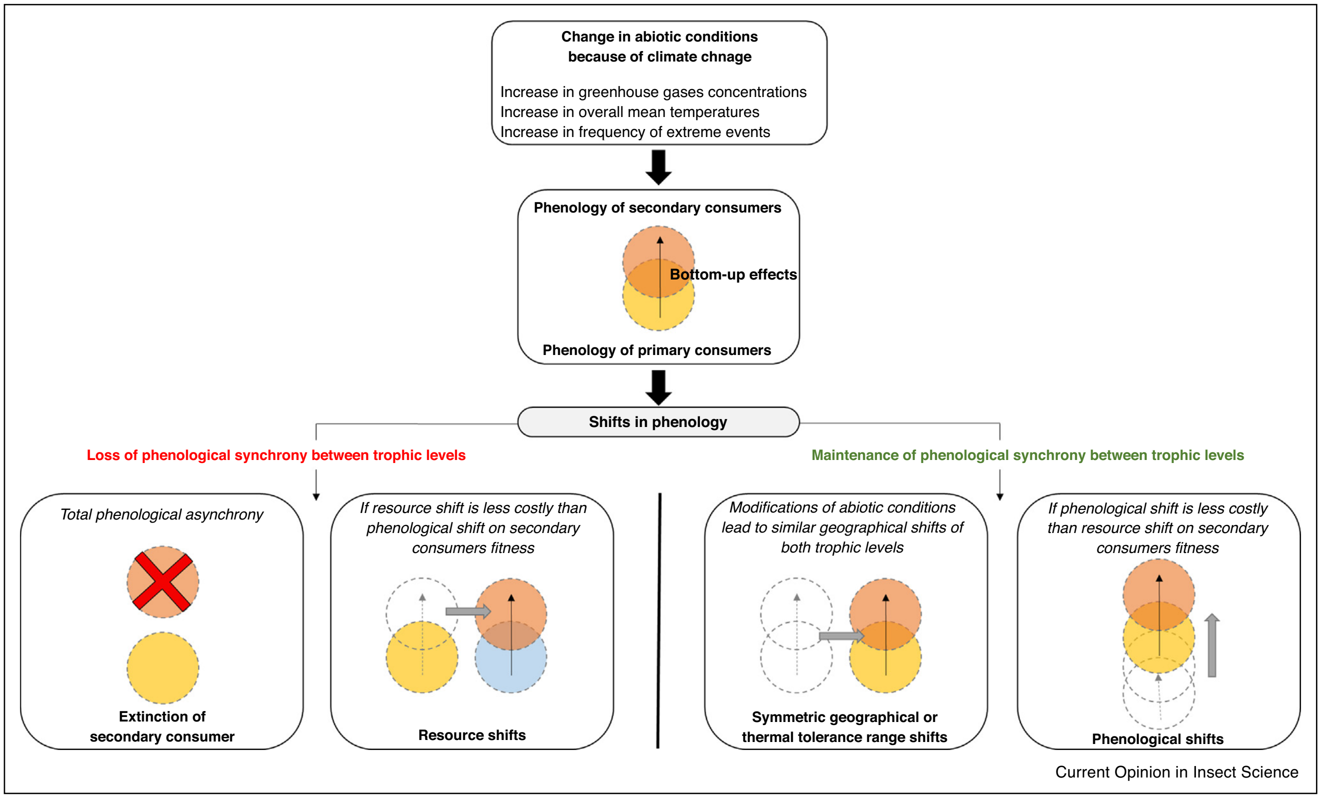
Quite a few ecological variables can affect the extent to which phenology synchrony is affected; there is, for example, expected differences between specialist and generalist species [76]. The rate of ecological niche modifications is expected to depend on the strength of specialisation from secondary consumers (predators or parasitoids) to primary consumers (prey or hosts) [77], as fitness from the former group is directly linked to the strength and maintenance of these ecological interactions with the latter [75]. Generalist consumers, because of their broad diet breadth or host range, are expected to have more plasticity and to be less directly affected by extinctions than specialist species. Reversely, a specialist predator species cannot occupy a temporal niche where its prey is absent, even if it has the physiological capacity to extend its active period later in the year, which can constrain the evolution of the predator phenology. A specialist could also switch to a generalist strategy, or specialise on another prey species. In this case, it has to be considered the selective advantage that a predator species has in modifying its phenology even if it means exploiting suboptimal prey species. Reversely, if a prey species extends its activity period later in the year, it can represent an adaptive advantage for the predator species to shift its own phenology, even if it represents physiological costs in terms of abiotic environmental conditions encountered. Thus, according to the strength of the co-evolution histories shared between specialised secondary consumers for their prey or their host comparing to generalist ones, they are more likely to follow phenological shift from primary consumers they exploit or to extinct in the absence of plasticity or adaptation.

The most obvious change resulting from a strong phenological asynchrony would be the extinction of secondary consumers, particularly highly specialised ones, in response to the phenological shift of organisms from lower trophic level they depend on (Figure 1). So far, this situation has not been empirically described under natural conditions. However, according to model predictions this situation appeared as highly probable in some interaction systems with high dependence towards the lower trophic level and were populations at low abundances suffer from additive effects such as Allee effects [78]. Extinction of higher trophic levels within interacting systems because of phenological shifts has notably started to be documented for plant-insect systems such as plant–pollinators [79,80], but is also expected to occur for straight linked trophic systems such as host–parasitoid ones [81].

Phenology is also a strong driver of organisms distribution [82]; in addition to being drove by modifications of abiotic parameters, geographical shift for secondary consumers are expected to occur in response to phenological asynchronies too, either following the geographical shift of their prey or host, either because secondary consumers cannot themselves face change in abiotic conditions in their initial geographical range (Figure 1). However, if this theoretical output can be expected, there is no direct observation to date in insect systems, probably due to the difficulty of designing experimental setup or the lack of long time-data. Nevertheless, this point is also most likely to be reflected at the community level and therefore underlying biotic interactions that are shaping species distributions. For instance, a dung beetles community along an aridity gradient has been shown to shift towards more generalist species the more arid the environment was, partially in response to change in resource quality along the gradient [83].

The two last possible outputs of phenological asynchronies on trophic interactions are for secondary consumers to follow the phenological shifts that occurred for their exploited resources, if selective pressures from bottom–up effects (i.e. primary consumers) are stronger than pressures from abiotic conditions, or to change their diet for new resources present in their own phenological windows (Figure 1). However, both of these situations are expected to occur with strong dependence to predator diet breadth (or parasitoid host range) (i.e. specialist versus generalist), and to cost of microevolution events or plasticity needed to adapt to a new niche. Generalist consumers defined by a high plasticity in resources exploited maybe expected to experience phenological shift only in response to the modification of abiotic conditions and to keep exploiting resources that are still or newly present in their phenological window [75] (Figure 1, second from left bottom panel). At the opposite, for specialist secondary consumers, shift towards new resources from their phenological window is expected to be selected only if

Figure 1



Conceptual diagram of pathways by which changes in abiotic conditions may affect interactions between primary and secondary consumers through changes in phenology. Climate change can act on phenology of both trophic levels through modifications in thermal tolerances capacities, changes in developmental rate and change in voltinism. Phenology change in response to new abiotic conditions may differ between trophic levels, creating asynchrony and disrupting the trophic interactions (bottom–left part). Otherwise, phenology changes may be similar between trophic levels, maintaining synchrony either directly in response to abiotic changes, or indirectly through stronger bottom–up selective pressures than abiotic selective pressures (bottom–right part).

it is less costly than the phenological change needed to follow primary consumers [84] (Figure 1, first from left bottom panel).

Consequences at the community scale

Climate change is expected to have direct consequences on organism interactions and ultimately on communities' structure and functioning, independently of phenology shifts [85,86,87•]. In addition, phenological asynchronies among species and across trophic levels can contribute to restructuring insect communities [88•]. By being closely related to insect fitness, consequences of phenological asynchronies on trophic interactions as described above may directly modify the relative abundance of secondary consumers that compose insect communities, disrupting existing trophic networks and resulting into new interaction systems.

Phenological asynchronies may modify insect communities' structures through the establishment of new biotic interactions. Indeed, for a given interaction network, consequences of phenological asynchrony between primary and secondary consumers may lead to the establishment of new non-trophic interactions among secondary consumers such as inter-specific competition [89]. Phenological asynchronies may also contribute to the establishment of new trophic interactions among secondary consumers themselves by promoting intra-guild predation in response to phenology shifts of initial exploited resources and/or to new overlapping phenology among secondary consumer species [86].

In such a context, as observed for aquatic ecosystems [90] it can be expected from this framework a switch from specialist to generalist strategies, or an increase in the proportion of generalist arthropod predatory species, which would be advantaged for facing the unpredictability of their own phenological shifts as well as ones occurring in lower trophic levels. For instance in Scotland, an increase of generalist species has been shown in carabid beetles assemblages across time following changes in precipitation rates and temperatures [91].

Increasing relative abundances of generalists may have a strong impact on ecological network structures, which will need to be considered in further trophic network studies under climate change. For instance, network connectance, which quantifies the whole network complexity, is expected to increase with higher proportion of generalist species as the number of links increases with diet breath [14]. Similarly, vulnerability, which quantifies the mean number of species from higher trophic levels attacking species from lower levels, is expected to increase [92].

Thereby, consequences of phenological asynchronies among species and trophic levels can be expected to alter insect communities' structure according to individual species' biology and their responses to new abiotic conditions, as well as to newly formed (or lost) interactions they are facing. It is also important to consider the existing variation at the meta-population and meta-community levels and the importance of colonisation events, as phenology among interacting species can range from complete synchrony to complete asynchrony due for example to differences in species' responses to rising temperatures in spring [27]. However, as hard it is to obtain empirical results about phenological asynchrony in a given interaction systems, harder it is to date to disentangle the relative effect of this process on community structures and functioning from individual species' responses to climate modifications and from feed-back effects arising from trophic interactions [48,93]. Moreover, complexity of trophic and non-trophic interactions themselves could be expected to mediate individual species responses to the modification of abiotic parameters as shown for dragonflies larvae [94•]. Consequently, further long-time surveys of insect communities and associated trophic networks would be necessary to emphasis on the relative contribution of phenological asynchronies to community restructuration under climate change.

Consequence for the provision of ecosystem services

Trophic interactions are involved in several ecosystems services provided by insects such as pollination or pest biological control [95]. Thereby, consequences of current climate change on organisms' biology and on species interactions are expected to modify both quantitatively and qualitatively benefits provided by biodiversity to human populations [96], which are already severely threatened by land-use changes [97]. Consequences of phenological asynchrony on species interactions and associated ecosystem services would depend on trophic network resilience to biotic and abiotic modifications. In this context, the tri-trophic system composed by *Vitis vinifera*, *Lobesia botrana* and *Trichogramma* spp., have been used to illustrate the complexity and issues of integrating phenological asynchronies into further evolution of food-webs and associated ecosystem services under a climate change context [98••]. Indeed, the authors highlighted in their review that climate change is modifying host plant availability and quality for herbivore pests and their parasitoids appeared to be more susceptible to climatic variation than herbivores. Thus, changes in accumulated degree-days induced phenological shifts that did not occur at the same rate between trophic levels and across geographical range. All these points are making hard to establish overall recommendations for Integrated Pest Management methods based on trophic interactions like biological control. In addition, there is a gap about roles played in phenological asynchrony outputs by species from higher trophic levels, such as hyperparasitoids, that may become increasingly active in agrosystems in a climate-change context as their phenology is changing [93,94•,99]. For instance, a recent study has shown how those organisms, from the highest trophic level, were exposed like others to specific response to increasing temperatures, but also to consequences of bottom–up pressures [100•]. Indeed, the authors demonstrated that as temperatures increased with simulated heatwaves, primary parasitoid development speed increased, resulting in a decrease of the temporal window favourable to hyperparasitoids reproduction. Under natural conditions, cumulated phenological mismatches among organisms along the trophic cascade can be expected to alter trophic interactions and community structures at the highest level, most likely with more severity, on the same way that stated above between second and third trophic levels.

Conclusion

Laboratory and field studies focusing on consequences of phenological asynchronies between primary and secondary consumers are still scattered comparing to studies on primary producers and primary consumers. So far, it is possible to build a conceptual framework about the main consequences of climate change on pairwise species interactions and on trophic network functioning (Figure 1). Phenology and development rates are undoubtedly shifting in response to increasing temperatures, although at different intensities depending on species and trophic levels. The most tightly interacting species such as hosts and parasitoids or highly specialised predators and their prey, reinforced by long-term coevolution under shared abiotic conditions, are most likely to maintain phenological synchronisation through convergent phenological shifts allowed by both phenotypic plasticity and high bottom–up selective pressures. However, when synchronisation maintenance cannot be achieved due to ecological, physiological or genetic constraints, these specialist species are likely to be highly threatened by climate-change, unless they can shift towards more generalist strategies. Conversely, highly polyphagous generalist predators will likely shift prey depending on the new environmental conditions (e.g. most ant species, spiders or pentatomid bugs) rather than shifting their phenology. In such interacting systems mainly based on opportunistic strategies, predators are expected to shift in phenology directly in response to abiotic constraints following climate-change, and then adapt to interact with new available preys in their new phenology window. Clearly, multiplication of experimental evidences of phenological mismatches among species combined with long-term monitoring of insect trophic networks in natural conditions will help considering this response diversity and realising accurate predictions in a context of climate change.

Conflict of interest statement

Nothing declared.

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