

2 Change in Diapause Strategy in Insects and Impacts on Pest Populations

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Abstract

Diapause is an ecological and physiological mechanism that enables insects to synchronize their periods of activity with a favourable environment. Climate change has a clear impact on this key event in the phenology of both insect pests and their natural enemies. Changes in diapause strategies have been observed in the face of rising average temperatures and less severe winters. Diapause can start later and end earlier than before, either in direct response to favourable environmental conditions (involving phenotypic plasticity) or via longer-term changes in species-specific critical daylength (involving genetic evolution). The consequences are numerous, ranging from individual to population and community scales. Although predictions are complex, in the agricultural environment, the risk posed is desynchronization between the life cycles of plants, pests and their natural enemies (predators or parasitoids), leading to mismatches between trophic levels and potential disruption of the biological control service.

2.1 Introduction

As temperature imposes significant constraints on physiological, behavioural and ecological traits of ectotherms (Deutsch *et al.*, 2008; Huey *et al.*, 2012; Abram *et al.*, 2017), climate change has already started to impact the occurrence of insects, in both space and time (see Schleuning *et al.*, 2020; Harvey *et al.*, 2023 and references therein). Warmer temperatures have resulted in arthropods expanding their distribution poleward and prolonging their period of activity (Parmesan, 2007). Evidence of phenotypic plasticity and evolutionary adaptation to current global change has emerged for insects and should lead to different strategies to cope with not only the gradual

warming but also the increase in the frequency and duration of sporadic, extreme climatic events (e.g. heat waves, unseasonal cold spells, droughts, floods, fires).

The timing of seasonal biological events (phenology) is crucial to the survival and general fitness of all organisms (Forrest and Miller-Rushing, 2010) and climate change is restructuring several elements of the life cycle and year-round ecology of insects. For instance, in some species from temperate regions, warmer temperatures have been shown to speed development and reproduction, provide opportunities for more generations per year (voltinism), advance spring emergence and delay autumn migration or diapause induction (Altermatt,

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2010; Harvey *et al.*, 2023). These phenological shifts may also modify the nature, frequency and strength of guild and trophic interactions, leading to complex responses at the community level (Davis *et al.*, 1998; Petchey *et al.*, 1999; Suttle *et al.*, 2007; Post *et al.*, 2008). For one thing, phenological changes may modify the synchrony of closely interacting species (e.g. plant vs pollinator; plant vs herbivore; prey or host vs predator or parasitoid). Asynchrony can arise when the type, magnitude and pace of phenological responses to climate change differ between interacting species (Singer and Parmesan, 2010; Gallinat *et al.*, 2015). This issue has particularly become a matter of interest in biological control since temporal asynchrony between pests and their natural enemies may have negative economic impacts (Cock *et al.*, 2013). Understanding the effects of climatic variability on population and community dynamics therefore requires knowledge of how species interact and how these interactions are modulated by temperature variations (Stenseth *et al.*, 2002; Tylianakis *et al.*, 2008; van de Putten *et al.*, 2010; Sentis *et al.*, 2015).

In this chapter we focus on insect diapause in the context of climate change and the potential consequences for biological control of insect pests. We first briefly introduce the role and mechanisms of diapause, then we explore the capacity of insects to develop adapted diapause strategies in response to climate warming, and finally describe how potential diapause-induced asynchrony between pests and natural enemies may impact biological control.

2.2 Diapause

Diapause is a genetically preprogrammed physiological state of dormancy at the heart of the overwintering strategy of most temperate insects (Tauber *et al.*, 1986; Danks, 1987; Košťál *et al.*, 2017; Denlinger, 2022). It is a major adaptation evolved by insects to synchronize their seasonal activity with biotic resources and climatic constraints (Tauber *et al.*, 1986). Diapause is termed 'obligatory', when expressed at a particular time in each generation irrespective of environmental conditions, or 'facultative', when occurring only in the generation that precedes adverse

conditions. Diapause can be divided into three main phases: prediapause or induction (insects respond to cues triggering diapause pathways), diapause (period of developmental arrest and insensitivity to environmental cues), and post-diapause (development resumes under favourable conditions) (Tauber and Tauber, 1976; Košťál, 2006; Denlinger *et al.*, 2012) (Fig. 2.1).

The induction phase usually takes place at a given life stage of the insect – egg, larva, pupa or adult – in anticipation of seasonal changes and harsh conditions. Stimuli consist of changes in photoperiod, temperature, moisture, pH, plant secondary compounds and resources such as oxygen, water, food and host. Several cues can be involved in diapause induction, and interactions among stimuli may occur (Tauber *et al.*, 1986). Furthermore, in some cases, responses to diapause inducing cues can be transgenerational, i.e. perceived by the females and extended to their progeny (Saunders, 1965; Rockey *et al.*, 1989; Denlinger, 2022 and references therein). This complexity of response is well illustrated in *Aphidius nigripes* (Hymenoptera: Braconidae), a parasitoid of the potato aphid *Macrosiphum euphorbiae* (Homoptera: Aphididae), which exhibits a facultative prepupal diapause (Brodeur and McNeil, 1989). Abiotic and biotic stimuli are perceived by the female and the egg and first-instar larva. Low temperatures and short daylengths are significant stimuli for both females and immatures, as well as the interactions between these factors. Furthermore, maternal age and host size can also modulate the diapause induction process. The involvement of two generations and the multiplicity of interacting cues are adaptations of a multivoltine species with short developmental time to adequately assess seasonal changes in the environment and programme diapause.

For many temperate insects, a gradual decrease in photoperiod, the most consistent indicator of seasonal change, is the major external signal that initiates molecular, physiological and endocrinological processes associated with diapause induction. Temperature, a less predictable stimulus on a short-term basis, can modify the diapause-regulating role of day length, with high temperatures reinforcing long-day effects and vice versa. Temperature is usually more critical for diapause maintenance and termination, together with other environmental factors



Fig. 2.1. Photograph of a diapausing prepupa of *Aphidius avenaphis* taken out of its mummy (sample from Saskatchewan, Canada, 2015). Credits: Kévin Tougeron (CC BY-NC-SA). Permission received for commercial use.

(e.g. food, host, moisture). Furthermore, a chilling period is often required before an insect can come out of diapause, or a minimum threshold temperature must be attained and sustained for some days to terminate diapause (Lees, 1955; Tauber *et al.*, 1986; Danks, 1987; Košťál, 2006).

For any given insect species, at any given site, 'there is an optimal time to enter diapause that is an adaptive compromise between avoiding winter cold and conserving resources for overwintering and for development and reproduction the following spring' (Bradshaw and Holzapfel, 2008). This optimal timing, which likewise applies for diapause termination and spring emergence, is affected by climate warming and forces insects to respond differently to climatic cues involved in diapause induction and termination. Climate changes will also impact overwintering survival of insects due to decreased severity of winter duration

and cold, decreased snow cover and increased environmental stochasticity during the winter (Bale and Hayward, 2010). These conditions will probably affect postwinter fitness components of emerging insects such as body size, fecundity, longevity, dispersal and immune function (Ishihara and Shimada, 1995; Bradshaw *et al.*, 1998; Ellers and van Alphen, 2002). For example, in preparation for winter, most insect species accumulate lipids as energetic fuel for use during dormancy (Hahn and Denlinger, 2011; Sinclair and Marshall, 2018; Enriquez and Visser, 2023; Short and Hahn, 2023). CaraDonna *et al.* (2018) showed experimentally for a solitary bee that predicted future climatic conditions would reduce lipid reserves and survival of overwintering individuals.

Insect pest diversity, distribution and abundance are predicted to increase overall with climate change and thus negatively impact crop

production (Patterson *et al.*, 1999; Rosenzweig *et al.*, 2014; Deutsch *et al.*, 2018). In this context, from an applied perspective, studying diapause is important to develop and implement pest management strategies. Changes in the phenology, abundance and population cycles (voltinism) of insect pests have the potential to considerably modify crop productivity. For instance, it has been established or anticipated using predictive models that warmer temperatures speed up development and delay diapause in autumn of several pest species, thereby allowing the production of additional generations per year (e.g. Porter *et al.*, 1991; Altermatt, 2010; Bentz *et al.*, 2010). For example, Gagnon and Bourgeois (2024) showed for the carrot weevil *Listronotus oregonensis* (Coleoptera: Curculionidae) that recent increasing temperature in Québec, Canada, promotes the development of a second generation, primarily by disrupting reproductive diapause, resulting in increased pest pressure on carrot crops. Knowledge of diapause is also critical for understanding aspects of overwintering survival and timing of spring emergence of insects. Of significance in high latitudes, climate warming is generally associated with a reduction of the buffering effect of snow cover for insects diapausing in the soil, which has direct impact on their cold-hardiness and energetics (reviewed by Marshall *et al.*, 2020).

Similar considerations apply to biological control agents since diapause and overwintering survival influence their capacity to establish and spread once released in the habitat. Managing diapause can also be an issue when studying or mass-rearing a natural enemy. Gariépy *et al.* (2015) showed that an aphid parasitoid *Binodoxys communis* (Hymenoptera: Braconidae) lost its capacity to enter diapause when reared under non-diapause conditions for extended periods of quarantine and laboratory confinement. Increasing the storage, shelf-life and diapause termination of mass-produced predators and parasitoids through diapause management has also become a challenge for the biological control industry (Colinet and Boivin, 2011).

2.3 Change in Diapause Strategies

This section describes mechanisms allowing insects to cope with and adapt to new climatic

conditions. Insect diapause is a classic example of developmental plasticity and polyphenism, intrinsically associated with temperature conditions and other environmental parameters. As diapause is a syndrome selected by environmental variability, it is also liable to change through the action of natural selection (Tauber *et al.*, 1986). This is clearly seen over wide geographic gradients where populations are adapted to local environmental conditions, with greater diapause incidences and earlier initiation timings poleward (Paolucci *et al.*, 2013). In the context of climate change, insect diapause, in terms of both dates of induction and termination, and incidence within populations, is therefore likely to be altered, especially as environmental conditions change rapidly and with great intensity (Bale and Hayward, 2010; Kivelä *et al.*, 2013). Climate change may impact environmental stimuli which act directly on insects or indirectly through food resources or interacting partners (symbionts, prey, predators, competitors) (Tougeron *et al.*, 2019).

Most adaptive responses to climate change are complex and involve a variety of mechanisms acting in combination (Harvey *et al.*, 2023; Edelsparre *et al.*, 2024). Two main routes can lead to changes in diapause expression in insects. The first and most straightforward route is inherent to the definition of the diapause syndrome: phenotypic plasticity in timing and expression. For a given time of year, at a given photoperiod, average temperatures rise with climate warming. As a result, for most insects that rely on both temperature and photoperiod to initiate diapause, the date of entry may be delayed until later in the year through a plastic response to new environmental conditions. This may only be the case for multivoltine species, for which only one generation per year enters diapause. In univoltine species, for which diapause is obligatory, plastic adjustments are much more difficult to achieve (Saunders, 2002; Tougeron, 2019; Lindstad *et al.*, 2020). In some populations exposed to milder climates, only some of the individuals may enter into facultative diapause. For example, parasitoids of the genus *Aphidius* (Hymenoptera: Braconidae) in western France have for most species reduced the expression of their diapause to a small fraction of the population following the onset of increasingly short and warm winters (Tougeron *et al.*, 2017b). Plastic adjustments in diapause

strategies may allow insects to adapt to both heterogeneous environments and directional changes in the environment over the short term, but can potentially restrict the action of natural selection by keeping insects away from environmental pressures (Chevin *et al.*, 2013; Sgrò *et al.*, 2016; Abram *et al.*, 2017). Differences in diapause expression over time can also result from maternal effects (transgenerational plasticity), which may enhance or inhibit diapause in the offspring depending on environmental conditions encountered by the mother, and may play a role in the context of climate change (Mousseau and Dingle, 1991; Tougeron *et al.*, 2017a).

The second way in which diapause expression can change over the longer term (i.e. over generations) is through the genetic evolution of thresholds or conditions required to initiate, maintain and terminate diapause. For example, Bean *et al.* (2012) demonstrated an evolution towards a decline in the critical day length inducing diapause in the beetle *Diorhabda carinulata* (Coleoptera: Chrysomelidae), a biological control agent of invasive *Tamarix* sp (Caryophyllales: Tamaricaceae). It resulted in a closer match between the beetle life history and the phenology of the shrub. The change depends on the strength of directional selection on diapause-associated traits and on phenotypic plasticity itself (Bradshaw and Holzapfel, 2006; Forrest, 2016; Sgrò *et al.*, 2016). A genetic alteration affecting seasonal patterns in insects is seen in how the pitcher plant mosquito *Wyeomyia smithii* (Diptera: Culicidae) has adapted to extended growing periods in North America, by modifying the critical photoperiod for inducing larval diapause in the fall, shifting towards shorter daylight thresholds (Bradshaw and Holzapfel, 2001). Most examples of changes in insect phenology in the face of global warming imply strong selection caused by change in winter conditions, such as in the Asian tiger mosquito *Aedes albopictus* (Diptera: Culicidae) which shows genetic divergence in diapause-associated cold tolerance, timing and syndrome (Batz *et al.*, 2020).

Disentangling the relative effects of plasticity and genetic on phenological shifts and local adaptations of insects is a major challenge in evolutionary research on organisms' responses to climate changes (Merilä and Hendry, 2014; Tougeron *et al.*, 2018b). In a warming climate, strong selection pressure for diapause loss could also come from diapause termination requirements for some

insects which only resume development if they have first been chilled for a few days or weeks (Tauber and Tauber, 1976; Tougeron, 2019; Toxopeus *et al.*, 2021). For example, the parasitoid *Colpoclypeus florus* (Hymenoptera: Eulophidae) requires a chilling period of at least 5 weeks at 4°C to terminate diapause (Milonas and Savopoulou-Soultani, 2000).

Selection pressures apply to insect diapause expression, whether agricultural pests or their natural enemies, because there are inherent costs, and the cost–benefit balance may alter under climate change when considering timing and ecological costs (e.g. reproductive arrest under mild winters) or metabolic and production costs (e.g. producing unnecessary cryoprotectant molecules) (Hahn and Denlinger, 2007; Lahti *et al.*, 2009; Sgrò *et al.*, 2016; Short and Hahn, 2023). Diapause costs are associated to diapause duration and (mostly thermal) conditions experienced during diapause, by a normally linear consumption of the reserves in function of time, and resources (or time) may be compromised in trade-offs (Nylin and Gotthard, 1998; Danks, 2007; Roff and Fairbairn, 2007). Using *Aphalara itadori* (Hemiptera: Aphalaridae), a biological control agent introduced from Japan to North America and Europe to control an invasive weed *Reynoutria japonica* (Caryophyllales: Polygonaceae), Grevstad *et al.* (2022) suggested that in warmer climates, the insect may be diapausing too early, therefore not fully exploiting the weed throughout the growing season.

The capacity to delay or avert diapause may therefore provide a selective advantage in species that can avoid energetic and metabolic costs while maintaining overwinter activities, including foraging for resources and reproduction (Bale and Hayward, 2010). For example, in the parasitoid *Asobara tabida* (Hymenoptera: Braconidae) an increase in diapause duration led to increased mortality and reduced fecundity (Ellers and van Alphen, 2002). Conversely, when diapause is not expressed in environments that are too cold or variable, this poses serious problems in the context of biological control, for example by introducing species that have evolved in tropical or subtropical environments, or in mass rearing environments (Gariépy *et al.*, 2015).

Depending on the environmental variability and reliability of the diapause-inducing

signals, directional selection towards pure and conservative strategies of reduction in diapause expression may be favoured, or bet-hedging strategies can also be selected (i.e. risk minimization strategies) (Hopper, 1999). In many cases, diapause is a pure strategy, with 100% of the individuals in a population entering diapause when environmental and especially winter conditions are harsh. At the opposite end of the spectrum, if winter conditions remain favourable for maintaining activity, a pure strategy of abandoning diapause could theoretically be maintained, as in tropical environments. However, climate change may lead to more variable and unpredictable environments, which can select for bet-hedging strategies (Furness *et al.*, 2015; van Baaren *et al.*, 2024) in insect diapause and overwintering phenotypes to reduce the average fitness in favour of a smaller fitness variance. When a female cannot accurately assess which offspring phenotype would be favoured in the future environment – diapausing offspring or not – the proportion of each offspring phenotype may be adjusted to the probability of encountering a given environment, when biotic or abiotic cues make it at least partially predictable (Uller, 2008). Conditional strategies ('adaptive coin flipping') may therefore be adopted where the probability of expressing a phenotype is based on the probability of encountering a given environment (Cooper and Kaplan, 1982), such as stressful versus mild winter conditions. Alternative bet-hedging strategies may also increase the phenotypic variability produced within a generation or between generations (diversified bet-hedging) or produce the same phenotype (conservative bet-hedging) (Ripa *et al.*, 2010). To cope with a new selection pressure led by increasing environmental stochasticity (variability and unpredictability), mixed strategies such as bet-hedging strategies should become more frequent (Simons, 2011; Kivelä *et al.*, 2013). Selection may therefore act by both lowering diapause induction thresholds and modifying the proportion of diapausing offspring produced by each insect female.

In a nutshell, intrapopulation variability in diapause expression can originate from diversified bet-hedging strategies or from genetic polymorphism of mixed-pure strategies, maintained by balancing selection (Bradshaw and Holzapfel, 2001; Soula and Menu, 2003), which results

in different plastic responses to environmental cues within a population. Interpopulation variability results from local adaptation in diapause induction thresholds (i.e. critical day length). Accordingly, climate change is expected to alter the expression of diapause, but a certain degree of unpredictability may be anticipated due to interindividual response elements and environmental variability in relation to global climate change trends. The three forms of adaptations (phenotypic plasticity, genetic evolution, bet-hedging) are not mutually exclusive and depend on climate predictability, variability and rate of change (DeWitt and Scheiner, 2004; Tufto, 2015).

2.4 Matches and Mismatches Across Trophic Levels

Climate change affects insect pest populations and their natural enemies in a variety of ways, which have been extensively reviewed in this book and review articles (see Thomson *et al.*, 2010; Cock *et al.*, 2013; Eigenbrode *et al.*, 2015; Furlong and Zalucki, 2017; Furlong *et al.*, 2021). Many scenarios are possible, but a main pattern is that climate change is expected to increase damage caused by agricultural pests through increasing population growth, accumulative pest generations per year, facilitation of pest dispersion, earlier pest outbreaks and both decreasing natural enemy efficiency and plant resistance (Klapwijk *et al.*, 2012; Björkman and Niemelä, 2015; Pincebourde *et al.*, 2016).

The case of diapause is interesting to explore in detail, as it is a predominant phenological event in the life of insects of temperate environments, and a syndrome with various traits and phenotypes expressed. It is also a polyphenism, i.e. binary situation, which by definition results in either developmental arrest or direct development, with no intermediate situation that might be found in other phenotypes such as heat tolerance (Hance *et al.*, 2007). Different pathways can lead to total or partial phenological desynchronization between interacting organisms, depending on the intensity of selection pressures applied to diapause expression at each trophic level, the response variability of each species and the associated costs for each

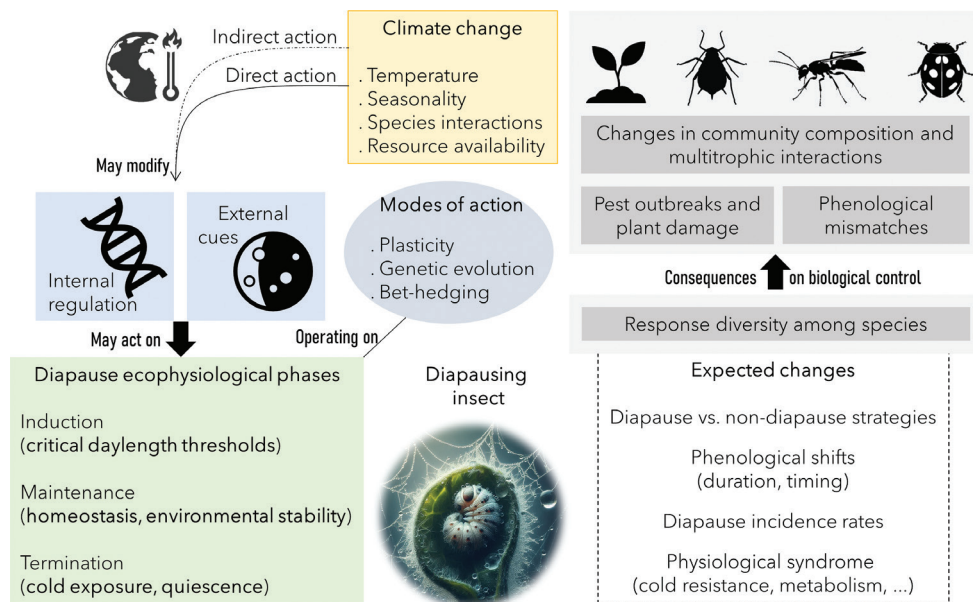


Fig. 2.2. General pathway by which change in the expression of diapause is possible and observed in insects. The consequences are visible on individuals, population dynamics and therefore communities. Biological control services may then be affected.

individual (Renner and Zohner, 2018; Damien and Tougeron, 2019). Therefore, the effects of climate change have to be considered at the species level but also for the entire community because asynchrony and asymmetrical changes in diapause or phenology patterns across trophic levels potentially lead to shift in species interactions (van de Putten *et al.*, 2010; Forrest, 2016; Thackeray *et al.*, 2016; Damien and Tougeron, 2019; Harvey *et al.*, 2023). For example, if diapause persists in natural enemies under future climates but not in pests (primary consumers), warmer winters may favour greater pest population increases during crop auxiliaries diapause and greater damage to crops in spring, as for example expected in orchards infested with aphids in New Zealand (Gerard *et al.*, 2013) (Fig. 2.2).

In any given community, some plant–herbivore, prey–predator or host–parasitoid interactions will reduce in intensity or disappear, and novel interactions will emerge, altering the abundance, distribution and function of each species in a food web (Tylianakis *et al.*, 2008; Gilman *et al.*, 2010). Rapid change in community composition following climate change can

be linked to modifications in diapause expression of all or some species of a community (Tougeron *et al.*, 2018a). For example, in parasitoid communities of cereal aphids experiencing warmer winters, the generalist aphid parasitoid *Aphidius avenae* (Hymenoptera: Braconidae) reduced winter diapause expression and became the dominant species in winter, inducing the rarefaction of the previously most abundant host species *A. rhopalosiph* and *A. matricariae* (Andrade *et al.*, 2016; Tougeron *et al.*, 2017b).

Because early suppression of pests is often crucial for efficient biological control, the loss or decrease of diapause expression in natural enemies could favour biological control, especially if natural enemies can exploit more host or prey for a longer time window. In the parasitoid *Cotesia melitaearum* (Hymenoptera: Braconidae), van Nouhuys and Lei (2004) showed that warmer springs improved the synchrony with its host, the butterfly *Melitaea cinxia*, (Lepidoptera: Nymphalidae) leading to increased parasitoid colonization at the metapopulation scale. However, with climate change, modifications in food web composition may *in fine* decrease biological control efficiency through increasing

intraguild competition, intraguild predation (Frances and McCauley, 2018) or activity of new antagonist species. For example, hyperparasitism levels tend to rise in most cropping systems (Gómez-Marco *et al.*, 2015; Tougeron *et al.*, 2021), suggesting that the loss of diapause expression can occur across different trophic levels and that hyperparasitoid pressure may increase in winter or early spring, leading to poorer pest control by primary parasitoids (Tougeron and Tena, 2018).

Herbivorous pests, in particular sap-sucking insects, are often associated with facultative symbionts that provide nutritional functions and resistance to environmental disturbance (Zytynska *et al.*, 2021). Although diapause as such is not directly affected by these symbionts (Mushegian and Tougeron, 2019), their effects on heat tolerance, and conversely the effects of temperature on their maintenance, can jeopardize interactions with natural enemies present in the environment (Kashima *et al.*, 2006; Cayetano and Vorburger, 2013; Tougeron and Iltis, 2022). Bacterial symbionts are therefore important elements to consider in the context of climate change, as they are partly decisive in the persistence of certain pest populations and in the maintenance of host–parasitoid or prey–predator interactions.

Phenological mismatches and absence of accurate temporal host tracking by natural enemies may result in important yield losses,

especially if the natural enemy is highly specialized on a given prey (Eigenbrode *et al.*, 2015). For example, due to warmer winters and springs, parasitoids of the invasive horse chestnut leaf miner (*Cameraria ohridella* (Lepidoptera: Gracillariidae)) broke diapause too early, resulting in poor synchronization between species and reduced control of the host populations (Grabenweger *et al.*, 2007). For the biocontrol agent *Torymus sinensis* (Hymenoptera: Torymidae), a lower parasitism pressure due to phenological mismatch with its host *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae) increases the probability of pest outbreaks at warmer temperatures (Ferracini *et al.*, 2022). Natural enemies that rely on their hosts or prey to initiate their own diapause (Tougeron *et al.*, 2021), or in which there is strong selection pressure to follow the same diapause-inducing signals, will be less likely to desynchronize and reduce the effectiveness of the biological control service (Furlong and Zalucki, 2017; Renner and Zohner, 2018). In addition, diapause asynchrony may not be an issue for biological control when there is enough functional redundancy within a guild of natural enemies to control a host (Hance *et al.*, 2007; Damien and Tougeron, 2019). However, it is necessary to include potential changes in diapause in population and community dynamic models destined to inform pest control decisions (Lalonde, 2004; Kalinkat and Rall, 2015).

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