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INVITED REVIEW

How climate change affects the seasonal ecology of insect parasitoids

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Abstract. 1. In the context of global change, modifications in winter conditions may disrupt the seasonal phenology patterns of organisms, modify the synchrony of closely interacting species and lead to unpredictable outcomes at different ecological scales.

2. Parasites are present in almost every food web and their interactions with hosts greatly contribute to ecosystem functioning. Among upper trophic levels of terrestrial ecosystems, insect parasitoids are key components in terms of functioning and species richness. Parasitoids respond to climate change in similar ways to other insects, but their close relationship with their hosts and their particular life cycle – alternating between parasitic and free-living forms – make them special cases.

3. This article reviews of the mechanisms likely to undergo plastic or evolutionary adjustments when exposed to climate change that could modify insect seasonal strategies. Different scenarios are then proposed for the evolution of parasitoid insect seasonal ecology by exploring three anticipated outcomes of climate change: (i) decreased severity of winter cold; (ii) decreased winter duration; and (iii) increased extreme seasonal climatic events and environmental stochasticity.

4. The capacities of insects to adapt to new environmental conditions, either through plasticity or genetic evolution, are highlighted. They may reduce diapause expression, adapt to changing cues to initiate or terminate diapause, increase voltinism, or develop overwintering bet-hedging strategies, but parasitoids' responses will be highly constrained by those of their hosts.

5. Changes in the seasonal ecology of parasitoids may have consequences on host–parasitoid synchrony and population cycles, food-web functioning, and ecosystem services such as biological pest control.

Key words. Climatic scenarios, food webs, host–parasitoid relationships, insect seasonality, overwintering strategies, phenology.

Introduction

In temperate regions, warmer average temperatures, extended growing seasons, higher climate variability, and lower predictability of climatic conditions constitute important aspects of climate change (Easterling *et al.*, 2000; IPCC, 2014). Through either plasticity or local adaptations, there are three ways in which ectotherms may respond to climate changes. They can shift their geographic distribution to match their current thermal preferences, alter their phenology to cope with new patterns of seasonal climatic conditions, or adjust their thermal tolerance capacities to match local changes in temperature (Walther *et al.*, 2002; Parmesan & Yohe, 2003), with consequences at the population and community levels, and

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for the evolution of species (Blanckenhorn, 2018). For insects from temperate and polar regions, modifications in phenology (seasonal strategies) are the most commonly reported responses to climate change (Forrest, 2016). Insects in these regions have been shown to migrate and reproduce earlier, to increase the number of generations per year, and to delay, reduce, or abandon diapause expression (e.g. Musolin, 2007; Tobin *et al.,* 2008; van Asch *et al.,* 2012; Bell *et al.*, 2015).

Among upper trophic levels, insect parasitoids are key components of terrestrial ecosystems through their diversity, abundance, and functions (Quicke, 2014). The life histories of parasitoids are closely linked to those of their hosts (Godfray, 1994), a primary feature being the seasonal synchrony between host availability and parasitoid activity (Danks, 1987). Asymmetric changes in the seasonal activities of species between closely interacting sympatric species, such as pollinators and plants, predators and prey, or parasites and hosts, are likely to disrupt the synchronisation of their life cycles (Visser & Both, 2005; Jeffs & Lewis, 2013; Ovaskainen *et al.*, 2013; Martinez-Bakker & Helm, 2015). Such temporal mismatches may lead to complex outcomes in the structure and dynamics of populations and communities (Damien & Tougeron, 2019). The trophic-rank hypothesis predicts that organisms from high trophic levels should be more strongly affected by environmental changes and ecological disturbances than organisms from low trophic levels, because of cascading effects in the food chain (Holt *et al.*, 1999; Gilman *et al.*, 2010). Predicting the consequences of climate change on host–parasitoid relationships is thus challenging because it affects both organisms separately as well as their interactions (Jeffs & Lewis, 2013; Le Lann *et al.*, 2014a).

This review examines the potential effects of climate change on the seasonal ecology of insects, and considers the biological particularities of parasitoids. We first briefly summarise the current knowledge on diapause and seasonal adaptations in insects. Second, we examine the mechanisms through which environmental changes could influence these adaptations in parasitoids. Finally, we propose different scenarios for the evolution of parasitoid seasonal ecology in the context of rapid climate change and highlight the consequences on food webs and ecosystem functioning and services.

Diapause as an adaptation to temperate climates

Temperature is the primary abiotic factor affecting insect development, reproduction, foraging behaviour, distribution range, and the timing of their activities (Angilletta, 2009; Abram *et al.*, 2016; Sánchez-Guillén *et al.*, 2016; Córdoba-Aguilar *et al.*, 2018). In temperate and polar regions, insects have evolved different strategies to survive recurring environmental conditions that are unsuitable for growth and reproduction. Within the different types of dormancy, insects can rapidly enter quiescence when they face non-cyclic, often short, periods of atypical environmental conditions (Leather *et al.*, 1993). Quiescence is, as opposed to diapause, an immediate and direct physiological or behavioural response to a stressful event, most often a thermal or water stress, that is not related to seasonal recurrence (Tauber *et al.*, 1986). Quiescence is quickly terminated as soon as the environment becomes favourable again. Insects can also enter diapause, which is an obligate (univoltinism) or facultative (multivoltinism) hormonally mediated and pre-programmed state of low metabolic activity characterised by arrested development, suspended activity, and increased resistance to environmental extremes (Tauber *et al.*, 1986; Hodkova & Hodek, 2004; Koštál, 2006). Typically, insects enter diapause in advance of the onset of adverse conditions and terminate it some time after the return of favourable conditions, thereby providing a 'safety' margin against unseasonal conditions. An early or a late entry into diapause may reduce fitness because the insect either forgoes growth and breeding opportunities or dies from adverse conditions (Bradshaw *et al.*, 2004).

Within a population, there are interindividual differences in environmental thresholds at which diapause is induced and terminated. These act as a developmental buffer against seasonal variability and unpredictability because only some individuals enter diapause while others remain active or become quiescent (Tauber & Tauber, 1981). This intrapopulation variability in diapause expression originates from different plastic responses to environmental cues, bet-hedging strategies or from genetic polymorphism of mixed pure strategies that are maintained by balancing selection (Bradshaw & Holzapfel, 2001; Soula & Menu, 2003).

Cues acting on diapause initiation and termination are diverse and their complexity varies among species. Photoperiod is a reliable signal of seasonal change and is undoubtedly the main cue inducing facultative diapause before the onset of adverse conditions. Temperature, maternal effects, diet, resource availability, and other biotic (e.g. species interactions) and abiotic factors can also mediate photoperiodic diapause expression (Tauber *et al.*, 1986; Denlinger, 2002). For parasitoid insects, host characteristics (species, size, development stage, density, physiological state) represent additional strong evolutionary forces acting on diapause (Tauber *et al.*, 1986; Brodeur & McNeil, 1989; Polgár & Hardie, 2000). The specific characteristics of diapause in parasitoids are detailed in the following sections. Diapause termination is triggered by the same environmental stimuli as the ones triggering diapause initiation, as well as others (photoperiod, temperature, moisture, resource availability) (Tauber & Tauber, 1976; Koštál, 2006). A cold period is often required to break diapause before the return of spring-like conditions (Koštál, 2006). Diapause is thus a pivotal anticipatory strategy in insect life cycles, as it is affected by environmental conditions and controls growth and reproduction (Tauber *et al.*, 1986).

Mechanisms through which environmental changes could modify seasonal strategies

Climate changes may impact environmental stimuli acting directly on the parasitoid, indirectly through its host, or on both the parasitoid and its host. The ability of hosts and parasitoids to cope with a changing seasonal environment is determined both by plastic adjustments to their diapause syndrome and by the strength of directional selection on diapause-associated traits or on phenotypic plasticity (Bradshaw & Holzapfel, 2006; Sgrò *et al.*, 2016). Thus climate change will probably act on the syndrome of associated traits, in a way that diapause expression

is unlikely to change alone, but will rather change alongside with other traits. Changes in diapause expression can arise either directly from plastic responses of pre-overwintering individuals or from transgenerational plasticity. Transgenerational plasticity, including maternal effects, occurs when environmental cues experienced by the previous generation(s) modify phenotypic reaction norms of the following generation (Burgess & Marshall, 2014; Sgrò *et al.*, 2016). Transgenerational plasticity is beneficial to the insect when the environment experienced by previous generations (e.g. thermal conditions) is similar to that of the next generation(s), so that adaptive phenotypes can be produced (Galloway & Etterson, 2007). Disentangling the relative effects of genetic changes and plasticity on shifts in phenology has been identified as one of the greatest challenges in evolutionary research on organism responses to climate change (Merilä & Hendry, 2014; Schilthuizen & Kellermann, 2014). In this section, we will discuss plastic and genetic responses of insect seasonal strategies to changes in the main abiotic (i.e. temperature) and biotic (i.e. host) cues within and among parasitoid generations, and fitness costs associated with diapause in a changing world.

Responses to cues for diapause induction, duration, and termination

Temperature increases with climate warming while the photoperiod cycle remains unaffected. This could lead to a maladaptive response to photoperiod by parasitoids when suitable conditions (e.g. warm temperature, host availability) remain available (Forrest, 2016). Conflicting information from different environmental cues may strongly impact their fitness and drive plastic or evolutionary changes in the induction, duration, and termination of diapause (Bradshaw & Holzapfel, 2006; Forrest, 2016).

Within one generation. In insects with wide geographic distributions, a genetically determined critical day length optimises the timing of diapause induction in each population to match local seasonal variations (Tauber *et al.*, 1986). Current local adaptations to early and harsh winters at high latitudes and temperature-dependent clines are expected to be modified by climate warming in terms of incidence, onset, duration, and termination of diapause (Hut *et al.*, 2013). Climate change could thus act on diapause expression through adjustments of the plastic response to environmental cues by the overwintering generation. For example, when aphid parasitoids that had adapted to harsh winters in Canada were translocated to western France, where mild winters occur, they entered diapause at a lower incidence and later in the season than in their area of origin (Tougeron *et al.*, 2018a).

For diapause termination, temperature is often a major determinant, either directly on the parasitoid or indirectly through the host. Some species require sufficiently high temperatures during a certain period to end diapause. In many species, diapausing insects have to be exposed to freezing temperatures before they can resume development and terminate diapause (Tauber & Tauber, 1976). For example, the parasitoid *Colpoclypeus florus* (Hymenoptera: Eulophidae) must remain at 4 °C for more than 5 weeks to terminate diapause (Milonas & Savopoulou-Soultani, 2000). For species like this, winter warming could interfere with these mechanisms of diapause regulation, and no indication of possible adaptation has yet been identified. For the parasitoid *Psyllaephagus pistaciae* (Hymenoptera: Encyrtidae), cold conditions are not necessary to break diapause, although cold conditions decreased the number of days required for adult emergence after diapause (Mehrnejad & Copland, 2005). For the tachinid parasitoid *Eucarcelia rutilla* (Diptera: Tachinidae), a hormonal stimulus from its host *Bupalus piniarius* (Lepidoptera: Geometridae) is required to end diapause (Schoonhoven, 1963). The effects of long-term temperature increases on diapause termination have never been explored, so the plasticity and evolutionary potential of diapause termination mechanisms in a warming climate remain unknown.

Among generations. Rapid evolutionary changes through natural selection can occur within the timescale of current climate warming (Bradshaw & Holzapfel, 2006; Hoffmann & Sgrò, 2011). Indeed, seasonal photoperiodism is regulated by clock genes in insects which may be subject to selection, and which could consequently modify the response thresholds at which diapause is induced or terminated. A specific example of rapid genetic changes altering insect seasonality is the adaptation of the pitcher-plant mosquito *Wyeomyia smithii* (Diptera: Culicidae) to longer growing seasons in North America through the modification of its critical photoperiod for larval diapause induction in the autumn (i.e. towards shorter day-length thresholds) (Bradshaw & Holzapfel, 2001). Similar genetic responses are expected in parasitoids (Jeffs & Lewis, 2013).

Transgenerational plasticity, which is subject to evolutionary change, can allow adaptive responses to rapid environmental changes (Sheriff & Love, 2013; Donelson *et al.*, 2018), e.g. when ovipositing parasitoid females are sensitive to environmental diapause cues and diapause is initiated in the offspring (Saunders, 1965). When environmental cues associated with upcoming deleterious conditions are detected (Danks, 1987; Mousseau & Dingle, 1991), females can adjust the contents of carbohydrates and polyols in the eggs to induce diapause (Denlinger, 2002). Voinovich *et al.* (2015) showed that diapause was induced by maternal effects in the parasitoid *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) when females were reared at a low temperature. Conversely, diapause was averted in the offspring when females were reared at a high temperature. Critical photoperiod for maternally induced diapause usually varies geographically in an adaptive manner, in such a way that northern mothers show a sharper transition from the production of non-diapausing offspring to diapausing offspring (Mousseau & Dingle, 1991). The maternal impact on offspring diapause also varies among populations depending on the selective importance attributed to the female's perception of the environment. The more the maternal environment can predict the offspring environment, the more impactful should maternal effects be on diapause, because it has a positive effect on fitness (Mousseau & Dingle, 1991). In populations living in more unpredictable environments, we should expect low maternal impact on offspring diapause.

In some parasitoid species, diapause cannot be induced in the non-photothermosensitive generation, as a potential adaptation to avoid diapause induction in parasitoids developing in late spring (when some environmental conditions are similar to those in autumn) (Reznik & Samartsev, 2015). This phenomenon probably arises from an 'epigenetic counter', where DNA methylation induced by overwintering parasitoids inhibits diapause induction in offspring (Reznik & Samartsev, 2015) and could last over several generations (Uller, 2008). Epigenetic regulation of insect diapause through DNA methylation, histone modifications, and small RNA interference is discussed further in the review by Reynolds (2017).

Host signal

Any change in host quality (species, size, physiological state) or abundance over time can act as a selective pressure for modification of diapause expression in parasitoids.

Parasitoid diapause can be triggered by the onset of host diapause through endogenous physiological synchronisation (Polgár & Hardie, 2000; Gerling *et al.*, 2009). For example, the hyperparasitoid *Catolaccus aeneoviridis* (Hymenoptera: Pteromalidae) enters diapause at high proportions when developing in cocoons of the diapausing primary parasitoids *Cotesia congregata* (Hymenoptera: Braconidae) (McNeil & Rabb, 1973). Interactions between this factor and abiotic factors played an important role in diapause initiation (McNeil & Rabb, 1973). On the other hand, parasitoid diapause can be decoupled from that of its host and be induced only by abiotic environmental cues. For example, the tachinid parasitoid *Myiopharus doryphorae* (Diptera: Tachinidae) is not affected by the diapause status of its host, the Colorado potato beetle, whereas diapause of *M. aberrans*, a congeneric parasitoid of the same host, is strongly influenced by the life cycle, endocrinological state, and physiological status of the host (Gollands *et al.*, 1991). In idiobiont parasitoids, which kill or paralyse their host at oviposition, the host may represent a less important signal for diapause induction than in koinobiont parasitoids, where the host continues to develop during parasitism (Polgár *et al.*, 1991).

Host size has been shown to influence several life-history parameters of parasitoids, including diapause. In the aphid parasitoid *Aphidius nigripes* (Hymenoptera: Braconidae), diapause incidence is higher when parasitising smaller hosts (Brodeur & McNeil, 1989). When aphids experience suboptimal conditions, in particular when feeding on suboptimal host plants, they can produce 'dwarf' phenotypes (Watt & Hales, 1996) that could influence the parasitoid's diapause. Despite these examples, the relative importance of host size as a diapause-inducing cue remains poorly studied in most host–parasitoid associations.

Summer diapause in parasitoids is an overlooked phenomenon (He *et al.*, 2010; Tougeron *et al.*, 2017a, and references therein). It can be induced by a shortage of resources (e.g. hosts) in the environment, competition among females, and food availability for adults (Masaki, 1980; Tsukada, 1999; Saulich & Musolin, 2017). For instance, female aphid parasitoids *Aphidius avenae* and *Aphidius rhopalosiphi* (Hymenoptera: Braconidae) produce diapausing offspring when exposed to conditions of high intraspecific competition for hosts (Tougeron *et al.*, 2017a). Such a biotic stimulus may act directly or indirectly (i.e. mediated by photoperiod or temperature) on summer diapause induction. Patterns of summer diapause may thus be sensitive to modifications in seasonal host densities, including those arising from climate changes. For example, heatwaves can strongly reduce the number of hosts in summer (Rabasse *et al.*, 1983; Sentis *et al.*, 2013).

Nothing is known about the influence plants may have on parasitoid diapause, but one could expect that the plant acts on parasitoid diapause indirectly through its impact on the herbivorous host, the emission of volatile organic compounds, or changes in plant quality (Polgár *et al.*, 1995; Hunter & McNeil, 1997). The nature and abundance of phytoecdysteroids change during a plant's life cycle and could influence diapause induction of the host (Polgár *et al.*, 1995). The host plant plays a crucial role in the seasonal polymorphism and heteroecy of aphids because most aphid species shift from a secondary to a primary host plant at the end of the growing season. This shift is accompanied by the production of sexual aphid morphs (Dixon, 1985), which can be a signal for diapause induction in parasitoids (Polgár *et al.*, 1991; Tougeron *et al.*, 2019). As another example, diapausing larvae of the pecan nut casebearer *Acrobasis nuxvorella* (Lepidoptera: Pyralidae) resume growth and development when exposed to pecan volatiles during the onset of pecan bud growth in spring (Vargas-Arispuro *et al.*, 2013). The influence of plants on seasonal strategies has been reported in other invertebrates, such as nematodes, that respond to root exudates to enter quiescence (Hiltpold *et al.*, 2015). Warmer temperatures and higher CO_2 levels will affect species' interactions mediated by chemical information (Holopainen & Gershenzon, 2010; Sentis *et al.*, 2015), with unknown consequences on parasitoid ecology (Hance *et al.*, 2007).

Costs of diapause

Climate changes may alter aspects of the cost–benefit balance of entering, maintaining, and terminating diapause, as well as the evolutionary trade-offs between two overwintering strategies: entering diapause or remaining active during the winter. Because the 'physiological decision' to enter diapause cannot be reversed (Bale & Hayward, 2010) and diapause is intrinsically linked to insect fitness, natural selection should favour changes in the seasonal ecology of parasitoids, depending on the costs/benefits of expressing diapause under changing environments.

Timing costs (e.g. entering diapause during warm winters), metabolic costs (e.g. producing unnecessary cryoprotectant molecules), and ecological costs (e.g. cessation of reproduction when hosts remain available in the environment) can be linked to a wrong decision to enter or terminate diapause in a rapidly warming environment (Sgrò *et al.*, 2016). For example, Stuhldreher *et al.* (2014) showed that the cold-adapted butterfly *Erebia medusa* (Lepidoptera: Nymphalidae) terminated diapause earlier than usual under simulated warmer winters, which led to lower adult survival. Parasitoids are constrained by the energetic resources they can derive from their hosts or from the environment (Visser & Ellers, 2008); they are therefore

sensitive to increasing metabolic costs during diapause or following spring emergence.

Fecundity and survival are often reduced in insects, including parasitoids, emerging from diapause due to physiological stress, cryoprotectant production, and consumption of energetic reserves (Zhou *et al.*, 1995; Ellers & Van Alphen, 2002; Hahn & Denlinger, 2007). Diapause costs are directly linked to diapause duration by a linear consumption of the reserves through time. For example, in the parasitoid *Asobara tabida* (Hymenoptera: Braconidae), an increase in diapause duration led to increasing mortality and decreasing fecundity (Ellers & Van Alphen, 2002). One way for insects to save energy during diapause is to enter into a state where metabolic and respiratory rates are very low (Wadsworth *et al.*, 2013), particularly during cold winters (Irwin & Lee, 2003).

Scenarios for the evolution of seasonal strategies under climate changes

In this section, we present different scenarios for the evolution of insect seasonal strategies under climate changes based on the mechanisms detailed earlier. Many considerations can be generalised to other insects but we aim to demonstrate specificities of host–parasitoid relationships. Scenarios stem from the predictions that: (i) winter cold severity will decrease; (ii) suitable conditions for resuming activities such as reproduction will appear earlier in spring and extend later in autumn; and (iii) extreme and/or unexpected climatic events such as heatwaves, cold spells, or drought episodes will be more frequent (Easterling *et al.*, 2000). We highlight which of these predictions could have the highest impact on insect ecology (Fig. 1).

Decrease in winter cold severity

Decrease of diapause expression. In a climatic scenario where relatively warm conditions are sustained during the winter, one can first predict that the reliability of photoperiod as a signal for upcoming winter conditions will decrease and that parasitoids will adopt new cues (or modify thresholds for existing cues) to enter diapause. In addition, we can envisage two opposite scenarios. In the first, because metabolic rates increase with temperature (Gillooly *et al.*, 2001) and lead to higher energy consumption before the return of favourable conditions (Williams *et al.*, 2012; Xiao *et al.*, 2016), maintaining relatively high metabolic rates during diapause or extended quiescence under a warmer climate would be costly (Perez & Noriega, 2013). Accordingly, the capacity to delay, avert, or reduce diapause duration may be selected in insect populations (Bale & Hayward, 2010), especially when overwintering conditions allow individuals to remain active and reproduce (Forrest, 2016). In the second prediction, diapause costs would diminish through a reduction in diapause duration (Ellers & Van Alphen, 2002; Ito, 2007).

The best strategy for parasitoids under warmer winters in areas where frost conditions still occur would be to enter a deep state of diapause late in autumn and terminate diapause early in spring. Studies are required to examine the degree of metabolic suppression during diapause as a proxy of diapause intensity, because the intensity of diapause may be linked to the type of response to global climate warming (Wadsworth *et al.*, 2013). Additionally, species for which a cold period is required to end diapause will suffer more from warm winters than others, because cold periods may become less frequent. By contrast, for species with diapause termination exclusively under photoperiodic control, the effect of warming temperatures on diapause termination should be weak.

A likely scenario following a decrease in winter cold severity would be a reduction in diapause by the selection of lower induction thresholds (i.e. less sensitive to environmental cues). This could result in an increase in the frequency of quiescence events, which represents a more plastic strategy because the time needed to react to climatic changes is shorter for quiescence than for diapause (Perez & Noriega, 2013). A quiescent strategy would allow parasitoids to more accurately track temperature changes (e.g. Rundle & Hoffmann, 2003). Quiescence would also be less costly, as the production of cryoprotective molecules would not be required as often and, when it was, it would be for shorter periods (winters will be shorter and less intense). Quiescence may thus allow insects to cope with warmer and more variable winter temperatures if they can sporadically increase their cold tolerance, e.g. through rapid cold-hardening (Owen *et al.*, 2013). There are few studies concerning the proportion of species shifting from diapause to quiescence strategies, or of the plasticity of such shifts depending on the thermal and photoperiodic environment. The development of metabolic tools and metrics to disentangle diapause from quiescence syndromes would greatly help in identifying the type of dormancy expressed in a given population.

The scenario of a complete loss of diapause has already been documented in some host–parasitoid associations. Functional traits can be lost through the process of selection or reduced through plastic adjustments when their expression involves costs under some environmental conditions. Strong shifts in diapause incidence have been detected when parasitoids were reared in the laboratory over many generations under constant temperature and photoperiod conditions, such as parasitoids used in biological control. For example, the aphid parasitoid *Binodoxys communis* (Hymenoptera: Braconidae) lost its capacity to enter diapause in less than 300 generations when reared in the laboratory, leading to 100% mortality when the parasitoid was next exposed to overwintering conditions in Canada (Gariepy *et al.*, 2015). Andrade *et al.* (2016) and Tougeron *et al.* (2017b, 2018b) showed that since 2010, because of warming winters in western France, the braconid parasitoids *A. avenae* and *A. ervi* (Hymenoptera: Braconidae), which were known to enter diapause in winter in the past, now remain active as reproducing adults in cereal fields. Also, in mild-winter areas of north-western Spain, the parasitoid *Anaphes nitens* (Hymenoptera: Mymaridae) does not express a true diapause but rather enters winter quiescence to adjust dormancy duration to temperatures experienced during winter (Santolamazza-Carbone *et al.*, 2009).

Trait convergence within communities can be expected when environmental conditions are particularly harsh and influence

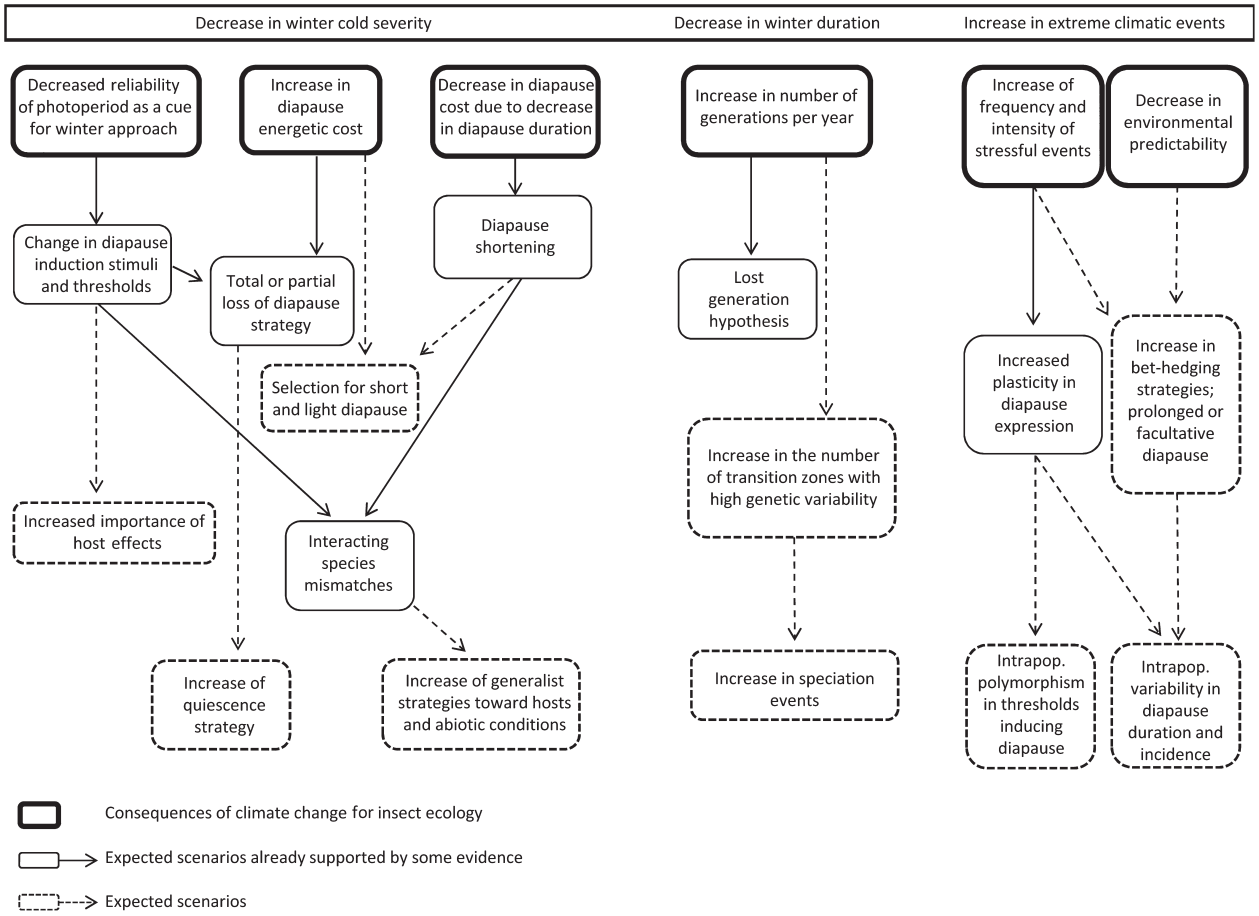

Fig. 1. Schematic of the consequences of decreased winter cold severity and winter duration, and increased extreme climatic events for the seasonal ecology of parasitoids. The three panels refer to the main climate changes that are already well established in the literature, the consequences for insect ecology (bold boxes), and empirical evidence (solid-line boxes and arrows) or expected patterns (dashed-line boxes and arrows).

coexisting species (Cornwell *et al.*, 2006; Le Lann *et al.*, 2014b). Diapause should be maintained in parasitoid communities experiencing both harsh temperatures and host scarcity during winter. With climate changes, we expect traits linked to overwintering strategies to become more convergent among parasitoid species because of increasing environmental filtering at the community level (i.e. warmer temperatures leading to diapause avoidance) (Le Lann *et al.*, 2014b; Outreman *et al.*, 2017). By contrast, traits are expected to diverge in communities where niche partitioning favours high levels of competition (MacArthur & Levins, 1967) and leads to the formation of populations/communities with both diapausing and non-diapausing individuals/species.

Modifications in host–parasitoid interactions. Climate changes could result in asymmetrical changes in overwintering strategies between hosts and parasitoids because: (i) phenology is shifting at different rates between species and trophic levels (Thackeray *et al.*, 2016); and (ii) parasitoids and hosts may rely on different cues to initiate or terminate diapause (Walther, 2010). Modifications in the timing of diapause induction, duration, and termination could thus compromise the seasonal synchrony of parasitoids with their hosts and other resources. Desynchronisation in host–parasitoid phenology can in turn induce shifts in diapause expression for parasitoids.

Parasitoids that enter and maintain diapause under the strict control of their host (e.g. McNeil & Rabb, 1973) will probably remain synchronised following climate change. Predictions are more challenging for parasitoid species that rely on multiple diapause-inducing cues, including those from their host. For example, the parasitoids *Aphidius matricariae* and *A. ervi* (Hymenoptera: Braconidae) enter diapause at high levels when parasitising sexual aphids, probably in response to aphid metabolic or hormonal content, whereas diapause is induced by photoperiod and temperature when parasitoids exploit asexual aphids (Polgár *et al.*, 1991; Tougeron *et al.*, 2019). Indeed, sexual female morphs of the pea aphid have been shown to contain more polyols and sugar molecules than asexual females, which may increase diapause incidence in aphid parasitoids (Tougeron *et al.*, 2019). Yet aphids produce fewer sexual morphs in warmer environments (Dedryver *et al.*, 2001). In these species, we predict that climate warming will modify parasitoid diapause expression through both modifications in host phenology and

the emergence of contradictory environmental signals for parasitoids if sexual morphs induce parasitoid diapause, even if winters are warm enough for them to remain active. However, because aphid diapause and aphid sexual morphs are often induced by the same cues as for parasitoid diapause, it is unlikely that conflicting cues would appear for parasitoids between host signals and abiotic signals. In warm environments, aphid parasitoids would more likely stop using aphid sexual morphs as a diapause-inducing signal (Tougeron *et al.*, 2019).

Physiological and behavioural thermal preferences often differ between parasitoids and their hosts (van Baaren *et al.*, 2010; Le Lann *et al.*, 2014a; Moiroux *et al.*, 2016; Furlong & Zalucki, 2017), which is common among trophic levels (Berg *et al.*, 2010; Visser, 2016). For example, parasitoids and their hosts differ in thermal acclimation responses when facing microclimatic variations across a landscape (Tougeron *et al.*, 2016; Alford *et al.*, 2017). A potential scenario would be that parasitoid success decreases when hosts are more resistant to climate variability than parasitoids (Le Lann *et al.*, 2014a). Moreover, because of higher reproductive and growth rates, adaptations to new climatic conditions could arise more rapidly for hosts than for parasitoids, thereby contributing to a loss of synchronisation (Hance *et al.*, 2007). Mismatches in phenology could thus occur through differences in thermal responses between interacting species (Wetherington *et al.*, 2017). For example, black, thermophilic caterpillars of the Finnish butterfly *Melitaea cinxia* bask in the sun to accelerate their development, an option not available for their immobile, white-cocooned specialist parasitoids (*Cotesia melitaearum*). As a result, caterpillars can generate adaptive phenological asynchrony with parasitoids and thereby change the temporal dynamics of the interactions (Van Nouhuys & Lei, 2004).

Species that are generalists for traits like thermal tolerance or degree of host specialisation should adapt better to climate changes than specialist species; thus the latter should be under stronger selective pressure for phenological adjustments (Rand & Tscharntke, 2007; Tylianakis *et al.*, 2008; Vázquez *et al.*, 2015). For example, generalist parasitoids can switch to suboptimal host species at a specific period of the year if their preferred host species modifies its phenology. By contrast, specialist parasitoids cannot track their hosts beyond their own temporal range. This would be a major issue for parasitoids if their seasonal phenology, including diapause expression, did not adapt to changing climates.

Parasitoids have the capacity to manipulate the behaviour of their hosts to increase their own fitness (Brodeur & Boivin, 2004), even in the context of diapause. Brodeur and McNeil (1989) observed that the behaviour of parasitised aphids varies as a function of the physiological state of the parasitoid. Mummies containing non-diapausing *A. nigripes* are located in the apical stratum of the plant canopy, whereas aphids containing parasitoid larvae destined to enter diapause frequently leave the host plant and mummify in concealed microhabitats where the effect of adverse climatic conditions is reduced during the lengthy dormant period. Josso *et al.* (2011) showed that drosophilid larvae parasitised by *A. tabida* pupate nearer to a humid substrate than do unparasitised larvae, to avoid desiccation at high temperatures. These examples imply that parasitoids can drive their hosts to favourable overwintering sites as a form of behavioural plasticity that could then reduce negative impacts of climate changes.

Climate changes have the potential to disrupt trophic interactions and to force evolutionary responses in interacting species, because spatially and temporally co-occurring species do not necessarily respond in a similar way to global changes (Schweiger *et al.*, 2008). In a recent review, Johansson *et al.* (2015) suggested that phenological asynchrony can shape life-history traits and have consequences on the population dynamics of interacting species. They proposed different scenarios for the evolution of synchrony between interacting species under climate change. However, the effects of asynchrony remain unclear because of the lack of empirical evidence, especially when considering potential extinctions (Dunn *et al.*, 2009). The synchrony between *Euphydryas aurinia* (Lepidoptera: Nymphalidae) and its parasitoid *Cotesia bignellii* (Hymenoptera: Braconidae) was not altered under scenarios of climate warming because the variance in developmental duration of the parasitoid is large enough to ensure an overlap between host availability and parasitoid emergence (Klapwijk *et al.*, 2010).

Decrease in winter duration

Shifts in voltinism. Because it is a product of multiple environmental constraints (Tobin *et al.*, 2008), changes in voltinism are difficult to predict, especially for interacting species such as parasitoids and their hosts. However, for insects with facultative diapause, several studies have shown that species/populations have added one or more generations to their seasonal cycle (Altermatt, 2010), through either an increase in developmental rate or a reduction in diapause duration (Tobin *et al.*, 2008; Bentz & Powell, 2014). For example, the grape-berry moth *Paralobesia viteana* (Lepidoptera: Tortricidae) can add a partial fifth generation per year in the southern United States when temperatures exceed normal values (Tobin *et al.*, 2003). In insects, small modifications in temperature can result in large shifts in voltinism (Parmesan & Yohe, 2003), which may also be true for parasitoids as long as hosts are available. A decrease in voltinism could also be expected if some insects fail to prevent diapause or enter diapause early because of mismatches between photoperiod and thermal signals, as discussed by Forrest (2016).

When populations are compared among latitudes, many insect species with a facultative diapause show a sawtooth pattern in life-history traits like development time or body size, because the expected gradual change of these traits in relation to season length is interrupted by abrupt changes in voltinism (Kivelä *et al.*, 2013). In transition areas between populations with different numbers of generations (e.g. Winterhalter & Mousseau, 2007; Aalberg Haugen & Gotthard, 2015; van Dyck *et al.*, 2015), the genetic variability is expected to be high, resulting in higher life-history variability (Nylin *et al.*, 1994; Blanckenhorn & Fairbairn, 1995) and possibly hybridisation between different voltinism patterns (Wadsworth *et al.*, 2013, and references therein). Studies on geographic gradients (e.g. Bradshaw & Holzapfel, 2001; Winterhalter & Mousseau, 2007; Paolucci

et al., 2013) may help to forecast where such populations with mixed strategies would occur and predict the proportion of diapausing individuals at a given location under different climate-warming scenarios by examining analogous spatial and thermal conditions. In addition, differences in dormancy patterns between populations may ultimately lead to speciation following reproductive isolation when their life cycles greatly diverge (Wadsworth *et al.*, 2013).

Obligatory diapause is strongly genetically conserved within species (Koštál, 2006), and plasticity is unlikely to be involved in any kind of resynchronisation with seasonality. We expect high mortality and potential local extinctions when univoltine species do not adapt to new climatic environments. Species with obligatory diapause occurring at a genetically determined development stage may be more affected by the rapidly rising global temperatures than species with facultative diapause because of mismatches between diapause timing and abiotic conditions (i.e. they may enter diapause too early in the season due to temperature effects on developmental rate). At this point, we can only predict that species with an obligatory diapause may be subject to strong selective pressures on the period of diapause initiation and termination (Forrest, 2016). Strong physiological and ecological costs for the insect may force the selection toward increasing voltinism.

The adaptive value of shifts in voltinism in response to climate change remains to be determined (Duputié *et al.*, 2015) because physiological and ecological costs may arise from such developmental responses (Sgrò *et al.*, 2016). In some cases, the extended period before diapause induction is a developmental trap resulting in the production of a complete or partial additional generation in the autumn that cannot survive or enter diapause (the 'lost-generation hypothesis' following Musolin, 2007; van Dyck *et al.*, 2015). Delayed diapause induction could result from constraints (i.e. high temperatures acting on plasticity) rather than an adaptive phenotypic plasticity response of the insect. For example, an increase in temperature by 1–2 °C in the Osaka region of Japan from the 1950s to the 1990s allowed the stink bug *Nezara viridula* (Hemiptera: Pentatomidae) to enter diapause later in the season, leading to a late generation that was unable to survive winter (Musolin, 2007). By contrast, insect populations from mild winter areas that remain active throughout winter may gain a selective advantage that could be maintained in the populations (Bale & Hayward, 2010).

Increasing maternal effects. Transgenerational plasticity may become increasingly important for diapause induction in the context of longer growing seasons. Parasitoids need to accurately assess seasonal changes by using more reliable proxies of upcoming winter or of the return of favourable conditions. In a changing environment, maternal perception of abiotic conditions and host availability could contribute more to adaptive induction and/or termination of diapause at the appropriate period of the year (Mousseau & Dingle, 1991). Van Asch *et al.* (2010) showed that the winter moth *Operophtera brumata* (Lepidoptera: Geometridae) adjusted its phenology to spatial variations in the timing of oak bud opening through maternal effects on offspring developmental time. The authors argued that such maternal effects should also play a role in adaptation to shifts in host plant phenology induced by climate change without the need for genetic change.

However, mother–offspring conflicts in overwintering strategies have been shown to occur in some areas: females exposed to high temperatures in the autumn do not induce diapause in their progeny, leading to offspring death due to mismatches in the transgenerational transfer of environmental information (Coleman *et al.*, 2014). Depending on environmental correlations between generations, maternal effects may either decrease or increase the rate of response to selection and thus speed up or slow down evolutionary changes in diapause following climate warming (Kirkpatrick & Lande, 1989). Under conditions of environmental autocorrelation, transgenerational plasticity may be beneficial for the offspring, whereas an unpredictable environment should decrease its adaptive value (Marshall & Uller, 2007; Sgrò *et al.*, 2016; Donelson *et al.*, 2018). Experimental designs that are able to distinguish transgenerational plasticity from selection and from within-generation plasticity should be used to dissociate the role of such mechanisms in organism responses to climate change (Blanckenhorn, 2018; Donelson *et al.*, 2018).

Increase in the frequency of extreme events and environmental stochasticity

Hopper (1999) argued that yearly variations in the thermal environment are too small to select for risk-spreading in insects. Accordingly, the evolution of bet-hedging strategies has been overlooked in the context of climate changes (Sgrò *et al.*, 2016). To cope with a new selective pressure associated with increasing environmental stochasticity (variability and unpredictability), mixed strategies such as bet-hedging should become more frequent (Simons, 2011; Kivelä *et al.*, 2013) and could arise from maternal effects or directly from the diapausing generation, as discussed earlier. Bet-hedging strategies should be widespread among univoltine insects with obligatory diapause (e.g. Bradford & Roff, 1993; Menu *et al.*, 2000). Conservative risk-spreading strategies may occur with early obligatory diapause induction as well as delayed post-diapause emergence (Hopper, 1999). For multivoltine species with facultative diapause, diversifying risk-spreading strategies could lead to variable diapause induction and termination thresholds within a population; individuals of the same genotype may or may not enter diapause under identical environmental cues (i.e. intra-populational risk-spreading strategy; Hopper, 1999).

Increased climatic variability could select for increased phenotypic plasticity within a population (Vázquez *et al.*, 2015), with some individuals undergoing diapause and the other individuals remaining active in the environment or entering adult quiescence, as observed in aphid parasitoids (Starý, 1970; Andrade *et al.*, 2016). Diapause induction may become a flexible conditional strategy (Blanckenhorn & Fairbairn, 1995). In an adaptive 'coin-flipping' strategy, the proportion of parasitoids entering diapause each winter should match the probability of a parasitoid undergoing harsh winters and experiencing host shortage (Hopper, 1999; Rajon *et al.*, 2014). This raises the question of

the role of environmental predictability in the establishment of such mixed strategies (Burgess & Marshall, 2014).

Parasitoids overwinter inside their immobile hosts or in the habitat (e.g. plant, soil) and are consequently exposed to unpredictable climatic variations as they are not able to perform behavioural thermoregulation to seek microclimatic refuges during diapause (Hance *et al.*, 2007). Therefore, they select overwintering sites before entering diapause to cope with microclimatic variability (Hance *et al.*, 2007). As mentioned earlier, host manipulation may allow parasitoids to select proper overwintering sites in a timely manner. Climate warming can lead to a decrease in snow cover and reduce the insulating effect for organisms overwintering in leaf litter or in the soil (Zhang, 2005); this may increase parasitoid mortality during diapause (Hance *et al.*, 2007). Indeed, reduced snow cover leads to an increased exposure to freeze–thaw cycles and cold spells (Roland & Matter, 2016). In both obligate and facultative diapause species, unpredictable snow-cover conditions should favour behavioural bet-hedging strategies in the selection of overwintering sites (e.g. Boivin, 1994). For example, the mymarid parasitoid *Anaphes victus* (Hymenoptera: Mymaridae) lays its diapausing eggs in different sites, and their survival depends on the probability of these sites being snow-covered in winter (Boivin, 1994).

Prolonged diapause, when individuals from a population terminate diapause over successive years (Menu *et al.*, 2000), is perhaps the most well-studied seasonal bet-hedging strategy in arthropods (Menu & Debouzie, 1993; Soula & Menu, 2003, and references therein), but it has been overlooked for parasitoids (Valera *et al.*, 2006). Prolonged diapause favours the survival of at least a few individuals in case of a catastrophic year (Ringel *et al.*, 1998). However, in favourable years, individuals remaining in diapause face ecological costs because they miss reproductive opportunities and remain exposed to predators, parasites, and pathogens for longer periods of time (Denlinger, 1981; Menu & Desouhant, 2002). Parasitoids can enter and terminate prolonged diapause when their hosts adopt the same strategy, indicating that they are both timed by the same external cues, potentially due to strong coevolution (Hanski, 1988; Corley *et al.*, 2004). We can expect prolonged diapause occurrence and duration variability to increase in several insect species with increasing climatic variability and unpredictability (Hanski, 1988; Lalonde, 2004).

As discussed earlier, climate change should have a greater effect on specialist than on generalist species, including resistance to non-optimal temperatures. For example, a thermal specialist (stenotherm) strain of the parasitoid *Venturia canescens* (Hymenoptera: Ichneumonidae) was more severely affected by temperature fluctuations than was a generalist (eurytherm) strain for a set of life-history traits (Foray *et al.*, 2014). Evolution often favours the selection of climate specialist populations at high or low latitudes (Hoffmann, 2010; Nilsson-Örtman *et al.*, 2012), because adaptations to a wide range of temperatures is energetically costly, especially when temperature variations are low or occur between generations (Hoffmann *et al.*, 2013). In eurythermic species, diapause could be lost more quickly with climate warming than in stenothermic species, because eurytherms have a better capacity to survive both warm winters and cold spells without the need to enter diapause. Furthermore, they could track their host's phenology more accurately than stenotherms.

Consequences of changes in diapause expression

Predictive models on the consequences of global changes increasingly explore the response of multiple species within a food web, because changes in phenology (e.g. diapause expression) can translate into modifications in the strength, occurrence, and frequency of multi-trophic interactions (Davis *et al.*, 1998; Thomson *et al.*, 2010; Gilbert *et al.*, 2014). Key questions relate to potential outcomes of shifts in the interactions of species on food-web functioning and ecosystem services such as biological pest control (Gilman *et al.*, 2010; Chaianunporn & Hovestadt, 2015; Valiente-Banuet *et al.*, 2015).

Changes in community structure and food-web functioning

In a meta-analysis, Tylianakis *et al.* (2008) showed that every type of species interaction can be modified by climate changes. Consequently, the effects of climate changes should be considered not only at the individual level (e.g. physiological acclimation, thermal stress) but also for the entire community (e.g. shifts in interactions involving more than two species), from plants to the highest trophic levels (van der Putten *et al.*, 2010; Thackeray *et al.*, 2016; Visser, 2016). Following changes in overwintering strategies, novel interactions will appear that alter the abundances, distributions, and functions of species in a food web (Walther *et al.*, 2002; Gilman *et al.*, 2010), potentially leading to increased antagonism (predation, parasitism, competition) and affecting the fitness of newly interacting species because of a lack of co-evolutionary history (Gilman *et al.*, 2010).

In insect communities, some species stop entering diapause; this has consequences on food-web functioning, especially for keystone species. For example, in the parasitoid community of cereal aphids in western France, diapause incidence of the generalist aphid parasitoid *A. avenae* has been greatly reduced over the past 10 years because of warmer winters (Tougeron *et al.*, 2017b). As a result, this species has become the dominant species in winter, with a concomitant decline in the previously most abundant parasitoid species *A. rhopalosiphi* and *A. matricariae* (Andrade *et al.*, 2016). When parasitoids extend their activity to a new period during the year, the trophic niche could overlap with other species and lead to intraguild competition.

Finally, the role bacterial endosymbionts might play in structuring communities (e.g. Sanders *et al.*, 2016) or shaping host–parasitoid interactions in the context of climate change remains poorly understood (Jeffs & Lewis, 2013; Mushegian & Tougeron, 2019; Thierry *et al.*, 2019). Endosymbiont effects on insect life-history traits and species interactions are highly diverse (Oliver *et al.*, 2014), and it is known that they become less effective when temperatures rise (Bensadia *et al.*, 2006; Cayetano & Vorburger, 2013). In addition, symbionts can be involved in overwintering insect survival by improving the thermal tolerance of their hosts (Kashima *et al.*, 2006; Dunbar *et al.*, 2007; Koehler *et al.*, 2013). Host–microbe interactions, from

pathogenic to mutualistic, may have an impact on diapause phenotypes. Conversely, diapause can affect the ecology of microbial communities and the evolution of host–microbe interactions (Mushegian & Tougeron, 2019).

Impacts on biological control

Climate change is expected to increase damage caused by agricultural pests through increasing population growth, advance in pest outbreaks, and facilitation of pest dispersion, but also to increase the number of pest generations year^{-1}, and to decrease the effectiveness of natural enemies and plant resistance (Thomson *et al.*, 2010; Klapwijk *et al.*, 2012; Björkman & Niemelä, 2015; Eigenbrode *et al.*, 2015; Pincebourde *et al.*, 2016). Inaccurate temporal host-tracking by a specialised parasitoid may result in significant yield losses (Eigenbrode *et al.*, 2015). For example, Grabenweger *et al.* (2007) showed that parasitoids of the invasive horse chestnut leaf miner *Cameraria ohridella* (Lepidoptera: Gracillaridae) broke diapause too early in spring when hosts were not available. Changes in host–parasitoid food-web composition (see the previous section) under global change may decrease the efficiency of biological control through increasing intraguild competition or the presence of new antagonist species (Tylianakis & Binzer, 2014; Thierry *et al.*, 2019). In addition, hyperparasitism levels have been shown to increase during winter following climate warming (Tougeron *et al.*, 2017b), which may lead to poorer pest control by primary parasitoids (Gómez-Marco *et al.*, 2015). Little information is available on hyperparasitoid ecology and on whether climate change will negatively or positively affect biological pest control through hyperparasitism (Tougeron & Tena, 2018).

It is possible that host–parasitoid desynchronisation would not be problematic for biological control if there were enough functional redundancy within a guild of parasitoid species to control a pest population (Hance *et al.*, 2007). In some instances, climate warming could be beneficial to biological control agents in terms of abundance and richness, as they would be able to parasitise more hosts over a longer time window (Péré *et al.*, 2013) and be present in crops at the beginning of pest infestations. Warmer springs improved the synchrony of the specialist parasitoid *Cotesia melitaearum* (Hymenoptera: Braconidae) with its host, the butterfly *Melitaea cinxia* (Lepidoptera: Nymphalidae), leading to increased parasitoid colonisation at the metapopulation scale (Van Nouhuys & Lei, 2004).

From a biological control perspective, manipulation of parasitoid diapause for cold storage and inundative release is a promising field of research (Denlinger, 2008; Colinet & Boivin, 2011). It is thus crucial, finally, to: (i) determine diapause incidence, diapause induction thresholds, and mechanisms of diapause initiation and termination in candidate species (e.g. Gariepy *et al.*, 2015); and (ii) include overwintering strategies as well as host–parasitoid seasonal synchrony in population dynamics models destined to guide pest control decisions (Lalonde, 2004). Simulation models on insect seasonality (e.g. Powell & Logan, 2005) and host–parasitoid interactions (e.g. Kalinkat & Rall, 2015) in response to temperature changes could provide useful insights into the phenological responses of pests and natural enemies to climate change and help to predict changes in biological pest control.

Conclusion

Forecasting scenarios on the evolution of insect seasonality is challenging because dormancy is not simply an active versus inactive state but a whole spectrum of states (syndrome), i.e. it is a physiologically complex and dynamic alternative developmental pathway that is part of a continuing process within the insect's life cycle, with varying characteristics throughout diapause induction, maintenance, termination, and insect ontogenesis. Further investigations on the cost–benefit balance of diapause are required to foresee how insects will adapt diapause timing and incidence under future environmental conditions. Incorporating trade-offs between diapause and other traits is crucial to understanding the action of natural selection on parasitoids and their response to modifications in the seasonal environment. As discussed throughout the manuscript, physiological, metabolic, morphological and behavioural trade-offs with diapause may limit the adaptation potential of parasitoids to climate change. Conversely, trade-offs between diapause and other life histories (e.g. size) mostly occur when time to complete development is limited (Danks, 2007), and climate change may modify the duration of the growing season, thus limiting the occurrence and strength of trade-offs.

Parasitoids will obviously share common responses to climate change with other insects, but we have highlighted that some of these responses are unique to parasitoids because of their unique lifestyle. These singularities mostly include the relationship with the host: generalist versus specialist host species, koinobiont versus idiobiont parasitoids, host-diapause-conformer versus independent cues perceived by the parasitoid, and species capable of host manipulation. According to their life-history strategies, parasitoids may thus be more or less subject to shifts in overwintering strategies along with climate change. This also raises the question of which are the best stimuli for parasitoids to rely on to enter and terminate diapause in a changing climate, given that the reliability of photoperiod as an indicator of upcoming seasonal changes in temperature and host availability could diminish.

In the light of this discussion, we see that current climate changes can affect several aspects of parasitoid ecology, and parasitoids can rely on different strategies to cope with these changes. As a plausible general scenario, we suggest that parasitoids will locally modify their seasonal strategy to adapt to their new thermal environment and maintain the relationship with their hosts. Successful adaptations to rapid climate change should involve both local adaptations by genetic changes in diapause expression and behavioural and physiological plastic responses, including maternal effects.

Future research will have to assess the relative importance and potential of these mechanisms in mediating the responses of parasitoid species to climatic change (Bradshaw & Holzapfel, 2006; Merilä & Hendry, 2014; Duputié *et al.*, 2015; Abram *et al.*, 2016). This could be achieved by experimental evolution frameworks, community-scale experiments, and by exploring datasets

on long-term host–parasitoid interactions. More generally, a better appreciation of the processes governing insect phenology is needed to forecast the consequences of such changes on species interactions and synchrony across multiple trophic levels, community functioning, and ecosystem services such as biological pest control (Forrest, 2016; Visser, 2016), especially because these responses might be taxonomically constrained (Thackeray *et al.*, 2016).

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