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Hyperparasitoids as new targets in biological control in a global change context

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Abstract

Agricultural and forest insect pests generate important yield losses worldwide. Global-change is expected to increase pest outbreaks and their impact on human-managed ecosystems. Pest control performed by natural enemies is also likely to be influenced by global-change. Yet, pests and their natural enemies are part of complex food-webs and interact with other species, notably at upper trophic levels (e.g. hyperparasitoids, predators). These interactions have to be considered as important facets of food-web structure, functioning, and pest control efficiency. Relatively recent evidence suggests that global-change may translate to modifications in upper-trophic level abundance, phenology, and geographic range. The combination of these shifts at different trophic-levels may ultimately threaten ecosystem services such as biological pest control, yet these shifts have largely been overlooked. Little information is available on hyperparasitoid ecology and therefore little is known about the potential impact of climate change on these species. Improving our knowledge on this topic is important if we aim at adopting biological control programs in the near future. In this overview, we first emphasize that hyperparasitoids may have huge potential to disrupt biological control in natural and agricultural settings. We then stress that this disruption may increase in frequency and magnitude in the near future due to global-change. We finally propose that hyperparasitoids may become new targets in biological control and recommend different methods to control them, or limit their impact.

Key-words: Pest-control; intraguild interactions; food-web; climate-change; parasitoid; conservation; ecosystem services

1. Introduction

Agricultural and forest productivity will likely increase to meet intensifying human demand for food, manufactured goods and houses (Foley et al., 2005). In the meantime, the Earth is experiencing rapid changes in both climatic conditions and land-use (Tilman, 1999; Karl and Trenberth, 2003). These changes have led to a drastic decrease in biodiversity and to important consequences on species ecology, including distribution ranges, phenology and physiology, ultimately threatening the stability of ecosystems (Hautier et al., 2015; Walther et al., 2002) and degrading ecosystem services (Tscharntke et al., 2005; Montoya and Raffaelli, 2010). One of the most important ecosystem services is biological pest control, which helps to maintain pest damage below tolerable thresholds in human-managed ecosystems, such as agrosystems or forests, and can help to sustain the increasing production demand (van Lenteren, 2012; van Lenteren et al., 2018). Whether global-change will negatively or positively impact the efficiency of biological-control service remains unclear, but every type - either natural, classical, conservation or augmentative biological control - is likely to be impacted (Aguilar-Fenollosa and Jacas, 2014; Andrew and Hill, 2017; Björkman and Niemelä, 2015).

Global change is expected to increase damage caused by agricultural pests by increasing their population growth, generations per year, and dispersal, by inducing earlier pest outbreaks, decreasing natural enemies' efficiency, and decreasing plant resistance (Björkman and Niemelä, 2015; Klapwijk et al., 2012; Pincebourde et al., 2016). Environmental changes might also be beneficial for biological control agents if, for example, they are able to find more hosts/prey for a longer time window (Hance et al., 2007; Thomson et al., 2010) since early suppression of pests is crucial for efficient biological control (Gómez-Marco et al., 2016a; Langer et al., 1997; Neuville et al., 2015). Parasitoids are among the main natural enemies, and have been widely used in biological control against insect pests (Jervis, 2007; van Lenteren et al., 2018). Global-change will either (i) enhance biological control by parasitoids if they adapt better to new conditions than their hosts, (ii) maintain unchanged biological control by parasitoids if they are able to keep pace with their hosts' distribution or phenology shifts, or (iii) disrupt biological control by parasitoids if they adapt less well to new environmental conditions than their hosts.

However, parasitoids and their hosts are not alone in their environment and they interact with other species in complex food-webs. Following global-change, novel interactions will appear through shifts in geographic ranges (Van der Putten, 2012) or in phenology (Forrest, 2016; Visser, 2016), altering the abundance, distribution, and functions of species in a food-web (Facey et al., 2014; Gilman et al., 2010; Walther et al., 2002), potentially leading to increased antagonism among natural enemies (predation, parasitism or competition). These changes in food-web interactions are an additional challenge that biological control practitioners will have to face in the upcoming years (Andrew and Hill, 2017; Hance et al., 2007). Thus, if we aim at predicting the effect of global-change on biological control, there is a need to consider such effects not only at the pest-parasitoid scale, but at the whole community scale (e.g. shifts in interactions involving more than two species) (Frago, 2016; Thackeray et al., 2016; Thompson et al., 2013; Tylianakis et al., 2008; van der Putten et al., 2010; Visser, 2016).

Intraguild interactions among parasitoid species (i.e. species sharing the same host) are good examples of the complexity underlying food-web functioning and of the difficulty to develop successful biological control programs (Gómez-Marco et al., 2015; Traugott et al., 2008). Specifically, the effects of intraguild competition (i.e. direct competition, multiparasitism) (reviewed in Boivin and Brodeur, 2006; Harvey et al., 2013) and intraguild predation (i.e. when at least two species that share the same prey or host also predate or parasitize each other) (reviewed in Rosenheim et al., 1995) on biological control have been well explored. Surprisingly, and despite their importance in biological control and their ubiquity in food-webs, the effects of upper trophic levels such as hyperparasitoids on pest population regulation have been neglected relative to interactions mentioned above. Hyperparasitoids are secondary parasites of immature stages of primary parasitoids and belong to the fourth (or upper) trophic levels (Sullivan, 1987) and are the only specific natural enemies of parasitoids (Boivin and

Brodeur, 2006). Hyperparasitoids have a wide host range and harbor complex life-cycles and host-foraging behaviour since they can be either facultative or obligate (Brodeur, 2000; Hunter and Woolley, 2001). They come from a few taxa but are present in a wide variety of ecosystems, including forests, crops, orchards and greenhouses (Brodeur, 2000; Frago, 2016; Prado et al., 2015). As high trophic level species, they are more susceptible to perturbations because of bottom-up effects in the food-web, as predicted by the trophic rank hypothesis (Holt et al., 1999; Gilman et al., 2010). Yet, hyperparasitoids did not gain the attention that they deserve in most biocontrol studies. We first review the effect of hyperparasitoids on biological control provided by parasitoids; we then analyze the potential effect of climate change on hyperparasitoids and biological control; and, finally, we propose several methods to overcome the effect of hyperparasitoids on biological control.

2. Hyperparasitoids and biological control disruption

When any type of biological control fails, it is often because scientists overlooked natural enemies as part of a food web (Goldson et al., 2014). Studies of natural host–parasitoid communities reveal that hyperparasitoids are common in many networks (Gómez-Marco et al., 2015; Müller and Godfray, 1999; Tena et al., 2008; Traugott et al., 2008). In fact, numerous field studies have reported hyperparasitism levels up to 90% (e.g. Holler et al., 1993). Prado et al., (2015) also state that high hyperparasitism rates may be reached in greenhouses due to temperature advantage. Naturally occurring hyperparasitism is traditionally thought to disrupt biological control by primary parasitoids on target pests because hyperparasitoids develop at the expense of parasitoids and are, thus, likely to limit the control of herbivorous hosts by the following parasitoid generation (Rosenheim, 1998; Sullivan and Völkl, 1999). Among the detrimental effects on primary parasitoids, hyperparasitoids may affect their establishment, occurrence and abundance not only through direct parasitism but also by acting as intraguild competitors (i.e., facultative hyperparasitoids that exploit herbivores and primary parasitoids) (Boivin and Brodeur, 2006; Snyder and Ives, 2008). For example, Pérez-Lachaud et al. (2002) showed that *Cephalonomia hyalinipennis*, a facultative bethylid hyperparasitoid of the coffee berry borer, affected the primary biocontrol agents through direct behavioural contests for hosts. In another example, primary parasitoids *Metaphycus* and the facultative hyperparasitoid *Coccophagus lycimnia* compete for hosts of the same size when they parasitize the citricola scale *Coccus pseudomagnoliarum* leading to reduced levels of biological control (Bernal et al., 2001). As a consequence, the potential negative impact of hyperparasitoids may be different between obligate and facultative hyperparasitoids. Obligate hyperparasitoids generally hinder the effect of primary parasitoids but may circumstantially play a role in stabilizing host-parasitoids interactions through density-dependent effects (Beddington and Hammond, 1977; Hassell and Waage, 1984; Holt and Hochberg, 1998), and may thus in some cases enhance biological control by primary parasitoids (Rosenheim, 1998; Sullivan and Völkl, 1999). The latter (facultative hyperparasitoids) may both outcompete and parasitize primary parasitoids, in addition to ovicide and larvicide effects (Bernal et al., 2001; Pérez-Lachaud et al., 2004), but may still be efficient at controlling pests since some facultative hyperparasitoids have been considered as candidate species for classical or augmentative biological control (Boivin and Brodeur, 2006). Thus, the debate about the extent to which hyperparasitoids can disrupt or even enhance biological control remains open, and would benefit from more theoretical and empirical studies (Brodeur, 2000; Rosenheim et al., 1995; Schooler et al., 2011; Snyder and Ives, 2008).

In biological control, the actual impact of naturally occurring hyperparasitoids on the efficacy of primary parasitoids can be confused with other biotic and abiotic factors. For example, immature mortality of the primary host can be due not only to hyperparasitoids but also to host defenses or extreme climatic conditions (Godfray, 1994). Moreover, the effect of hyperparasitoids can go beyond the direct mortality of immature parasitoids. For example, they can deter primary parasitoids of foraging on host patches through volatiles (Höller et al., 1994; Petersen et al., 2000); or be responsible of the apparent competition between primary

parasitoids, leading to the extinction of the loser species (Van Nouhuys and Hanski, 2000). From a population dynamics point of view, hyperparasitoids are likely to act similarly as superpredators on the prey/pest trophic level (e.g. Mbava et al., 2017), which can be observed directly by monitoring food-webs over time or recording behavioural activities. In addition to direct population monitoring, other indirect molecular tools such as barcoding or stable isotopes analyses can be used to assess and quantify the impact of hyperparasitoids on lower trophic levels (Sanders et al., 2016; Traugott et al., 2008).

Hyperparasitoids can act on the efficiency of natural (discussed above), classical, augmentative or conservation biological control.

2.1. Hyperparasitoids in classical biological control

In classical biological control, native hyperparasitoids can already be present at the location of introduction and can therefore reduce its own potential, although complex density-dependent interactions can appear in some other host-parasitoid-hyperparasitoid systems (Hougardy and Mills, 2008). For example, the native hyperparasitoid *Conura albifrons* was shown to attack the primary parasitoid *Diadromus pulchellus*, an exotic biological control agent released in North America to control the leek moth (Miall et al., 2014). Hyperparasitoids can also be fortuitously released with the new primary parasitoid, in both cases impairing the long-term establishment of the primary parasitoid (Goldson et al., 2014). Although great care is made to exclude hyperparasitoids when importing insects, several cases of fortuitous introduction of hyperparasitoids – such as in Southern California at the beginning of the 20th century – reinforced the importance of quarantine procedures before the introduction (Sawyer, 2002). Moreover, the important steps taken to reduce the risks associated with biological control introductions over the past 20 years have led to greatly improved safety of introductions (Heimpel and Mills, 2017; Van Lenteren et al., 2003). Therefore, it seems unlikely that the fortuitous introduction of hyperparasitoids will occur in the coming years.

2.2. Hyperparasitoids in augmentative biological control

Hyperparasitoids can also disrupt augmentative biological control. The best known example is the augmentative releases of *Aphidius colemani* (Hymenoptera: Braconidae) in greenhouses to control aphids (Prado et al., 2015). There are several species of hyperparasitoids that attack and hinder the effect of *A. colemani* (Acheampong et al., 2012; Bloemhard et al., 2014; van Steenis, 1995). These hyperparasitoids are more abundant and active in summer (van Steenis, 1995; Bloemhard et al., 2014). For this reason, augmentative releases of *A. colemani* are recommended in spring, when hyperparasitism does not interfere with aphid control (Prado et al., 2015). The use of banker plants can also hinder the efficacy of *A. colemani* releases if hyperparasitoids can find hosts and overwinter there (Nagasaka et al., 2010).

Naturally present primary parasitoid and hyperparasitoid populations around agricultural fields can interact with released parasitoids. This should be taken into account for the development of pest management strategies in the future. However, as mentioned before, little is known about what hyperparasitoid species are present around cultivated fields, and we know even less about their behaviour and ecology. Several questions remain to be answered if our aim is to include hyperparasitoids as an important factor when making management decisions. For example; how do they interact with other species, especially with released and naturally present primary parasitoids, and with the abiotic environment?

2.3. Hyperparasitoids in conservation biological control

In conservation biological control, hyperparasitoids can take advantage of the conservation procedures aimed to improve the fitness of primary parasitoids (Müller and Godfray, 1999). In conservation biological control, there may be a trade-off between improving primary parasitoid efficiency and attracting hyperparasitoids or improving their fitness. For instance, nectar sources added around the fields to improve efficiency of *Aphidius ervi*, a primary parasitoid of aphids,

could also benefit hyperparasitoids such as *Dendrocerus aphidum* (Araj et al., 2006, 2009). Several elements in the landscape such as the composition of field margins may also provide hyperparasitoid alternative host species or suitable over-wintering sites (Plećaš et al., 2014).

3. The effects of global-change on hyperparasitoids

As global-changes are altering trophic interactions (Tylianakis et al., 2008), and the scheduling of species activities in a food-web (Forrest, 2016), the effect of hyperparasitoids on biological control could be modified. Predicting hyperparasitoids' range or phenology shifts following global-change is problematic because their life-cycles are often understudied and strongly linked to those of lower trophic levels (primary parasitoids, hosts and host-plants). Land-use change and climate change are the main drivers of global environmental changes and are expected to have both additive and synergistic effects on organisms ecology (Oliver and Morecroft, 2014). Among potential interactions between both global-change drivers, one could expect that due to climate warming, the build-up of hyperparasitoid populations would be faster in simplified landscapes with more host resources (e.g. aphids) than in more complex landscapes, especially for facultative hyperparasitoids and generalist species. Predictions may vary between generalist and specialist hyperparasitoids species because the latter are not expected to shift their range or phenology beyond that of their hosts, while generalist hyperparasitoids are more likely to find an alternative host and spread to other systems in the global-change context.

Landscape complexity tends to increase species diversity and the action of primary parasitoids as well as hyperparasitoids (Ortiz-Martínez and Lavandero, 2018; Plećaš et al., 2014), especially for generalist species such as parasitoid communities associated with aphids (Brodeur, 2000; Heimpel and Mills, 2017). By analysing food-webs of cereal aphids along an agricultural landscape gradient of structural complexity, Gagic et al. (2011) have shown that both parasitism and hyperparasitism levels are higher in complex landscapes with little percentage of arable lands. Yet, Rand et al. (2012) found that generalist hyperparasitoids benefit landscape complexity more than specialist primary parasitoids. Therefore, the question remains as to the extent to which landscape simplification may act on the services/disservices balance (i.e. will landscape simplification decrease more hyperparasitism than it decreases primary parasitism and favor pests). More studies are necessary to understand how agricultural intensification and landscape simplification can act indirectly on hyperparasitoids by modifying trophic interactions between pests and primary parasitoids, which can in turn trigger effects on the upper trophic level through bottom-up effects (Gagic et al., 2012; Lohaus et al., 2013; Zhao et al., 2013).

Concerning the effects of climate-change, higher temperatures will likely lead to a decrease in longevity in insects from all trophic levels through increasing metabolic rates (van Baaren et al., 2010). In the hyperparasitoid *Asaphes vulgaris* (Hymenoptera: Pteromalidae), the lifespan is four months at 15°C while it decreases to only 46 days at 25°C (Brodeur and McNeil, 1994). However, hyperparasitoids may benefit from higher temperatures for several reasons. First, climate-change may allow hyperparasitoids to terminate diapause earlier than reported in past decades, thus increasing their damage on early-season parasitoids (Gómez-Marco et al., 2015; Tougeron et al., 2017). Hyperparasitoids can be active in winter only if primary parasitoids are available, which in turn requires the presence of hosts. Such a scenario is now present in western and southern Europe where winters are mild enough to allow insect activity throughout the year, including by hyperparasitoids (Andrade et al., 2016; Gómez-Marco et al., 2016a; Lumbierres et al., 2007). Hyperparasitoids were only observed from spring to fall a few decades ago (Krespi et al., 1997; Rabasse and Dedryver, 1982) but, as in many insect species, their phenology seems to be changing following both softening of climatic conditions and modifications in their host's phenology (Tougeron et al., 2017). Secondly, although no long term analysis on hyperparasitoid voltinism (i.e. the production of supplementary generation

each year) are available to our knowledge, we expect an increase in voltinism in hyperparasitoids as occurs in many insects under warmer climates (Sgrò et al., 2016). Finally, basal thermal tolerance and thermal optima can differ between trophic levels which may condition the way hyperparasitoids interact with lower trophic levels in a warmer climate (Furlong and Zalucki, 2017; Gilman et al., 2010), and therefore change the way pest populations are controlled. Rice and Allen (2009) showed that the developmental threshold from larva to adult was 3°C higher for the hyperparasitoid *Mesochorus* sp. (Hymenoptera: Mesochorinae) than for three primary parasitoids species it attacks. Differences in plastic response and in adaptive potential to rapid temperature warming among trophic levels are thus critical to consider in this context and can be viewed as a "thermal arming race" between interacting species (Ferris and Wilson, 2012; Somero, 2010). Nevertheless, the extent to which higher temperatures would benefit hyperparasitoids more than it would primary parasitoids or pest insects still remains to be clarified in most host-parasitoid-hyperparasitoid systems.

If temperatures remain in an optimal or quasi-optimal range for hyperparasitoids, we expect an overall positive effect of climate-change on hyperparasitoid abundances and species richness at a given location, likely due to increase in foraging capacities, and increasing voltinism and seasonal activity levels. However, whether these responses will negatively or positively affect biological pest control is a question that remains to be answered, especially because many crop-specific and species-specific situations will likely appear. Numerous gaps exist concerning our understanding of hyperparasitoid ecology and biology. However, we can speculate that both evolutionary and plastic adjustments, including maternal effects and bet-hedging strategies, will be involved in their adaptation to environmental changes. The response of hyperparasitoids to ongoing global-changes is likely to be the same as the response of primary parasitoids to changing environments (Figure 1, Tougeron, 2017). More insights on plant-herbivore interactions in a global-change context are proposed in Pincebourde et al. (2016) and in Björkman and Niemelä (2015) regarding the impact on biological control.

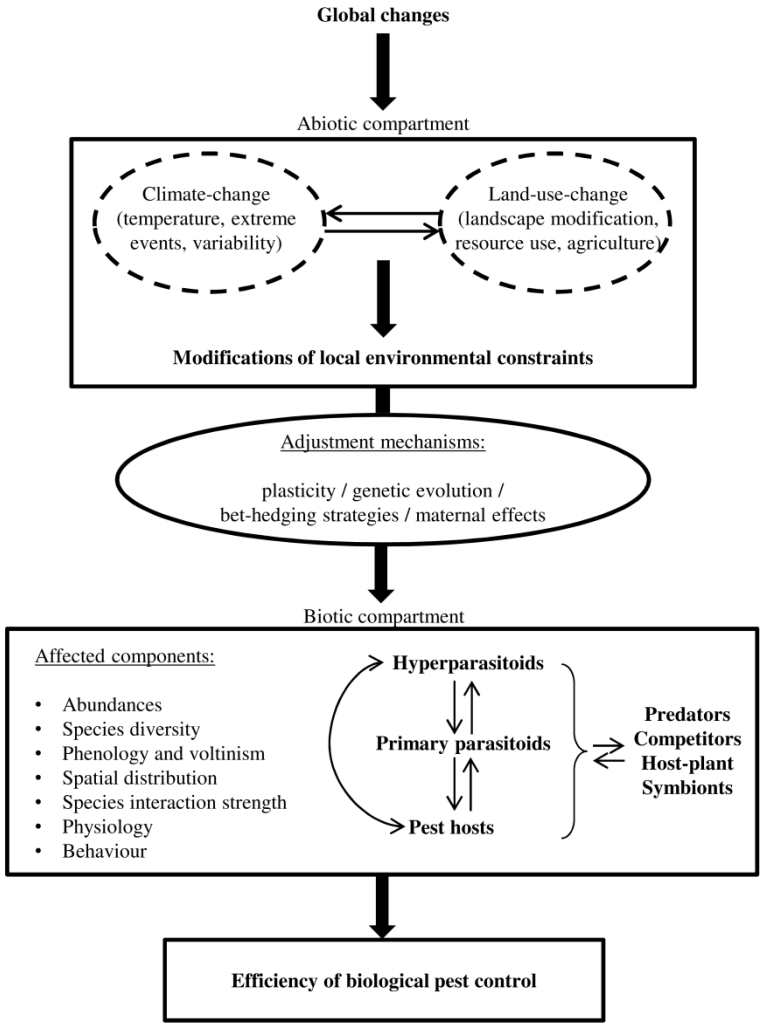

Figure 1: Schematic summarizing the factors involved in modulating the efficiency of biological pest control when hyperparasitoids are present in the ecosystem, and in the context of global changes. These processes are described in the main text of the manuscript. In brief, both climate and land-use changes will modify local environmental conditions. Hyperparasitoids may adapt to new conditions through environmental plasticity or natural selection. These adjustments may not only affect different components of hyperparasitoid ecology, but also of species with which they interact. These changes in the biotic compartment ultimately act on the efficiency of biological pest control, although both positive and negative outcomes could be predicted. This figure is not exhaustive and other mechanisms (e.g., pesticides, artificial light at night) may be involved.

4. Hyperparasitoids as new targets in biological control?

In light of the above, it would be interesting to consider hyperparasitoids as potential targets in biological control and investigate methods to buffer their negative impacts on pest suppression. As species at high trophic levels, hyperparasitoids undergo many ecological and physiological constraints on which we could act to reduce their fitness or their establishment and persistence in the target environment. Some methods have already proved efficient in classical biological control such as quarantine procedures to avoid the introduction of hyperparasitoids. However, controlling hyperparasitoids in conservation and augmentative biological control without also impairing primary parasitoids' fitness is thorny because hyperparasitoids often are ecologically, behaviourally and physiologically very close to their hosts due to their common evolutionary origin (Buitenhuis et al., 2017).

4.1. Use of chemical volatiles

A first promising method is to unravel hyperparasitoid host-foraging behaviour and determine whether there are volatile chemicals that could lure hyperparasitoids away from primary parasitoids without disrupting the latter. If this occurs, the use of attractants or repellents could be a promising approach to keep hyperparasitoids away from target crops. Limited information on hyperparasitoid foraging behaviour indicates that they exploit host and plant volatile chemicals to find their parasitoid hosts (Buitenhuis et al., 2005; Poelman et al., 2012; Sullivan and Völkl, 1999). Host-related kairomones also elicit behavioural responses in the hyperparasitoid. For example, hyperparasitoid females of *Alloxysta victrix* (Hymenoptera: Figitidae) show arrested development and antennal examination behaviour when exposed to aphid cornicle secretions, honeydew and solvent extracts of parasitized aphids by the primary parasitoid (Grasswitz, 1998). Exploiting plant volatiles and/or insect-induced plant volatiles to manipulate target species such as pests or their natural enemies is a commonly used strategy (e.g., push-pull methods in biological control) (Cook et al., 2007). However, as pointed out by Poelman and Kos (2016), there is a risk that both primary and secondary hyperparasitoids are attracted by the same volatile chemicals. Efforts may thus concentrate in finding chemical lures – or concentrations or mixes of these chemicals – that are specific to hyperparasitoids. If these volatile chemicals are attractive only to hyperparasitoids and are affordable, they could be used to control hyperparasitoids without interfering with the activity of primary parasitoids. To the same extent, chemical volatiles used to attract primary parasitoids to crops should ideally not be attractors to hyperparasitoids. An interesting but yet untested approach arises from the fact that primary and secondary parasitoids may be attracted in a different way by plant and host cues (discussed in Poelman and Kos, 2016).

4.2. Environmental management

In a conservation biological control approach, it would be interesting to evaluate whether specific flower mixes and/or specific sugars (for sugar spraying) could benefit primary parasitoid more than hyperparasitoids. In this sense, it has been recently demonstrated that two *Aphidius* parasitoids increase their longevity much more than their hyperparasitoid *Dendrocerus aphidum* when they feed on melibiose (Goelen et al., 2018), a common sugar of honeydew (Wäckers, 2001). This knowledge can be exploited in tailoring food sources to selectively support *Aphidius* parasitoids, enhancing the biological control of aphids (Damien et al., 2017). As trophic levels can have different thermal requirements or plastic adjustment capacities to microclimatic conditions (Thackeray et al., 2016) appropriate landscape management to manipulate pests', parasitoids' and hyperparasitoids' thermal niches could also be considered (Alford et al., 2017; Tougeron et al., 2016).

Another potential solution in conservation biological control would be to enhance predator presence at the beginning of the season, when hosts are at low densities. For example, in citrus, the aphid *Aphis spiraecola* (Hemiptera: Aphididae) has a large and diverse complex of hyperparasitoids which may make unfeasible its biological control with parasitoids in the Mediterranean Basin (Gómez-Marco et al., 2015). There, the biological control services of these predators can be improved by means of cover crops based on Poaceae plants that increase their presence at the beginning of the season (Gómez-Marco et al., 2016a, 2016b).

4.3. Use of natural enemies of hyperparasitoids

Another method is to use the specific natural enemies of hyperparasitoids. For this, we first need to identify them and then determine the extent to which hyperparasitoids' negative effects on primary parasitoids can be limited by their predators, pathogens and parasites in the food-web. Focus should be made on finding hyperparasitoid or predator species that are able to attack a target hyperparasitoid without interfering with the lower trophic levels (i.e., primary parasitoids). At least two groups of insects have been identified as potential natural enemies of hyperparasitoids. Among specialists, some hyperparasitoids are in the fifth trophic level (i.e.

tertiary parasitoids) and parasitize hyperparasitoids. or interfere with their development through larval or adult competition (Harvey et al., 2009). For example, the use of molecular techniques have allowed researchers to untangle the role of hyperparasitoids in food-webs that include the aphid *A. spiraecola* in citrus, and some hyperparasitoids appeared to be in the fifth trophic level (Gómez-Marco et al., 2015). Ants generally protect aphids from primary parasitoids. However, ants are also the best known generalist natural enemy of hyperparasitoids and can provide an "enemy-free space" for the primary parasitoid. For example, the primary parasitoid of aphids *Lysiphlebus cardui* (Hymenoptera: Braconidae) can avoid ants attending aphids, whereas hyperparasitoids are detected and attacked by ants (Völkl, 1992). This interaction is, however, quite specific as some hyperparasitoids can handle ant attendance (Hübner and Völkl, 1996). The presence of tertiary hyperparasitoids and/or ants could be promoted in future conservation biological control programs. To rear tertiary parasitoids for their release in augmentative biological control seems unfeasible, however, because of their cost (van Lenteren et al., 2018). Development of specific strains of microbial biological control agents targeting hyperparasitoids could also be interesting solutions in the future.

4.4. Recommendations for augmentative biological control

In augmentative biological control, we would recommend, when possible, to select and release primary parasitoids that can avoid/escape hyperparasitism, either behaviorally or immunologically, (Brodeur and McNeil, 1989; Höller, 1991), even if they are less effective. In case species with different suitability for hyperparasitoids and efficacy as biological control agents can be released, we would recommend releasing first the "tolerant to hyperparasitism but less effective species", and then release the "intolerant but effective" at the end of the season once hyperparasitoids cannot built up their populations. In terms of augmentative releases, it is also important to determine the correct timing to control a pest while avoiding the presence of hyperparasitoids. For this, it is crucial to include diapause and changes in diapause expected in insects of all trophic levels under climatic change in population dynamic models and phenology models intended to biological control practitioners (Bale and Hayward, 2010; Lalonde, 2004). Moreover, as hyperparasitoid population dynamics seem to depend on both pest hosts and primary parasitoids (Gagic et al., 2011), future research needs to focus on how manipulating either or both of these lower-trophic-level populations could make hyperparasitoid populations crash (e.g., by establishing complex multitrophic-level population dynamics models to identify the levers on which acting to eliminate hyperparasitoids from a system).

4.5. Potential of endosymbionts

Endosymbionts are important players in many food-webs. They are known to be involved in host-parasitoid interactions (Dion et al., 2011; Oliver et al., 2014), but have only recently been studied regarding higher trophic levels. Protective symbionts in pests may have effects that extend to higher trophic levels, including hyperparasitoids (Oliver and Martinez, 2014; Ye et al., 2018). For example, in populations of the pea aphid *Acyrthosiphon pisum* (Hemiptera: Aphididae) that are protected by the bacterial endosymbiont *Hamiltonella defensa* against primary parasitism, there is a reduction in hyperparasitoid emergence not by a direct effect of the endosymbiont on the hyperparasitoid, but through indirect cascading effect resulting from the reduction of specific hosts available for primary parasitism (Mclean et al., 2017). In this sense, protection by endosymbionts is an additional type of bottom-up effect that influences the composition of a parasitoid-hyperparasitoid community (Rothacher et al., 2016; van Nouhuys et al., 2016; Ye et al., 2018). There are, however, no empirical analyses available on how protective symbionts in the host pest or in the primary parasitoid might directly impact hyperparasitoids, nor on how we could control hyperparasitoid fitness through manipulation of endosymbiosis within food-webs (McLean et al., 2016). Moreover, endosymbionts within hyperparasitoids remain, to our knowledge, poorly studied and their potential ecological and evolutionary implications are yet unknown, especially concerning species interactions within food-webs. Endosymbionts are also involved in insect resistance to stress such as thermal stress (Dunbar et al., 2007). They are themselves sensitive to thermal stress (Tada et al., 2011) and

their interaction with the host and the parasitoid differs depending on temperature (Cayetano and Vorburger, 2013; Guay et al., 2009; Thomas and Blanford, 2003). Through changes in temperatures in greenhouses, it could thus be possible to manipulate the efficiency of endosymbiotic microorganisms to change the outcome of plant-pest-parasitoid-hyperparasitoid interactions. This option would however impact plant production and development of other pests such as fungi.

5. Conclusion

It is now clear that the study of binary pest-parasitoid interactions is not sufficient to assess the impacts of global-change on biological pest control, and that multitrophic interactions from the host-plant to the hyperparasitoid (Dicke and Baldwin, 2010; Duffy et al., 2007; Harvey, 2015; Pincebourde et al., 2016), as well as endosymbiotic interactions (McLean et al., 2016; Ye et al., 2018) should be considered. Predicting interaction shifts within food-webs and their ecological consequences in a changing world is currently one of the greatest challenges in community ecology (Chevin et al., 2010; Gilman et al., 2010). Hyperparasitoids may positively respond to global-change through increasing population growth and activity rates, but whether this will negatively or positively affect biological pest control is still unknown. While their potential detrimental effects on primary parasitoids must be evaluated and limited as part of biological control programs, we also need to account for their potential positive influence on food-web stabilization through top-down effects (stabilization of host-parasitoids interactions).

Realistically, hyperparasitoids cannot be removed from food-webs, aside from food-webs maintained in greenhouses and other highly controlled systems. Some of the control methods exposed in the last section of our manuscript are promising, but remain limited because their application will depend on both the crop system (greenhouses, fields, orchards, forests, etc.) and local biotic and abiotic constraints. In order to reduce the negative effect of hyperparasitoids in the future and to better adopt pest management decisions, more empirical studies are required on the ecology of hyperparasitoids in different environmental contexts. In particular, research priorities should be given to: (i) improving knowledge on hyperparasitoid ecophysiology, including determining their current thermal tolerance ranges and seasonal strategies under diverse environmental conditions; (ii) determining the extent to which hyperparasitoids' physiology and behaviour are liable to plastic or evolutionary adjustments in the face of climate-change; and (iii) focusing on plant-host-parasitoid-hyperparasitoid community assembly rules, species interactions and food-web functioning in various systems.

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References

Acheampong, S., Gillespie, D.R., Quiring, D., 2012. Survey of parasitoids and hyperparasitoids (Hymenoptera) of the green peach aphid, Myzus persicae and the foxglove aphid, Aulacorthum solani (Hemiptera: Aphididae) in British Columbia. Journal of the Entomological Society of British Columbia 109, 12–22.

Aguilar-Fenollosa, E., Jacas, J.A., 2014. Can we forecast the effects of climate change on entomophagous biological control agents? Pest management science 70, 853–859.

Alford, L., Tougeron, K., Pierre, J.-S., Burel, F., Van Baaren, J., 2017. The effect of landscape complexity and microclimate on the thermal tolerance of a pest insect. Insect Science.

Andrade, T.O., Krespi, L., Bonnardot, V., van Baaren, J., Outreman, Y., 2016. Impact of change in winter strategy of one parasitoid species on the diversity and function of a guild of parasitoids. Oecologia 180, 877–888. https://doi.org/10.1007/s00442-015-3502-4

Andrew, N.R., Hill, S.J., 2017. Effect of Climate Change on Insect Pest Management, in: Environmental Pest Management: Challenges for Agronomists, Ecologists, Economists and Policymakers. p. 197.

Araj, S.A., Wratten, S.D., Lister, A.J., Buckley, H.L., 2006. Floral nectar affects longevity of the aphid parasitoid Aphidius ervi and its hyperparasitoid Dendrocerus aphidum. New Zealand Plant Protection 59, 178.

Araj, S.-E., Wratten, S., Lister, A., Buckley, H., 2009. Adding floral nectar resources to improve biological control: Potential pitfalls of the fourth trophic level. Basic and Applied Ecology 10, 554–562. https://doi.org/10.1016/j.baae.2008.12.001

Bale, J.S., Hayward, S.A.L., 2010. Insect overwintering in a changing climate. Journal of Experimental Biology 213, 980–994. https://doi.org/10.1242/jeb.037911

Beddington, J.R., Hammond, P.S., 1977. On the Dynamics of Host-Parasite-Hyperparasite Interactions. The Journal of Animal Ecology 46, 811. https://doi.org/10.2307/3642

Bernal, J.S., Luck, R.F., Morse, J.G., Drury, M.S., 2001. Seasonal and Scale Size Relationships between Citricola Scale (Homoptera: Coccidae) and Its Parasitoid Complex (Hymenoptera: Chalcidoidea) on San Joaquin Valley Citrus. Biological Control 20, 210–221. https://doi.org/10.1006/bcon.2000.0905

Björkman, C., Niemelä, P. (Eds.), 2015. Climate change and insect pests, CABI climate change series. CAB International, Wallingford, Oxfordshire.

Bloemhard, C., van der Wielen, M., Messelink, G., 2014. Seasonal abundance of aphid hyperparasitoids in organic greenhouse crops in The Netherlands. IOBC/WPRS Bull 102, 15–19.

Boivin, G., Brodeur, J., 2006. Intra- and Interspecific Interactions among Parasitoids: Mechanisms, Outcomes and Biological Control, in: Brodeur, J., Boivin, G. (Eds.), Trophic and Guild in Biological Interactions Control. Springer Netherlands, Dordrecht, pp. 123–144.

Brodeur, J., 2000. Host specificity and trophic relationships of hyperparasitoids, in: Parasitoid Population Biology. pp. 163–183.

Brodeur, J., McNeil, J.N., 1994. Life history of the aphid hyperparasitoid Asaphes vulgaris Walker (Pteromalidae): possible consequences on the efficacy of the primary parasitoid Aphidius nigripes Ashmead (Aphidiidae). The Canadian Entomologist 126, 1493–1497. https://doi.org/10.4039/Ent1261493-6

Brodeur, J., McNeil, J.N., 1989. Seasonal microhabitat selection by an endoparasitoid through adaptive modification of host behaviour. Science 244, 226–228.

Buitenhuis, R., Harvey, J.A., Vet, L.E.M., Boivin, G., Brodeur, J., 2017. Comparing and contrasting life history variation in four aphid hyperparasitoids. Ecological Entomology. https://doi.org/10.1111/een.12390

Buitenhuis, R., Vet, L.E.M., Boivin, G., Brodeur, J., 2005. Foraging behaviour at the fourth trophic level: a comparative study of host location in aphid hyperparasitoids. Entomologia Experimentalis et Applicata 114, 107–117. https://doi.org/10.1111/j.1570-7458.2005.00234.x

Cayetano, L., Vorburger, C., 2013. Effects of Heat Shock on Resistance to Parasitoids and on Life History Traits in an Aphid/Endosymbiont System. PLoS ONE 8, e75966. https://doi.org/10.1371/journal.pone.0075966

Chevin, L.-M., Lande, R., Mace, G.M., 2010. Adaptation, Plasticity, and Extinction in a Changing Environment: Towards a Predictive Theory. PLoS Biology 8, e1000357. https://doi.org/10.1371/journal.pbio.1000357

Cook, S.M., Khan, Z.R., Pickett, J.A., 2007. The Use of Push-Pull Strategies in Integrated Pest Management. Annual Review of Entomology 52, 375–400. https://doi.org/10.1146/annurev.ento.52.110405.091407

Damien, M., Le Lann, C., Desneux, N., Alford, L., Al Hassan, D., Georges, R., van Baaren, J., 2017. Flowering crops in winter increases pest control but not trophic link diversity. Agriculture, Ecosystems & Environment 247.

Dicke, M., Baldwin, I.T., 2010. The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help.' Trends in Plant Science 15, 167–175. https://doi.org/10.1016/j.tplants.2009.12.002

Dion, E., Polin, S.E., Simon, J.-C., Outreman, Y., 2011. Symbiont infection affects aphid defensive behaviours. Biology Letters 7, 743–746. https://doi.org/10.1098/rsbl.2011.0249

Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thébault, E., Loreau, M., 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecology Letters 10, 522–538. https://doi.org/10.1111/j.1461-0248.2007.01037.x

Dunbar, H.E., Wilson, A.C., Ferguson, N.R., Moran, N.A., 2007. Aphid thermal tolerance is governed by a point mutation in bacterial symbionts. PLoS Biol 5, e96.

Facey, S.L., Ellsworth, D.S., Staley, J.T., Wright, D.J., Johnson, S.N., 2014. Upsetting the order: how climate and atmospheric change affects herbivore–enemy interactions. Current Opinion in Insect Science 5, 66–74. https://doi.org/10.1016/j.cois.2014.09.015

Ferris, R., Wilson, R.S., 2012. The physiological arms race: Exploring thermal acclimation among interacting species. Journal of Thermal Biology 37, 236–242. https://doi.org/10.1016/j.jtherbio.2012.01.006

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global Consequences of Land Use. Science 309, 570. https://doi.org/10.1126/science.1111772

Forrest, J.R.K., 2016. Complex responses of insect phenology to climate change. Current Opinion in Insect Science. https://doi.org/10.1016/j.cois.2016.07.002

Frago, E., 2016. Interactions between parasitoids and higher order natural enemies: intraguild predation and hyperparasitoids. Current Opinion in Insect Science 14, 81–86. https://doi.org/10.1016/j.cois.2016.02.005

Furlong, M.J., Zalucki, M.P., 2017. Climate change and biological control: the consequences of increasing temperatures on host–parasitoid interactions. Current Opinion in Insect Science. https://doi.org/10.1016/j.cois.2017.03.006

Gagic, V., Hänke, S., Thies, C., Scherber, C., Tomanović, Ž., Tscharntke, T., 2012. Agricultural intensification and cereal aphid–parasitoid–hyperparasitoid food webs: network complexity, temporal variability and parasitism rates. Oecologia 170, 1099–1109. https://doi.org/10.1007/s00442-012-2366-0

Gagic, V., Tscharntke, T., Dormann, C.F., Gruber, B., Wilstermann, A., Thies, C., 2011. Food web structure and biocontrol in a four-trophic level system across a landscape complexity gradient. Proceedings of the Royal Society B: Biological Sciences 278, 2946–2953. https://doi.org/10.1098/rspb.2010.2645

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. Trends in Ecology & Evolution 25, 325–331. https://doi.org/10.1016/j.tree.2010.03.002

Godfray, H.C.J., 1994. Parasitoids: behavioral and evolutionary ecology. Princeton University Press.

Goelen, T., Baets, D., Kos, M., Paulussen, C., Lenaerts, M., Rediers, H., Wäckers, F., Jacquemyn, H., Lievens, B., 2018. Gustatory response and longevity in Aphidius parasitoids and their hyperparasitoid Dendrocerus aphidum. Journal of Pest Science 1–10.

Goldson, S.L., Wratten, S.D., Ferguson, C.M., Gerard, P.J., Barratt, B.I.P., Hardwick, S., McNeill, M.R., Phillips, C.B., Popay, A.J., Tylianakis, J.M., Tomasetto, F., 2014. If and when successful classical biological control fails. Biological Control 72, 76–79. https://doi.org/10.1016/j.biocontrol.2014.02.012

Gómez-Marco, F., Tena, A., Jaques, J.A., García, A.U., 2016a. Early arrival of predators controls Aphis spiraecola colonies in citrus clementines. Journal of Pest Science 89, 69–79. https://doi.org/10.1007/s10340-015-0668-9

Gómez-Marco, F., Urbaneja, A., Jaques, J.A., Rugman-Jones, P.F., Stouthamer, R., Tena, A., 2015. Untangling the aphid-parasitoid food web in citrus: Can hyperparasitoids disrupt biological control? Biological Control 81, 111–121. https://doi.org/10.1016/j.biocontrol.2014.11.015

Gómez-Marco, F., Urbaneja, A., Tena, A., 2016b. A sown grass cover enriched with wild forb plants improves the biological control of aphids in citrus. Basic and Applied Ecology 17, 210–219. https://doi.org/10.1016/j.baae.2015.10.006

Grasswitz, T.R., 1998. Contact Kairomones Mediating the Foraging Behavior of the Aphid Hyperparasitoid Alloxysta victrix (Westwood) (Hymenoptera: Charipidae). Journal of Insect Behavior 11, 539–548. https://doi.org/10.1023/A:1022315413516

Guay, J.-F., Boudreault, S., Michaud, D., Cloutier, C., 2009. Impact of environmental stress on aphid clonal resistance to parasitoids: Role of Hamiltonella defensa bacterial symbiosis in association with a new facultative symbiont of the pea aphid. Journal of Insect Physiology 55, 919–926. https://doi.org/10.1016/j.jinsphys.2009.06.006

Hance, T., van Baaren, J., Vernon, P., Boivin, G., 2007. Impact of Extreme Temperatures on Parasitoids in a Climate Change Perspective. Annual Review of Entomology 52, 107–126. https://doi.org/10.1146/annurev.ento.52.110405.091333

Harvey, J.A., 2015. Conserving host–parasitoid interactions in a warming world. Current Opinion in Insect Science 12, 79–85. https://doi.org/10.1016/j.cois.2015.09.001

Harvey, J.A., Poelman, E.H., Tanaka, T., 2013. Intrinsic Inter- and Intraspecific Competition in Parasitoid Wasps. Annual Review of Entomology 58, 333–351. https://doi.org/10.1146/annurev-ento-120811-153622

Harvey, J.A., Wagenaar, R., Bezemer, T.M., 2009. Interactions to the fifth trophic level: secondary and tertiary parasitoid wasps show extraordinary efficiency in utilizing host resources. Journal of Animal Ecology 78, 686–692. https://doi.org/10.1111/j.1365-2656.2008.01516.x

Hassell, M.P., Waage, J.K., 1984. Host-Parasitoid Population Interactions. Annual Review of Entomology 29, 89–114.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T., Reich, P.B., 2015. Anthropogenic environmental changes affect ecosystem stability via biodiversity. Science 348, 336–340. https://doi.org/10.1126/science.aaa1788

Heimpel, G.E., Mills, N.J., 2017. Biological control: ecology and applications. Cambridge University Press.

Höller, C., 1991. Movement away from the feeding site in parasitized aphids: host suicide or an attempt by the parasitoid to escape hyperparasitism. Behaviour and impact of Aphidophaga 45–49.

Holler, C., Borgemeister, C., Haardt, H., Powell, W., 1993. The Relationship between Primary Parasitoids and Hyperparasitoids of Cereal Aphids: An Analysis of Field Data. The Journal of Animal Ecology 62, 12. https://doi.org/10.2307/5478

Höller, C., Micha, S.G., Schulz, S., Francke, W., Pickett, J.A., 1994. Enemy-induced dispersal in a parasitic wasp. Cellular and Molecular Life Sciences 50, 182–185.

Holt, R.D., Hochberg, M.E., 1998. The Coexistence of Competing Parasites. Part II—Hyperparasitism and Food Chain Dynamics. Journal of Theoretical Biology 193, 485–495. https://doi.org/10.1006/jtbi.1998.0717

Holt, R.D., Lawton, J.H., Polis, G.A., Martinez, N.D., 1999. Trophic rank and the species–area relationship. Ecology 80, 1495–1504.

Hougardy, E., Mills, N.J., 2008. Comparative life history and parasitism of a new colour morph of the walnut aphid in California. Agricultural and Forest Entomology 10, 137–146.

Hübner, G., Völkl, W., 1996. Behavioral strategies of aphid hyperparasitoids to escape aggression by honeydew-collecting ants. Journal of Insect Behavior 9, 143–157.

Hunter, M.S., Woolley, J.B., 2001. Evolution and behavioral ecology of heteronomous aphelinid parasitoids. Annual review of entomology 46, 251–290.

Jervis, M.A., 2007. Insects as natural enemies: a practical perspective. Springer Science & Business Media.

Karl, T.R., Trenberth, K.E., 2003. Modern Global Climate Change. Science 302, 1719–1723. https://doi.org/10.1126/science.1090228

Klapwijk, M.J., Ayres, M.P., Battisti, A., Larsson, S., 2012. Assessing the impact of climate change on outbreak potential. Insect outbreaks revisited 429–450.

Krespi, L., Dedryver, C.-A., Creach, V., Rabasse, J.-M., Le Ralec, A., Nenon, J.-P., 1997. Variability in the development of cereal aphid parasitoids and hyperparasitoids in oceanic regions as a response to climate and abundance of hosts. Population Ecology 26, 545–551.

Lalonde, R.G., 2004. Some dynamical consequences of parasitoid diapause. Oikos 107, 338–344.

Langer, A., Stilmant, D., Verbois, D., Hance, T., 1997. Seasonal activity and distribution of cereal aphid parasitoids in Belgium. Entomophaga 42, 185–191.

Lohaus, K., Vidal, S., Thies, C., 2013. Farming practices change food web structures in cereal aphid–parasitoid–hyperparasitoid communities. Oecologia 171, 249–259. https://doi.org/10.1007/s00442-012-2387-8

Lumbierres, B., Starý, P., Pons, X., 2007. Seasonal parasitism of cereal aphids in a Mediterranean arable crop system. Journal of Pest Science 80, 125–130. https://doi.org/10.1007/s10340-006-0159-0

Mbava, W., Mugisha, J.Y.T., Gonsalves, J.W., 2017. Prey, predator and super-predator model with disease in the super-predator. Applied Mathematics and Computation 297, 92–114. https://doi.org/10.1016/j.amc.2016.10.034

Mclean, A.H.C., HrčEk, J., Parker, B.J., Godfray, H.C.J., 2017. Cascading effects of herbivore protective symbionts on hyperparasitoids: Symbionts and hyperparasitoids. Ecological Entomology 42, 601–609. https://doi.org/10.1111/een.12424

McLean, A.H.C., Parker, B.J., Hrček, J., Henry, L.M., Godfray, H.C.J., 2016. Insect symbionts in food webs. Philosophical Transactions of the Royal Society B: Biological Sciences 371, 20150325. https://doi.org/10.1098/rstb.2015.0325

Miall, J.H., Abram, P.K., Cappuccino, N., Mason, P.G., 2014. Potential impact of the native hyperparasitoid *Conura albifrons* (Hymenoptera: Chalcididae) on the exotic biological control agent *Diadromus pulchellus* (Hymenoptera: Ichneumonidae). Biocontrol Science and Technology 24, 611–624. https://doi.org/10.1080/09583157.2014.883361

Montoya, J.M., Raffaelli, D., 2010. Climate change, biotic interactions and ecosystem services. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 2013–2018. https://doi.org/10.1098/rstb.2010.0114

Müller, C.B., Godfray, H.C.J., 1999. Indirect interactions in aphid–parasitoid communities. Researches on Population Ecology 41, 93–106.

Nagasaka, K., Takahasi, N., Okabayashi, T., 2010. Impact of secondary parasitism on Aphidius colemani in the banker plant system on aphid control in commercial greenhouses in Kochi, Japan. Applied Entomology and Zoology 45, 541–550.

Neuville, S., Le Ralec, A., Outreman, Y., Jaloux, B., 2015. The delay in arrival of the parasitoid Diaeretiella rapae influences the efficiency of cabbage aphid biological control. BioControl. https://doi.org/10.1007/s10526-015-9702-3

Oliver, K.M., Martinez, A.J., 2014. How resident microbes modulate ecologically-important traits of insects. Current Opinion in Insect Science 4, 1–7. https://doi.org/10.1016/j.cois.2014.08.001

Oliver, K.M., Smith, A.H., Russell, J.A., 2014. Defensive symbiosis in the real world - advancing ecological studies of heritable, protective bacteria in aphids and beyond. Functional Ecology 28, 341–355. https://doi.org/10.1111/1365-2435.12133

Oliver, T.H., Morecroft, M.D., 2014. Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities: Interactions between climate change and land use change. Wiley Interdisciplinary Reviews: Climate Change 5, 317–335. https://doi.org/10.1002/wcc.271

Ortiz-Martínez, S.A., Lavandero, B., 2018. The effect of landscape context on the biological control of Sitobion avenae: temporal partitioning response of natural enemy guilds. Journal of Pest Science 91, 41–53. https://doi.org/10.1007/s10340-017-0855-y

Pérez-Lachaud, G., Batchelor, T.P., Hardy, I.C.W., 2004. Wasp eat wasp: facultative hyperparasitism and intra-guild predation by bethylid wasps. Biological Control 30, 149–155. https://doi.org/10.1016/j.biocontrol.2004.03.003

Pérez-Lachaud, G., Hardy, I.C.., Lachaud, J.-P., 2002. Insect gladiators: competitive interactions between three species of bethylid wasps attacking the coffee berry borer, Hypothenemus hampei (Coleoptera: Scolytidae). Biological Control 25, 231–238. https://doi.org/10.1016/S1049-9644(02)00103-2

Petersen, G., Matthiesen, C., Francke, W., Wyss, U., 2000. Hyperparasitoid volatiles as possible foraging behaviour determinants in the aphid parasitoid Aphidius uzbekistanicus (Hymenoptera: Aphidiidae). European Journal of Entomology 97, 545–550.

Pincebourde, S., van Baaren, J., Rasmann, S., Rasmont, P., Rodet, G., Martinet, B., Calatayud, P.-A., 2016. Plant–Insect Interactions in a Changing World, in: Advances in Botanical Research. Academic Press.

Plećaš, M., Gagić, V., Janković, M., Petrović-Obradović, O., Kavallieratos, N.G., Tomanović, ž., Thies, C., Tscharntke, T., Ćetković, A., 2014. Landscape composition and configuration influence cereal aphid–parasitoid–hyperparasitoid interactions and biological control differentially across years. Agriculture, Ecosystems & Environment 183, 1–10. https://doi.org/10.1016/j.agee.2013.10.016

Poelman, E.H., Bruinsma, M., Zhu, F., Weldegergis, B.T., Boursault, A.E., Jongema, Y., van Loon, J.J.A., Vet, L.E.M., Harvey, J.A., Dicke, M., 2012. Hyperparasitoids Use Herbivore-Induced Plant Volatiles to Locate Their Parasitoid Host. PLoS Biology 10, e1001435. https://doi.org/10.1371/journal.pbio.1001435

Poelman, E.H., Kos, M., 2016. Complexity of Plant Volatile-Mediated Interactions Beyond the Third Trophic Level, in: Deciphering Chemical Language of Plant Communication. Springer, pp. 211–225.

Prado, S.G., Jandricic, S.E., Frank, S.D., 2015. Ecological Interactions Affecting the Efficacy of Aphidius colemani in Greenhouse Crops. Insects 6, 538–575. https://doi.org/10.3390/insects6020538

Rabasse, J., Dedryver, C., 1982. Overwintering of primary parasites and hyperparasites of cereal aphids in western France. In Aphid antagonists. Proceedings of a meeting of the EC Experts' Group, Portici, Italy, 23-24 November 1982 (pp. 57-64). Presented at the Aphid antagonists. Proceedings of a meeting of the EC Experts' Group, Portici, Italy, 23-24 November 1982, AA Balkema, pp. 57–64.

Rand, T.A., van Veen, F.J.F., Tscharntke, T., 2012. Landscape complexity differentially benefits generalized fourth, over specialized third, trophic level natural enemies. Ecography 35, 97–104. https://doi.org/10.1111/j.1600-0587.2011.07016.x

Rice, A.D., Allen, G.R., 2009. Temperature and developmental interactions in a multitrophic parasitoid guild. Australian Journal of Entomology 48, 282–286. https://doi.org/10.1111/j.1440-6055.2009.00717.x

Rosenheim, J.A., 1998. Higher-order predators and the regulation of insect herbivore populations. Annual review of entomology 43, 421–447.

Rosenheim, J.A., Kaya, H.K., Lester, E.E., Marois, J.J., Jaffee, B.A., 1995. Intraguild predation among biological-control agents: theory and evidence. Biological Control 5, 303–335.

Rothacher, L., Ferrer-Suay, M., Vorburger, C., 2016. Bacterial endosymbionts protect aphids in the field and alter parasitoid community composition. Ecology 97, 1712–1723. https://doi.org/10.1890/15-2022.1

Sanders, D., Moser, A., Newton, J., van Veen, F.J.F., 2016. Trophic assimilation efficiency markedly increases at higher trophic levels in four-level host–parasitoid food chain. Proceedings of the Royal Society B: Biological Sciences 283, 20153043. https://doi.org/10.1098/rspb.2015.3043

Sawyer, R.C., 2002. To make a spotless orange: Biological control in California. Purdue University Press.

Schooler, S.S., De Barro, P., Ives, A.R., 2011. The potential for hyperparasitism to compromise biological control: Why don't hyperparasitoids drive their primary parasitoid hosts extinct? Biological Control 58, 167–173. https://doi.org/10.1016/j.biocontrol.2011.05.018

Sgrò, C.M., Terblanche, J.S., Hoffmann, A.A., 2016. What Can Plasticity Contribute to Insect Responses to Climate Change? Annual Review of Entomology 61. https://doi.org/10.1146/annurev-ento-010715-023859

Snyder, W.E., Ives, A.R., 2008. Behavior influences whether intra-guild predation disrupts herbivore suppression by parasitoids. Behavioral ecology of insect parasitoids. Blackwell Pub, Malden, MA, USA 71–91.

Somero, G.N., 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine "winners" and "losers." Journal of Experimental Biology 213, 912–920. https://doi.org/10.1242/jeb.037473

Sullivan, D.J., 1987. Insect hyperparasitism. Annual review of entomology 32, 49–70.

Sullivan, D.J., Völkl, W., 1999. Hyperparasitism: multitrophic ecology and behavior. Annual review of entomology 44, 291–315.

Tada, A., Kikuchi, Y., Hosokawa, T., Musolin, D.L., Fujisaki, K., Fukatsu, T., 2011. Obligate association with gut bacterial symbiont in Japanese populations of the southern green stinkbug Nezara viridula (Heteroptera: Pentatomidae). Applied Entomology and Zoology 46, 483–488. https://doi.org/10.1007/s13355-011-0066-6

Tena, A., Soto, A., Garcia-Marí, F., 2008. Parasitoid complex of black scale Saissetia oleae on citrus and olives: parasitoid species composition and seasonal trend. BioControl 53, 473–487. https://doi.org/10.1007/s10526-007-9084-2

Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S., Helaouet, P., Johns, D.G., Jones, I.D., Leech, D.I., Mackay, E.B., Massimino, D., Atkinson, S., Bacon, P.J., Brereton, T.M., Carvalho, L., Clutton-Brock, T.H., Duck, C., Edwards, M., Elliott, J.M., Hall, S.J.G., Harrington, R., Pearce-Higgins, J.W., Høye, T.T., Kruuk, L.E.B., Pemberton, J.M., Sparks, T.H., Thompson, P.M., White, I., Winfield, I.J., Wanless, S., 2016. Phenological sensitivity to climate across taxa and trophic levels. Nature. https://doi.org/10.1038/nature18608

Thomas, M.B., Blanford, S., 2003. Thermal biology in insect-parasite interactions. Trends in Ecology & Evolution 18, 344–350. https://doi.org/10.1016/S0169-5347(03)00069-7

Thompson, R.M., Beardall, J., Beringer, J., Grace, M., Sardina, P., 2013. Means and extremes: building variability into community-level climate change experiments. Ecology Letters 16, 799–806. https://doi.org/10.1111/ele.12095

Thomson, L.J., Macfadyen, S., Hoffmann, A.A., 2010. Predicting the effects of climate change on natural enemies of agricultural pests. Biological Control 52, 296–306. https://doi.org/10.1016/j.biocontrol.2009.01.022

Tilman, D., 1999. Global environmental impacts of agricultural expansion: the need for sustainable and efficient practices. Proceedings of the National Academy of Sciences 96, 5995–6000.

Tougeron, K., 2017. Diapause variability in aphid parasitoids in the context of climate changes; implications for biological control. Université de Rennes 1 & Université de Montréal.

Tougeron, K., Le Lann, C., Brodeur, J., van Baaren, J., 2017. Are aphid parasitoids from mild winter climates losing their winter diapause? Oecologia 183, 619–629. https://doi.org/10.1007/s00442-016-3770-7

Tougeron, K., van Baaren, J., Burel, F., Alford, L., 2016. Comparing thermal tolerance across contrasting landscapes: first steps towards understanding how landscape management could modify ectotherm thermal tolerance. Insect Conservation and Diversity 9, 171–180. https://doi.org/10.1111/icad.12153

Traugott, M., Bell, J.R., Broad, G.R., Powell, W., Van Veen, F.J.F., Vollhardt, I.M.G., Symondson, W.O.C., 2008. Endoparasitism in cereal aphids: molecular analysis of a whole parasitoid community. Molecular Ecology 17, 3928–3938. https://doi.org/10.1111/j.1365-294X.2008.03878.x

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. Ecology letters 8, 857–874.

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11, 1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

van Baaren, J., Le Lann, C., JM van Alphen, J., 2010. Consequences of Climate Change for Aphid-Based Multi-trophic Systems, in: Kindlmann, P., Dixon, A.F.G., Michaud, J.P. (Eds.), Aphid Biodiversity under Environmental Change. Springer Netherlands, Dordrecht, pp. 55–68.

Van der Putten, W.H., 2012. Climate Change, Aboveground-Belowground Interactions, and Species' Range Shifts. Annual Review of Ecology, Evolution, and Systematics 43, 365–383. https://doi.org/10.1146/annurev-ecolsys-110411-160423

van der Putten, W.H., Macel, M., Visser, M.E., 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philosophical Transactions of the Royal Society B: Biological Sciences 365, 2025–2034. https://doi.org/10.1098/rstb.2010.0037

van Lenteren, J.C., 2012. The state of commercial augmentative biological control: plenty of natural enemies, but a frustrating lack of uptake. BioControl 57, 1–20. https://doi.org/10.1007/s10526-011-9395-1

Van Lenteren, J.C., Babendreier, D., Bigler, F., Burgio, G., Hokkanen, H.M.T., Kuske, S., Loomans, A.J.M., Menzler-Hokkanen, I., Van Rijn, P.C.J., Thomas, M.B., others, 2003. Environmental risk assessment of exotic natural enemies used in inundative biological control. BioControl 48, 3–38.

van Lenteren, J.C., Bolckmans, K., Köhl, J., Ravensberg, W.J., Urbaneja, A., 2018. Biological control using invertebrates and microorganisms: plenty of new opportunities. BioControl 63, 39–59. https://doi.org/10.1007/s10526-017-9801-4

Van Nouhuys, S., Hanski, I., 2000. Apparent competition between parasitoids mediated by a shared hyperparasitoid. Ecology Letters 3, 82–84.

van Nouhuys, S., Kohonen, M., Duplouy, A., 2016. Wolbachia increases the susceptibility of a parasitoid wasp to hyperparasitism. The Journal of Experimental Biology 219, 2984–2990. https://doi.org/10.1242/jeb.140699

van Steenis, M., 1995. Evaluation of four aphidiine parasitoids for biological control of Aphis gossypii. Entomologia Experimentalis et Applicata 75, 151–157.

Visser, M.E., 2016. Phenology: Interactions of climate change and species. Nature. https://doi.org/10.1038/nature18905

Völkl, W., 1992. Aphids or their parasitoids: who actually benefits from ant-attendance? Journal of Animal ecology 273–281.

Wäckers, F., 2001. A comparison of nectar-and honeydew sugars with respect to their utilization by the hymenopteran parasitoid Cotesia glomerata. Journal of Insect Physiology 47, 1077–1084.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.

Ye, Z., Vollhardt, I.M.G., Parth, N., Rubbmark, O., Traugott, M., 2018. Facultative bacterial endosymbionts shape parasitoid food webs in natural host populations: A correlative analysis. Journal of Animal Ecology 87, 1440–1451. https://doi.org/10.1111/1365-2656.12875

Zhao, Z.-H., Hui, C., Ouyang, F., Liu, J.-H., Guan, X.-Q., He, D.-H., Ge, F., 2013. Effects of inter-annual landscape change on interactions between cereal aphids and their natural enemies. Basic and Applied Ecology 14, 472–479. https://doi.org/10.1016/j.baae.2013.06.002