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SPECIAL ISSUE: 6TH INTERNATIONAL ENTOMOPHAGOUS INSECTS CONFERENCE

Biological control of invasive stink bugs: review of global state and future prospects

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Abstract

Invasive stink bugs (Hemiptera: Pentatomidae) are responsible for high economic losses to agriculture on a global scale. The most important species, dating from recent to old invasions, include *Bagrada hilaris* (Burmeister), *Halyomorpha halys* (Stål), *Piezodorus guildinii* (Westwood), *Nezara viridula* (L.), and *Murgantia histrionica* (Hahn). *Bagrada hilaris*, *H. halys*, and *N. viridula* are now almost globally distributed. Biological control of these pests faces a complex set of challenges that must be addressed to maintain pest populations below the economic injury level. Several case studies of classical and conservation biological control of invasive stink bugs are reported here. The most common parasitoids in their geographical area of origin are egg parasitoids (Hymenoptera: Scelionidae, Encyrtidae, and Eupelmidae). Additionally, native parasitoids of adult stink bugs (Diptera: Tachinidae) have in some cases adapted to the novel hosts in the invaded area and native predators are known to prey on the various instars. Improving the efficacy of biocontrol agents is possible through conservation biological control techniques and exploitation of their chemical ecology. Moreover, integration of biological control with other techniques, such as behavioural manipulation of adult stink bugs and plant resistance, may be a sustainable pest control method within organic farming and integrated pest management programs. However, additional field studies are needed to verify the efficacy of these novel methods and transfer them from research to application.

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Introduction

Invasive insect herbivores are responsible for an annual loss of at least 70 billion USD globally (Bradshaw et al., 2016), with the biggest agricultural producers, USA and China, experiencing the highest costs and also representing the main potential sources of invasive pests (Paini et al., 2016). The economic loss caused by invasive insects is growing, mostly due to market globalization and climate change (Bradshaw et al., 2016). Herbivorous stink bugs (Hemiptera: Pentatomidae) serve as a good example of this, as many species are agricultural pests in their native range as well as serious invasive pests with high economic impact (Panizzi et al., 2000; McPherson, 2018). Stink bug damage is due to the feeding punctures of adults and nymphs on plant tissues, especially those of fruits and seeds and sometimes leaves and stems, resulting in large reductions in crop yield and/or quality (Panizzi et al., 2000; McPherson, 2018). Additionally, several species transmit plant pathogens (Mitchell et al., 2018).

At least two polyphagous pentatomid species, the brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hamilton et al., 2018), and the southern green stink bug, *Nezara viridula* (L.) (Esquivel et al., 2018), are globally important pests. *Halyomorpha halys* is a temperate/subtropical species native to eastern Asia that has established in North America and Europe, where it damages many crops (reviewed by Leskey & Nielsen, 2018), has recently established in Chile (Faúndez & Rider, 2017), and has regularly been intercepted at New Zealand's border in recent years (Avila & Charles, 2018; Charles et al., 2019). Unlike *H. halys*, the native geographical range of *N. viridula* (Africa, southwest Asia, or Mediterranean region) is not yet clearly defined, but this species has spread into tropical, subtropical, and warm-temperate zones of five continents and might expand further (Panizzi & Slansky, 1985; Todd, 1989; Panizzi & Lucini, 2016; Esquivel et al., 2018).

The most recent widespread invasive pentatomid species, the painted bug or Bagrada bug, *Bagrada hilaris* (Burmeister), which has African and Asian origins, now has an almost worldwide distribution and has recently become a serious concern on brassicaceous crops in the USA (Bundy et al., 2018b). To date, two additional stink bugs, *Murgantia histrionica* (Hahn) and *Piezodorus guildinii* (Westwood), are less widely distributed than *B. hilaris*, having expanded their ranges only within the American continent. Historically, *M. histrionica*, native to Central America and Mexico, could be considered the first recorded invasive stink bug, having invaded the southern part of the USA during the 19th century where it is still causing economic losses on brassicaceous crops (McPherson et al., 2018). *Piezodorus guildinii*, originally described from the Caribbean, is now a major pest of soybean and other Fabaceae in many parts of the American continent (Bundy et al., 2018a).

Stink bug expansion into new areas, especially when transported over long distances by global trade and tourism, can often be attributed to the overwintering behaviour of adults (Panizzi et al., 2000; Musolin et al., 2018). In autumn, several species aggregate in buildings and other artificial shelters to hibernate. Overwintering *H. halys* adults have been transported while hidden inside many types of material (Maistrello et al., 2018; Nixon et al., 2019). This has affected international trade due to the mandatory phytosanitary importation measures required by some countries (e.g., New Zealand and Australia). These regulations impose treatments on any type of commodities imported from countries where *H. halys* is confirmed as present (MPI, 2020).

Following the introduction of exotic species into new areas, native natural enemies sometimes adapt to the non-coevolved species. Fortuitous biological control of invasive stink bugs by native parasitoids and predators has been observed, but in most cases, native parasitoids are not considered effective for biological control, especially when compared with coevolved species from the native area (McPherson, 2018). Because of a lack of effective natural enemies, combined with stink bug biology, locally favourable ecological conditions, and their capacity to cause direct damage to marketable produce, the impact of stink bugs in invaded agroecosystems is often significant, both in terms of crop loss and by disrupting established integrated pest management (IPM) practices (Panizzi et al., 2000; McPherson, 2018). It is therefore vital to develop new sustainable control methods that can be included within revised IPM strategies. In this paper, we review a century of biological control programs for invasive stink bugs and discuss the global biocontrol strategies developed against them through six case studies. These strategies include classical, augmentative, and conservation biological control, as well as an innovative pre-emptive classical biocontrol approach. Additionally, based on knowledge of stink bug and parasitoid behaviour, biology, and chemical ecology, we discuss the prospects of using semiochemical and other novel approaches to increase natural enemy efficacy and manage stink bug pests as part of sustainable, integrated control strategies.

Management of invasive stink bugs over a century of classical biological control

Recent stink bug invasions have renewed the interest in classical biological control as a potential pest control strategy. Evaluation of suitable candidates for classical

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biological control of *B. hilaris* is underway in North America, with research focusing on egg parasitoids, as the tachinid parasitoids of adult stink bugs (Diptera: Tachinidae) that have been recorded in Asia are poorly known and do not seem to have a significant impact on this host (Sforza et al., 2017; Bundy et al., 2018b). Similarly, the most important natural enemies of *H. halys* appear to be coevolved egg parasitoids in the native range of Eastern Asia (Zhang et al., 2017; Buffington et al., 2018; Hamilton et al., 2018; Leskey & Nielsen, 2018). The egg parasitoid *Trissolcus japonicus* (Ashmead) [Hymenoptera: Scelionidae (syn. Platygastridae s.l.; Sharkey, 2007, but see Popovici et al., 2017)] is the predominant natural enemy of *H. halys* in Asia and is therefore considered a promising biocontrol agent for this invasive pest (Zhang et al., 2017; Buffington et al., 2018; Leskey & Nielsen, 2018). However, environmental risk assessment of *T. japonicus* as candidate biocontrol agent, conducted in the USA and in Europe, raised ecological concerns due to the apparent low host specificity of *T. japonicus* and consequent risk that this species might attack non-target species in the areas of introduction, including beneficial predatory stink bugs (Hedstrom et al., 2017; Botch & Delfosse, 2018; Haye et al., 2020). Legislative restrictions in Europe and the USA severely limit the introduction of exotic species by focusing on perceived risks for non-targets rather than the benefits of pest reduction (van Lenteren et al., 2006; Rondoni et al., 2020). Now that the occurrence of *T. japonicus* has been reported in northern Italy (Sabbatini Peverieri et al., 2018), in early 2020 the Italian government authorized the mass production and release of this parasitoid in Italy, where *H. halys* has caused the highest economic losses in Europe since its arrival in 2012 (Maistrello et al., 2016, 2018). This is the first officially authorized release of the parasitoid against *H. halys* in Europe. As has occurred in Italy, constraints are probably becoming less relevant in the USA because of the recent finding of adventive populations of *T. japonicus* in the invaded areas (Talamas et al., 2015).

About 1 century ago, the first attempts with biological control of stink bugs started with *N. viridula* and they are still in progress globally. Classical biological control mostly involved the egg parasitoid *Trissolcus basalis* (Wollaston) (Hymenoptera: Scelionidae), which was introduced and released in nearly all geographical areas invaded by *N. viridula* (Esquivel et al., 2018). Additionally, the native parasitoids of adults, *Trichopoda pennipes* (Fabricius) and *Trichopoda giacomellii* (Blanchard) (Diptera: Tachinidae), were found parasitizing this species in North and South America, respectively, and were subsequently introduced into Hawaii (USA) and Australia for classical biological control of *N. viridula* (Liljesthröm & Rabinovich, 2004; Esquivel et al., 2018). *Trichopoda pennipes*, which attacks adults and occasionally nymphs, was then accidentally introduced in Italy (Colazza et al., 1996) from where it spread to several countries in Europe and the Mediterranean (Tschorsnig, 2017). Despite the numerous classical biocontrol programs against *N. viridula*, this species is still an economically important pest worldwide except in South America (Panizzi & Lucini, 2016).

In contrast with other invasive stink bugs, no biocontrol efforts have been made against *M. histrionica* in the USA. However, several native natural enemies – the most common ones the parasitoids *Trissolcus brochymenae* (Ashmead), *Trissolcus euschisti* (Ashmead) (Hymenoptera: Scelionidae), and *Ooencyrtus johnsoni* (Howard) (Hymenoptera: Encyrtidae) – have been recorded since the end of the 19th century but generally with low reported efficacy (McPherson et al., 2018).

Overall, naturally occurring and classical biological control of stink bugs, although useful in significantly reducing the exotic pest populations, are often inadequate in maintaining the pest below the economic injury level (McPherson, 2018). Therefore, additional approaches are being evaluated and developed regularly to improve the efficacy of parasitoids as biocontrol agents and to integrate biocontrol programs with other sustainable management methods, targeting adult stink bugs. In the following sections, we report relevant case studies and discuss the potential application of conservation biological control and other sustainable control methods (Figure 1).

Case study 1: Selection of candidates for classical biological control of *Bagrada hilaris*

History, invasion, and pest status

The painted or Bagrada bug, *B. hilaris*, is a worldwide pest of brassicaceous crops (Bundy et al., 2018b). Like other stink bugs, it can also be a nuisance pest for humans by sheltering in homes (Faúndez, 2018). *Bagrada hilaris* is native to Africa, the Middle East, and Asia where it sporadically damages local crops (Gunn, 1918; Ahuja et al., 2008). Since its first introduction in California (USA) in 2008, it has become invasive in southern states of the USA (Reed et al., 2013) and in Hawaii (USA), Mexico, and Chile (Faúndez et al., 2016). In the Mediterranean basin, *B. hilaris* was accidentally introduced into Italy and Malta. Pinpointing the origin of invasive populations in the Americas will enable an understanding of the invasion routes of *B. hilaris* and ultimately help to find the parasitoid best suited to control this pest. A preliminary phylogeographical study using the DNA barcode region COI identified Pakistan as a source for the invasive *B. hilaris* in North America (Sforza et al., 2017).

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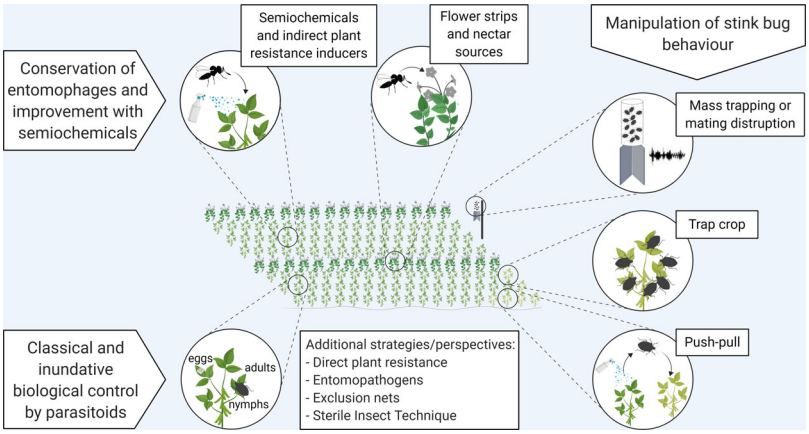


Figure 1 Possible strategies for successful stink bug management based on the integration of biological control (classical, inundative, or conservation) with manipulation of the natural enemy and/or herbivore behaviour, or with additional strategies.

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This pest is multivoltine with gregarious behaviour (Reed et al., 2013; Bundy et al., 2018b). Unlike most of the 4 722 species of Pentatomidae (Rider, 2016) that glue eggs together in clusters onto plant material, *B. hilaris* deposits many of its eggs singly into the soil (Gunn, 1918; Taylor et al., 2014), which may affect egg parasitism (see below). Due to the economic impact of *B. hilaris* injury on crops in southwestern USA, its control currently relies on pesticide applications (Palumbo et al., 2016). Classical biological control could provide sustainable and long-term control, especially if implemented as part of an IPM program. To date, no classical biocontrol program is in place in any of the countries in the invaded range. However, the egg parasitoids *Gryon myrmecophilum* (Ashmead), *Telenomus podisi* (Ashmead), and *Tr. basalis* (all Hymenoptera: Scelionidae) were found parasitizing *B. hilaris* in Mexico (Felipe-Victoriano et al., 2019), suggesting a possible role for them in conservation biological control.

Exploration for natural enemies in the native range

Surveys for natural enemies began in countries where *B. hilaris* is native, including South Africa and India. As for other invasive stink bugs (see below), predators and resident North American parasitoids have been reported (Bundy et al., 2018b). However, we present only data on egg parasitoids from the native geographical range of the pest. Gunn (1918) first recorded the presence of an egg parasitoid emerging from artificially buried eggs of *B. hilaris* in cabbage and cauliflower fields. Subsequently, egg parasitoids in the scelionid genera *Telenomus*, *Typhodytes* (Mani, 1942; Samuel, 1942), and *Trissolcus* (Chacko & Katiyar, 1961) were collected from India. After the invasion of *B. hilaris* in the Americas, surveys were conducted in 2015 in Pakistan. Three species were collected, viz., *Trissolcus hyalinipennis* Rajmohana & Narendran (syn. *Allophanurus indicus* Subba Rao & Chacko), *Gryon gonikopalense* Sharma (Scelionidae), and an *Ooencyrtus* sp. (Encyrtidae) (Mahmood et al., 2015). The latter was the first report of an *Ooencyrtus* species on *B. hilaris* eggs. These egg parasitoid candidates are currently under evaluation in the USA and European quarantine facilities. Since 2016, new surveys for *B. hilaris* biocontrol candidates have been conducted in Kenya and South Africa (Mason et al., 2018). Various collecting protocols, including sentinel eggs and Malaise trapping, are being used to study the native biodiversity of egg parasitoids of *B. hilaris* (RFH Sforza, M Kasina, P Addison, MC Bon & E Talamas, unpubl.).

Promising candidates

Among the parasitoid species collected in Pakistan in 2015, only two have been studied in the laboratory. The basic biological traits of *Tr. hyalinipennis* were described by Subba Rao & Chacko (1961). Their studies reported a very high fecundity level of 158 progeny per female and a longevity of over 1 month. Studies of *G. gonikopalense* at the USDA-ARS European Biological Control Laboratory (Montpellier, France) suggest this species is a promising biocontrol candidate (Martel et al., 2019). Both the host and parasitoid share the same thermal requirements for their development and reproduction, suggesting that their development will be synchronous in the field.

An important criterion for an effective candidate biocontrol agent is its foraging capacity for *B. hilaris* eggs buried in the soil, as was highlighted by Bundy et al. (2018b). Recent investigations under laboratory conditions have shown that *Tr. hyalinipennis* is unable to parasitize buried eggs, whereas *G. gonikopalense* readily finds and parasitizes *B. hilaris* eggs in the soil (G Martel & RFH Sforza, unpubl.). This information provides a basis for investigating whether *G. gonikopalense* effectively parasitizes *B. hilaris* eggs under natural conditions, especially considering that *B. hilaris* is able to oviposit both in the soil and on

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its host plant (Taylor et al., 2014). Another criterion is the host specificity of the selected egg parasitoids, which is currently under investigation in USA quarantine facilities for *B. hilaris* and several other stink bugs. If the above-mentioned criteria are met, the release of *G. gonikopalense* in North America can be considered. In the meantime, foreign exploration in Africa will continue to search for other coevolved parasitoids.

Case study 2: Biological control of *Halyomorpha halys* in North America

History, invasion, and pest status

The brown marmorated stink bug, *H. halys*, was first detected in the USA in the mid-1990s (Leskey & Nielsen, 2018) in Allentown, PA (Hoebeke & Carter, 2003), and has since spread to more than 42 states (Leskey & Nielsen, 2018). In Canada, it was first detected in Ontario and Quebec in 2010 (Fogain & Graff, 2011) and subsequently in British Columbia (Abram et al., 2017c). This species is a polyphagous pest with a host range of more than 300 plant species (Lee et al., 2013; Bergmann et al., 2016). In North America, this includes over 170 plants from more than a dozen families, and apples, peaches, nectarines, pears, grapes, sweet corn, soybeans, and hazelnuts are among the most susceptible cultivated hosts (Leskey & Nielsen, 2018).

Natural control by native parasitoids and predators

Early biological control research in North America focused on identifying the indigenous natural enemies of *H. halys*. These studies mainly concentrated on the egg stage, using sentinel (fresh and frozen) *H. halys* egg masses to assess predation and parasitism (Dieckhoff et al., 2017; Abram et al., 2017b; Leskey & Nielsen, 2018). In general, control by existing natural enemies has been considered ineffective (Ogburn et al., 2016; Cornelius et al., 2016a; Abram et al., 2017b). In agreement with the enemy release hypothesis (Keane & Crawley, 2002), *H. halys* seems to have escaped from its natural enemies in the invaded North American areas. For example, in organic agro-ecosystems across the eastern USA, maximum levels of natural biological control were estimated at 20%, primarily caused by chewing predators (Ogburn et al., 2016) whose efficacy is dependent on the *H. halys* life stage (Morrison et al., 2016; Pote & Nielsen, 2017). In the laboratory, late-instar *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae), katydids (Orthoptera: Tettigoniidae), earwigs (Dermaptera: Forficulidae), jumping spiders (Araneae: Salticidae), crickets (Orthoptera: Gryllidae), and ground beetles (Coleoptera: Scarabaeidae) were effective predators of *H. halys* eggs (Abram et al., 2015; Morrison et al., 2016). Grasshoppers (Orthoptera: Acrididae), *Coccinella septempunctata* (L.) (Coleoptera: Coccinellidae), and the spined soldier bug *Podisus maculiventris* (Say) (Pentatomidae) also preyed on eggs, whereas several hemipteran predators attacked young nymphs (Pote & Nielsen, 2017). Using surveillance cameras, Pote (2018) reported katydids feeding on *H. halys* eggs in the field. Possibly, indigenous generalist predators use pentatomid semiochemical cues to locate *H. halys* (Fraga et al., 2017).

Mortality from parasitism of *H. halys* eggs by indigenous parasitoids in North America tends to be lower than that from predation (Ogburn et al., 2016), accounting for less than 5% of parasitoid emergence from eggs in 87% of all surveys (Abram et al., 2017b). However, levels of parasitism and predation seem to vary depending on habitat (Cornelius et al., 2016a; Tillman et al., 2020), with parasitism greater than predation in woody ornamental nurseries (Jones et al., 2017), whereas the opposite is true for organic agroecosystems (Ogburn et al., 2016). Three parasitoid families are commonly found attacking *H. halys* eggs in the USA and Canada: Scelionidae (*Telenomus*, *Trissolcus*, and *Gryon* spp.), Eupelmidae (*Anastatus* spp.), and Encyrtidae (*Ooencyrtus* spp.) (Abram et al., 2017b; Leskey & Nielsen, 2018). According to Abram et al. (2017b), *Anastatus* and *Trissolcus* tend to dominate ornamental, semi-natural/urban, and forest habitats, whereas *Te. podisi* dominates field/vegetable crops and orchard habitats (see also Herlihy et al., 2016, and Tillman et al., 2020). One explanation for the low parasitism rates observed of *H. halys* eggs is that even when eggs are attacked, the native parasitoids frequently fail to develop to emergence, although they may still kill the host (Cornelius et al., 2016b). Abram et al. (2014) showed that *H. halys* eggs are attacked by *Te. podisi* at rates similar to indigenous *P. maculiventris* eggs. However, successful development occurred only in the latter species. They argued that *H. halys* acts as an evolutionary trap for this parasitoid, which could result in an increase in population levels of indigenous pentatomids. It is also worth noting that, although convenient, studies using sentinel eggs may underestimate the levels of parasitism (Jones et al., 2014; but see Herlihy et al., 2016, and Dieckhoff et al., 2017). This reduced parasitism could be due to the absence of cues used by indigenous parasitoids in host finding and recognition, i.e., host kairomones (Conti et al., 2003; Laumann et al., 2009; Tognon et al., 2016, 2017; Rondoni et al., 2017; Boyle et al., 2020) and oviposition-induced plant synomones (Colazza et al., 2004a; Conti & Colazza, 2012; Rondoni et al., 2017).

Exploration for natural enemies in the native range and biological control

To improve *H. halys* biological control, efforts were initiated in the late 2000s in the USA to introduce natural

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enemies from its native range. Classical biocontrol efforts targeted egg parasitoids of the genus *Trissolcus*, including *Tr. japonicus*, the predominant egg parasitoid and most important natural enemy of *H. halys* in Asia capable of inflicting high rates of parasitism in landscapes and orchard crops (Zhang et al., 2017; Buffington et al., 2018; Leskey & Nielsen, 2018). In 2014, although still under evaluation in quarantine facilities in the USA, a population of *Tr. japonicus* was found during routine sentinel egg surveys in a wooded habitat in Beltsville, MD (Talamas et al., 2015; Buffington et al., 2018). Molecular analyses revealed that the *Tr. japonicus* specimens found were different than those maintained in quarantine, indicating that it was introduced into the USA by other means via an unknown pathway (Buffington et al., 2018). Since then, *Tr. japonicus* has been reported in at least 13 states across the USA (Milnes et al., 2016; Hedstrom et al., 2017; Morrison et al., 2018; Leskey & Nielsen, 2018; Jarrett et al., 2019) and two provinces in Canada (Abram et al., 2019; Gariepy & Talamas, 2019). They comprise three distinct haplotype populations, indicating that there have been several independent introductions whose source regions have not yet been clearly identified (MC Bon, pers. comm.). Although *Tr. japonicus* has been reported mainly from unmanaged landscape habitats, it has also been found in peach orchards (Kaser et al., 2018).

Laboratory testing of *Tr. japonicus* against North American pentatomids has shown a marked preference for *H. halys* but not complete host specificity (Hedstrom et al., 2017; Botch & Delfosse, 2018; Lara et al., 2019). Potential alternate hosts may be less physiologically suitable for development than *H. halys* if they are accepted for oviposition, producing smaller and less fit progeny (Botch & Delfosse, 2018). The first field study of a *Tr. japonicus* population in North America appears to confirm these laboratory studies, at least for several native pest stink bugs in the Pacific Northwest (Milnes & Beers, 2019). A degree of specificity is also conferred by chemicals associated with *H. halys* that are used by *Tr. japonicus* in host finding and recognition. In choice tests, *Tr. japonicus* remained longer on surfaces with *H. halys* contact kairomones (Hedstrom et al., 2017). Furthermore, they responded more strongly to *H. halys* kairomone traces deposited on leaves of apple, maple, and soybean than to traces of the predatory *P. maculiventris* (Boyle et al., 2020), a non-target species that is an important predator in agricultural habitats of several pests, including *H. halys* (Pote & Nielsen, 2017). Parasitoid females detected and responded in a similar manner to kairomone traces on leaves of host plants, increasing their search time in a Y-tube olfactometer, and female *Tr. japonicus* were attracted to *n*-tridecane but repelled by (*E*)-2-decenal, two defensive compounds emitted from *H. halys* males and females (Zhong et al., 2017). In other experiments, *Tr. japonicus* females were attracted to volatiles from gravid females and mature males of *H. halys* and to volatiles induced in tomato plants by oviposition and feeding of this coevolved host, but females did not respond to similar cues associated with *P. maculiventris* (Bertoldi et al., 2019).

Although *Tr. japonicus* is also capable of parasitizing *P. maculiventris* (Hedstrom et al., 2017; Botch & Delfosse, 2018), the probability of *Tr. japonicus* locating and parasitizing *P. maculiventris* under field conditions is likely to be lower than for encountering *H. halys* (Bertoldi et al., 2019; Boyle et al., 2020). *Trissolcus japonicus* did not appear to be attracted to the *H. halys* aggregation pheromone (Morrison et al., 2018), and it was never captured in stink bug traps baited with *H. halys* and *P. maculiventris* pheromones (Boyle, 2017). Whether populations of indigenous pentatomids in North America will be negatively impacted by *Tr. japonicus* and whether this foreign parasitoid will provide better biological control of *H. halys* remain open questions that must be answered with continued field studies.

Case study 3: Biological control of *Halyomorpha halys* in Europe

Invasion of Europe and pest status

The European invasion by *H. halys* started in Switzerland in 2004 (Haye et al., 2015b) followed by the colonization of neighbouring countries and interceptions at customs/ports/airports (Claerebout et al., 2018). Genetic analyses demonstrate a high diversity of the invading *H. halys* populations, especially in Italy (Cesari et al., 2017) and Greece (Morrison et al., 2017), indicating multiple introductions that are still ongoing from their native range in Asia and other invaded countries. Serious damage in Italy was observed on peach, pear, and hazelnut, starting from 2013 (Maistrello et al., 2017; Bosco et al., 2018). Outbreaks in northern Italy in 2019 caused more than € 356 million damage on pear, peach, and nectarine, with up to 80–100% yield losses (CSO, 2019). Damage was reported also on apple, kiwi, and other fruit crops, as well as on horticultural and row crops (peppers, tomatoes, maize, and beans). Following *H. halys* invasion, previous IPM programs were seriously disrupted and official IPM guidelines had to be revised to allow for increased numbers of treatments with broad-spectrum insecticides.

Natural control by native parasitoids and predators

Due to restrictions on the practice of classical biological control in Europe, initial studies aimed to discover native natural enemies that were able to adapt to the new invasive

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species. Field surveys were performed in Switzerland, Italy, and Georgia, mainly to detect egg parasitoids and predators either using sentinel egg masses (frozen or fresh) or by collecting naturally laid egg masses. Overall, egg parasitism ranged from 3 to 39% in Switzerland (using frozen sentinel eggs), from 1 to 3% in Emilia Romagna, Italy (using fresh sentinel eggs), and from 12 to 21% in Piedmont, Italy (collecting naturally laid eggs). The generalist egg parasitoid *Anastatus bifasciatus* (Geoffroy) (Eupelmidae) was the predominant species in all surveys (Haye et al., 2015a; Costi et al., 2018; Kereselidze et al., 2018; Moraglio et al., 2020b), confirming its ability to develop in both frozen and fresh eggs. Other species found included *Trissolcus cultratus* (Mayr) (Scelionidae) in Switzerland (Haye et al., 2015a), and *Trissolcus kozlovi* Rjachovsky, *Trissolcus belenus* (Walker) [syn. *Tr. semistriatus* (Nees von Esenbeck) sensu Talamas et al., 2017] (Tortorici et al., 2019), *Tr. basalis*, *Telenomus turesis* Walker (Scelionidae) and the hyperparasitoid *Acroclisoides sinicus* (Huang & Liao) (Pteromalidae) in Piedmont (Sabbatini Peverieri et al., 2019; Moraglio et al., 2020b). In these surveys, a wide range of eggs were lost or showed symptoms of predation (chewing or sucking): up to 31% in Switzerland (Haye et al., 2015a), 2–5% in Emilia Romagna (Costi et al., 2018), and 0.4–9% in Piedmont (Moraglio et al., 2020b).

Laboratory no-choice tests were carried out to evaluate the potential of several parasitoid species to attack eggs of European native pentatomids as well as some generalist predators. *Ooencyrtus telenomicida* (Vassiliev) (Encyrtidae) achieved 36% parasitism of *H. halys* eggs, followed by *Ooencyrtus pityocampae* (Mercet) (21%), *A. bifasciatus* (20%), and *Telenomus chloropus* Thomson (6%) (Roversi et al., 2016). In another study, seven scelionid species (six *Trissolcus* spp. and *Te. turesis*) were tested on *H. halys* eggs. All the *Trissolcus* spp. caused significantly higher egg abortion compared with unexposed eggs, but only *Tr. kozlovi* was able to produce offspring from fresh eggs (Moraglio et al., 2020a), confirming what was observed in field surveys in Piedmont (Moraglio et al., 2020b).

Several species of wild-collected native European generalist predators were tested for their ability to feed on eggs and nymphs of *H. halys* in no-choice tests (Bulgarini et al., 2019). Only the omnivorous *Pholidoptera littoralis* (Fieber) (Orthoptera: Tettigoniidae) was capable of preying on eggs and first and second instars. The other predators did not feed on the eggs. Young *H. halys* nymphs were preyed on by *Nagusta goedelii* (Kolenati), *Rhynocoris iracundus* (Poda) (both Hemiptera: Reduviidae), and two *Himacerus* species (Hemiptera: Nabidae), and *R. iracundus* also fed on the adults (Bulgarini et al., 2019.). In a laboratory study, the arboreal ant *Crematogaster scutellaris* (Olivier) (Hymenoptera: Formicidae) did not prey on eggs but proved to be effective at preying on all nymphal instars (Castracani et al., 2017). In addition, the predatory potential of bats (Chiroptera) was assessed by screening for the presence of *H. halys* DNA (Piemontese et al., 2019) in guano samples from nine Italian bat species collected in natural and agricultural environments. Two genera of bats, *Myotis* and *Nyctalus* (both Vespertilionidae), showed evidence of feeding on *H. halys* (Piemontese et al., 2019). In a similar approach, analysis of the gut contents of field-collected arthropods identified *H. halys* DNA in predatory insects and arachnids belonging to Dermaptera, Orthoptera, Hemiptera, Opiliones, and Araneae (G Bulgarini, L. Piemontese, M. Cesari, R. Guidetti, L. Maistrello, unpubl.).

Control by exotic parasitoids and possible impact on native non-target stink bugs

Recently, field surveys in Switzerland and Italy discovered the presence of populations of *Tr. japonicus* and *Trissolcus mitsukurii* (Ashmead), which are considered the most effective egg parasitoids in China and Japan, respectively (Arakawa & Namura, 2002; Zhang et al., 2017), although the higher prevalence of *Tr. mitsukurii* over *Tr. japonicus* in Japan is debated (KA Hoelmer, unpubl.). *Trissolcus japonicus* was found first in Canton Ticino, Switzerland, in 2017 and in Piedmont and Lombardy, Italy, in 2018 (Sabbatini Peverieri et al., 2018; Stahl et al., 2019b; Moraglio et al., 2020b). A genetic analysis using the barcode mitochondrial DNA determined the closest match of the 'Ticino populations' with Japanese populations, but the pathways of entry into Switzerland remain unknown (Stahl et al., 2019b). *Trissolcus mitsukurii* was first recorded in northeastern Italy starting from 2016 (Scaccini et al., 2020). After the discovery of populations of *Tr. japonicus* and *Tr. mitsukurii* in Italy, the situation has been changing, as highlighted by the increased parasitism rate in the site in Piedmont where, together with *A. bifasciatus*, *Tr. japonicus* was detected in 2018 (Moraglio et al., 2020b). Given the availability of their host, the distribution of these exotic egg parasitoids is expected to expand, even in the absence of human intervention.

The prospective host range of *Tr. japonicus* in Europe was evaluated in no-choice tests, followed by large-arena choice tests (Haye et al., 2020). The developmental suitability of European non-target host species for *Tr. japonicus* was demonstrated in no-choice tests by offspring emergence from 11 out of 13 non-target species tested (85%). In large-arena choice tests, the degree of non-target parasitism was substantially reduced (three out of four suitable species were parasitized), whereas parasitism of *Palomena prasina* L. (Pentatomidae) eggs was comparable to that of *H. halys* (Haye et al., 2020). Field data from the

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invaded areas in Switzerland and Italy can contribute to a risk-benefit evaluation of releasing or re-locating *Tr. japonicus* populations into other parts of Europe.

Augmentative releases and efficacy of native parasitoids

Given that *A. bifasciatus* is the most prevalent native egg parasitoid of *H. halys* in field surveys (Haye et al., 2015a; Costi et al., 2018; Moraglio et al., 2020b) and that it is capable of developing in viable *H. halys* eggs (Roversi et al., 2016; Abram et al., 2017b), this species was selected as a candidate for augmentative releases. *Anastatus bifasciatus* can exploit cues associated with the non-coevolved host during its searching, as parasitoid females responded positively both to adult *H. halys* male volatiles and to *H. halys*-induced plant volatiles (Rondoni et al., 2017). Trials were performed in four apple orchards in Switzerland for 3 years and in an organic pear orchard in northern Italy for 1 year, releasing an equivalent of 11 000–26 000 *A. bifasciatus* females per ha (Stahl et al., 2019a). Parasitism averaged 6% (range: 2–16%) on frozen *H. halys* sentinel egg masses and 8% on frozen egg masses of lepidopteran non-target species. At the Italian site, parasitism on naturally laid eggs was considerably higher (49%) than on frozen sentinel eggs (16%). This suggests that although large quantities of frozen eggs are easier to obtain for experiments, data based upon their use in the field are likely to underestimate the actual impact of parasitism.

In 2019, further trials were performed in Emilia Romagna, Italy, where 10 000 *A. bifasciatus* females per ha were released over 5 weeks from the beginning of egg laying by *H. halys* (June–early July) in a small wooded area adjacent to a pear orchard. Parasitism averaged 9% on naturally laid eggs and 2.5% on frozen sentinel egg masses (Maistrello et al., 2020). However, these field trials underestimated the overall impact of *A. bifasciatus*, as they did not account for host eggs killed due to host feeding. According to previous laboratory trials, host feeding by *A. bifasciatus* may double the estimated host mortality (Stahl et al., 2019a).

Case study 4: Pre-emptive biological control of *Halyomorpha halys* in New Zealand – a world first

Risk of invasion, potential impact, and pre-emptive biocontrol approach

In New Zealand, *H. halys* presents a major risk not only to the sustainability and economics of food production but also to conservation due to its biology and very broad host range (Duthie, 2012; Lee et al., 2013; Bergmann et al., 2016). A recent assessment of the potential economic impact of *H. halys* in New Zealand found that if it established, it could cost the horticulture and arable industries 4.2 billion NZD in 2038 (New Zealand Institute of Economic Research, 2017). In addition, some New Zealand native plant species may be at risk of attack by *H. halys* as well (Duthie, 2012).

Although *H. halys* is not yet known to be present in New Zealand, there is a high risk of entry and establishment, with more than 212 live interceptions of *H. halys* adults at New Zealand's border during the latest high-risk season (i.e., September 2018–April 2019), totalling more than 1 500 adults. Invasive pests can sometimes be eradicated on arrival, but if eradication attempts fail or are deemed technically or economically unfeasible, then there will be a need to undertake area-wide pest management. If this is the case, classical biological control is expected to become a key strategy for reducing *H. halys* populations throughout New Zealand. The severity and imminent nature of *H. halys* incursion meant that there was an urgency for developing a pre-emptive classical biocontrol approach before the arrival of *H. halys*. Pre-emptive biological control is a novel approach that has the potential to enhance preparedness for a possible invasion of pest species and accelerate the response to invasive pests. With this approach, natural enemies can be selected, risk assessment studies carried out, and their potential release pre-approved by regulators for timely release after arrival of the pest. This would significantly reduce pest densities and rates of spread, ultimately reducing the economic or environmental damage associated with the pest (Hoddle et al., 2018). In preparation for a potential arrival/establishment of *H. halys* in New Zealand, a pre-emptive classical biocontrol program for this pest using the egg parasitoid *Tr. japonicus*, the most promising biocontrol agent of *H. halys*, was initiated in December 2015. This program aimed to determine the biosafety of *Tr. japonicus* to potential non-target species in New Zealand and to pre-approve its release to be ready for the anticipated arrival of *H. halys*.

Risk assessment for biological control of *Halyomorpha halys*

The potential host range of *Tr. japonicus* in New Zealand was investigated in quarantine using imported parasitized *H. halys* eggs from USDA-ARS (Newark, DE, USA) between November 2015 and December 2016. Egg masses of seven species of New Zealand Pentatomidae, including one sub-species, were individually exposed to naive mated female *Tr. japonicus* in no-choice laboratory experiments. All tested species were non-endemic but naturalised species to New Zealand. The only Pentatomidae species endemic to New Zealand, *Hypsithocus hudsonae* Bergroth, was not available at the time and could not be tested (Charles et al., 2019). Results from laboratory host-specificity testing demonstrated that the predatory Pentatomidae *Cermatulus nasalis* (Westwood) *nasalis*, *C.*

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nasalis hudsoni, and *Oechalia schellenbergii* (Guérin), and the phytophagous *Monteithiella humeralis* (Walker), *Dictyotus caenosus* (Westwood), *Glaucias amyoti* (Dallas), and *Cuspicona simplex* Walker were all physiological hosts for *Tr. japonicus*, although not all were equally susceptible to parasitism (Charles et al., 2019). No development or emergence of *Tr. japonicus* from eggs of *N. viridula* was observed (Charles et al., 2019).

In addition, a CLIMEX bioclimatic model was developed to estimate the potential global distribution of *Tr. japonicus* with particular reference to New Zealand and to investigate possible overlaps with the current distribution of potential non-target species (Avila & Charles, 2018). In the native range of *Tr. japonicus*, the model predicts its presence or potential expansion coinciding with the native range of *H. halys* (confirmed by specimen collection records that show it occurs throughout the entire native range of *H. halys*) into most humid-subtropical and humid-continental areas (Avila & Charles, 2018). Globally, the model projected that many temperate, Mediterranean, and subtropical areas could be suitable for the establishment of *Tr. japonicus*. Laboratory studies also demonstrated that *Tr. japonicus* and *Tr. cultratus* could survive periods of winter temperatures as cold or colder as tolerated by their host, *H. halys* (Nystrom et al., 2017). In New Zealand, the north appears moderately to highly suitable for *Tr. japonicus*, whereas southern regions are mostly marginal. The risk posed by *Tr. japonicus* to non-target species in New Zealand is predicted to vary between different pentatomids (Avila & Charles, 2018). CLIMEX projections of the potential distribution of *Tr. japonicus* provide useful guidance for selecting release sites if importation/release of this parasitoid needs to be carried out in New Zealand or worldwide.

Approval to release *Trissolcus japonicus* in New Zealand

The importation, development, and release of new organisms into New Zealand are under strict regulation and must be approved by the Environmental Protection Authority (EPA), which implements the Hazardous Substances and New Organisms (HSNO) Act 1996 (Ehlers et al., 2019). An applicant seeking approval to release a candidate biocontrol agent must submit an application that includes a risk/benefit analysis providing evidence to support the proposal for release and demonstrating that it meets the minimum standards of the HSNO Act. The application submitted to the EPA must provide information about potential adverse effects and the expected economic, social, and cultural benefits of the introduction. The EPA then conducts a full evaluation and review of the benefits and risks associated with the proposed biocontrol agent (Barratt & Ehlers, 2017; Ehlers et al., 2019). If the perceived benefits outweigh the risks, then EPA may grant approval for release, subject (or not) to further conditions.

In March 2018, an application was submitted to the EPA by a representative group from the horticultural industries (BMSB Council) to seek pre-approval to import and release *Tr. japonicus* into New Zealand in the event of a *H. halys* incursion. The application included host range testing, bioclimatic modelling, and substantial additional information on economic and social benefits. As a result of this application, in August 2018, the EPA granted approval for a conditional release of *Tr. japonicus* in the event that a *H. halys* incursion is detected in New Zealand, and it is subject to the development of an appropriate release plan (EPA, 2018). This is the first approval granted to release a biocontrol agent into New Zealand prior to the arrival of its target pest and the first example worldwide to approve the future release of *Tr. japonicus* before the arrival of *H. halys*. The successful implementation of this approach will provide New Zealand with the opportunity for a quicker response against a *H. halys* invasion and a greater chance of achieving an eradication or implementing an early area-wide pest management plan. This novel example of pre-emptive biological control might provide the impetus for biocontrol practitioners to adopt such an approach in the future for the early management of exotic pest incursions.

Case study 5: Biological control of stink bugs in South America

General overview of stink bugs as pests in South America

In South America, stink bugs are major pests primarily in arable crops, such as soybean, beans, and maize (Panizzi & Silva, 2012), which cover large agricultural areas. For example, the total area planted with soybean in Brazil, Paraguay, Uruguay, and Argentina is approximately 56 million ha (Trase, 2018). Since the start of soybean production and its expansion in South America, increasing problems with stink bugs have been reported. In general, these are species complexes with the dominant species varying among regions (Saluso et al., 2007; Ribeiro et al., 2009; Panizzi & Lucini, 2016; Aquino et al., 2019). The first serious pest mentioned in the literature was the cosmopolitan *N. viridula* (Panizzi & Lucini, 2016). Interestingly, its importance has changed over time. Currently, *N. viridula* is found at very low population levels in various regions of Brazil and Argentina (Panizzi & Lucini, 2016). This phenomenon could be due to adaptation to new cropping systems, expansion of soybean culture to hotter regions and broad adoption of non-tillage practices that favour native species. As a result, the dominant stink bugs in crops are currently native species such as *Euschistus*

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heros (Fabricius) (Pentatomidae) in hot regions (e.g., central and north Brazil) (Aquino et al., 2019) and *P. guildinii* in cold regions (e.g., southern Brazil, Paraguay, Uruguay, and Argentina) (Panizzi & Lucini, 2016). Other than *N. viridula*, no serious problems have been observed with invasive stink bugs in South America. However, because in recent years *H. halys* and *B. hilaris* have been reported in Chile, both species represent a serious threat to South American agriculture (Faúndez et al., 2016; Faúndez & Rider, 2017).

Classical and inundative biological control

The use of parasitoids for stink bug management in Brazil started in the 1990s with inundative biological control as part of an IPM program developed in the southern region of the country (Parana state). This biocontrol program was based on the use of the exotic *Tr. basalis*, which was already established in South America for the biological control of *N. viridula*, the main soybean pest at that time, and was shown to be especially useful for small to medium cultured areas surrounded by rivers. After demonstrating effective levels of control, the program was extended to more than 18 000 ha (Corrêa-Ferreira et al., 2000; Corrêa-Ferreira, 2002). In spite of its success, the program was eventually abandoned by growers who adopted new cropping systems with non-tillage practices, transgenic cultivars, and pest management based on cheap insecticides (Panizzi, 2013).

In Brazil, current efforts focus on *E. heros* control with *Te. podisi* as its main natural enemy. Because of the high dispersal capacity of this parasitoid, release of large numbers of individuals (ca. 5 000 individuals ha^{-1}) is necessary (Corrêa-Ferreira, 2002), requiring the rearing not only of many wasps but also their host. Mass rearing systems for stink bugs, including the use of artificial diets, have improved parasitoid production (Silva et al., 2008; Mendoza et al., 2016; Hayashida et al., 2018; Silva et al., 2018). This rearing system, together with new technologies – such as the preservation of host eggs and parasitoids at low temperatures until field release (Silva et al., 2018), protection of parasitized eggs in cardboard capsules, drone-based deployment systems, and accurate spatio-temporal field releases – could favour biocontrol programs in the near future. The high susceptibility of egg parasitoids to insecticides (Corrêa-Ferreira et al., 2010) is also important, so the identification and use of selective products are critical for successful inundative biocontrol strategies (Stecca et al., 2017). The commercial production of *Te. podisi* in Brazil is currently under consideration for license approval, which will allow a wider availability of parasitoids to growers.

In Argentina, a biocontrol program against *N. viridula* was implemented in 1981 with the introduction of *Tr. basalis* from Australia. A few years after the release of *Tr. basalis*, *N. viridula* was reduced to low densities (Crouzel & Saini, 1983). This was the only classical biocontrol effort for stink bugs in Argentina, and no subsequent evaluations were made regarding the success of the biocontrol program in the regions of release (Molinari et al., 2008).

In Uruguay, a multi-institution project was launched in 2005 that combined public and private interests for mass rearing and release of *Te. podisi*, with the aim of increasing the levels of parasitism of *P. guildinii* and reducing the use of insecticides. Releases were initially made of parasitized eggs as a source of parasitoids, but because of high levels of natural predation, adult wasps were released in the second stage of the project. Post-release parasitism of *P. guildinii* eggs by *Te. podisi* in two regions (Dolores and Paysandú) was 67 and 69%, respectively, which was higher than natural parasitism in areas without releases, i.e., 52 and 47% respectively (Castiglioni et al., 2007).

Conservation biological control and semiochemical-based strategies to enhance parasitoid efficacy

Because of the high diversity of natural enemies (Cingolani, 2012), especially of egg parasitoids (Scelionidae), which can reach high natural parasitism rates of 60–80% (Corrêa-Ferreira & Moscardi, 1995; Cingolani et al., 2014a,b; Paz-Neto et al., 2015; Zerbino & Panizzi, 2019), conservation biological control appears to be an effective approach for stink bug management in South America. However, due to the expansion of agricultural fields, landscape and habitat management may be necessary to enhance the ecological services provided by parasitoids (Aquino et al., 2019). Other tools that could improve conservation biological control of stink bugs include the recruitment of parasitoids using semiochemicals (Vieira et al., 2013, 2014) and the use of soybean cultivars producing volatiles attractive to parasitoids (Michereff et al., 2014, 2016). Moreover, attract-and-reward (Simpson et al., 2011) and push-pull (Khan et al., 2016) strategies could increase parasitism rates of semiochemically or naturally attracted parasitoids in the field. The potential of flowering plants to improve *Tr. basalis* attraction and parasitism rates of *N. viridula* eggs has also been demonstrated (Foti et al., 2017, 2019). An attract-and-reward strategy for *Te. podisi* and other species of South American scelionids is under investigation (RA Laumann, MF Aquino, MC Blassioli Moraes & M Borges, unpubl.). Conservation biological control of *N. viridula* and semiochemical-based strategies against stink bugs are also discussed more in detail below.

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Case study 6: Conservation biological control of *Nezara viridula*

Global pest status of *Nezara viridula*

Perhaps as a result of climate warming, *N. viridula* seems to be rapidly expanding its range in both hemispheres to regions that were previously not warm enough to sustain the survival of the species. For instance, in Japan, *N. viridula* was confined to the southwestern part of the archipelago since its earliest record there in the late 19th century. However, the species has recently expanded its range into the warm-temperate zone and now reaches the central part of the archipelago (Tougou et al., 2009). Similarly, *N. viridula* is currently expanding its geographical range in Europe to the north (Salisbury et al., 2009; Marcu & Grozea, 2018). Reports of its occurrence have been documented in Slovakia (Hemala & Kment, 2017) and in The Netherlands, where an estimated 10-15% of sweet pepper greenhouses were infested in 2019 (H Hoogerbrugge, pers. comm.). Currently, *N. viridula* is considered a key pest in only a limited number of agricultural crops, mainly tomatoes and legumes (Esquivel et al., 2018). Changes in geographical distribution may profoundly affect its status as agricultural pest, particularly in the newly invaded areas. Given the need for sustainable management solutions, the possibility of combining the release of natural enemies with cost-effective approaches that involve habitat manipulation as a conservation biocontrol measure can be a valuable alternative to pesticides for controlling stink bug populations (Tillman, 2017).

Conservation biological control: habitat manipulation and cultural practices

Conservation biological control comprises a variety of methods, including habitat manipulation and cultural practices that aim at supporting natural enemy populations in the vicinity and within agricultural areas and thus reducing herbivory on crops (Gontijo, 2019). A particularly favoured measure is the planting of flower strips to provide parasitoids and predators with sugar resources, shelter, alternative prey, and a suitable microclimate (González-Chang et al., 2019). Although increasing habitat diversity per se may not lead to a consistent enhancement of pest control (Karp et al., 2018), it has been advocated that the 'right kind of diversity' is necessary, meaning that the traits of selected flowering plants must match the requirements of the targeted biocontrol agent (van Rijn & Wäckers, 2016). For example, corolla length and floral scent have been shown to be decisive features that confer a certain degree of specificity in the interactions between flowers and visiting insects (Tillman, 2017). In recent years, conserving and enhancing natural enemies for controlling phytophagous stink bugs by providing floral resources have been receiving increased interest (Tillman, 2017). Several studies have demonstrated that a strategic arrangement of flowering plants can attract and enhance the efficacy of these parasitoids (Tillman, 2017). In the southeastern USA, where peanuts and cotton are widely grown, stink bugs such as *N. viridula* and *Chinavia hilaris* (Say) (Pentatomidae) have become important pests in cotton. Field experiments with potted milkweed, *Asclepias curassavica* L. (Apocynaceae), placed at peanut-cotton interfaces to serve as a nectar source for natural enemies, showed that parasitism of both adult stink bug species was significantly higher in the 2 years of the experiment. In this case, parasitism was mainly due to the tachinid fly *Tric. pennipes* (Tillman & Carpenter, 2014). Similarly, flowering buckwheat, *Fagopyrum esculentum* Moench (Polygonaceae), was able to increase the efficacy of *Tric. pennipes* parasitizing *N. viridula* in cotton (Tillman, 2017).

Studies conducted in Sicily, Italy, have shown differing impacts of buckwheat floral nectar on the abundance of *Tr. basalis* and *O. telenomicida*, two sympatric egg parasitoids of *N. viridula* (Foti et al., 2017, 2019). In the case of *Tr. basalis*, laboratory tests to screen for suitable non-crop plants showed that buckwheat and basil flowers have a positive effect on parasitoid longevity (Rahat et al., 2005; Foti et al., 2017). Buckwheat was more attractive to *Tr. basalis* than other companion plants because of characteristic compounds in the floral scent (Foti et al., 2017). When buckwheat margins were grown alongside tomato plots, *Tr. basalis* located and parasitized more *N. viridula* egg masses during the growing season (Foti et al., 2019). However, such beneficial effects cannot be generalized and may not apply to all *N. viridula* egg parasitoids. In fact, laboratory tests showed that buckwheat scent repels female *O. telenomicida* and flowering buckwheat margins fail to increase stink bug parasitism under field conditions (Foti et al., 2019). Although a beneficial effect overall can be expected due to the dominance of *Tr. basalis*, the possibility that there may be contrasting effects of floral scent within the parasitoid guild highlights the importance of selecting appropriate companion plants on a case-by-case basis. Researchers might even need to go one step further, as it can be necessary to select not only a suitable species but also the right cultivar of a given companion plant. Field studies in Florida, USA, for instance, demonstrated large differences between three sweet alyssum varieties, *Lobularia maritima* (L.) Desv. (Brassicaceae), in attracting predators of *N. viridula* when grown within tomato crops (Haseeb et al., 2018). Another obstacle for conservation biological control of *N. viridula* is the fact that parasitoids such as *Tr. basalis* tend to stay within a limited range of the flower margin, rather than moving deeper into the crop.

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Future work will need to focus on the question of how this obstacle can be overcome. Parasitoid distribution could be enhanced, e.g., by planting flower strips within fields and using modern GPS technology to avoid accidental spraying. Large-scale trials testing this concept are currently underway in the UK (ASSIST programme; https://www.assist.ceh.ac.uk).

Future prospects for improving stink bug control

The role of biological control in reducing invasive pest populations is widely recognized, although only a small amount (around one-tenth) of past natural enemy introductions provided satisfactory control (Cock et al., 2016). Therefore, because of the generally low economic injury levels of stink bugs (McPherson, 2018), it is not surprising that the efficacy of egg parasitoids alone is often insufficient to keep their populations under control; although it could be improved through conservation biological control (see case study 6) and applied chemical ecology methods (see below). Additionally, the prospects for integrating biological control with other sustainable control methods could improve stink bug control efficacy (Figure 1). Below, we review prospective methods for improving the efficacy of egg parasitoids and, when available, parasitoids attacking adults by using a chemical ecology approach. Also, we evaluate their possible integration with other sustainable methods targeting stink bugs.

Chemical ecology for manipulating parasitoid behaviour

In recent years, the development of semiochemical-based tactics has increased greatly, as they are considered efficient tools for manipulating insect behaviour with the aim of enhancing the biological control of crop pests (Wajnberg & Colazza, 2013). Feeding and/or oviposition by herbivorous insects induce changes in a plant's ecophysiological traits and their emission of volatile organic compounds (VOCs), either as herbivore-induced plant volatiles (HIPVs) or oviposition-induced plant volatiles (OIPVs) (Hilker & Fatouros, 2015; Pashalidou et al., 2015). Changes in VOC emission can occur locally and/or systemically and at either quantitative or qualitative levels (Dicke & van Loon, 2000; Martinez et al., 2013). Emission of HIPVs or OIPVs might alert the neighbouring plants of the same or other species (Baldwin & Schultz, 1983; Arimura et al., 2000; Karban & Maron, 2002) and/or act as an indirect plant defence by recruiting natural enemies of the herbivorous insects (Meiners & Peri, 2013; Hilker & Fatouros, 2015; Pashalidou et al., 2015). Many parasitoids and predators are known to respond to HIPVs or OIPVs during their host/prey location behaviour and can discriminate between volatiles produced by undamaged or infested plants (D'Alessandro & Turlings, 2006; Hare, 2011).

Egg parasitoids in systems involving stink bugs optimize their foraging behaviour by efficiently exploiting OIPVs (Conti & Colazza, 2012). OIPVs reliably indicate the presence of host egg masses and are produced by plants in large quantities, making them easily detectable (Fatouros et al., 2008; Conti & Colazza, 2012). For example, *Tr. basalis* (Colazza et al., 2004a,b; Frati et al., 2017; Salerno et al., 2019) and *Te. podisi* (Blassioli Moraes et al., 2005, 2009; Michereff et al., 2011) are attracted to leguminous plants infested by *N. viridula* or *E. heros* respectively. By providing reliable information to female egg parasitoids on the presence of suitable target hosts, OIPVs increase wasp recruitment on the host-infested plants, likely increasing parasitism rates.

Feeding and oviposition by the zoophytophagous predator *P. maculiventris* also induce the emission of VOCs in *Vicia faba* L. (Fabaceae) plants that attract *Te. podisi* females (Martorana et al., 2019). Interestingly, both *Tr. basalis* (Martorana et al., 2017; Rondoni et al., 2017) and *Te. podisi* (Martorana et al., 2019) show specificity in their response to OIPVs emitted by infested plants, as neither species are attracted by plants on which the alien *H. halys* had fed and oviposited. This lack of response, probably due to the absence of a history of coevolution between the interacting species, might allow egg parasitoids to optimize their time and energy budgets by exploiting cues only from suitable (coevolved) hosts (Martorana et al., 2017, 2019).

Stink bug activity may also leave short-range cues that are exploited by egg parasitoids once they have landed on plants. For instance, *Tr. brochymenae* shows an intense egg foraging behaviour on the leaf surface, exploiting substrate-borne chemical cues emitted by brassicaceous plants as a consequence of feeding and oviposition of *M. histrionica* (Conti et al., 2010). Several egg parasitoids are also able to detect chemical traces released by stink bugs and retained by the plant epicuticular waxes (Conti et al., 2003; Colazza et al., 2009; Frati et al., 2013; Boyle et al., 2020). *Trissolcus basalis* females were shown to discriminate traces left by *N. viridula* females from those left by males, due to the absence of *n*-nonadecane, a cuticular hydrocarbon present in *N. viridula* males but absent in females (Colazza et al., 2007). In doing so, wasps can restrict their searching behaviour to an area of the plant where host eggs are more likely to be found.

Laboratory studies that demonstrated the role of HIPVs, OIPVs, and contact cues in mediating host searching behaviour of egg parasitoids have opened up new opportunities for developing strategies for herbivorous stink bug control. However, the application of semiochemical-based

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techniques in the field is often difficult and provides results that are sometimes inconsistent. Several potential limitations and risks have been reported in the literature, including a potential increase in intraguild predation on natural enemies that in turn induces a reduction in the top-down control of the pests (Poelman & Kos, 2016; Peri et al., 2018). These techniques are applied in complex environments in which plants are subjected to various biotic and abiotic stresses and in which several intra- and inter-specific interactions can occur simultaneously. For example, the chewing damage from *Sitona lineatus* (L.) (Coleoptera: Curculionidae), whose adults feed on leaves and larvae feed on roots, induces a change in the OIPV profile emitted by *V. faba* plants that are concurrently infested by *N. viridula*, which in turn reduces the recruitment of the latter's egg parasitoid *Tr. basalis* (Moujahed et al., 2014). Similar disruptive effects on host egg location by parasitoids were observed in the presence of concurrent infestations of both alien (*H. halys*) and local (*N. viridula* or *P. maculiventris*) stink bugs (Martorana et al., 2017, 2019). Moreover, changes in the volatile blend emitted by plants infested by stink bugs that resulted in modification of egg parasitoid searching behaviour were also observed as a result of abiotic factors, such as water stress (Salerno et al., 2017).

To manipulate parasitoid behaviour on crops, semiochemicals can be applied directly onto the plants by spraying or by using slow-release dispensers, their emission can be induced by applying elicitors such as plant hormones (JA, methyl jasmonate, cis-jasmone, and SA) or plants themselves could be genetically engineered to increase their emission of HIPVs (Blassioli Moraes et al., 2013; Colazza et al., 2013; Simpson et al., 2013; Peri et al., 2018). However, few examples are reported in the literature on parasitoids of stink bugs, and the results are somewhat contradictory. Positive results were obtained in attracting the tachinid parasitoid *Gymnosoma rotundatum* (L.) to persimmon orchards using methyl (*E*,*E*,*Z*)-2,4,6-decatrienoate, the aggregation pheromone of the brown-winged green stink bug *Plautia stali* Scott (Pentatomidae) (Jang & Park, 2010; Jang et al., 2011). Positive results were also obtained in soybean crops using the aggregation pheromone of *Riptortus pedestris* (= *clavatus*) (Fabricius) (Hemiptera: Alydidae), which led to an increased abundance of its egg parasitoids, *Ooencyrtus nezarae* Ishii (Encyrtidae) and *Gryon japonicum* (Ashmead) (Scelionidae) (Lim & Mainali, 2013). Similarly, application of a racemic mixture of methyl 2,6,10-trimethyltridecanoate, a component of *E. heros* pheromone, attracted scelionid egg parasitoids (Borges et al., 1998). Conversely, although an increase in parasitoid recruitment in soybean fields was observed by using slow-release dispensers impregnated with (*E*)-2-hexenal, a compound present in the metathoracic glands of *E. heros* (Laumann et al., 2007), a more in-depth study demonstrated only early parasitoid recruitment but not a sustained increase in abundance (Vieira, 2010). Moreover, the application of cis-jasmone in soybean plants had positive effects on the foraging behaviour of scelionid stink bug egg parasitoids, leading to an increase in their abundance (Blassioli Moraes et al., 2009; Vieira, 2010), but this did not lead to an improvement of parasitism rate (Vieira et al., 2013). Parasitoid recruitment using semiochemicals can be affected by the experience of the foraging females, for example when the hosts are scarce or lacking. Without the reward of suitable host eggs, scelionid parasitoid females were shown to reduce their responses to semiochemicals due to habituation (Peri et al., 2006, 2016; Abram et al., 2017a). Additionally, most parasitoids are more dependent on other cues than those from the host-plant complex, such as floral odours from nectar plants. Therefore, manipulating the habitat by creating ecological infrastructures, e.g., using companion flowering plants such as buckwheat that serve as feeding sites for recruitment of stink bug egg parasitoids, might increase parasitism efficacy (see case study 6). The integration of semiochemical-based manipulation of parasitoid behaviour and habitat manipulation, e.g., the attract-and-reward strategy (Khan et al., 2008; Simpson et al., 2011), might limit the possible negative effects of parasitoid recruitment in the absence of hosts.

Chemical ecology for manipulating stink bug behaviour

The use of semiochemicals against stink bugs might be combined with biological control to increase pest control efficacy within organic farming systems. The chemical ecology of stink bugs is characterized by a wide array of signals that drive their behaviour at both intra- and inter-specific levels. Although sex and aggregation pheromones of stink bugs are commonly used as lures for trapping (Borges et al., 1998, 2011; Leskey & Nielsen, 2018), few studies have reported the application of other semiochemicals.

Stink bugs exploit host plant volatiles to find their feeding and oviposition substrates (Martinez et al., 2013; Guarino et al., 2017a; Weber et al., 2018). The types of semiochemicals they use depend on their feeding habits and their level of polyphagy. Polyphagous species respond to blends of common plant volatiles in precise proportions, whereas monophagous and oligophagous species are more attracted by key plant-specific compounds (Guarino et al., 2017a). For example, *Eurydema pulchrum* Westwood (Pentatomidae) positively responds to volatiles from host plants belonging to different families, such as *Brassica oleracea* L., *Raphanus sativus* L. (Brassicaceae) and

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Solanum lycopersicum L. (Solanaceae) (Rather et al., 2010). In contrast, *B. hilaris*, a specialist of Brassicaceae that exhibits a strong preference for certain species at the seedling stage (Huang et al., 2014; Guarino et al., 2017b), preferred *B. oleracea* and *B. napus* over *B. carinata*. This behaviour seems to be mediated by a novel diterpene hydrocarbon, still uncharacterized, emitted by *B. oleracea* and *B. napus* but missing in *B. carinata* blends (Guarino et al., 2018).

Stink bug preference for certain host plant species could be exploited for pest management using trap crops, which rely on an attractive host plant to arrest the pest and/or to concentrate it in certain zones of the field, where it can be eliminated (Hokkanen, 1991). Trap crops have shown the potential to effectively manage stink bugs in conventional and organic crop production systems (Todd & Schumann, 1988; Tillman, 2006). For example, the use of sorghum as a trap crop for *N. viridula* reduced insecticide applications in cotton, and black mustard used as a trap in sweet corn reduced pest damage by 22% (Rea et al., 2002; Tillman, 2006). Similarly, soybean and a mixture of triticale, sorghum, and sunflower were successfully used as trap crops in cotton fields for *Euschistus servus* (Say), *C. hilaris*, and *N. viridula* (Mizell et al., 2008; Tillman et al., 2015). The efficacy of the trap crop technique has also been demonstrated by combining it with pheromone-baited traps for suppressing *E. servus* attacking cotton. Such combinations of attractant stimuli increased the trap crop effectiveness in terms of numbers of attracted individuals and also consistently reduced the dispersal of *E. servus* in cotton fields (Tillman & Cottrell, 2012) and of *P. stali* in kaki persimmon orchards (Yamanaka et al., 2011). Recently, trap crops have been used for the management of invasive stink bug species. For example, *H. halys* has been controlled in pepper fields by using sunflower alone or in combination with sorghum as trap crops (Soergel et al., 2015; Mathews et al., 2017).

The use of trap crops for stink bug control may be particularly useful because there are few biologically based strategies that are available for the suppression of stink bugs in small organic farms or homeowner gardens (Mathews et al., 2017). Trap cropping might lead to (1) reduction in the use of pesticides, thus reducing the cost of pest control; (2) reduction in the selective pressure for development of pest resistance; and (3) preservation of natural enemies (Gordon et al., 2017). However, none of the cases reported have yet led to commercial implementation (Weber et al., 2018).

In order to manipulate pest behaviour more effectively, the trap crop technique can also be implemented by using a stimulus that is deterrent or repellent in nature, applied on the crop, leading to a push-pull strategy (Pickett et al., 2014). Information on the successful application of this strategy against stink bugs is scarce. However, a study carried out by Zhang et al. (2014) showed that several plant extracts obtained from clove, lemongrass, spearmint oil, and ylang-ylang plants acted as repellents toward *H. halys* and could be candidates as 'push stimuli' for this pest. The repellent stimuli could be used as extracts in dispensers or as intercropping plants to repel the pest that simultaneously could be attracted by a trap crop that serves as a 'pull stimulus'.

Intercropping with a non-host plant can directly reduce the damage to cash crops by masking the host from the pests, as some plants might have a repellent effect on herbivores (Smith & McSorley, 2000). In stink bug management, intercropping soybean with millet, cow pea, and groundnut reduced damage by *N. viridula* by 50% compared with a system containing soybean and millet only (Sastawa et al., 2004).

Future research on behavioural manipulation of stink bugs will be able to take advantage of new genomic and transcriptomic technology (Sparks et al., 2014) to identify the genes responsible for their pheromone production and behavioural responses to various odours. The objective will be, for example, to use plants or yeasts as 'factories' of stink bug attractants that can be used as 'dead end' trap crops (Møldrup et al., 2012).

Prospects for additional sustainable control methods

Additional sustainable control methods that could be considered in combination with parasitoids within organic farming systems include implementation of vibratory cues to disrupt stink bug sexual communication (Laumann et al., 2017; Čokl et al., 2019; Polajnar et al., 2019), direct plant resistance (Rondoni et al., 2018; Serteyn et al., 2020), exploitation of stink bug entomopathogens (Hajek et al., 2018), exclusion netting for fruit orchards (Candian et al., 2018), attract-and-kill methods (Morrison et al., 2019), and a novel mode of application of the sterile insect technique that combines the release of sterilized stink bugs with sterile parasitoids for pest eradication (Horrocks et al., 2020). Several of these possible methods are discussed below.

The reproductive behaviour in many stink bug species is mediated by multimodal communication, based on long-range attraction on a common substrate via chemical signals and the involvement of combinations of vibratory, chemical, and visual cues during calling and courtship behaviours (Čokl et al., 2019). Vibratory signals have been proposed as tools for mass trapping, using a bi-modal trap based on the aggregation pheromone and vibratory signal (Polajnar et al., 2019), and for mating disruption (Laumann et al., 2017). Considering that females of *Te. podisi* specifically respond to stink bug vibratory signals for

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spatial orientation, such signals might also be exploited for parasitoid recruitment on infested crops (Laumann et al., 2017).

Host plant (*V. faba*) resistance to stink bugs has been investigated recently at the biological, molecular, and behavioural level (Rondoni et al., 2018; Serteyn et al., 2020). Rondoni et al. (2018) showed that plants recognize *H. halys* oviposition as a warning signal and respond by activating defences against *H. halys* nymphs, resulting in reduced size of juvenile offspring. This is possibly related to the priming of JA-dependent genes, including a cysteine proteinase inhibitor. The use of proteinase inhibitors in agriculture can be implemented through the development of transgenic plants, the use of recombinant microorganisms, or production of biopesticides (reviewed by Rodríguez-Sifuentes et al., 2020).

Conclusions

This review summarises more than a century of research on the biological control of invasive stink bugs. Invasive stink bugs are difficult to control, especially when they have already colonized entire regions and population outbreaks have occurred. A new pest often spreads rapidly after its introduction, and effective management is often subject to delays while available short-term tools are identified and a classical biological control program is initiated. Pre-emptive biological control is an innovative strategy for appropriate situations to reduce delays in research and implementation, by preparing in advance for the arrival of a pest. When a pest has already established in a new region, classical biological control can be an effective means of reducing the reservoir of populations in the wider landscape, thus reducing immigration to crops. However, classical biological control of stink bugs has limitations that have been addressed here and have been recently analysed by Abram et al. (2020). Using stage-structured matrix models, these authors showed that stink bug mortality at the adult stage would be expected to provide a greater reduction of population growth than mortality at the egg stage and that a multi-tactic approach targeting different stages would be much more effective in reducing populations below the economic injury level. Here, we show that egg parasitoids are the most common natural enemies of stink bugs globally, and for this reason they have been the most commonly studied parasitoids of stink bugs. However, parasitoids attacking adults also provide interesting perspectives, although these are only known for a few invasive stink bug species.

The combination of classical biological control followed by conservation methods and integrated with other sustainable control methods targeting the various instars should provide interesting prospects for the improvement of stink bug control efficacy (Figure 1). Conservation biological control, through a provision of suitable nectar-producing flowering plants, can attract and improve the efficacy of both parasitoids attacking adults (Tillman & Carpenter, 2014; Tillman, 2017) and egg parasitoids (Foti et al., 2017, 2019). The application of semiochemicals on crops or inducing them in plants by applying elicitors might also facilitate recruitment of parasitoid species attacking adults (Jang & Park, 2010; Jang et al., 2011) or eggs (Borges et al., 1998; Lim & Mainali, 2013), although a consequent improvement of parasitism has yet to be demonstrated with these applications (Blassioli Moraes et al., 2009; Vieira, 2010; Vieira et al., 2013). The attract-and-reward strategy, which combines behavioural manipulation and habitat manipulation, might further improve parasitoid efficacy (Khan et al., 2008; Simpson et al., 2011). Semiochemicals can be used to manipulate not only natural enemies but also stink bug behaviour by using either trap crops (Todd & Schumann, 1988; Tillman, 2006; Nielsen et al., 2016) or push-pull strategies (Pickett et al., 2014). Moreover, future tactics might exploit vibratory cues to disrupt stink bug sexual communication (Laumann et al., 2017; Čokl et al., 2019; Polajnar et al., 2019) or direct plant resistance (Rondoni et al., 2018). Ultimately, as most research has been conducted only under laboratory conditions, there is an urgent need for field validation of these data before effective implementation can become a reality.

Author Contribution Statement

All authors contributed to the writing of the paper. EC and GR conceived the idea of the article and designed the layout. EC coordinated the paper and wrote the general parts. GA and BB wrote about the pre-emptive classical biological control of *H. halys* in New Zealand. FC and RAL focused on the biocontrol of stink bugs in South America. SC and MR wrote about the conservation biocontrol of *N. viridula*. EP, SG, and EW contributed with the chemical ecology of stink bugs and egg parasitoids. RS and MG wrote about the classical biological control of *B. hilaris*. LM and LT focused on the biocontrol of *H. halys* in Europe. CRS and KH focused on the biocontrol of *H. halys* in North America.

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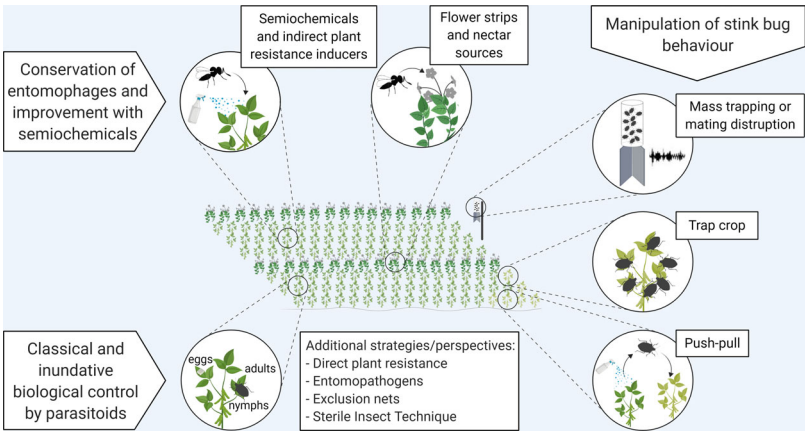
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Graphical Abstract

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We present a century of classical biological control of invasive stink bugs and review the biocontrol strategies on a global scale. These strategies include classical, augmentative, and conservation BC, as well as innovative proactive classical biological control, all of which are described through case studies. Based on information on stink bug and parasitoid chemical ecology, we discuss semiochemical-based approaches and other methods to increase natural enemy efficacy and to manage stink bug pests as part of sustainable control strategies.