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FORUM PAPER

The underestimated role of pest pentatomid parasitoids in Southern South America

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Abstract

Stink bugs are pests of economic importance of extensive crops (commodities) in the Neotropics, particularly in Southern South America. They are abundant, have a broad geographical distribution, and cause severe damage. Main species include the Neotropical brown-stink bug, *Euschistus heros* (F.), the red-banded stink bug, *Piezodorus guildinii* (Westwood), the Southern green stink bug, *Nezara viridula* (L.), the green-belly stink bugs, *Dichelops furcatus* (F.), and *D. melacanthus* (Dallas), and the brown-winged stink bug, *Edessa meditabunda* (F.). The management of these pest species on crops is complex because they can cause economic damage in low numbers, and it is difficult to control by the commonly used insecticides. Therefore, biological control appears as the most important tactic to be implemented in stink bug management programs. Among the many natural enemies present on the various agroecosystems, egg parasitoids (Hymenoptera) and parasitoids of adult stink bugs (Diptera and Hymenoptera) are the most promising groups to be exploited as biological control agents of pest species. Despite attempts in the past, implementation of biological control of stink bugs on major commodities in Southern South America still remains at a low level of adoption, and its high potential is, generally, underestimated. In this review article, we present extensive data from the literature on the two main groups of biological control agents referred above. Moreover, we discuss ways to promote biological control as the most important tactic to manage stink bugs in Southern South America.

Keywords Heteroptera · Pentatomidae · Adult parasitoids · Egg parasitoids · Southern South America

Introduction

The Neotropics, especially Southern South America, is actually one of the most important regions of the world for production of agricultural commodities. Cotton, rice, maize, soybean, and wheat are the most important crops, which account for 14% of the agricultural area and 43% of the gross agriculture production value (FAOstat 2017). The Southern Cone Region, which includes Argentina, Bolivia, Brazil, Chile, Paraguay, and Uruguay, is responsible for more than 90% of maize, rice, soybean, and wheat production, and 66% of cotton cultivated in South America. Therefore, we will concentrate our discussion on this area of the Neotropics.

Phytophagous stink bugs (Heteroptera: Pentatomidae) are important pests of afore mentioned crops. They feed mostly on seeds and on immature fruits, causing severe damage (e.g., Corrêa-Ferreira and Panizzi 1999; Chocorosqui and Panizzi 2004; Gamundi and Sosa 2008; Luna and Iannone 2013). Stink bug-feeding results in fruit abscission and/or malformation of seeds and fruits, directly affecting yield and quality (Panizzi 1997; Panizzi et al. 2000). The management of stink bugs is a complex and difficult task because they cause economic damage at low population levels, and have intrinsic tolerance to the commonly used insecticides. Therefore, their control requires multiple applications of broad-spectrum organophosphate and/or pyrethroid insecticides.

The integrated pest management (IPM) concept was developed more than 40 years ago because of the dependence of pest control on chemicals. Overreliance on pesticides led to outbreaks of secondary pests, resurgence of pest populations, insecticide resistance, and adverse effects on

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the environment and human health. The IPM concept entails the coordination of multiple tactics to optimize the control of all types of pests in a compatible economic and ecological way (Prokopy and Kogan 2003). These tactics include biological, cultural, behavioral (e.g., semiochemicals), plant resistance (including transgenic plants), and chemical control. In a holistic IPM program, biological control should play a fundamental role. Natural enemies are responsible for the equilibrium in agroecosystems, so their populations should be maintained and/or increased (Parra 2014).

In the Neotropics, where biodiversity is high, the development of biological control programs faces several challenges. One of them is the size of field crops reaching 20–30 or even 100 thousand hectares (Parra 2014). Moreover, the cropping systems create a continuum of crops year round, facilitating the build up of pests and demanding intensive use of chemicals. In this context, there is a critical need to reassess biological control in highly disturbed or temporary agroecosystems, such as annual crops (Michaud 2018). Therefore, it is necessary to create a biological control model adapted to extensive farmlands bearing dynamic features in its agricultural system (Parra 2014). In Latin America, augmentation has been widely adopted and vigorously promoted primarily to reduce the hazardous use of insecticides (Michaud 2018). Given the current concern over non-target effects of introduced biocontrol agents, the future of classical biological control in annual crops does not look favorable. Augmentation biological control is not an ecological solution, because it does not move agriculture closer to becoming a self-sustaining ecosystem that naturally retains pests below economic thresholds without continued human intervention (Michaud 2018). Conserving and enhancing resident natural enemies, particularly in the Neotropics, shows a much greater potential in annual crops and should receive increased emphasis. The ephemeral nature of annual crops can present impediments to conservation of biological control, especially in ecologically depauperate landscapes, which may justify inoculative releases of key natural enemies, but the greater permanence of perennial cultures should facilitate more permanent biological control solutions (Michaud 2018).

Stink bugs have a diverse and complex set of natural enemies in the Neotropics. The main ones are parasitoids of eggs and of adults (Corrêa-Ferreira and Panizzi 1999). Egg parasitoids (Scelionidae) (Fig. 1) have biological attributes and behavioral responses to host density that could lead to density-dependent parasitism and efficient local regulation of stink bug populations (Corrêa-Ferreira and Moscardi 1995, 1996; Laumann et al. 2010; Cingolani 2011; Bueno et al. 2012). Some species were successfully used in biological control programs in Brazil (Corrêa-Ferreira and Moscardi 1995; Bueno et al. 2012). Several species of flies (Diptera: Tachinidae) and micro-Hymenoptera (Encyrtidae) parasitize adults (Corrêa-Ferreira and Peres 2003; Cingolani 2011). Tachinids stand out for their diversity and abundance (Fig. 2). In spite of this, the taxonomic, biological, and ecological knowledge of this group is scarce and fragmented (Aquino 2016; Corrêa-Ferreira and Schoavengerst 2017; Dios and Nihei 2017; Agostinetto et al. 2018).

In this review article, we present the main stink bug pests of major commodities in Southern South America, and their pest status. Within the IPM programs, we present and discuss the role of biological control, particularly egg and adult parasitoids. We emphasize in particular the current underestimated role of these parasitoids, the lack of considering them as major component of IPM programs, and the possibilities to enhance their effectiveness and use.

Stink bugs as major pests in Southern South America

Considering abundance, geographical distribution, and magnitude of damage caused, the main pest species of major commodities include the Neotropical brown-stink bug, *Euschistus heros* (F.), the red-banded stink bug, *Piezodorus guildinii* (Westwood), the Southern green stink bug, *Nezara viridula* (L.), the green-belly stink bugs, *Dichelops furcatus* (F.), and *D. melacanthus* (Dallas), the brown-winged stink bug, *Edessa meditabunda* (F.), the rice stem bug *Tibraca limbativentris* Stal, and the *Oebalus* spp. complex.

The relative economic importance of each species is variable according to countries or regions within each country. For example, in Brazil, *E. heros* is the most important soybean pest, followed by *Dichelops* spp. and *P. guildinii*. *E. heros* is more abundant in the warmer areas (Panizzi and Slansky 1985; Kuss et al. 2012; Tuelher et al. 2016), while *P. guildinii* has been reported as the main pest in Southern fields (Corrêa-Ferreira and Panizzi 1999; Thomazini and Thomazini 2001; Tuelher et al. 2016).

In the last 10 + years, a drastic increase in *D. melacanthus* and *D. furcatus* abundance in Southern Brazil on soybean, wheat, and maize was observed (Chocorosqui and Panizzi 2004; Crosariol-Netto et al. 2015; Panizzi et al. 2016). In Argentina, *D. furcatus* is the second species in importance on soybean. Its abundance has significantly increased relative to the other stink bugs species, becoming dominant in recent years (Frana et al. 2006; Luna and Iannone 2013). In Uruguay, *D. furcatus*, *E meditabunda,* and *N. viridula* have a similar relative abundance on soybean, each one representing about 10% of the total population (Zerbino et al. 2016a).

The red-banded stink bug, *P. guildinii* is the most abundant species in Argentina, Bolivia, and Uruguay (Arroyo and Kamawura 2003; Massoni and Frana 2006; Saluso et al. 2011a; Zerbino et al. 2010, 2016a). In Paraguay, Colmán (2010) reported *P. guildinii*, *E. heros,* and *D. furcatus* as

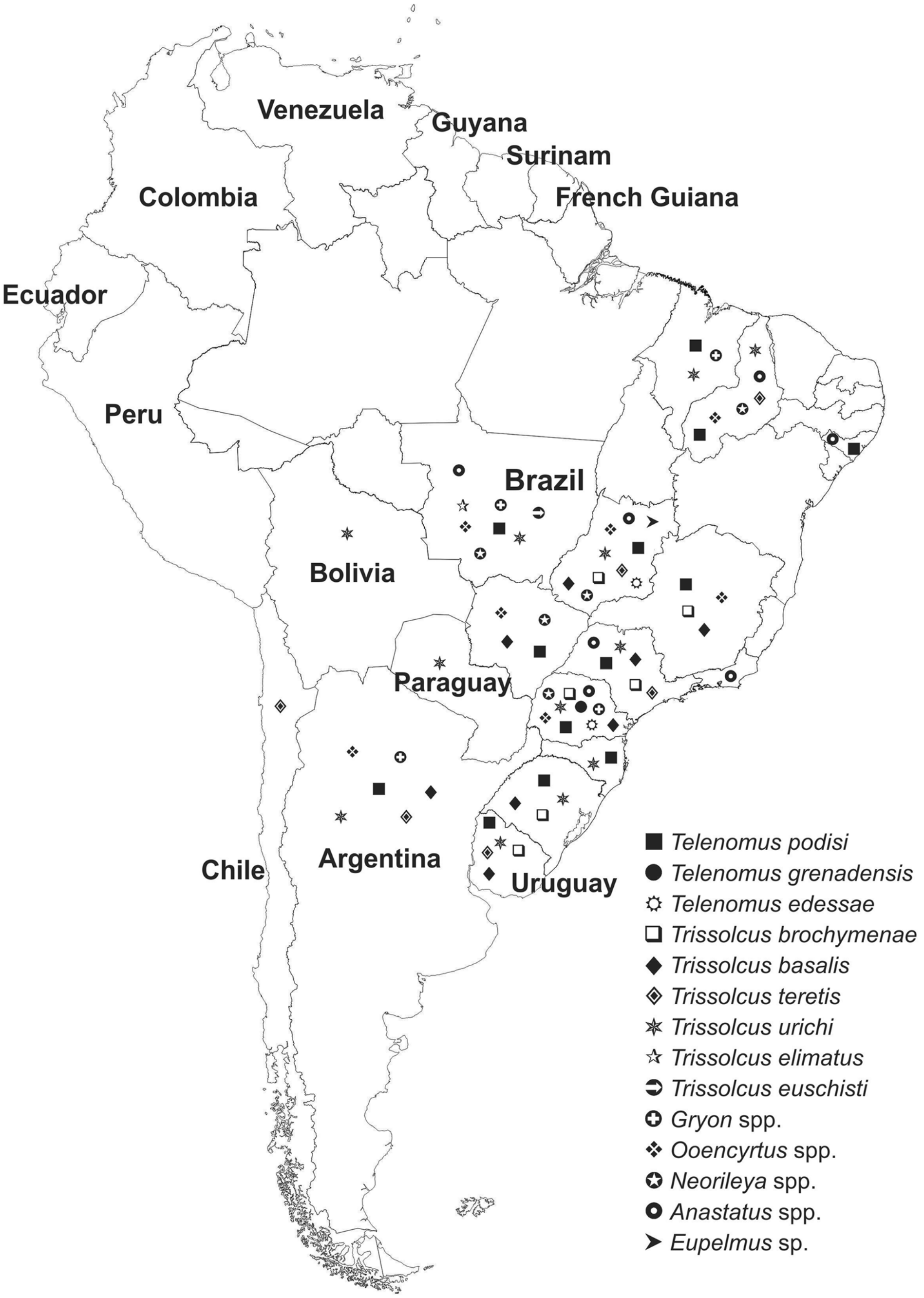

Fig. 1 Geographical distribution of egg parasitoids of stink bug (Pentatomidae) pests of crops in Southern South America based on literature records (Link and Concatto 1979; La Porta and Crouzel 1984; Corrêa-Ferreira 1986, 1993; Foerster and Queiroz 1990; Corrêa-Ferreira and Moscardi 1995; Cividanes et al. 1995; Venzon and Virissimo 1995; Medeiros et al. 1998; Loiácono and Margaría 2002; Maruyama et al. 2002a, b; Godoy et al. 2005; Massoni and Frana 2006; Santos 2008; Ribeiro and Castiglioni 2008; Castiglioni et al. 2010; Laumann et al. 2010; Golin et al. 2011; La Porta et al. 2013; Cingolani et al. 2014; Paz-Neto et al. 2015; Talamas et al. 2015)

regular species on soybean fields during March, with *P. guildinii* frequent, and *E. heros* and *D. furcatus* less frequent; *N. viridula* and *E. meditabunda* were considered rare. However, in recent years, *E. heros* became predominant (Gómez López et al. 2015).

The composition of the stink bug species on major crops in the Americas has changed over the years. Panizzi and Lucini (2016) presented and discussed the possible reasons to explain this phenomenon. For example, *N. viridula* was the predominant species in Brazil, Argentina, and Uruguay, when the expansion of soybean cultivation began in the 1970s (Bimboni 1978; Panizzi and Slansky 1985; Panizzi and Lucini 2016). Nowadays, it is considered a secondary species, which abundance decreased considerably (Panizzi and Lucini 2016; Zerbino et al. 2016a). On the other hand, *E. heros* has colonized new territories such as Argentina in the 2009–2010 soybean season (Saluso et al. 2011b).

Oebalus poecilus and *T. limbativentris* have wide geographic distribution, occurring throughout Latin America. In Brazil and Argentina, they are pests of rice, while in Uruguay they do not require chemical control (Panizzi et al. 2000; Martínez et al. 2018).

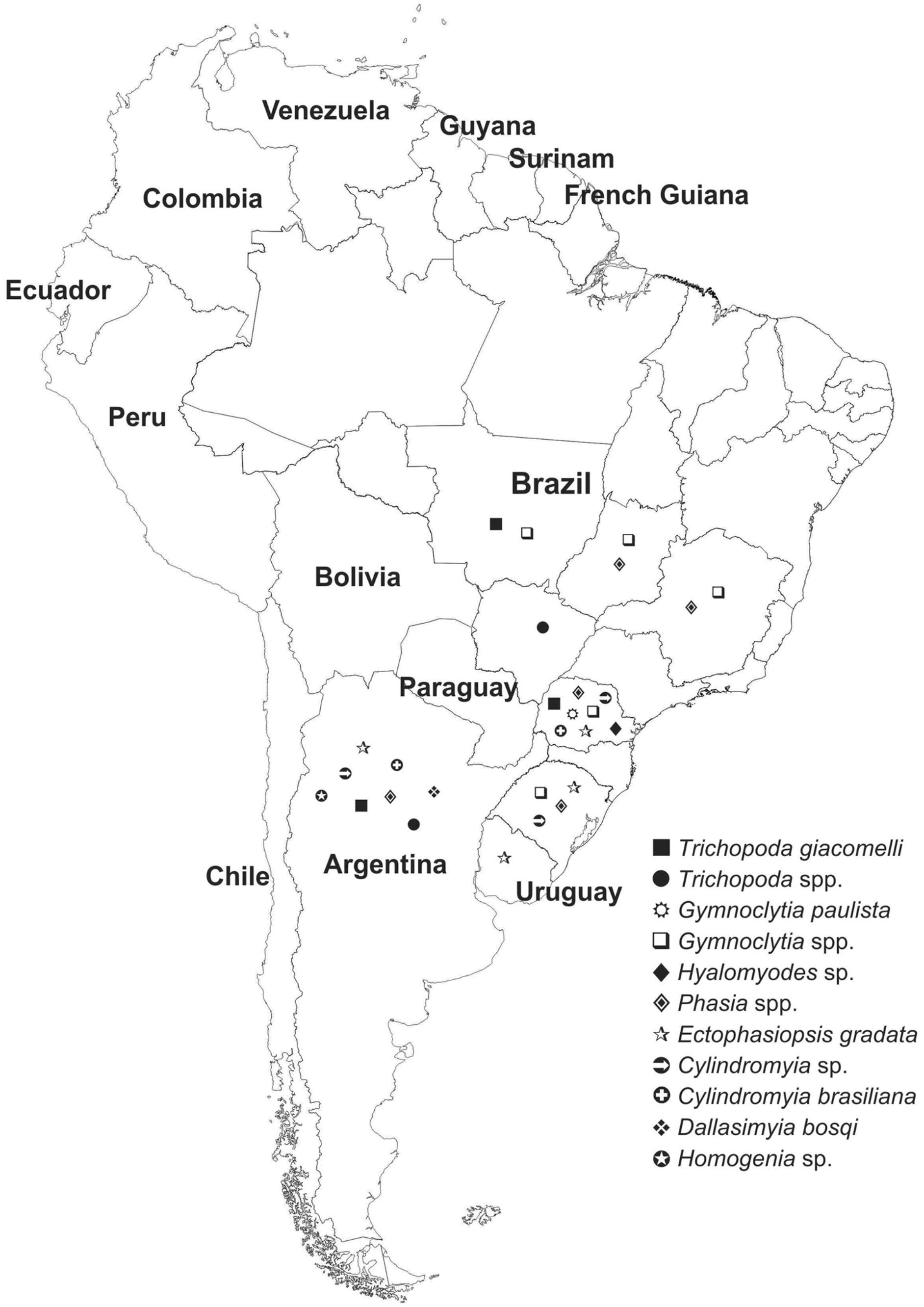

Fig. 2 Geographical distribution of tachinid parasitoids of stink bug (Pentatomidae) pests of crops in Southern South America based on literature records (Corrêa-Ferreira 1984; La Porta 1990; Panizzi and Corrêa-Ferreira 1997; Corrêa-Ferreira et al. 1998, 2005; Panizzi and Oliveira 1999; Pereira et al. 2009; Werdin González et al. 2011; Liljesthröm and Avalos 2015; Aquino 2016, Corrêa-Ferreira and Schoavengerst 2017; Dios and Nihei 2017; Agostinetto et al. 2018)

Phytophagous pentatomids feed on various structures of the host plants and therefore, the nature of the injury is variable. They feed by inserting their stylets into plant tissues and injecting a watery saliva, which contains digestive enzymes, and then sucking out the liquefied food contents. The gelatinous saliva solidifies around the stylet to form a stylet sheath. These sheaths remain in the plant tissue after feeding and serve as a record of feeding activity. Seeds and immature fruits are preferred feeding sites (Panizzi 1997).

The damage to plant tissues results from the frequency of stylet penetration and feeding duration, associated with salivary secretions that may be toxic and cause tissue necrosis. On soybean, different species cause different magnitudes of damage at the same population level, because of differences in feeding behavior, morphology of the mouth parts, and composition of the saliva (Sosa-Gómez and Moscardi 1995; Corrêa-Ferreira and Azevedo 2002; Depieri and Panizzi 2010, 2011). *P. guildinii* is considered the most damaging species due to its feeding behavior and the chemical dissolution of seed tissues caused by its saliva (Depieri and Panizzi 2011). Although *E. heros* causes less damage than *P. guildinii* and *N. viridula*, in Brazil it is the most economically important species because of its greater distribution and abundance (Corrêa-Ferreira and Panizzi 1999; Depieri and Panizzi 2011).

On cotton, *E. heros* in particular, and *E. meditabunda* and *N. viridula* are the three main stink bug pests in Brazil, causing significant losses in the production and quality of the fiber (Cruz-Júnior 2004; Soria et al. 2011).

Dichelops spp. and *N. viridula* have been reported on maize and wheat (Chocorosqui and Panizzi 2004; Roza-Gomes et al. 2011; Panizzi et al. 2016). *D. melacanthus* and *D. furcatus* may cause severe damage to maize seedlings, by sap sucking and introduction of toxic salivary enzymes resulting in withering of leaves and, eventually, of the whole plant (Ávila and Panizzi 1995; Crosariol-Netto et al. 2015). Their damage reduces the plant height, the number of expanded leaves, and the roots dry mass (Roza-Gomes et al. 2011). Severe attacks can cause seedling death, with reduction of the crop stand (Chocorosqui and Panizzi 2004). *N. viridula* has been mentioned as a sporadic pest in maize seedlings, with injuries caused similar in type and intensity to those caused by *Dichelops* spp. (Roza-Gomes et al. 2011)

On wheat, the feeding activity of *Dichelops* spp. causes characteristic lesions on leaves, with perforation and destruction of tissues, occasionally leading to leaf folding, which can present wrinkles that resemble viruses. Damage during the vegetative period increases the number of tillers (Chocorosqui and Panizzi 2004; Panizzi et al. 2016). *D. melacanthus* significantly reduces the number of wheat seed heads and grain yield (Chocorosqui and Panizzi 2004). *D. furcatus* high infestation at the booting stage causes significant damage to wheat grain yield and quality (Panizzi et al. 2016). *D. furcatus* and *N. viridula* do not reproduce on wheat plants in the field in the Neotropics, despite their reported occurrence as nymphs and as adults causing damage to the crop (Panizzi et al. 2016).

Oebalus poecilus affects the quantity and quality of rice production by feeding on developing grains. The damage depends on the stage of grain development at the time of attack. Seed heads with liquid endosperm (milky) and in the form of dough (paste) may be completely damaged or become atrophied, in which case small dark spots on the glumes are noted. The impact of *T. limbativentris* on paddy rice also depends on plant growth stage. Adults and nymphs feed on stems, sucking sap, and injecting saliva with toxins. Young tillers may die, and damage in the plant reproductive stage causes white panicles, because of total or partial panicle abortion (Panizzi et al. 2000).

Egg and adult parasitoids of stink bugs in Southern South America

Egg parasitoids

Among the natural enemies of stink bugs, eggs parasitoids are a good example of successfully applied biological control (Corrêa-Ferreira and Moscardi 1995; Pacheco and Corrêa-Ferreira 2000; Corrêa-Ferreira and Peres 2003; Bueno et al. 2012). They have biological and behavioral attributes that lead to density-dependent parasitism and efficient local regulation of stink bug populations. The egg parasitoids (Scelionidae) are used worldwide for biological control of stink bugs by mass or inoculative liberations, especially the cosmopolitan *Trissolcus basalis* (Wollaston) and the Neotropical *Telenomus podisi* (Ashmead) (Corrêa-Ferreira 1993). These parasitoids use chemical signals to locate their hosts, and they can be managed using semiochemicals from their hosts or from the plants (Borges et al. 2011, see discussion ahead).

In the Neotropics, several species of egg parasitoids of stink bugs have been recorded (Table 1). Only in Brazil, more than 23 species have been reported (Corrêa-Ferreira 1984; Corrêa-Ferreira and Moscardi 1995; Foerster and Queiroz 1990; Medeiros et al. 1998; Venzon et al. 1999; Godoy et al. 2005; Santos 2008; Paz-Neto et al. 2015; Talamas et al. 2015). In Argentina and in Uruguay, fewer species are reported (Massoni and Frana 2006; Ribeiro and Castiglioni 2008; Castiglioni et al. 2010; Cingolani et al. 2014) (Table 1), which include *Te. podisi, Tr. urichi* (Crawford)*, Tr. teretis* (Johnson), and *Tr. basalis*, in Argentina, and *Te. podisi*, *Tr. urichi*, *Tr. basalis*, *Tr. brochymenae* (Ashmead), *Tr. teretis,* and one specimen of Encyrtidae in Uruguay (Castiglioni et al. 2010; Cingolani 2011).

Although scelionids are the most frequent and abundant, species of Encyrtidae and Eurytomidae, such as *Ooencyrtus* spp. and *Neorileya* spp., are observed (Corrêa-Ferreira and Moscardi 1995). *P. guildinii* hosts the greatest, while *E. heros* and *Dichelops* spp. the lowest number of egg parasitoids (Table 1).

Te. podisi, *Tr. basalis*, and *Tr. urichi*, are polyphagous although they show preferences for particular hosts (Cingolani et al. 2014; Paz-Neto et al. 2015). *Tr. basalis* prefer *N. viridula*, while *Te. podisi* prefer *E. heros*, *P. guildinii,* and *D. furcatus* (Corrêa-Ferreira and Moscardi 1995; Talamas et al. 2015). *Gryon scutellatum* (Masner), *Te. edessae* (Fouts) and *Anastatus* sp., are very specific, and each parasitize one stink bug species only (Table 1).

Polyphagous egg parasitoids tend to have a wider distribution (Paz-Neto et al. 2015) as is the case of *Te. podisi* registered in at least 10 of the 26 states of Brazil;

Table 1 Egg parasitoids reported for different species of stink bugs (Pentatomidae) major pests in Southern South America

Family	Egg parasitoid species	Stink bug species						
		Euschistus heros	*Piezodorus guildinii*	*Nezara viridula*	*Dichelops* spp.	*Edessa meditabunda*	*Tibraca limbativentris*	*Oebalus poecilus*
Scelionidae	*Telenomus podisi*	X	X	X	X	–	X	X
	Telenomus edessae	–	–	–	–	X	–	–
	Telenomus grenadensis	–	–	–	–	X	–	–
	Telenomus sp. 2	–	X	–	–	–	–	–
	Telenomus mormidae	–	X	–	–	–	–	X
	Trissolcus basalis	X	X	X	X	X	–	–
	Trissolcus urichi	X	X	X	X	X	X	–
	Trissolcus brochymenae	X	X	–	X	–	–	–
	Trissolcus teretis	X	–	–	X	–	–	–
	Trissolcus sp. 2	X	X	–	–	–	–	–
	Trissolcus edessae	–	–	–	–	X	–	–
	Trissolcus euschisti	–	–	–	–	X	–	–
	Trissolcus elimatus	–	–	–	–	X	–	–
	Gryon scutellatum	–	–	–	–	X	–	–
	Gryon obesum	X	X	X	–	–	–	–
Eurytomidae	*Neorileya* sp.	X	X	X	X	X	–	–
	Neorileya ashmeadi	–	–	–	X	–	–	–
	Neorileya flavipes	–	–	X	–	X	–	–
Encyrtidae	*Ooencyrtus anasae*	–	X	X	–	–	–	–
	Ooencyrtus sp. 1	X	X	X	X	X	–	–
	Ooencyrtus sp. 2	–	X	–	–	–	–	–
	Ooencyrtus submetallicus	–	X	X	–	–	X	–
Eupelmidae	*Anastatus* sp.	–	–	–	X	–	–	–
	Eupelmus sp.	X	X	X	–	–	–	–
Pteromalidae	Pteromalidae sp. 1	–	X	X	–	–	–	–
	Pteromalidae sp. 2	–	X	X	–	–	–	–
	Pteromalidae sp. 3	–	X	X	–	–	–	–

Source: Corrêa-Ferreira and Moscardi (1995, 1996), Medeiros et al. (1998), Maciel et al. (2007), Castiglioni et al. (2010), Godoy et al. (2005), Massoni and Frana (2006), Santos (2008), Margaría et al. (2009), Cingolani (2011), Paz-Neto et al. (2015), Talamas et al. (2015) Hymenoptera Online (HOL). [Online] (Accessed 18 July 2018)

Tr. basalis predominates in the Central-Southern and *Tr. urichi* in the Central-Northern Regions.

Composition and predominance of egg parasitoid species are related to composition and predominance of stink bug species (Corrêa-Ferreira 1984; Foerster and Queiroz 1990; Venzon et al. 1999; Godoy et al. 2005; Paz-Neto et al. 2015; Talamas et al. 2015). In the 80s and 90s when *N. viridula* predominated, *Tr. basalis* was the prevalent species. Currently, *Te. podisi,* which is associated with the widespread *E. heros* and the abundant *Dichelops* spp., is the most common species. These two species of egg parasitoids, abundant and efficient, are commonly used in stink bug biological control programs (Corrêa-Ferreira and Moscardi 1995; Corrêa-Ferreira and Panizzi 1999; Corrêa-Ferreira and Peres 2003; Bueno et al. 2012).

In addition to the stink bug species present, the natural incidence of egg parasitoids is also directly associated with management practices (e.g., adoption of IPM concepts, and selective use of insecticides, among others) in different regions. According to literature, on average, the natural incidence of egg parasitoids is higher for *E. heros* and *P. guildinii* than for *N. viridula* (see Table 2 and references therein). These egg parasitoids should be preserved from the beginning of the crop implantation to achieve success in management of stink bug populations during the entire cycle of cultivation (Corrêa-Ferreira and Panizzi 1999; Smaniotto et al. 2013).

Table 2 Percentage of eggs of stink bug (Pentatomidae) species parasitized by different species of parasitoids in agroecosystems of different countries in Southern South America

Country	Stink bug species				
	Euschistus heros	*Piezodorus guildinii*	*Nezara viridula*	*Dichelops furcatus*	Sources[a]
Argentina	–	60	–	44	13
	–	37	–	–	17
	–	–	–	63	18
	–	–	25	–	19
Brazil	–	18	–	–	1
	–	–	24	–	2
	–	42	–	–	3
	50	50	14	50	4
	60	62	54	–	5
	30	50	–	–	6
	–	30	–	–	7
	82	60	33	–	8
	53	40	–	–	9
	20–100	5–60	15–50	–	10
	61	32	–	–	11
	40	–	–	–	12
	–	0	14	17	14
Uruguay	–	41–59	–	–	16
	–	66	–	–	15
Mean (± SE)	53.7 ± 6.3	43.9 ± 5.3	27.5 ± 6.0	43.5 ± 9.7	

[a] Sources: Link and Concatto (1979)[1], Moreira and Becker (1986)[2], Corrêa-Ferreira (1986)[3], Foerster and Queiroz (1990)[4], Corrêa-Ferreira and Moscardi (1995)[5], Venzon and Virissimo (1995)[6], Cividanes et al. (1995)[7], Medeiros et al. (1998)[8], Thomazini (1999)[9], Pacheco and Corrêa-Ferreira (2000)[10], Godoy et al. (2005[11], 2007)[12], Castiglioni et al. (2010)[13], Massoni and Frana (2006)[14], Santos (2008)[15], Ribeiro and Castiglioni (2008)[16], Cingolani (2011)[17], La Porta et al. (2013)[18], Liljesthröm et al. (2013)[19]

Adult parasitoids

The main parasitoids of adult stink bugs include Hymenoptera (Encyrtidae) and Diptera (Tachinidae) (Corrêa-Ferreira and Panizzi 1999). *Hexacladia smithii* (Ashmead) is the most frequent hymenopteran in adults of *E. heros* on soybean (Corrêa-Ferreira et al. 1998; Godoy et al. 2010; Turchen et al. 2015).

Tachinid parasitoids belong to the subfamily Phasiinae, tribes Trichopodini and Cylindromyiini (Liljesthröm and Avalos 2015). These flies attack Heteroptera only, primarily stink bugs (Pentatomidae) and leaf-footed bugs (Coreidae), making them important natural enemies in agricultural and natural habitats.

Adult parasitoids search for more conspicuous hosts than egg parasitoids, considering size, mobility, and cues associated with them. Unlike parasitoids of immatures, they allow their hosts to remain active (including reproductively) after parasitism. Another important feature of adult parasitoids is that because hosts are exposed, mobile, with defense and escape abilities, they developed skills for fast oviposition (Pilkay et al. 2013).

In the Southern Cone of South America, more than 12 species of tachinid flies attack adult stink bugs (Corrêa-Ferreira 1984; Panizzi and Corrêa-Ferreira 1997; Nunes et al. 1998; Panizzi and Oliveira 1999; Corrêa-Ferreira et al. 1998, 2005; Liljesthröm and Avalos 2015; Aquino 2016; Agostinetto et al. 2018). *E. heros* and *D. furcatus* show the highest, while *P. guildinii* and *N. viridula* show the lowest number of associated species (Table 3) (Corrêa-Ferreira and Panizzi 1999; Massoni and Frana 2005; Bueno et al. 2012; Liljesthröm and Avalos 2015).

Trichopoda giacomelli (Blanchard) is the most common and polyphagous species of tachinid reported from Brazil and Argentina, with preference for *N. viridula* (Sgarbanti 1979; Corrêa-Ferreira 1984; Liljesthröm and Bernstein 1990). It reduces the longevity and reproductive capacity of host bugs, especially when they are parasitized during late nymphal or young adult stages (La Porta 1987; Corrêa-Ferreira et al. 1991; Liljesthröm 1991; Nunes et al. 1998; Bueno et al. 2012). *Trichopoda giacomelli* has been used in biological control programs in Argentina (Liljesthröm and Bernstein 1990). Based on its performance in this country (Liljesthröm 1991), it was considered a potential biological control agent of *N. viridula* in Australia, especially in pecan orchards. Recovery of parasitized *N. viridula* from a range of host plants within 10 km of the release site indicates active dispersal by the agent and/or parasitized host. Parasitism

Table 3 Species of tachinids reported from different species of stink bug (Pentatomidae) pests of major crops in Southern South America

Tachinid Species	*Euschistus heros*	*Piezodorus guildinii*	*Nezara viridula*	*Dichelops furcatus*	*Dichelops melacanthus*	*Edessa meditabunda*	*Tibraca limbatriventris*
Cylindromyia brasiliana	–	–	–	X	X	–	X
Cylindromyia sp.	–	–	–	X	–	–	–
Gymnoclytia paulista	X	–	X		–	–	–
Gymnoclytia sp. 1	–	–	–	X	–	–	–
Gymnoclytia sp. 2	–	–	–	X	–	–	–
Hyalomyodes sp.	X	–	–		–	–	–
Phasia sp. 1	–	X	–	X	–	–	–
Phasia sp. 2	X	–	–	–	–	–	–
Phasia sp.	X	–	–	–	–	–	X
Trichopoda giacomelli	X	X	X	–	X	X	–
Ectophasiopsis gradata	–	–	–	X	–	–	–
Homogenia sp.	–	–	–	–	–	X	–
Dallasimyia bosqi	–	–	–	–	–	X	–

Sources: Sgarbanti (1979), Corrêa-Ferreira (1984), Panizzi and Corrêa-Ferreira (1997), Nunes et al. (1998), Panizzi and Oliveira (1999), Corrêa-Ferreira et al. (1998, 2005), Menegaz De Farias et al. (2012), Liljesthröm and Avalos (2015), Aquino (2016), Dios and Nihei (2017), Agostinetto et al. (2018)

ranged from 9 to 72% during summer; 42% of adults were parasitized during diapause (Coombs and Sands 2000). In Brazil, it can also parasitize *E. heros*, *E. meditabunda*, *D. melacanthus,* and *P. guildinii,* although in a much lower level, particularly *P. guildinii* (Nunes et al. 1998; Corrêa-Ferreira et al. 2005; Bueno et al. 2012). In Argentina and Uruguay, *T. giacomelli* has never been recorded from *P. guildinii* (Liljesthröm and Avalos 2015; Ribeiro and Castiglioni 2008).

In general, the highest rates of tachinid parasitism on stink bug species are observed at the beginning of the crop development (Corrêa-Ferreira and Panizzi 1999; Corrêa-Ferreira et al. 2005). The parasitism rate is largely variable throughout the year; these oscillations are related to stink bug abundance and overwintering strategies, climatic conditions, and crop management (Liljesthröm and Bernstein 1990; Panizzi and Oliveira 1999; Aquino 2016). The highest incidence of parasitism on *N. viridula* occurs in winter (mild) and spring, when bugs concentrate on a few wild and perennial-cultivated plants (Corrêa-Ferreira 1984; Panizzi and Oliveira 1999). For other stink bug species, such as *E. heros* and *D. furcatus*, tachinid parasitism is low during autumn and winter (Panizzi and Oliveira 1999; Agostinetto et al. 2018). These differences occur because these two latter species remain sheltered underneath crop residues in partial diapause during autumn and winter, which behavior prevents parasitism by tachinid flies at this time.

The incidence of tachinid parasitism on stink bug pests is affected by the use of chemical control. On soybean, the reduction in use of insecticides following IPM practices increased 63% the parasitism rate of tachinids (Aquino 2016). Therefore, the observed abandonment of IPM programs and the increase in use of insecticides explain why in many cases the parasitism rate recorded is low (see Table 4 and references therein).

It is important to note that parasitism by tachinids on stink bugs is easily overlooked or underestimated. This occurs because some flies lay eggs under the bug wings, which make them unnoticeable (Aldrich et al. 2006). For example, eggs of tachinids parasitizing *D. furcatus* in southern Brazil were laid preferably on the bugs' dorsal surface (82%) and the majority (42%) deposited under the wings (Agostinetto et al. 2018). In addition, eggs/egg shells may rub off preventing been noticed.

Limitations of applied biological control of stink bugs by parasitoids in Southern South America

In recent past decades, successful stink bugs biological control programs have been developed and implemented in Brazil (Corrêa-Ferreira and Moscardi 1996; Corrêa-Ferreira and Peres 2003). However, as the cultivation systems changed with the adoption of intense multiple cropping and the no-tillage cultivation, the interactions of stink bugs with their associated plants changed drastically. This has also adversely affected biological control.

The no-tillage cultivation system widely adopted by growers provides bugs with shelter (i.e., crop residues year round) and food (fallen seeds from the previous crop) (Panizzi 2013). These facts boosted some stink bug populations (e.g., *E. heros*, *D. melacanthus, D. furcatus, O. poecilus,* and *T. limbativentris*) (Panizzi 2007; Panizzi and Parra

Table 4 Percentage of tachinid parasitism on adult stink bugs (Pentatomidae) pests of major crops in Southern South America

Country	Stink bug species				Sources[a]
	Euschistus heros	*Piezodorus guildinii*	*Nezara viridula*	*Dichelops furcatus*	
Argentina	–	–	65	–	1
	–	–	26–32 (SP, SU)	–	3
	–	–	36	–	4
	–	*	–	*	6
	–	–	14 (WI)	–	9
	–	0	50	19	10
Brazil	–	–	27–53	–	2
	0 (WI)–37 (SU)[†]	–	30 (SU)–55(AU) 65 (WI)–100 (SP)	–	5
	**	–	–	–	8
	–	–	–	7(AU)–23 (SU)	12
	**	–	–	–	11
Uruguay	–	0	–	–	7

[a] Sources: Sgarbanti (1979)[1], Corrêa-Ferreira (1984)[2], La Porta and Crouzel (1984)[3], La Porta (1990)[4], Panizzi and Oliveira (1999)[5], Massoni and Frana (2005)[6], Ribeiro and Castiglioni (2008)[7], Pereira et al. 2009[8], Werdin González et al. (2011)[9], Liljeström and Avalos (2015)[10]; Aquino (2016)[11], Agostinetto et al. (2018)[12]

[†] *SU* summer, *AU* autumn, *WI* winter, *SP* spring

*Only one specimen parasitized

**Predominant specimens parasitized

2009). The abandonment of the successful use of the classical IPM, because of the tremendous increase of cultivated areas, the reduction of the costs of conventional insecticides, and the absence of effective extension services, added additional limitations (Panizzi 2013; Parra 2014). In this new reality, there is an urgent need to develop new procedures, such as novel sampling techniques using pheromones and/or remote sensing in order to release natural enemies at the right time and place (Parra 2014). The development of mass rearing techniques of stink bugs using artificial diets still presents a challenge to be overcome in order to meet the market demand for mass production of their biological control agents (Panizzi 2013; Parra 2014).

Perspectives and challenges of biological control of stink bugs on major crops in Southern South America

In Southern South America, the landscape has been transformed over time, from one that featured agricultural patches in a "sea" of natural habitats, to one that features remnant patches of natural habitats in a "sea" of agricultural enterprises (Panizzi 2013; Parra 2014). Usually, the pest management practice has been focused on the crop rather than on the whole farm or farmscape (Michaud 2018). Due to the changes in the agricultural landscape, it is time to broaden the perspective shifting to a more holistic approach.

Sustainable agriculture requires management of the ecosystem to conserve the natural enemies, which are important tools in suppressing pest populations (ecosystems services). In this context, there is a critical need to reassess biological control in a highly disturbed or temporary agroecosystems, such as annual crops (Michaud 2018). Given the concern over non-target effects of introduced biological control agents, the future for classical biological control in annual crops does not look favorable. Applied biological control with inoculative releases of natural control agents to increase their populations has great potential for use in annual crops. However, considering the amount of land dedicated to extensive crops, it becomes critical to meet the market demand for biocontrol agents. In contrast to classical and applied biological approach, conserving and enhancing resident natural enemies has great potential to use in annual crops. There may be agronomic constraints that render certain pests impossible to manage via conservation biological control in some agroecosystems, but in many cases, small changes in agronomic practices might tip the balance in favor of a more permanent solution. Natural enemies are capable of evolution just the same as pests, and sometimes it is possible to assist this process when their needs are understood. The field subdivision into smaller units could facilitate their penetration into planted areas by virtue of increasing edge habitat natural enemies. Although efforts to foster greater local plant diversity often require some reduction of the area planted to crops, marginal areas around fields are often underutilized and could be planted with species that provide floral resources for natural enemies. However, for that is required an improved understanding of the biology, behavior, and ecological requirements of these native species to improve their natural effectiveness and potentially preclude the need to rear them at all (Michaud 2018).

The quality of the habitat fragments, together with weather conditions, influences the development and survival of stink bugs and their natural enemies, which in turn affects the subsequent growth and dynamics of pests (Cingolani et al. 2014). It is necessary to consider that, because annual crops are temporary, pests and natural enemies must move in a landscape of patches consisting of bare ground, crop, and non-crop vegetation, to be successful.

The interactions between herbivorous insects, their host plants, and their natural enemies are implicit in a tri-trophic context closely related to the search behavior by hosts or prey of natural enemies (Price et al. 1980). The manipulation of the plant biodiversity and the behavior of parasitoids using semiochemicals offer as means to enhance the effectiveness of biological control. Stink bugs explore a variety of host plants within and between generations, which can be colonized in sequence. Throughout the growing season, they move between associated plants in response to deterioration of suitability of their current host plants (Panizzi 1997; Panizzi and Silva 2009; Tillman 2017). The sequence of the crop/wild hosts and their influence in natural enemy guilds could be useful to develop biological control strategies. Additionally, the semiochemical complex related to crop/wild host plants chemicals could be used in the field to recruit and retain parasitoids in these areas (Borges et al. 2011).

Plant biodiversity management and semiochemicals

Stink bugs and plants

Although the relationships between plants and stink bugs occur all over the different zoogeographical zones, perhaps in no other area of the world this relationship is as intense as in the Neotropics (Panizzi and Lucini 2017). This feature provides the opportunity to develop management tactics, before these insects colonize and damage the crops (Panizzi and Parra 2009; Zerbino et al. 2015).

Stink bugs spend most of the year on hosts and associated plants, or shelters, and only 3 or 4 months during spring–summer on the main crop (Panizzi and Silva 2009). The specific knowledge of cultivated and wild hosts is relevant to design strategies to stink bugs management. It is necessary to know which host plants are used by pentatomids, how suitable they are for nymphal development and adult reproduction, what sequence of hosts are used by sequential generations, and when dispersal occurs from these plants to crop plants and vice versa (Panizzi 1997).

The host plant/stink bug interactions are related to the bioecology of the insect. Often, a plant species on which a particular species of stink bug is collected, feeding or not, is regarded as a host plant; however, this is not always the case. A host plant is defined as a plant that the bug feeds on and that allows reproduction, i.e., the complete development of nymphs that will yield adults able to continue breeding to produce future generations. On the other hand, associated plants are those that the bugs may feed on, use as shelter, lay eggs on, but the nymphs are unable to develop and complete their life cycle; in addition, any resulting adults do not breed (Smaniotto and Panizzi 2015; Panizzi and Lucini 2017).

In temperate climates, adult stink bugs enter reproductive diapause during the fall and spend the winter protected in different hibernation sites (Panizzi 1997; Mourão and Panizzi 2000; Chocorosqui and Panizzi 2003; Zerbino et al. 2014, 2015). During spring they develop a first generation on alternate hosts (wild or cultivated plants), and later in summer they move to the main crop where they breed and cause damage (Panizzi 1997; Zerbino et al. 2015).

Among the host plants, there are those that are preferred, which present high nutritional qualities. When insects feed on them, it is expected that the next generation will be able to reach its maximum reproductive potential, thus maximum fitness occurs, i.e., the maximum reproductive contribution of each individual to the next generation. In those cases, nymphal development and adult reproductive performance will be the greatest (Panizzi 2007). For example, there is a close association between *P. guildinii* with indigo plants in Brazil, and with alfalfa in Argentina and Uruguay (Panizzi 1997, 2007; Cingolani et al. 2014; Zerbino et al. 2015, 2016b). Similarly, in Brazil, pigeon pea, *Cajanus cajan* (L.), which is used on contour lines as wind barrier, is explored by *P. guildinii* and other pentatomids, such as *E. heros* and *N. viridula* (Panizzi 1997, 2007). These host plants have the potential use as traps, where the release of eggs parasitoids may reduce the stink bug population that will colonize the main crop (Panizzi 2007; Zerbino et al. 2015, 2016b). This procedure will reduce the amount of parasitoids needed, which will be more easily provided by producers.

Parasitoids and plants

The egg parasitism of stink bug should be studied in the context of the ecosystem in which stink bug species and their parasitoids co-exist. The parasitoid species emerging from stink bugs eggs are influenced by the habitat, and by the spatial and temporal composition of host plants (Tillman 2016). Understanding the natural biological control of stink bugs in both non-crops and crops is necessary to develop effective management strategies for these pests. In particular, the proximity of natural vegetation is a main factor that influences stink bugs–natural enemy relationships.

Several studies have investigated egg parasitism of stink bugs on crops (e.g., Foerster and Queiroz 1990; Corrêa-Ferreira and Moscardi 1995; Medeiros et al. 1998; Pacheco and Corrêa-Ferreira 2000; Godoy et al. 2005; Castiglioni et al. 2010; Bueno et al. 2012; Cingolani et al. 2014), but data on parasitism of eggs in non-crop habitats and/or secondary crops are scarce (Maruyama et al. 2002a, b). Even though the sequence of host plants has been studied for stink bugs, as previously mentioned, stink bug egg parasitization and predation have been assessed primarily for the main crops (see references on Tables 2 and 4). Considering the crop-to-crop dispersal of stink bugs, their parasitoids are likely to respond to host plant switching by their hosts (Tillman 2016).

The diversity of vegetation provides greater availability of floral resources, such as pollen and nectar for natural enemies, particularly parasitoids. These resources, mainly nectar, positively influence the longevity, survival, and reproduction of egg and adult parasitoids with direct consequences on their aptitude (Tillman 2017). Feeding on floral resources can also influence searching behavior of parasitoids. In addition, diverse habitats also provide alternative hosts, places for hibernation, and places of refuge, favoring the permanence of populations of natural enemies on a temporal and spatial scale (Landis et al. 2000; Bianchi et al. 2006).

Providing nectar-producing plants in peanut-cotton farmscapes enhanced parasitism of multiple stink bug species by adult and egg parasitoid in southwest Georgia, United States. However, only in a few studies, supplying nectar-producing flowers has been demonstrated to reduce damage, mainly because the parasitized pest continues to feed on the crop. Therefore, nectar provision should be considered alongside other management tactics, such as crops and physical barriers (Tillman 2017).

In Southern South America, there is a major lack of information on landscape ecology of stink bugs parasitoids. Some studies were carried out evaluating the parasitism and the behavior of parasitoids considering the preferred host plants of stink bugs. In Brazil, Maruyama et al. (2002a, b) evaluated the eggs parasitism of *P. guildinii* and *N. viridula* in non-crops plants after soybean harvest. On the wild legume, *Indigofera hirsuta* L., recorded rates of egg parasitism ranged from 9.7 to 18.1% for *P. guildinii* and 4.8–47.6% for *N. viridula.* Cingolani et al. (2014), in Argentina, compared the parasitism rate of *P. guildinii* eggs in alfalfa and soybean crops during the soybean season; they found that in both, soybean and alfalfa, the values of egg parasitism were similar (36 and 38%, respectively). In Uruguay, the egg parasitism rate of *P. guildinii* using sentinel eggs in alfalfa in spring and in soybean during summer resulted in similar parasitism rate (15%) (Zerbino, unpublished).

Plants also play a very important role in producing chemicals that affect the egg parasitoids in many ways. For example, when pigeon pea, *Cajanus cajan* L. was attacked by *E. heros*, the blend of volatiles released was similar to the volatiles released by the *E. heros*–soybean interaction, and the pigeon pea volatile blend was attractive to egg parasitoids (Blassioli-Moraes et al. 2005—see also below).

Parasitoids and semiochemicals

Semiochemicals are the main stimuli used by egg parasitoids in host searching and selection (Borges et al. 2011; Blassioli-Moraes et al. 2013, 2016). They have different origins: from the host plant, from the host itself, and from the mixture of both; and they are classified as pheromones or allelochemicals, considering these possible interactions. In general, information from plants, such as herbivory- or oviposition-induced volatiles, is used as long-range signals to locate the host (Blassioli-Moraes et al. 2016). Host or host-associated cues are used during different steps of host searching and selection behavior, as in habitat location, host location, or host selection (Tognon et al. 2016, 2017).

Semiochemicals have the potential to be used for behavioral manipulation of parasitoids, improving biological control (Borges et al. 2011; Vieira et al. 2013). This strategy may be useful by itself, but if combined with other strategies, its success may be improved (Blassioli-Moraes et al. 2016).

Most studies using semiochemicals are being conducted with herbivore-induced plant volatiles, and less attention has been dedicated to the semiochemicals from hosts or host-related compounds. Work developed in arable crops has concentrated on testing the effects of semiochemicals on parasitoids, usually Hymenoptera, with some studies focused on Platygastridae (Vieira et al. 2013, Tognon et al. 2016, 2017).

Plant volatiles are used in the field with different approaches: (1) Application of synthetic compounds that induce plants defense or attract natural enemies; (2) use in intercropping or multiple cropping systems, with plants that release volatile substances that attract natural enemies and repel herbivores, moving pests away from the target crop; and (3) provide trap crops that attract pests close to the target crop (Blassioli-Moraes et al. 2016).

Although the number of studies using semiochemicals has increased in recent years, information on their application under field conditions to favor the action of parasitoids remains limited. Besides the difficulties of identifying the compound attractive to parasitoids in laboratory bioassays, various other aspects should be considered to improve the use of semiochemicals in arable crops. Among them, dosages, time, mode of application (e.g., dispenser, sprays, plants emitting semiochemicals), and other technical aspects need to be better established (Blassioli-Moraes et al. 2013; Michereff et al. 2013). The response of parasitoids to herbivore-induced plant volatiles is affected by a variety of factors, such as the chemical context within the environment (i.e., concentration and particularly the relative proportion of compounds released by plants) and the odor of the surroundings of the plant (i.e., odor from soil, other plants, and fungi) (Michereff et al. 2013). Therefore, the use of semiochemicals for parasitoid management needs to be studied case-by-case, and adaptations should be tested in each particular situation (Blassioli-Moraes et al. 2016).

Two main strategies have been developed to apply semiochemicals in the field. One is the use of synthetic semiochemicals, which can be applied using a slow-release dispenser to act directly on parasitoids' behavior. The other strategy includes chemical application of synthetic compounds or phytohormones as sprays, inducing the production of defensive volatiles, which attract parasitoids (Blassioli-Moraes et al. 2013; Vieira et al. 2013). In Brazil, these strategies were evaluated in soybean fields. The use of rubber septa with (E)-2-hexenal, a stinkbug's pheromone component, that is also a volatile produced by plants, increased the number of scelionid wasps in relation to non-treated areas (Vieira et al. 2013). Other compound evaluated was cis-jasmone, a natural phytohormone that induces indirect defense of soybean plants. When sprayed on plants, they induced the production of volatiles (Moraes et al. 2009; Vieira et al. 2013). Results indicated that the total number of Scelionidae, mainly *Telenomus* spp. and *Trissolcu*s spp., was significantly higher in treated plots, but no significant difference in rates of parasitism and number of stink bugs was found between plots. Therefore, other factors such as lack of pollen and nectar to retain adult parasitoids, may explain these results (Vieira et al. 2013).

In contrast to egg parasitoids, much less attention has been given to tachinid adult parasitoids regarding semiochemicals. Several studies show the response of these parasitoids to pheromones of their hosts in pheromone-baited traps, but this group did not respond to volatiles from plants damaged by their herbivorous hosts (Aldrich et al. 2006; Blassioli-Moraes et al. 2013). The sensitivity of some tachinids to host pheromones and the precision of these kairomonal messages in some cases exceeds that of the bugs for their own pheromones (Aldrich et al. 2006). Host location by these flies occurs via antennal reception to the pheromones of their hosts; however, little is known regarding the mechanisms that underlie host selection.

The adult parasitoid guild appears to follow a similar trend as herbivorous stink bugs. Some tachinid species (*Trichopoda* spp.) are known to preferably oviposite on male's body compared to females (e.g., Liljesthröm 1991). In the host search, adult parasitoids follow the sexual and/or defensive pheromones as indicative of host presence in the area (Aldrich et al. 2006).

Studies with semiochemicals have focused mostly on increasing the effectiveness of biological control in the main crop. Perhaps, a better alternative would be to consider the use of semiochemicals to attract eggs and adults' parasitoids for the host plants that stink bugs colonize during spring, when female stink bugs deposit the eggs of the first generation. On the other hand, it is necessary to consider that the large-scale production of semiochemicals demanded by the extensive use of land by arable crops needs specific solutions from the chemical industry (Blassioli-Moraes et al. 2016).

Concluding remarks

This review article on parasitoids of major stink bug pests in Southern South America demonstrates that a great deal of research has been conducted on this topic. In spite of this, large-scale management of these insects is still primarily based on the intensive use of insecticides. This fact explains the relatively low parasitism incidence in different regions, and the differences in the diversity of parasitoids observed.

Considering the tremendous biodiversity in the Neotropics, as previously discussed, it is hard to believe that biological control of insect pests is not a main tactic of current IPM programs in the region. Compared with other areas of the world, biological control in the Neotropics is poorly exploited as a pest control tool. For example, about 230 species of natural enemies of insect and mite pests are commercialized in the world (van Lenteren 2012). In contrast, in the greatest country of the region, Brazil, only ca. ten species of natural enemies are available for purchase (Parra 2011). This means that less than 5% of total commercialized natural enemies are being used. Clearly, considering the biodiversity of the Neotropics, there is a tremendous potential to substantially increase the use of biocontrol agents to mitigate pests.

To overcome this challenge, a model biological control program should be developed and adapted to the large-scale farmlands of Southern South America. The parasitism incidence on eggs by microhymenopterans, and on adults, particularly by tachinids, can and should be much improved. Considering natural enemies diversity and abundance, as here demonstrated, efforts should be concentrated on conservation biological control, as advocated by Michaud (2018). Also, this concerted biocontrol effort should be integrated with other tactics, such as the use of trap crops and semiochemicals. Landscape planning providing parasitoids with food, hibernation, and refuge sites favors their permanence, and cultivation spatially and temporally planned should be developed. Finally, the use of selective insecticides should be encouraged or even mandatory to allow, not only parasitoids, but natural enemies in general to express their full ecosystem services to mitigate the impact of pests.

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