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Parasitism rates and parasitoid complexes of the wheat midges, *Sitodiplosis mosellana*, *Contarinia tritici* and *Haplodiplosis marginata*

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Abstract Three species of cecidomyiid midges (Diptera: Cecidomyiidae), whose larvae overwinter in the soil, can cause significant yield losses on wheat in Europe: the orange wheat blossom midge, *Sitodiplosis mosellana* (Géhin), the yellow wheat blossom midge, *Contarinia tritici* (Kirby), and the saddle gall midge, *Haplodiplosis marginata* (von Roser). The biological control of wheat midges by their parasitoids can contribute to reduce the midge populations. Soil samples were collected in several fields in Belgium in 2012–2014 in order to characterize the parasitism rates and parasitoid complexes in overwintering larvae. The parasitism rates varied greatly between the sampled fields: 3–100, 0–100 and 2% for *S. mosellana*, *H. marginata* and *C. tritici*, respectively. The parasitism rate was not related to the larval density of wheat midge. The three wheat midges have totally distinct parasitoid complexes in Belgium. Eight species (Hymenoptera: Pteromalidae and Platygastridae) were found as parasitoid of *S. mosellana*: *Macroglenes penetrans* (Kirby), *Amblypasis tritici* (Walker), *Euxestonotus error* (Fitch), *Euxestonutus* sp. Fouts, *Leptacis* sp. Foerster, *Platygaster gracilipes* (Huggert), *Platygaster nisus* Walker, and *Platygaster tuberosula* (Kieffer). According to their abundance, *M. penetrans*, *E. error* and *P. tuberosula* appeared as the main parasitoids of *S. mosellana* in Belgium. For the two other wheat midges, only one species of the family Platygastridae was found for each midge: *Platygaster equestris* (Spittler) for *H. marginata* and *Synopeas myles* (Walker) for *C. tritici*.

Keywords Cecidomyiidae · Wheat midge · Hymenopterous parasitoid · Pteromalidae · Platygastridae

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Introduction

Three species of cecidomyiid midges (Diptera: Cecidomyiidae), whose larvae overwinter in the soil, are common pests of wheat (*Triticum aestivum* L.) in Europe: the orange wheat blossom midge, *Sitodiplosis mosellana* (Géhin), the yellow wheat blossom midge, *Contarinia tritici* (Kirby) and the saddle gall midge, *Haplodiplosis marginata* (von Roser). These wheat

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midges are univoltine species and overwinter as larvae in the soil. Under favourable conditions, the larvae move towards the soil surface where they pupate. Adults emerge from the soil during the spring and generally mate at the emergence site. The mated females fly off to find a host plant to lay their eggs in the spikes for *S. mosellana* and *C. tritici*, and on the leaves for *H. marginata*. Eggs hatch a few days later. The larvae of *S. mosellana* and *C. tritici* feed on the developing kernels and on the flower parts, respectively. The young larvae of *H. marginata* move down under the leaf sheath to feed on the stem, where they induce the development of saddle-shaped galls. In early July, when the feeding period is over, larvae leave the spikes or the stems with rainfall and burrow into the soil, where they enter diapause (Barnes 1956).

The infestation of wheat crops by these pests can cause significant yield losses. In the last decade, serious damage caused by *S. mosellana* and *H. marginata* was observed in Europe, particularly in the United Kingdom (Oakley et al. 2005; Pope and Ellis 2013), Germany (Gaafar et al. 2011; Mölck 2007) and Belgium (Censier et al. 2016; Chavalle et al. 2015b). For example in the United Kingdom, the yield losses due to *S. mosellana* attacks reached up to 30% in 1993 (Oakley 1994), while those due to *H. marginata* attacks reached up to 70% in 2010 and 2011 (Pope and Ellis 2013).

To manage populations of wheat midges and minimize damage, the main control strategies are based on insecticide treatments (Censier et al. 2016; Chavalle et al. 2015b), and, only for *S. mosellana*, on growing resistant wheat cultivars (Chavalle et al. 2017). Others strategies using biopesticides such as insect pathogen, jasmonic acid and azadirachtin have also been developed (El-Wakeil et al. 2013; Shrestha and Reddy 2018).

Natural enemies can be also important regulators of wheat midge populations. Apart from predators, such as Carabidae, Staphylinidae and Araneae (Affolter 1990; Holland and Thomas 2000), several species of parasitoid wasps have been known for many years to attack *S. mosellana*, *C. tritici* and *H. marginata*. The information concerning the parasitoids of *S. mosellana* and *C. tritici* is confused because these midges have not always been distinguished correctly (Barnes 1956). According to the literature, 27 species have been recorded for the parasitoid complex of the wheat blossom midges: *S. mosellana* and *C. tritici* (Affolter 1990; Barnes 1956). Affolter (1990) showed that this parasitoid complex comprised only eight species in Switzerland and that the two midge species had totally distinct parasitoid complexes. *Macroglenes penetrans* (Kirby) (Pteromalidae) is the most common parasitoid of *S. mosellana*, but other species from the family Platygastridae are also known, such as *Euxestonotus error* (Fitch) and *Platygaster tuberosula* (Kieffer) (Affolter 1990; Barnes 1956; Chavalle et al. 2015a; Doane et al. 1989; Echegaray et al. 2016; Olfert et al. 2003). Among the common parasitoids of *C. tritici*, three species of Platygastridae were often recorded: *Isostasius punctiger* (Nees), *Leptacis tipulae* (Kirby) and *Synopeas myles* (Walker) (Affolter 1990; Buhl and Notton 2009; Speyer and Waede 1956; Weigand 1974).

Five species are known to parasitize *H. marginata*: two from the family Platygastridae, *Platygaster equestris* (Spittler) and *Platygaster taras* Walker, and three from the family Eulophidae, *Chrysocharis amyite* (Walker) (= *C. seiunctia*), *Holarcticesa clinius* (Walker) (= *Grahamia clinius*) and *Holarcticesa tatrica* (Erdös) (= *Grahamia tatrica*) (Baier 1964; Darvas et al. 2000; Emschermann 1969; Hansson 1988; Spittler 1969).

These parasitoids contribute to the biological control of wheat midges and to the regulation of their population dynamics (Affolter 1990; Barnes 1956; Censier et al. 2015; Oakley 1994; Olfert et al. 2009; Thompson and Reddy 2016). However the impact of parasitoids on wheat midge populations is variable because the parasitism rates differ greatly with field, location and year. Variable parasitism rates were observed in the United Kingdom with 4–99 and 0.1–72% in 1929–1956 (Barnes 1956), in Germany with 9.3–74.4 and 0.5–41.3% in 1970–1979 (Basedow and Schütte 1982) and in Switzerland with 5–50 and 0–21% (Affolter 1990) in 1985–1989 for *S. mosellana* and *C. tritici*, respectively. For *H. marginata*, variable parasitism rates were also observed in Germany with less than 1–69.4% (Spittler 1969), in Belgium with a maximum of 10% in 1965–1970 (De Clercq and D'Herde 1972), and in the Netherlands with 1.9–40.6% in 1965–1966 (Nijveldt and Hulshoff 1968).

Despite the significant damage observed in the last decade in Europe, no recent study has been conducted on the identification and quantification of these parasitoids in the wheat midge populations and none

has studied the parasitoid complex of the three wheat midges present in the same agro-ecosystem. In this study conducted in Belgium in 2011–2014, the identification of species composing the parasitoid complex of each wheat midge was carried out by rearing wheat midge larvae extracted from soil samples collected in autumn and in winter. The overwintering larvae are the most adequate stage to collect wheat midges in order to identify with certainty the link between the parasitoid species and their host. The occurrence of each parasitoid species was determined for each sample as well as the parasitism rate of each wheat midge.

Materials and methods

Fields and soil sampling

To study the parasitism of wheat midges, soil samples were collected in 2011–2014 in several fields of two different cereal-growing regions of Belgium (Fig. 1 and Table 1). The first one is the Limestone region, a region of deep loamy soils where the cereals are often cropped at least twice in a three-crop rotation scheme, alternately with spring crops such as potato, sugar beet, maize, chicory or vegetables. The second region is the Polders, located near the North Sea cost, 200 km away from the first one. The region of Polders is characterized by heavy clay soils where wheat is often grown in monoculture. Each of the three studied wheat midge can be found in both regions, but the Limestone region is mostly infested by *S. mosellana*, whereas the Polders by *H. marginata* and *C. tritici*. The soil of each field was sampled by taking randomly at least 16 soil cores (10 cm deep, 28.3 cm^2 in area) at a given date using a bulb planter. These cores, collected at least 10 m apart, were bulked in one soil sample to represent the field at a given date. The exact number of soil cores taken per sample is given in the Table 1.

Wheat midge larvae extraction and insect rearing

For the extraction of midge larvae, the method used was adapted from Doane et al. (1987). Each soil sample was put in a 5 l bucket filled with water and kneaded until full dispersion. The water, still containing the soil, was then poured through three successive sieves with mesh sizes of 2.8, 1.0 and 0.3 mm. This operation was repeated until the entire sample had been filtered. Only the sieve with the 0.3 mm mesh size retained the larvae of *S. mosellana* and *C. tritici*, whereas the larvae of *H. marginata* were also retained by the 1.0 mm mesh size. The larvae were isolated

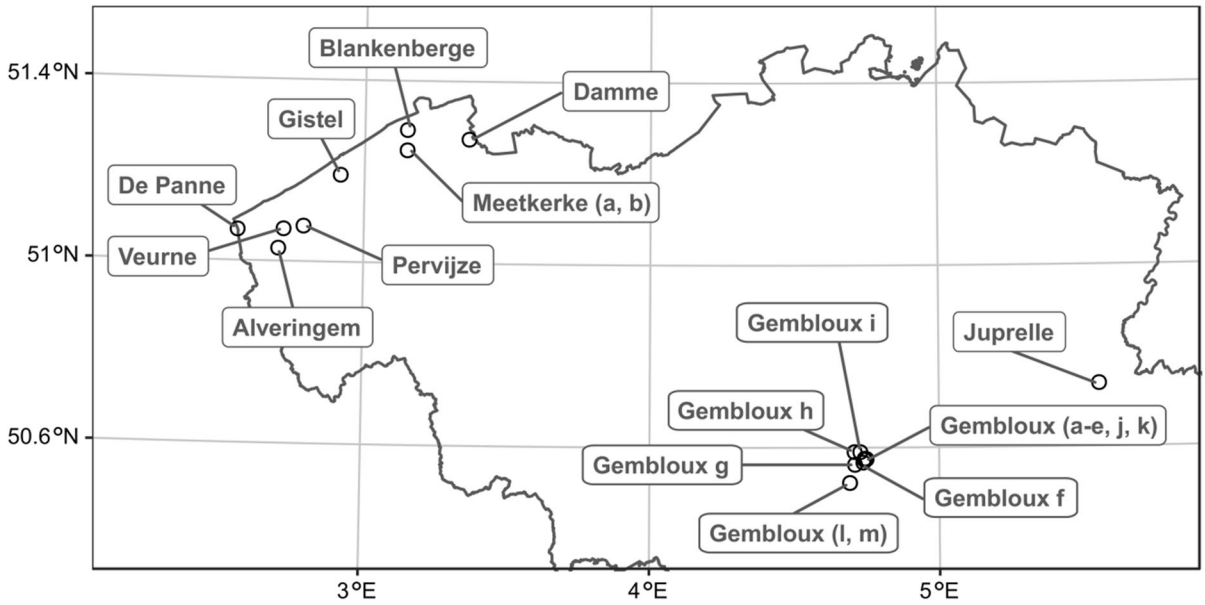

Fig. 1 Location of the sampled fields to study the parasitism of wheat midges, *S. mosellana*, *C. tritici* and *H. marginata* in Belgium in 2011–2014. Samples (1–31) from these fields are described in Table 1

Table 1 Description of samples used to study the parasitism of wheat midges, *S. mosellana*, *H. marginata* and *C. tritici* in 2011–2014. All fields are located in two cereal-growing regions of Belgium

Sample	Field	Cereal-growing region	Soil sampling date	Number of soil cores	Previous crop
1	Gembloux a	Limestone region	20 September 2011	40	Winter wheat
2	Gembloux b	Limestone region	29 November 2011	80	Winter wheat
3	Juprelle	Limestone region	15 December 2011	40	Winter barley
4	Juprelle	Limestone region	06 March 2012	40	Winter barley
5	Gembloux a	Limestone region	29 January 2013	20	Chicory
6	Gembloux c	Limestone region	19 February 2013	40	Winter wheat
7	Gembloux d	Limestone region	19 February 2013	40	Winter wheat
8	Gembloux e	Limestone region	27 February 2013	40	Sugar beets
9	Gembloux b	Limestone region	08 April 2013	20	Winter wheat
10	Gembloux f	Limestone region	24 April 2013	20	Winter wheat
11	Gembloux g	Limestone region	24 February 2014	50	Winter wheat
12	Gembloux h	Limestone region	04 March 2014	40	Winter wheat
13	Gembloux i	Limestone region	04 March 2014	40	Winter wheat
14	Gembloux a	Limestone region	19 March 2014	40	Winter wheat
15	Gembloux c	Limestone region	19 March 2014	40	Winter wheat
16	Gembloux j	Limestone region	19 March 2014	40	Winter wheat
17	Gembloux k	Limestone region	19 March 2014	40	Winter wheat
18	Gembloux l	Limestone region	24 March 2014	40	Winter wheat
19	Gembloux m	Limestone region	24 March 2014	40	Winter wheat
20	Veurne	Polders	01 December 2011	40	Winter wheat
21	Meetkerke a	Polders	01 December 2011	40	Winter wheat
22	Alveringem	Polders	19 March 2012	24	Winter wheat
23	Pervijze	Polders	13 February 2013	16	Winter wheat
24	Gistel	Polders	13 February 2013	16	Winter wheat
25	Meetkerke a	Polders	13 February 2013	16	Ryegrass
26	Meetkerke b	Polders	13 February 2013	16	Winter wheat
27	Blankenberge	Polders	11 March 2013	60	Winter wheat
28	De Panne	Polders	11 March 2014	40	Winter wheat
29	Gistel	Polders	11 March 2014	40	Winter wheat
30	Meetkerke a	Polders	11 March 2014	40	Winter wheat
31	Damme	Polders	11 March 2014	40	Winter wheat

species by species on a moist filter paper in Petri dishes and were kept at room temperature (20 ± 2 °C) and at natural photoperiod until either the midge or parasitoid emerged, two weeks to three months later.

Identification of the insects

Sitodiplosis mosellana, Contarinia tritici and *Haplodiplosis marginata* were identified with the keys for Cecidomyiidae of Harris (1966) and Skuhrava (1997). *Macroglenes penetrans* was identified using the key for Pteromalidae of Graham (1969) and the description given by Johansson (1936). *Platygaster* spp. were identified with the key for *Platygaster* of Buhl (2006) and the specific descriptions for each species: *P. tuberosula* with Kieffer (1926) and Johansson (1936), *P. gracilipes* (Huggert) with Huggert (1975), *P. nisus* Walker with Vlug (1985) and *P. equestris* with Spittler (1969). *Euxestonotus* sp. and *Leptacis* sp. were identified using the key for Platygastridae of Kozlov (1978). The description given by Gahan (1933) was used for *Euxestonotus error*.

Amblyaspis tritici (Walker) and *Synopeas myles* were identified using the key for Platygastridae of Vlug (1985) and Buhl (1999), and the descriptions given by Kieffer (1926).

Wheat midge larval density and parasitism rate

For each wheat midge (*S. mosellana*, *H. marginata* and *C. tritici*), the density of larvae extracted from the soil of each sample was calculated. The results were expressed per 40 soil cores (= 1132 cm^2) for an easier comparison between samples (Table 2). The parasitism rate for each wheat midge and the proportion of larvae parasitized by each parasitoid species in the parasitoid complex were calculated. To test if the parasitism rate is related to the larval density in the soil, we fitted a Generalized Linear Mixed Model (GLMM) with a binomial distribution and logit link function with R 3.4.4 (R Development Core Team 2017) and the package lme4 1.1–15 (Bates et al. 2015). The parasitism rate was used as response, the larval density in the soil as fixed explanatory variable and the field as random effect to take into account the repeated sampling on the same field during different years. An observation level random effect was added to take into account the overdispersion. In addition to this GLMM we performed binomial Generalized Additive Mixed Models (GAMM) with an identical model structure and with a smoothing term for density (package mgcv 1.8–23, Wood 2017). The aim was to check whether a non-linear relationship (on the logit scale) would fit better the data. The GAMM results provide approximate significance testing for the the smoothing term along with "estimated degrees of freedom" (edf) that are an estimate of the "wigglyness" of the relationship. An edf value of 1 indicates a linear relationship while higher values appear for non linear relationships of increasing complexity. These analyses were made for *S. mosellana* and *H. marginata* and not for *C. tritici* because it was only parasitized in one sample.

Results

Wheat midge larvae

Sitodiplosis mosellana was the most commonly observed wheat midge: it was present in the 31 samples sites (Table 2). *Haplodiplosis marginata* was also often detected (27 out of 31 samples), whereas *C. tritici* was clearly less widespread (ten out of 31 samples). The same ranking can be seen from the frequency of high population densities: *S. mosellana* with 19 samples showing more than 50 larvae per 40 soil cores; *H. marginata* with three samples showing more than 50 larvae per 40 soil cores; *C. tritici* with one sample showing more than 50 larvae per 40 soil cores. The high levels of *H. marginata* and especially *C. tritici* were observed in the Polders region. Only one larva of *C. tritici* was found outside the Polders region. For *S. mosellana*, the highest levels were observed in the Limestone region, but high populations can also be observed in the Polders.

Parasitism of wheat midges

The rearing of wheat midge larvae extracted for each sample enabled the parasitism rates to be determined and the parasitoid species to be identified (Fig. 2 and Table 2). The parasitism rates varied greatly from sample to sample for each of the three species of wheat midge. According to the binomial GLMM, the parasitism rate was not related to the larval density in the soil neither for *S. mosellana* (Likelihood Ratio Test (LRT) $\chi^2 = 0.0016$, df = 1, p = 0.967) nor for *H. marginata* (LRT: $\chi^2 = 0.0462$, df = 1, p = 0.8297) (Fig. 3). The GAMM shows a very flat U shaped relationship for *S. mosellana* (Fig. 3) but the smoothing term for density is not significant (edf = 1.99, p = 0.104). The GAMM model for *H. marginata* is very close to the GLMM (almost linear on the logit scale) and the smoothing term for density is not significant either (edf = 1, p = 0.552). Our data does not support any clear relationship between the parasitism rate and the density in the soil.

For *S. mosellana*, eight parasitoid species belonging to two families of Hymenoptera were identified: *Macroglenes penetrans* (Kirby) (Pteromalidae), *Amblyaspis tritici* (Walker) (Platygastridae), *Euxestonotus error* (Fitch) (Platygastridae), *Euxestonotus* sp. Fouts (Platygastridae), *Leptacis* sp. Foerster (Platygastridae), *Platygaster gracilipes* (Huggert) (Platygastridae), *Platygaster nisus* Walker (Platygastridae) and *Platygaster tuberosula* (Kieffer) (Platygastridae). The parasitism rates varied greatly, from 3 to 100%, depending on the sample. Parasitoids of *S. mosellana* were present in all the samples infested by this midge, but the relative abundance of each species in the

Table 2 For each sample and for each wheat midge (*S. mosellana*, *H. marginata* and *C. tritici*), larval density extracted, total number of larvae extracted from soil and number of larvae parasitized by each parasitoid species. Larval density corresponds to number of larvae extracted per 40 soil cores (= 1132 cm^2). Parasitism rate for each wheat midge and proportion of each parasitoid species in the parasitoid complex are in italics. *M. penetrans* is the only parasitoid belonging to the Pteromalidae family. All the other parasitoids species belong to the Platygastridae family. All fields are located in two cereal-growing regions of Belgium: the Limestone region (a) and the Polders region (b)

a

		Sitodiplosis mosellana													*Haplodiplosis marginata*						*Contarinia tritici*				
		Larvae extracted				Parasitoid species									Larvae extracted				Parasitoid species		Larvae extracted				Parasitoid species
Sample	Field	Density (per 1132 cm^2)	Total	Unparasitized	Parasitized	*Macroglenes penetrans*	*Amblyaspis tritici*	*Euxestonotus error*	*Euxestonotus* sp.[1]	*Leptacis* sp.	*Platygaster gracilipes*	*Platygaster nisus*	*Platygaster tuberculosa*	Platygastridae spp.[2]	Density (per 1132 cm^2)	Total	Unparasitized	Parasitized	*Platygaster equestris*	Platygastridae spp.[2]	Density (per 1132 cm^2)	Total	Unparasitized	Parasitized	*Synopeas myles*
1	Gembloux a	134	134	130	4	1	0	0	0	0	0	0	0	3	14	14	10	4	2	2	0	0	-	-	-
				97%	*3%*	*25%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*75%*			*71%*	*29%*	*50%*	*50%*					
2	Gembloux b	71	142	138	4	1	0	0	0	0	0	0	0	3	14	27	19	8	0	8	0	0	-	-	-
				97%	*3%*	*25%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*75%*			*70%*	*30%*	*0%*	*100%*					
3	Juprelle	38	38	26	12	5	1	2	0	0	0	0	3	1	0	0	-	-	-	-	0	0	-	-	-
				68%	*32%*	*42%*	*8%*	*17%*	*0%*	*0%*	*0%*	*0%*	*25%*	*8%*											
4	Juprelle	126	126	71	55	27	0	13	0	0	0	1	11	3	7	7	6	1	0	1	0	0	-	-	-
				56%	*44%*	*49%*	*0%*	*24%*	*0%*	*0%*	*0%*	*2%*	*20%*	*5%*			*86%*	*14%*	*0%*	*100%*					
5	Gembloux a	52	26	18	8	7	0	1	0	0	0	0	0	0	2	1	1	0	-	-	0	0	-	-	-
				69%	*31%*	*88%*	*0%*	*13%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*			*100%*	*0%*							
6	Gembloux c	186	186	153	33	21	0	6	6	0	0	0	0	0	11	11	5	6	0	6	0	0	-	-	-
				82%	*18%*	*64%*	*0%*	*18%*	*18%*	*0%*	*0%*	*0%*	*0%*	*0%*			*45%*	*55%*	*0%*	*100%*					
7	Gembloux d	14	14	12	2	1	0	0	0	0	0	0	0	1	5	5	5	0	-	-	0	0	-	-	-
				86%	*14%*	*50%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*50%*			*100%*	*0%*							
8	Gembloux e	7	7	3	4	3	0	0	0	0	0	0	1	0	0	0	-	-	-	-	0	0	-	-	-
				43%	*57%*	*75%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*25%*	*0%*											
9	Gembloux b	50	25	17	8	6	0	0	0	0	0	0	1	1	10	5	5	0	-	-	0	0	-	-	-
				68%	*32%*	*75%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*13%*	*13%*			*100%*	*0%*							
10	Gembloux f	76	38	37	1	1	0	0	0	0	0	0	0	0	2	1	1	0	-	-	0	0	-	-	-
				97%	*3%*	*100%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*			*100%*	*0%*							
11	Gembloux g	234	292	198	94	66	0	16	7	0	0	0	0	5	2	2	2	0	-	-	1	1	1	0	-
				68%	*32%*	*70%*	*0%*	*17%*	*7%*	*0%*	*0%*	*0%*	*0%*	*5%*			*100%*	*0%*					*100%*	*0%*	
12	Gembloux h	29	29	25	4	4	0	0	0	0	0	0	0	0	0	0	-	-	-	-	0	0	-	-	-
				86%	*14%*	*100%*	*0%*	*0%*	*0%*	*0%*	0%	*0%*	*0%*	*0%*											
13	Gembloux i	18	18	16	2	2	0	0	0	0	0	0	0	0	2	2	2	0	-	-	0	0	-	-	-
				89%	*11%*	*100%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*			*100%*	*0%*							
14	Gembloux a	21	21	17	4	4	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	-	-	-
				81%	*19%*	*100%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*			*0%*	*100%*	*0%*	*100%*					
15	Gembloux c	47	47	30	17	16	0	0	0	0	0	0	1	0	3	3	2 67%	1	0	1	0	0	-	-	-
				64%	*36%*	*94%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*6%*	*0%*				*33%*	*0%*	*100%*					
16	Gembloux j	41	41	31	10	9	0	1	0	0	0	0	0	0	2	2	1 50%	1	0	1	0	0	-	-	-
				76%	*24%*	*90%*	*0%*	*10%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*				*50%*	*0%*	*100%*					
17	Gembloux k	80	80	67	13	4	0	6	0	1	0	0	2	0	5	5	5	0	-	-	0	0	-	-	-
				84%	*16%*	*31%*	*0%*	*46%*	*0%*	*25%*	*0%*	*0%*	*15%*	*0%*			*100%*	*0%*							
18	Gembloux l	235	235	152	83	55	0	8	0	0	0	0	16	4	3	3	3	0	-	-	0	0	-	-	-
				65%	*35%*	*66%*	*0%*	*10%*	*0%*	*0%*	*0%*	*0%*	*19%*	*5%*			*100%*	*0%*							
19	Gembloux m	35	35	19	16	9	0	0	1	0	0	0	4	2	3	3	3	0	-	-	0	0	-	-	-
				54%	*46%*	*56%*	*0%*	*0%*	*6%*	*0%*	*0%*	*0%*	*25%*	*13%*			*100%*	*0%*							

b

		Sitodiplosis mosellana													*Haplodiplosis marginata*						*Contarinia tritici*				
		Larvae extracted				Parasitoid species									Larvae extracted				Parasitoid species		Larvae extracted				Parasitoid species
Sample	Field	Density (per 1132 cm^2)	Total	Unparasitized	Parasitized	*Macroglenes penetrans*	*Amblyaspis tritici*	*Euxestonotus error*	*Euxestonotus* sp.[1]	*Leptacis* sp.	*Platygaster gracilipes*	*Platygaster nisus*	*Platygaster tuberculosa*	Platygastridae spp.[2]	Density (per 1132 cm^2)	Total	Unparasitized	Parasitized	*Platygaster equestris*	Platygastridae spp.[2]	Density (per 1132 cm^2)	Total	Unparasitized	Parasitized	*Synopeas myles*
20	Veurne	62	62	56	6	3	0	2	0	0	0	0	0	1	411	411	382	29	1	28	0	0	-	-	-
				90%	*10%*	*50%*	*0%*	*33%*	*0%*	*0%*	*0%*	*0%*	*0%*	*17%*			*93%*	*7%*	*3%*	97%					
21	Meetkerke a	3	3	0	3	3	0	0	0	0	0	0	0	0	96	96	96	0	-	-	5	5	5	0	-
				0%	*100%*	*100%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*			*100%*	*0%*					*100%*	*0%*	
22	Alveringem	197	118	88	30	7	0	7	0	0	0	1	3	12	112	67	61	6	0	6	3	2	2	0	-
				75%	*25%*	*23%*	*0%*	*23%*	*0%*	*0%*	*0%*	*3%*	*10%*	*40%*			*91%*	*9%*	*0%*	*100%*			*100%*	*0%*	
23	Pervijze	55	22	16	6	2	0	2	0	0	0	0	0	2	10	4	4	0	-	-	35	14	14	0	-
				73%	*27%*	*33%*	*0%*	*33%*	*0%*	*0%*	*0%*	*0%*	*0%*	*33%*			*100%*	*0%*					*100%*	*0%*	
24	Gistel	98	39	31	8	5	0	1	0	0	0	0	0	2	0	0	-	-	-	-	23	9	9	0	-
				79%	*21%*	*63%*	*0%*	*13%*	*0%*	*0%*	*0%*	*0%*	*0%*	*25%*									*100%*	*0%*	
25	Meetkerke a	30	12	10	2	1	0	0	0	0	0	0	0	1	3	1	1	0	-	-	0	0	-	-	-
				83%	*17%*	*50%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*50%*			*100%*	*0%*							
26	Meetkerke b	55	22	21	1	1	0	0	0	0	0	0	0	0	5	2	2	0	-	-	0	0	-	-	-
				95%	*5%*	*100%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*			*100%*	*0%*							
27	Blankenberge	95	143	140	3	2	0	0	0	0	0	0	1	0	45	68	67	1	0	1	1	1	1	0	-
				98%	*2%*	*67%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*33%*	*0%*			*99%*	*1%*	*0%*	*100%*			*100%*	*0%*	
28	De Panne	92	92	75	17	10	0	5	0	0	0	0	1	1	1	1	1	0	-	-	14	14	14	0	-
				82%	*18%*	*59%*	*0%*	*29%*	*0%*	*0%*	*0%*	*0%*	*6%*	*6%*			*100%*	*0%*					*100%*	*0%*	
29	Gistel	175	175	139	36	13	0	20	0	0	1	0	0	2	6	6	6	0	-	-	287	287	280	7	7
				79%	*21%*	*36%*	*0%*	*56%*	*0%*	*0%*	*3%*	*0%*	*0%*	*6%*			*100%*	*0%*					*98%*	*2%*	*100%*
30	Meetkerke a	72	72	46	26	20	0	3	0	0	1	0	1	1	1	1	1	0	-	-	2	2	2	0	-
				64%	*36%*	*77%*	*0%*	*12%*	*0%*	*0%*	*4%*	*0%*	*4%*	*4%*			*100%*	*0%*					100%	*0%*	
31	Damme	8	8	6	2	1	0	0	0	0	0	0	1	0	3	3	3	0	-	-	5	5	5	0	-
				75%	*25%*	*50%*	*0%*	*0%*	*0%*	*0%*	*0%*	*0%*	*50%*	*0%*			*100%*	*0%*					*100%*	*0%*	

[1]: Unidentified species of *Euxestonotus* but not *E. error*

[2]: Unidentified species of Platygastridae were parasitoids that had died before leaving their host or damaged by leaving their host, and that could not be identified up to the species

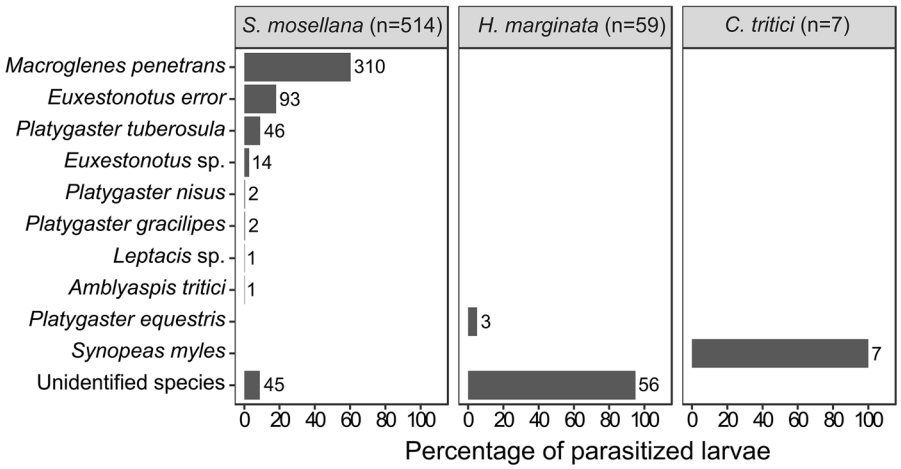

Fig. 2 Relative frequency of parasitoid species in the parasitoid complex of *S. mosellana*, *H. marginata* and *C. tritici*. n value corresponds to the total number of parasitized larvae

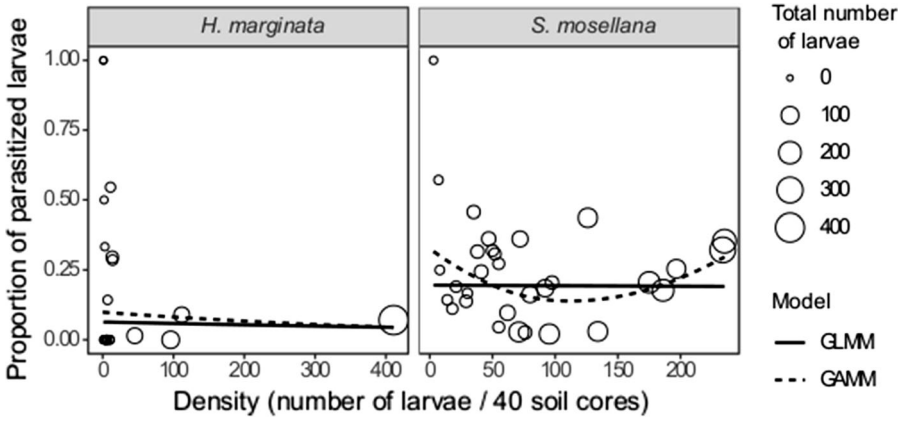

Fig. 3 Relationship between parasitism rate and larval density in the soil for *S. mosellana* and *H. marginata*. The x axis represents the density standardized to the same sampling effort (40 soil cores), while the size of circles represent the total number of observed larvae (not standardized). The continuous black lines are predictions from a binomial Generalized Linear Mixed Model (GLMM) and the dashed lines are predictions from a binomial Generalized Additive Mixed Model (GAMM). The parasitism rate versus density relationship is never statistically significant whatever the type of model used (see "Results" section for details)

parasitoid complex varied from sample to sample (Fig. 2). The Pteromalidae family, with only one species, *M. penetrans*, accounted for 23 to 100% of the parasitoid complex depending on the sample, whereas the Platygastridae family, with its seven identified species, accounted for 0–77% of the parasitoid complex. Of the seven species of Platygastridae, *E. error* and *P. tuberosula* are common parasitoid species of *S. mosellana*. The five other species of Platygastridae are rarer: *P. gracilipes* and *P. nisus* were found in two samples, whereas *A. tritici*, *Euxestonotus* sp. and *Leptacis* sp. were found in one sample.

For *H. marginata*, only one parasitoid species, belonging to the Platygastridae, was identified: *Platygaster equestris* (Spittler). The parasitism rates varied greatly, from 0 to 100%, and depended on the sample.

For *C. tritici*, only one parasitoid species belonging to the Platygastridae was identified: *Synopeas myles* (Walker). The population of only one sample out of the ten samples infested by *C. tritici* was parasitized with a low parasitism rate of 2%.

Discussion

The infestation levels by wheat midges varied strongly from sample to sample, even within the same cereal-growing region. This is not a surprise, because population levels of wheat midges are influenced by several factors specific to each field, such as the frequency with which susceptible cereals are cropped in the field itself but also in the surrounding area, the insecticide use habits, the reproductive success of midges in the last years (Barnes 1956; Elliott et al. 2011a; Oakley 1994), etc. Through this study, it appeared clearly that *H. marginata* and *C. tritici* are more abundant in the Polders region than in the Limestone region. All the high levels of *H. marginata* were found in the Polders. For *C. tritici*, results are even more contrasted: in the Limestone region only one sample out of 19 was very slightly infested by this midge with one specimen found, whereas 75% of the Polders samples were infested. This observation is probably connected to the type of soil in the Polders where heavy clay soils allowing higher moisture content, which could be more favourable for *H. marginata* and *C. triciti* (Basedow and Schütte 1982; Censier et al. 2015). Other explanatory factors like the climate cannot be excluded.

The parasitism rate varied greatly for the three species of wheat midge depending on the sample, but it was not related to the larval density of wheat midge in the soil. Similar results were observed by Smith et al. (2004) who showed that the parasitism rate of *S. mosellana* by *M. penetrans* was not related to the density of midge larvae in the wheat ears. In another study, however, Affolter (1990) found that the relationship between the absolute number of parasitized larvae and the midge density in the wheat ears followed (weakly) a Holling II functional response. With this model, the number of parasitized larvae is null for a density close to zero then increases with density and reaches slowly a plateau where the number of parasitized larvae is independent from the density. Several reasons might explain the contrasted results observed in these three studies in term of parasitism rate - host density relationship. Firstly, the Holling II relationship observed by Affolter (1990) implies that, when the host density is very low, the link between parasitism and host density is positive, whereas this link becomes weaker when the host density is very high (up to a plateau). This result suggests that when the reproductive success of the midges is very high, the population of parasitoids might not be able to saturate the host population. Hence, the result of the parasitism rate versus host density regression will depend highly on the range of host densities observed. Secondly, the parasitism rate - host density relationship can vary with the scale of observation (field, plant, etc.) (Norowi et al. 2000; Segoli 2016). In the present study, the host density measured is the density in the soil after winter, while the two other studies (Affolter 1990; Smith et al. 2004) measured the densities (and the parasitism rate) directly in the wheat ears before the winter. The density after winter takes into account the winter mortality that can be caused by several other factors than parasitism: predation, pathogens, climate, etc., which may explain the absence of parasitism rate - host density relationship. From the point of view of the protection of future cultures, the parasitism rate and midges density after winter is probably the most interesting measure. Indeed, it provides the real ratio between the midges that will emerge in the spring to attack new cultures and the number of parasitoids that might control their offspring. Third, Affolter (1990) present a curve of the absolute number of parasitized larvae while Smith et al. (2004) and Fig. 3 of the present study show the parasitism rate (i.e. the relative number of parasitized larvae). This difference makes the results difficult to compare. The absolute number of parasitized larvae is expected to increase at least monotonically when the density of the host increases (more hosts means potentially more parasitized hosts) unless a saturation point is reached (causing the plateau of the Holling II response). In the present study, using the absolute number of parasitized larvae instead of the parasitism rate does show indeed a logarithmic increase (Poisson GLMM and GAMM with log link) when the density in the soil increases and hence not any plateau in contrast with Affolter results (for details, see Sect. 3.6 in the figshare repository supplementary materials).

Of the eight hymenopterous species identified as parasitoids of *S. mosellana* in this study (Table 3), three are well-known parasitoid species of *S. mosellana* and were observed in previous studies: *M. penetrans*, *E. error* and *P. tuberosula*. The two species of the *Platygaster*, *P. gracilipes* and *P. nisus*, were never recorded as parasitoids of *S. mosellana* in the literature but they correspond perhaps to parasitoids identified as *Platygaster* sp. in several studies

Table 3 Referenced hosts for parasitoid species identified in this study and their geographical distribution. *Euxestonotus* sp. Fouts (Platygastridae) and *Leptacis* sp. Foerster (Platygastridae) are not included in this table because the specimens were not identified to the species. The parasitoid species are listed in alphabetic order within the two families of Hymenoptera (Platygastridae and Pteromalidae) and the host species for each parasitoid species are listed in alphabetic order

Parasitoid species	Geographical distribution	Host species (Cecidomyiidae)	References
Amblyaspis tritici (Walker) (Platygastridae)[a]	Europe	*Sitodiplosis mosellana* (Géhin)	Abram et al. (2012)
Euxestonotus error (Fitch) (Platygastridae)	Europe, North America and Asia	*Rhabdophaga* sp. (Westwood)	Various contributors (2018)
		Sitodiplosis mosellana (Géhin)	Affolter (1990), Barnes (1956), Chavalle et al. (2015a), Echegaray et al. (2016), Gahan (1933)
Platygaster equestris (Spittler)	Europe	*Haplodiplosis marginata* (von Roser)	Buhl and Koponen (2003), Buhl and Notton (2009), Spittler (1969)
Platygaster gracilipes (Huggert) (Platygastridae)[a]	Europe	*Sitodiplosis mosellana* (Géhin)	Buhl and Koponen (2003)
Platygaster nisus Walker (Platygastridae)[a]	Europe	*Sitodiplosis mosellana* (Géhin)	Buhl and Koponen (2003)
Platygaster tuberosula (Kieffer) (Platygastridae)	Europe and introduced in Canada for biological control	*Dasineura mali* (Kieffer)	Various contributors (2018)
		Sitodiplosis mosellana (Géhin)	Affolter (1990), Barnes (1956), Chavalle et al. (2015a), Johansson (1936), Olfert et al. (2003)
Synopeas myles (Walker) (Platygastridae)	Europe	*Contarinia medicaginis* (Kieffer)	Romankow and Dankowska (1993)
		Contarinia nasturtii (Kieffer)	Abram et al. (2012), Buhl and Notton (2009)
		Contarinia pisi (Winnertz)	Keller and Schweizer (1994)
		Contarinia tritici (Kirby)	Abram et al. (2012), Affolter (1990)
		Dasineura crataegi (Winnertz)	New record from Denmark, S. Haarder leg., Buhl det. 2017
		Dasineura ignorata (Wachtl)	Romankow and Dankowska (1994)
		Dasineura mali (Kieffer)	Buhl det.
		Dasineura marginemtorquens (Bremi)	Strong and Larsson (1992)
		Dasineura viciae (Kieffer)	Buhl and Notton (2009)
Macroglenes penetrans (Kirby) (Pteromalidae)	Europe, North America and Asia	*Sitodiplosis mosellana* (Géhin)	Affolter (1990), Barnes (1956), Chavalle et al. (2015a), Doane et al. (1989), Elliott et al. (2011b), Ellis et al. (2009), Noyes (2018)

[a]To our best knowledge, no data on the hosts of these three Platygastridae has been published in the literature until the present study

(Affolter 1990; Barnes 1956). *Amblyaspis tritici* has never been recorded as a parasitoid of *S. mosellana*. The exact species of the specimen *Euxestonotus* sp. and the specimen *Leptacis* sp. could not be identified because of their poor state of preservation, but it can be said with certainty that the specimen *Euxestonotus* sp. was not *E. error*, the only species of *Euxestonotus* genus recorded as a parasitoid of *S. mosellana* (Affolter 1990; Barnes 1956). The only species of *Leptacis* presented as a parasitoid of blossom wheat midges (i.e., *S. mosellana* and *C. tritici*) was *Leptacis tipulae* (Affolter 1990; Barnes 1956; Doeksen 1939;

Speyer and Waede 1956), which was also recorded as parasitoid of *Contarinia pisi* (Winnertz) (Barnes 1956; Bollinger 1968). Each parasitoid species identified for *H. marginata* and *C. tritici* in our study is a well-known parasitoid recorded in previous studies (Table 3): *Platygaster equestris* and *Synopeas myles*, respectively. For *S. mosellana* and *H. marginata*, several parasitoids were Platygastridae spp. for which the species could not be identified because they had died before leaving their host or had been damaged. The parasitoid complex identified for these two midges could be incomplete. Through this study conducted in Belgium, it appears that the three wheat midges have totally distinct parasitoid complexes as Affolter (1990) showed was the case in Switzerland for *S. mosellana* and *C. tritici*. They do not share any parasitoid species.

Although the three species of wheat midge are present in the same type of agro-ecosystem, attack the same host plants and are overlapping in their life cycle, their parasitoid complex is distinct. Several factors could explain these distinct parasitoid complexes such as the geographical distributions of hosts and of their parasitoids, the synchronization with host, the host specificity, the longevity and the fecundity of parasitoids, the searching behaviour of host, the larval competition in case of supernumerary parasitism, etc. At a large scale, the parasitoid complexes can be directly influenced by the distribution of wheat midges and this for each of their parasitoids. *S. mosellana* and *C. tritici* occur in Europe, North America and Asia (Barnes 1956; Affolter 1990), whereas *H. marginata* occurs only in Europe (Censier et al. 2015). Among the parasitoid species identified in this study, the distribution also varies, and all parasitoid species are not present in the geographical area of their host (Table 3). Among parasitoid species, the synchronization with their host and the host specificity varies because some parasitoids can attack also other hosts. *M. penetrans*, the only parasitoid from the family Pteromalidae, is considered as a specific parasitoid of *S. mosellana* (Affolter 1990). The biology of *M. penetrans* was described by Doane et al. (1989) and several studies have shown that its emergence is closely synchronized with the emergence of its single host and seems to coincide closely with the egg-laying date of the host (Affolter 1990; Chavalle et al. 2015a; Doane and Olfert 2008; Elliott et al. 2011b; Ellis et al. 2009). For the parasitoids from the family Platygastridae, the biology and phenology of many species are poorly known. However, they are probably similar to many Platygastridae species that are specialist parasitoids attacking a single host or a few very closely related species (Austin et al. 2005), though several species, especially in recent years, have been documented from a taxonomically wide range of midge hosts as well as host plants (Buhl, pers. observations), adding weight to the hypothesis of diverse refuges in agricultural environments. Among the parasitoid species of Platygastridae identified in this study, several species are known parasitoids of other midge species (Cecidomyiidae) (Table 3). The biology of *E. error* and *Platygaster* sp. was described by Affolter (1990) and several studies have shown that *E. error* and *P. tuberosula* emerge either before or after their host, depending on the meteorological conditions (Affolter 1990; Chavalle et al. 2015a; Olfert et al. 2003). If the host specificity of the parasitoids of Platygastridae is less strict (several hosts, emergences moderately synchronized with *S. mosellana*), they could be less effective parasitoids than *M. penetrans* for controlling *S. mosellana*, but the population of these generalist parasitoids could be maintained more easily on multiple hosts, in case of a population collapse of one of them. The searching behaviour of host by the parasitoids conditions also their effectiveness. For example, *M. penetrans* has a very long ovipositor allowing it to parasitize the eggs of *S. mosellana* which are deeply hidden in the spikelets and therefore inaccessible to *E. error* and *Platygaster* spp. with short ovipositors. Eggs on the rachis are almost never attacked by *M. penetrans* which only probes between glume and glumella (Affolter 1990). These searching behaviours can also explain why the parasitoid complex is distinct.

The parasitism rates observed in several fields suggest that parasitoids can contribute to the biological control of wheat midges and that they could play a role in the regulation of their populations. These observations have already been observed in previous studies, in particular for *S. mosellana* (Affolter 1990; Barnes 1956; Oakley 1994; Olfert et al. 2009). However, the results of this study seem to indicate that the population of parasitoids might not be able to saturate the host population when the levels of wheat midge populations are high. The main methods used to manage wheat midges and minimize the yield losses are based on insecticide treatments, and, only for *S.*

mosellana, on growing resistant wheat cultivars (Chavalle et al. 2017). Both practices can have a negative impact on its parasitoids. Growing resistant wheat cultivars could be a trap for parasitoids, and would decrease the parasitoid populations where their host has been decimated (Smith et al. 2004). The use of interspersed refuges, as recommended by Smith et al. (2004), would conserve a host population to preserve the parasitoid populations. Insecticide treatments against wheat midges use broad-spectrum insecticides that affect the pest as well as its parasitoids. Information on the abundance of parasitoids in a midge population could have an impact on the usefulness of insecticide treatments. The preservation and the promotion of parasitoid populations could reduce dependence on chemical control and improve the integrated management of wheat midges.

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Data availability All raw datasets and the R code used to perform the graphs and statistical analyses are available in a public repository: https://doi.org/10.6084/m9.figshare.5794551.v1.

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