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Revisiting Classical Biological Control Through the New Associations Between the Invasive Pest *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) and Local Parasitoids

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Abstract: *Spodopotera frugiperda* is a worldwide invasive pest that has caused major economic damage. According to classical biological control theory, natural enemies that can control invasive pests come from the area of origin as the pests that have gone through coadaptation processes. Our study, however, suggests that new associations between *S. frugiperda* and local natural enemies offer insights into the possibilities of biological control using local parasitoids. The research was conducted through a rapid survey in Yogyakarta, Indonesia, covering four districts in Sleman, Bantul, Gunung Kidul, and Kulon Progo from September 2019 to June 2022. The results showed a stable increase of parasitoid species richness found yearly, with 15 parasitoid species associated with *S. frugiperda*. Four egg parasitoids, eight larval parasitoids, and three pupal parasitoids were found to be associated with *S. frugiperda* for three years after it was first discovered in Indonesia. *Telenomus remus* is the most dominant parasitoid, with a higher abundance and parasitism rate than other parasitoids. A new association was found between *S. frugiperda* and twelve parasitoid species, consisting of three egg parasitoids (*Telenomus remus*, Hymenoptera sp.1 and Hymenoptera sp.2), six larval parasitoids (*Apanteles* sp., *Microplitis* sp., *Campoletis* sp., *Coccygidium* sp., *Eupelmus* sp., and *Stenobracon* sp.), and three pupal parasitoids (*Brachymeria lasus*, *B. femorata,* and *Charops* sp.). This study also reported the first findings of the association of *S. frugiperda* with the larval parasitoid *Megaselia scalaris* in Indonesia. The result suggests the revisit of classical biological control and that local natural enemies can foster quick adaptation to invasive pests.

Keywords: *Brachymeria*; *Eupelmus*; host-parasite interaction; local adaptation; Platygasteridae; *Telenomus remus*; *Stenobracon*

1. Introduction

The appearance of invasive pests is a problem that requires attention because it may threaten agriculture and the variety of local species [1] and cause biotic homogenization [2]. *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae) is an invasive pest from America. It has become a new pest in Indonesia since early 2019 [3]. This pest has a wide range of distribution. It has now spread to 32 provinces in Indonesia, including Sumatra [4], Java [5], Kalimantan [6], and Sulawesi [7]. *Spodoptera frugiperda* infestations should be severely considered since a population of 0.2 to 0.8 S. *frugiperda* larvae/plant can decrease maize productivity by 20 to 50% [3]. Reports of damage due to *S. frugiperda* have been reported in several countries, such as Ethiopia and Kenya (32 - 47%) [8], Zimbabwe (32 - 48%) [9], Ghana (22 - 67%) [10], and Indonesia (60%) [11]. *Spodoptera frugiperda* has reportedly replaced the position of Asian corn borer *Ostrinia furnacalis* Guenée (Lepidoptera: Crambidae) as the primary pest of maize in China [12]. Rizali et al. [2] mentioned that the presence of *S. frugiperda* significantly decreases the intensity of attack of other lepidopteran pests and indirectly causes negative effects on the diversity of their natural enemies (particularly predators) in different maize fields in Indonesia.

Several studies have been reported since *S. frugiperda* was first reported in Indonesia. The studies were mostly focused on the presence/absence, diversity, infestation level, and ecology of *S. frugiperda* [5,13–16]. Research on the performance of local parasitoid species in Indonesia in parasitizing *S. frugiperda* on a lab scale has even been reported [17,18]. Surveys on the infestation level of *S. frugiperda*, the association between S. *frugiperda* with local parasitoids, and its associated parasitism rate have also been carried out but limited within a specific period [2,5,19–28]. Preliminary research in Yogyakarta, Indonesia, showed a low attack rate from local parasitoids toward *S. frugiperda* [29]. Thus, there is scattered information regarding the possibility of a new association between *S. frugiperda* and local parasitoids.

According to classical biological control theory, invasive pest control can be carried out by importing parasitoids from the original habitat of the pest, which have been proven as potential biological agents [30]. For example, the introduction of *Rodolia cardinalis* Mulsant (Coleoptera: Coccinellidae) to control the cotton aphid, *Icerya purchasi* Maskell (Hemiptera: Margarodidae) in California [31], and the introduction of *Urophora affinis* Frauenfeld and *U. quadrifasciata* Meigen (Diptera: Tephritidae) to control spotted knapweed *Centaurea maculosa* Lam. and *C. diffusa* Lamarck in western North America [32]. In Indonesia, the introduction of biological control agents was also carried out several times, such as the introduction of *Curinus coeruleus* Mulsant (Coleoptera: Coccinellidae) from Hawaii to control *Heteropsylla cubana* Crawford (Hemiptera: Psyllidae) on mimosoid tree *Leucaena leucocephala* [33], the introduction of *Anagyrus lopezi* De Santis (Hymenoptera: Encyrtidae) from Thailand to control cassava mealybugs *Phenacoccus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae) [34], and the introduction *of Cecidochares connexa* Macquart (Diptera: Tephritidae) from Columbia to control the invasive species - siam weed *Chromolaena odorata* L. [35].

The latest example provides important information that 28 years after introduction, *C. connexa* has been reported to be associated with several local parasitoid species [36–39]. Another example is the association between leaf miner *Liriomyza* spp. and local parasitoids in Indonesia. *Liriomyza* spp. is an invasive pest found in Indonesia from America in the 1990s [40]. *Liriomyza* spp. was reported to be associated with 11 parasitoid species in 2000 [41], and in 2022, *Liriomyza* spp. was associated with 18 local parasitoid species [42]. These findings support Hokkanen and Pimentel's old hypothesis [43] on the possibility of new associations that can be formed between herbivores and their local natural enemies. Therefore, this research aimed to study the diversity of parasitoids associated with *S. frugiperda* for three years after it was first discovered in Indonesia. This is important to study as an effort to prepare local biological agents potentially to be used in controlling *S. frugiperda* in the future.

2. Materials and Methods

2.1. Sampling Location Determination

Sampling locations were determined using a stratified random sampling method in four central districts in Yogyakarta, including Sleman, Bantul, Kulon Progo, and Gunung Kidul. Parasitoid sampling activities were carried out in all sub-districts in each district. A total of 2-3 villages were selected from each sub-district as sampling points. From each village, a maize field was chosen as a sampling point using GPS Essentials (mictale.com), resulting in 143 sampling points (Figure 1, Supplementary file). Sampling of parasitoids was carried out on maize fields during the vegetative phase (2-3 weeks old) because the highest *S. frugiperda* infestation occurs at this stage [13].

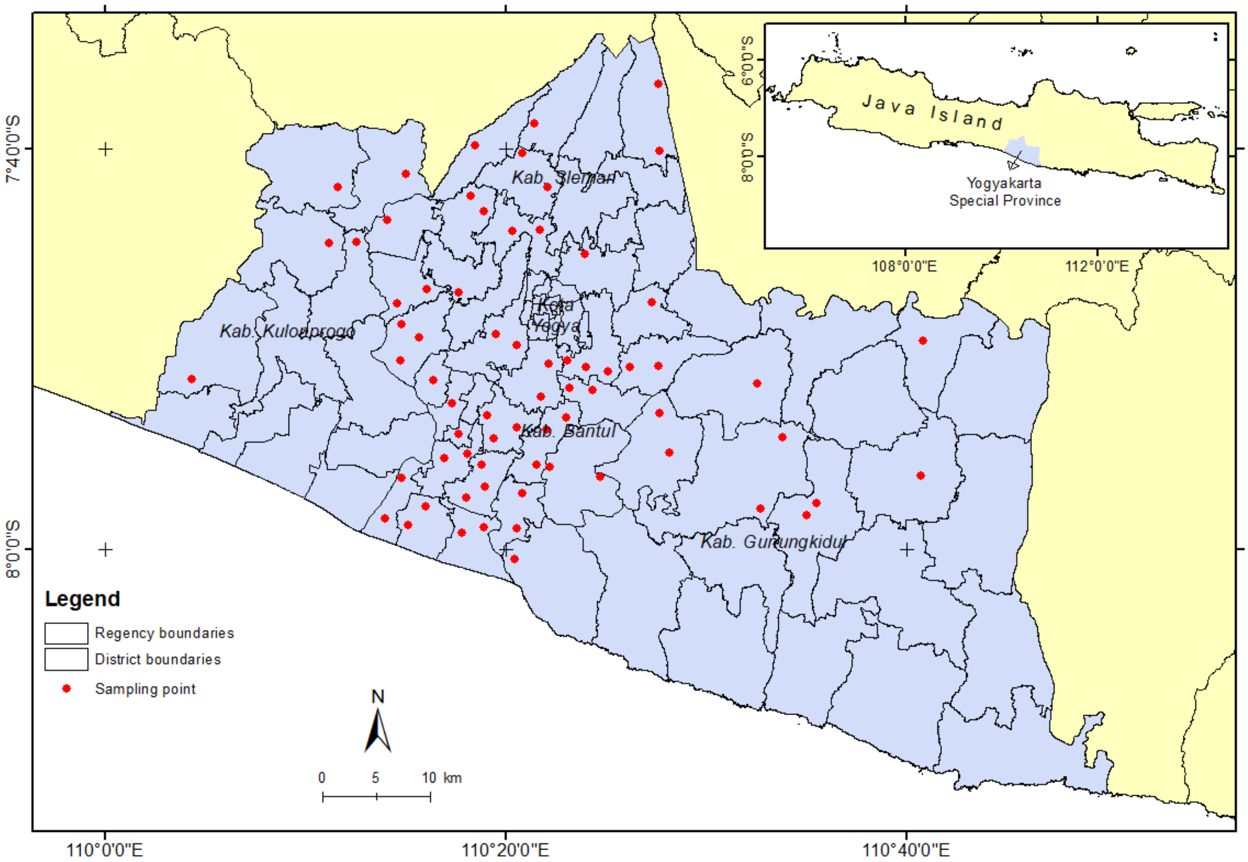

Figure 1. Sampling point of *S. frugiperda* parasitoid in Yogyakarta.

2.2. Sampling

The survey was carried out from September 2019 to June 2022. Sampling was carried out once on each field. Parasitoids were collected by collecting hosts (eggs, larvae, and pupae) of *S. frugiperda*, found on maize plants in every field. Sampling was carried out purposively by taking eggs, larvae, and pupae found. The samples obtained were brought from the field to the laboratory using an insect-rearing plastic container (21 x 21 cm) and then kept individually in plastic cups (400 ml) until moths or parasitoids appeared under laboratory conditions (26±1 °C, 60-80% r.h.). Parasitoids that appeared were counted, recorded, and grouped based on similar morphological characteristics, then preserved in a 1.5 ml microtube filled with 70% ethanol for further identification.

2.3. Parasitoid Identification

The parasitoids that appeared were identified at the Plant Protection Laboratory, Department of Agrotechnology, Universitas Muhammadiyah Yogyakarta. Identification of parasitoids was carried out by observing and matching the morphological characteristics of the parasitoids with some relevant literature [23,44–46]. The identified parasitoids were then documented and measured using TrueChromeII, TCapture 5.1 software (Fuzhou Tucsen Photonics Co., Ltd., China), and a Leica S6E Stereo Microscope (Leica Microsystems, Germany) at the Biological Control Laboratory, Department of Plant Protection, Faculty of Agriculture, IPB University. All identified parasitoids were confirmed at the Ecology and Systematics Laboratory, Faculty of Applied Science and Technology, Ahmad Dahlan University.

2.4. Data Analysis

The diversity (species richness and abundance) and parasitism rate of *S. frugiperda* parasitoids were tabulated using a pivot table on Microsoft Office Excel 365. Parasitoid distribution was mapped

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based on sampling points (regional administrative data) using ArcGis 10 (ESRI, Environmental Systems Research Institute, California, USA).

3. Results

The results showed that 15 species of parasitoids were associated with *S. frugiperda*. 80% (12/15) of the parasitoids discovered were new associations (Table 1). Four species were egg parasitoids, eight were larval parasitoids, and three were pupal parasitoids. The egg parasitoids found were *Hymenoptera* sp.1 (Figure 2a), *Hymenoptera* sp.2 (Figure 2b), *Trichogramma* sp. (Figure 2c), and *Telenomus remus* (Figure 2d). The larval parasitoids found were Hymenoptera, such as *Apanteles* sp. (Figure 3a), *Campoletis* sp. (Figure 3b), *Coccygidium* sp. (Figure 3c), *Eupelmus* sp. (Figure 3d), *Microplitis* sp. (Figure 3e), *Stenobracon* sp. (Figure 3f), and *Diptera* such as *Archytas marmoratus* (Figure 4a) and *Megaselia sp.* (Figures 4b). Based on its morphological characteristics, we confirmed that the last Dipteran species is *M. scalaris* (Figure 5). Meanwhile, the pupal parasitoids found were *Brachymeria femorata* (Figure 6a), *Brachymeria lasus* (Figure 6b), and *Charops* sp.

Table 1. Diversity of *Spodoptera frugiperda*'s parasitoid in Special Region Yogyakarta, Indonesia.

Order	Family	Species	Abundance			
			Bantul	Gunung Kidul	Kulonprogo	Sleman
		Egg parasitoid				
Hymenoptera	Unknown	Hymenoptera sp.1*		49		
	Unknown	Hymenoptera sp.2*				21
	Platygasteridae	*Telenomus remus**	8536	831	476	2324
	Trichogrammatidae	*Trichogramma* sp.	198			
		Larval parasitoid				
Hymenoptera	Braconidae	*Apanteles* sp.*		27	12	110
	Ichneumonidae	*Campoletis* sp.*		1		1
	Braconidae	*Coccygidium* sp.*		1		1
	Eupelmidae	*Eupelmus* sp.*			6	
	Braconidae	*Microplitis* sp.*		15		19
	Braconidae	*Stenobracon* sp.*	3			
Diptera	Tachinidae	*Archytas marmoratus*	1			
	Phoridae	*Megaselia scalaris*	1			
		Pupal parasitoid				
Hymenoptera	Chalcididae	*Brachymeria femorata**	5			
	Chalcididae	*Brachymeria lasus**	3			
	Ichneumonidae	*Charops* sp.*	1			2
	Species richness		8	6	3	7
	Total abundance		8748	924	494	2478

* New association.

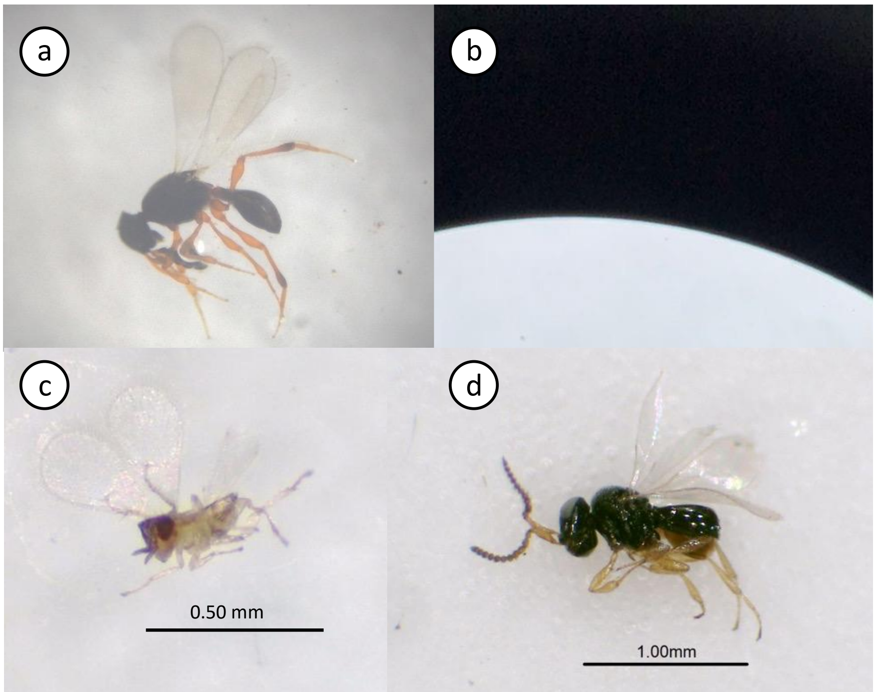

Figure 2. Egg parasitoid of *Spodoptera frugiperda* in Special Region Yogyakarta, Indonesia. a. *Hymenoptera* sp.1, b. *Hymenoptera* sp.2, c. *Trichogramma* sp., and d. *Telenomus remus*.

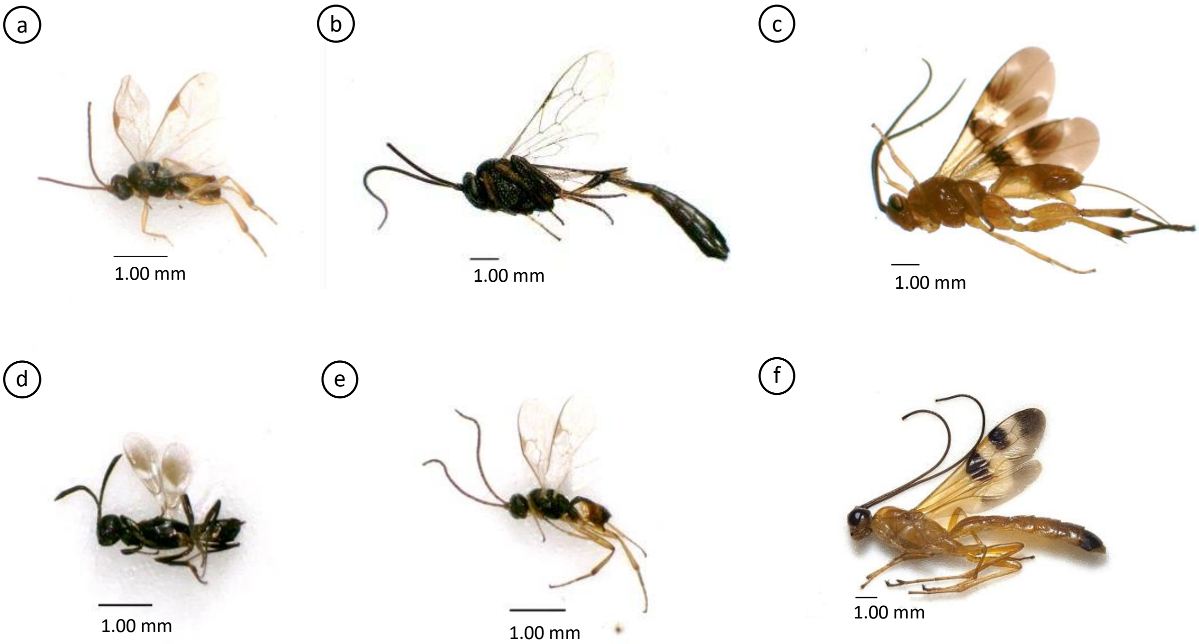

Figure 3. Larval parasitoid (Hymenoptera) of *Spodoptera frugiperda* in Special Region Yogyakarta, Indonesia. a. *Apanteles* sp., b. *Campoletis* sp., c. *Coccygidium* sp., d. *Eupelmus* sp., e. *Microplitis* sp., and e. *Stenobracon* sp.

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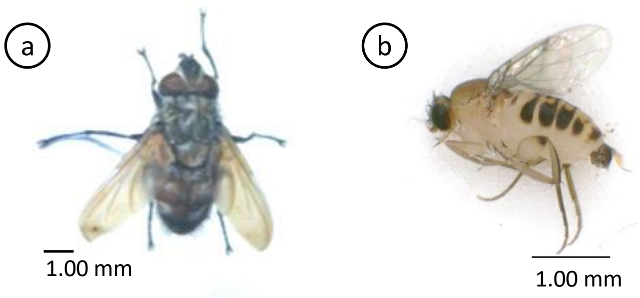

Figure 4. Larval parasitoid (Diptera) of *Spodoptera frugiperda* in Special Region Yogyakarta, Indonesia. a. *Archytas marmoratus* and b. *Megaselia scalaris.*

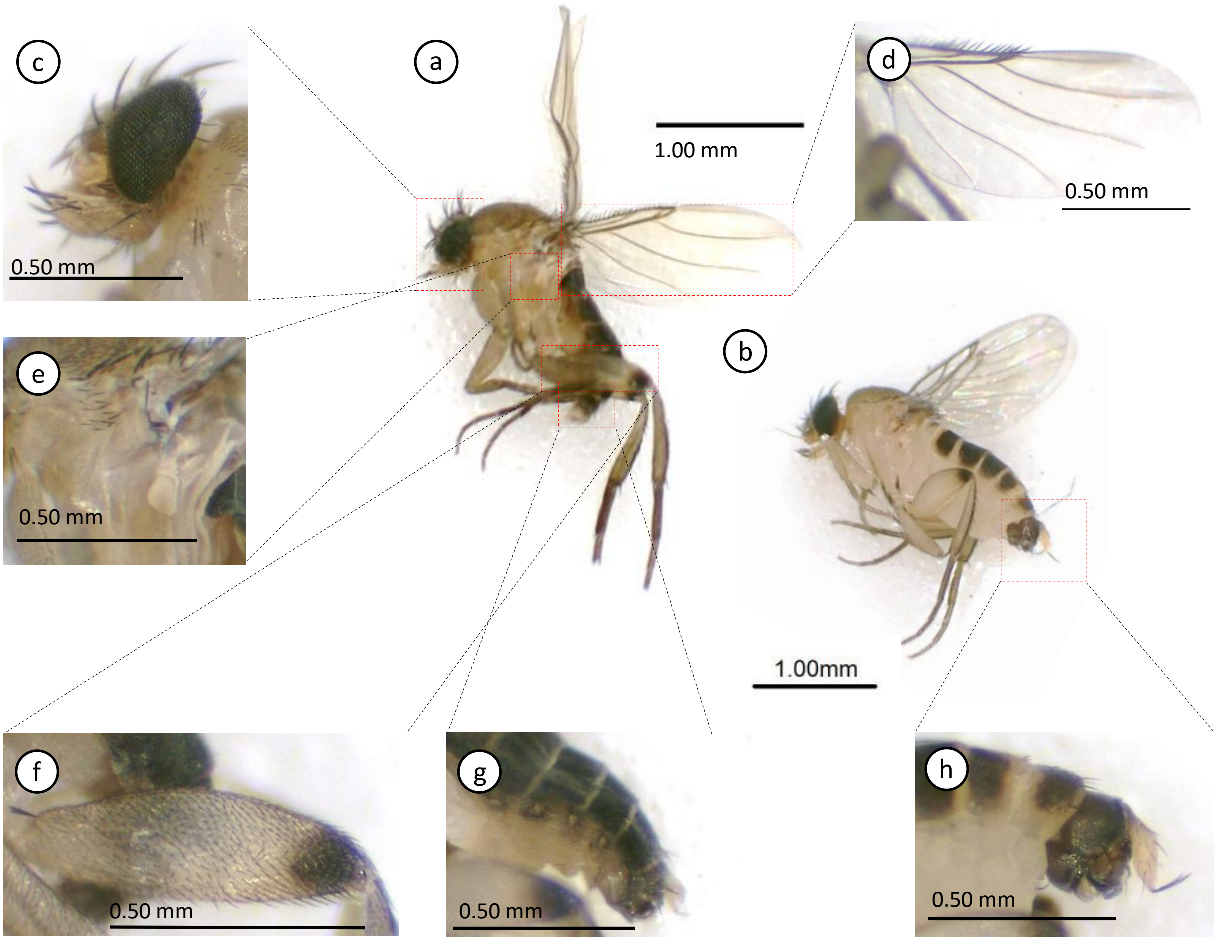

Figure 5. Morphological characters of *Megaselia scalaris*. a. female, b. male, c. head, d. wing, e. halter, f. hind tibia, g. female terminalia, and h. male terminalia.

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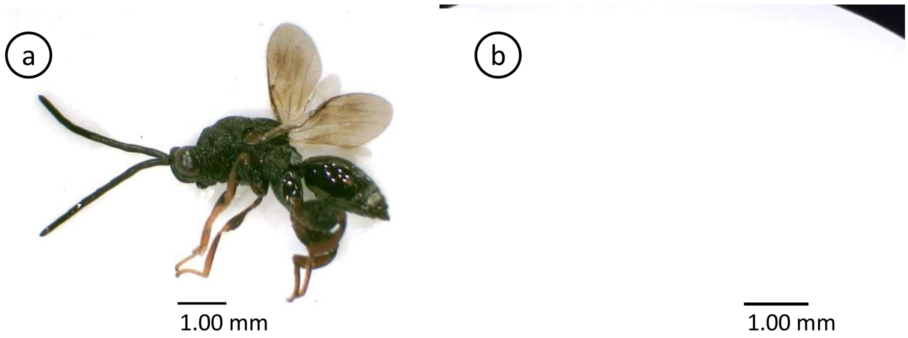

Figure 6. Pupal parasitoid of *Spodoptera frugiperda* in Special Region Yogyakarta, Indonesia. a. *Brachymeria femorata*, b. *Brachymeria lasus.*

However, not all parasitoid species were found in every location. Eight species of parasitoids were found in Bantul, seven in Sleman, six in Gunung Kidul, and only three in Kulonprogo. The richest and most abundant species of parasitoids were found in Bantul (8748 parasitoids). This amount is far higher than in other places. Two thousand seven hundred forty-eight parasitoids were obtained in Sleman, 924 in Gunung Kidul, and 494 in Kulon Progo (Table 1).

Based on a mapping analysis of the parasitoid species distribution found in the field, *S. frugiperda* has spread almost throughout the Yogyakarta region (Figure 7A). *Telenomus remus* was the most dominant parasitoid because of its abundance. However, *T. remus* was only distributed in a few areas (Figure 8), with the highest abundance found in Bantul.

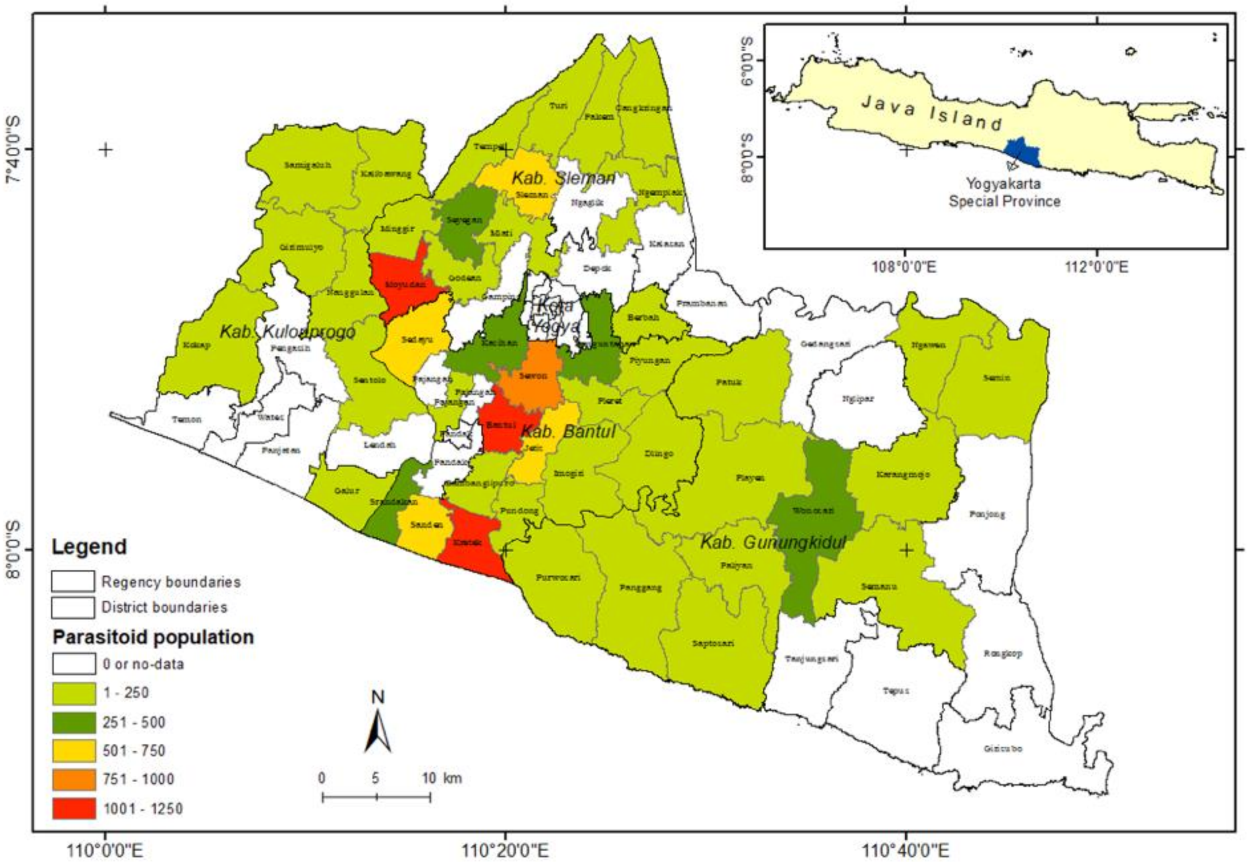

Figure 7. Distribution of *Spodoptera frugiperda*'s parasitoid in Special Region Yogyakarta, Indonesia.

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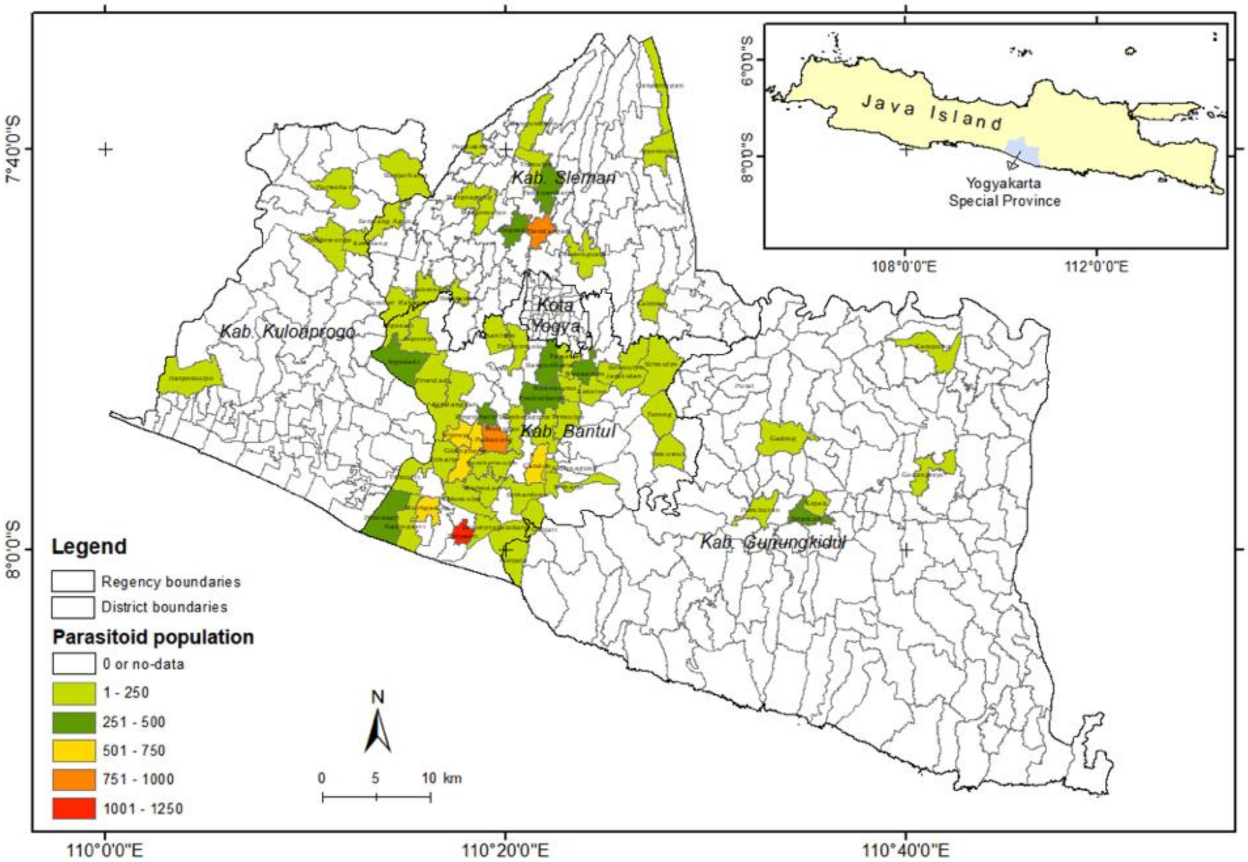

Figure 8. Distribution of *Telenomus remus* in Special Region Yogyakarta, Indonesia.

In addition to its high abundance, *T. remus* had the highest parasitism rate (26-87%). Other parasitoids such as *Hymenoptera* sp.1, *Campoletis* sp., *Coccygidium* sp., and *Microplitis* sp. had maximum parasitism rates of 12.81%, 12.69%, 17.54%, and 19.84% respectively. *Apanteles* sp. had a parasitism rate of 2-30%. The parasitism rate of other parasitoids occurred at lower rates, such as *Stenobracon* sp., *Brachymeria femorata*, and *B. lasus*, with 1 – 2% parasitism rate. Meanwhile, the other parasitoids, including *Hymenoptera* sp.2, *Megaselia scalaris*, *Archytas marmoratus*, and *Charops* sp., had a less than 1% parasitism rate (Figure 9).

Periodically, only one parasitoid was found associated with *S. frugiperda* in 2019. The number of parasitoid species associated with *S. frugiperda* increased to eight, thirteen, and fifteen species in 2020, 2021, and 2022, respectively (Table 2).

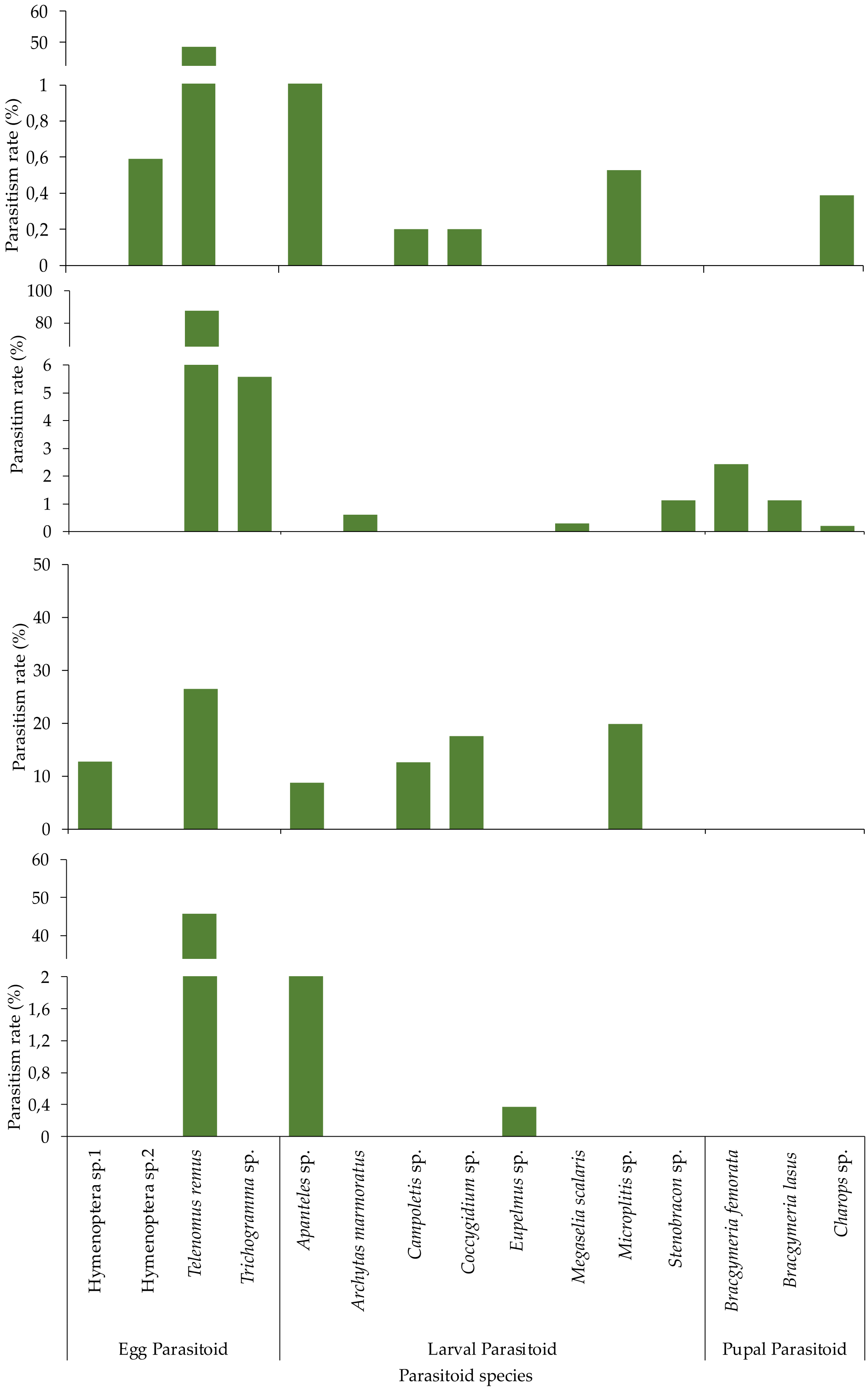

Figure 9. Parasitism rate of *Spodoptera frugiperda*'s parasitoid in Special Region Yogyakarta, Indonesia.

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Table 2. Parasitoid associated with *Spodoptera frugiperda* based on the time of observation.

Order	Family	Species Parasitoid	2019	2020	2021	2022
		Egg parasitoids				
Hymenoptera	Unknown	*Hymenoptera* sp.1			v	
	Unknown	*Hymenoptera* sp.2			v	
	Platygasteridae	*Telenomus remus*	v	v	v	v
	Trichogrammatidae	*Trichogramma* sp.				v
		Larval parasitoids				
Hymenoptera	Braconidae	*Apanteles* sp.		v	v	v
	Ichneumonidae	*Campoletis* sp.			v	
	Ichneumonidae	*Coccygidium* sp.			v	
	Eupelmidae	*Eupelmus* sp.				v
	Braconidae	*Microplitis* sp.		v	v	
	Braconidae	*Stenobracon* sp.			v	
Diptera	Tachinidae	*Archtyas marmoratus*		v		
	Phoridae	*Megaselia scalaris*		v		
		Pupal parasitoids				
Hymenoptera	Chalcididae	*Brachymeria lasus*		v		
	Chalcididae	*Brachmymeria femorata*		v		
	Ichneumonidae	*Charops* sp.			v	
Accumulated number of parasitoid species found			1	8	13	15

4. Discussion

A survey was conducted to study the diversity and the new associations between *S. frugiperda* and local parasitoids in the Special Region of Yogyakarta for three years after *S. frugiperda* was discovered in Indonesia to revise from the old to the new association biological control theoretical approach.

Classical Biological Control emphasizes old associations that invasive pests are controlled by the natural enemy from the country of origin because local natural enemies cannot control the invasive pest [30]. Meanwhile, a new association between invasive pests and local natural enemies will not result in suppression/regulation of the pest because adaptation will take too long. In fact, a physiological equilibrium that results from coevolution between a parasitoid and its hosts might prohibit such long-associated parasitoids from acting as efficient biological control agents [47]. Adaptation can happen relatively quickly, as we found during this study. Elton [48] said that when a parasite species is introduced into an ecosystem with a host or hosts it has never been associated with, the parasite population often rises quickly, often to outbreak levels, and its host population is suppressed.

Our research shows an increase in the number of parasitoids associated with *S. frugiperda*. These findings indicate a similar pattern in other areas of Indonesia. For example, one parasitoid (*T. remus*) was found to be associated with *S. frugiperda* at the beginning of survey activities in 2019. According to Jindal et al. [49], no parasitoids were seen in India in 2019 because *S. frugiperda* had just recently infected the crop in the late season. Maharani et al. [5] also reported no parasitoids directly associated with *S. frugiperda* in Bandung and Garut, West Java, Indonesia in 2019.

However, *A. marmoratus* and *Hymenoptera* larvae were found from *Mythymna separat*a obtained from the same field where *S. frugiperda* was collected. Furthermore, Pu'u and Mutiara [50] reported no parasitoids associated with *S. frugiperda* in Ende, East Nusa Tenggara, in 2020. Suroto et al. [24] reported one parasitoid (*Apanteles* sp.) associated with *S. frugiperda* in Banyumas, Central Java, in 2021. Then, Minarni et al. [21] reported the association of *S. frugiperda* with one egg parasitoid (*T. remus*) and three larval parasitoids from the Braconidae, Ichneumonida, and Chalcididae families in the same location in 2022.

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Based on the abundance of parasitoids, this study also showed differences in the abundance found in the four districts in Yogyakarta. The area with the highest abundance of parasitoids was Bantul. This is due to the characteristics of the sampling site, where Bantul Regency serves as Yogyakarta's primary maize-producing hub [51], making hosts (*S. frugiperda*) more accessible than in other districts. Kishinevsky et al. [52] said that an individual parasitoid would be more prevalent in a site if its host population is more numerous, as are its hosts.

Some parasitoids are similar to those found in the Western Hemisphere, while others differ. *Chelonus insularis* (Hymenoptera: Ichneumonidae) is identified as the primary parasitoid of *S. frugiperda* in most investigations conducted in North, Central, and South America. However, *Eiphosoma laphygmae* (Hymenoptera: Icheumonidae) is more recommended as a prospective candidate for introduction because of its specificity and significance as a parasitoid of the pest across most of its natural habitat [53]. These two parasitoids were not discovered during our research. They were not associated with *S. frugiperda* in other investigations, including those conducted in Cameroon [54] and India [55].

The most prevalent parasitoid identified in this investigation is *T. remus.* This study reported similar results from other investigations [56,57], where *T. remus* was the dominant parasitoid for *S. frugiperda* because this parasitoid has a high abundance and parasitism rate (26-87%). Kumela et al. [8] also reported that *T. remus* was a parasitoid of *S. frugiperda* eggs, with the highest parasitism rate (69.3%) in Kenya and Southern China (30-50%) [57]. Sari et al. [17] reported the potential of *T. remus* as a biological agent of *S. frugiperda* in Indonesia, with a parasitism rate of 69.40%. This value is quite comparative compared to other egg parasitoids such as *T. chilotraeae* [58]. The parasitism rate of *T. remus* may be higher in a situation with many potential hosts. Junaedi et al. [59] said that the availability of hosts for parasitoid survival could increase the parasitism rate. During sampling in the field, the population of *S. frugiperda* eggs was abundant. The high parasitism rate is also due to *T. remus'* ability to find and recognize its host [60]. Goulart et al. [61] said that the ability of *T. remus* to search and recognize its hosts is better than other *S. frugiperda* egg parasitoids such as *Trichogramma pretiosum*.

Telenomus remus is a native egg parasitoid from Malaysia and Papua New Guinea [62]. *Telenomus remus* is a common egg parasitoid used to control pests in the Noctuidae group, especially the *Spodoptera* genus [63]. *Telenomus remus* has been introduced to many countries, including America [63], despite having little success in controlling *S. frugiperda* [64]. In contrast to studies in Indonesia and other countries like Africa (Benin, Cameroon, Côte d'Ivoire, Ghana, Kenya, Niger, Nigeria, Uganda, South Africa, Tanzania, and Zambia) and Asia (China, India, and Nepal) [65] which claimed that *T. remus* is a potential biological control agent for controlling *S. frugiperda*. This could occur because *S. frugiperda* is not native to these regions. When a parasitoid can attack a new host species, the host typically suffers greatly [66]. In contrast to America, the existence of other parasitoids cannot successfully control *S. frugiperda* because they have evolved to its original natural enemies, making it resistant to effective control by other parasitoids [47].

Other egg parasitoids found were *Hymenoptera* sp.1 and *Hymenoptera* sp.2. Morphologically, these two parasitoid species are different from *T. remus*, even though they both

come from the Platygasteridae family, and these parasitoids are characterized by eight flagellum segments and a wider second metasoma segment, different from *T. remus,* which has dilation in the third metasoma [67]. Unfortunately, due to minimal sample conditions, identification could not be carried out to the genus level. Platygasteridae was found, with a lower abundance than *T. remus*. This might happen because the two are not the primary parasitoids of *S. frugiperda* eggs. *Hymenoptera* sp.1 has a similar morphological character to *Platygaster oryzae*, the main parasitoid of Asian rice gall midge *Orseolia oryzae* [68]. However, *Hymenoptera* sp.1 species could not be confirmed, even though this parasitoid emerged from the rearing of *S. frugiperda* egg clusters collected from maize fields adjacent to rice fields. Meanwhile, *Hymenoptera* sp.2 has a different body color from *P. oryzae*. *Platygaster oryzae* has a metallic black body color [69,70], while the parasitoids found were a bright yellow. The discovery of two different egg parasitoid species from *T. remus* and *Trichogramma* indicates the existence of two new associations between *S. frugiperda* and local egg parasitoids.

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Another new association has been found between *S. frugiperda* and larval parasitoids from Hymenoptera order, including *Apanteles* sp., *Microplitis* sp., *Campoletis* sp., *Coccygidium* sp., *Eupelmus* sp., and *Stenobracon* sp. All of these parasitoids are present in the Western hemisphere. However, *Apanteles* like *A. ruficrus* imported from the Australia [71], *M. manilae* from the Thailand [72], and *C. chloridae* from the India [73] to the US. *Apanteles* sp. is a larval parasitoid with the highest parasitism rate (2-30%) compared to other *S. frugiperda* larval parasitoids. Supeno et al. [23] and Suroto et al. [24] also reported the incidence of parasitism of *Apanteles* on *S. frugiperda* larvae with a 17 - 22% parasitism rate, higher than other *S. frugiperda* larval parasitoids. Moreover, *Microplitis* also has a significant parasitism rate (0.5 – 19.84%). The genus *Microplitis,* reported as a larval parasitoid of *S. frugiperda,* includes *M. manilae* [72]. *Microplitis* is a genera widely distributed throughout all biogeographic zones, with macrolepidopterans as their primary hosts [74]. The results of this study also indicate that *Apanteles* and *Microplitis* are parasitoids of *S. frugiperda* larvae potentially developed as biological agents. Association of *S. frugiperda* larvae with *Apanteles* and *Microplitis* was also reported from Bogor, West Java, with 0.39 and 12.3% parasitism rates, respectively [75]. Surprisingly, *Stenobracon* sp. and *Eupelmus* sp. have never been found in the western hemisphere or elsewhere. Meanwhile, *Coccygidium* sp. is reported from other regions. *Campoletis* and *Coccygidium* had 0.2-12.69% and 0.2-17.54% parasitism rate, respectively. *Campoletis* has also been reported in India, with a 2-4% parasitism rate [55]. Meanwhile, *Coccygidium* was also reported in India, with a 0.001% parasitism rate [55], and in Ghana, with a 3.9-19.3% parasitism rate [44].

Apart from the Hymenoptera order, there were also *S. frugiperda* larvae parasitoids from the Diptera order, such as *Archytas marmoratus* and *Megaselia scalaris*. *Archytas marmoratus* is a potential parasitoid for *S. frugiperda* in the American field [76]. However, the parasitism rate found in this study was very low. The parasitism level of *M. scalaris* was also very low. *Megalia scalaris* was first reported in Asian regions, including India [77] and China [78]. *Megalia scalaris* was also found in the Mexican region [79]. This finding is also the first report of an association between *S. frugiperda* and *M. scalaris* in Indonesia. *Megaselia scalaris* is an insect found in various regions, usually in decaying organic matter [80]. Besides being reported as a larval parasitoid of *S. frugiperda*, *M scalaris* was also reported to be associated with peach fruit fly, *Bactrocera zonata* (Saunders), Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) in Egypt [81], and fruit-piercing moths *Thyas coronota* (Fabricius) (Lepidoptera: Erebidea) in India [82]. However, according to a recent study, *M. scalaris* is not recommended as a potential biological control agent for *S. frugiperda. Megaselia scalaris* prefers to consume deceased larvae instead of acting as an endoparasitoid with parasitism rates of 2.2 and 0.7% in third- and fifth-instar larvae of *S. frugiperda*, respectively [83].

Besides the new association between S. *frugiperda* and several egg and larval parasitoids, there was another new association with three pupal parasitoids, such as *Brachymeria lasus* and *B. femorata* from the Chalcididae family, and *Charops* sp. from Ichneumonid family. Because these parasitoids also have never been documented in the western hemisphere. Several chalcidid families reported to be associated with *S. frugiperda* include *B. flavipes* (= robusta) (Fabricius), *B. ovata* (Say), *Conura femorata* (Fabricius), *C. hirtifemora* (Ashmead), *C. igneoides* (Kirby), *C. immaculata* (Cresson), and *C. meteori* (Burks) [84]. These two *S. frugiperda* pupal parasitoids were only found in Bantul. *Brachymeria lasus* and *B. femorata* usually attack hidden insects, such as the banana leafroller caterpillar *Erinota thrax* (Lepidoptera: Hesperiidae) [85], fire caterpillars, and other Noctuidae families. The proximity of banana plants to the sampling site in Bantul Regency suggests that there may be other hosts for these parasitoids. However, these two parasitoids have also been found parasitizing the pupae of *S. frugiperda* in Egypt [86]. Lastly, *Charops* sp. was identified through its pupal characteristics. *Charops* sp. was also reported as a pupal parasitoid of *S. frugiperda* in Cameroon [87], Ghana, and Benin [54] but has never been reported from the western hemisphere as well.

Our findings support Hokkanen and Pimentel's theory on using the New Association biological control approach for controlling *S. frugiperda* with local parasitoids such as *T. remus* and *Microplitis* sp. *Telenomus remus* has been used as a biological agent for *S. exigua* [88], and *Microplitis manilae* has

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also been around for a long time and is associated with other *Spodoptera* species, such as *S. litura* in Indonesia [89]. This evidence led us to conclude that these parasitoids existed earlier than *S. frugiperda* in Indonesia. Hokkanen and Pimental [43] also said that the original host of the most effective new association biocontrol agents is closely connected to the new host of the agent was introduced against. The original and subsequent hosts have typically belonged to the same genus. Longer taxonomic "jumps" to a new host from distinct families of hosts are also feasible, as exemplified by a pupal parasitoid *B. lasus*. Therefore, *T. remus* and *Microplitis* sp. are thus possible biological control agent options for use in control initiatives within the new association of biological control concepts equipped to regulate *S. frugiperda*.

5. Conclusions

This research supports Hokkanen and Pimentel's theory of using the new association biological control approach for controlling *S. frugiperda.* In contrast to Kenis [53], who recommends a classical biological control approach since introducing natural enemies may lead to an environmental risk. *Telenomus remus* is the most dominant parasitoid with a high abundance and parasitism rate compared to other parasitoids. *Telenomus remus* is a promising opportunity because *T. remus* is an egg parasitoid. Parasitoids can control pests early in life, thereby avoiding further attacks.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org.

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