



Re-evaluating the likely presence of *Spodoptera frugiperda* in Indonesia in 2015 through re-assessment of neglected maize field sample collections from Lampung

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Abstract The invasive fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith), poses a significant global threat with serious economic implications. Global concern heightened following the first major outbreak in Africa in 2016. Our research, which confirmed the presence of FAW in Indonesia in 2015 through re-examined samples from a maize field in Lampung region of Indonesia, supports the hypothesis that the invasion pattern does not follow the predicted west-to-east chronological timeline. Historical records and reidentification suggest that FAW may have been established in Indonesia, Africa, and Australia as early as nineteenth century, suggesting its potential presence in these regions much earlier than previously thought. The spread of FAW could

be linked to the movement of people and plants such as maize or Para grass (*Brachiaria mutica*), at least at the end of the nineteenth century. This underscores the importance of rigorous identification methods for accurately tracking invasive species like FAW. Analyzing these historical records alongside the genetic structure of populations in Southeast Asia, particularly in Indonesia, is crucial for future research aimed at developing effective management strategies to mitigate the impact on the global agriculture.

Keywords Early detection · Fall armyworm · Historical records · Invasion pattern · *Spodoptera*

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Introduction

The fall armyworm (FAW), *Spodoptera frugiperda*, emerged as an important agriculture pest, originating from the tropical and subtropical regions of the Americas. Renowned for its highly polyphagous nature, this noctuid moth demonstrates remarkable versatility, having been reported from over 353 crop and non-crop species spanning 76 plant families (Montezano et al., 2018). With its adaptability and voracious feeding habits, FAW has earned recognition as a significant invasive species. Its invasion saga began with the first identification in Western Africa during a series of outbreaks in early 2016 (Goergen et al., 2016), swiftly spreading eastward to India by May 2018 (Sharanabasappa et al., 2018).

The interception of FAW across Southeast Asia became apparent in 2019, with reports across various countries, including Indonesia, Cambodia, Laos, Malaysia, Vietnam, and the Philippines (Lestari et al., 2020; Sartiami et al., 2020; Trisyono et al., 2019; EPPO, 2021; Hang et al., 2020; Navasero et al., 2019). This invasion persisted into 2020, with the pest's presence confirmed in Papua New Guinea at the year's onset (Tay et al., 2023a). By early February 2020, FAW had established itself in maize fields in Queensland, Australia, marking an expansion of its geographical range. The most recent confirmed report in March 2022 indicated its presence in New Zealand (Rane et al., 2023), underscoring the rapid and extensive spread of FAW across diverse continents and climates.

However, the timeline of FAW interception and establishment in Indonesia and Southeast Asia maize fields remains unclear. Genomic studies have proposed an alternative pattern of FAW dispersal, with genome-wide SNP analyses indicating a close relationship between the FAW population in East Africa and those found in Asia and Southeast Asia (Rane et al., 2023; Tay et al., 2022, 2023b). This evidence suggests the potential existence of pre-established FAW populations in Southeast Asia before 2016 such as reported in 2008 in Vietnam (Vu, 2008, Nguyen & Vu, 2009; see also Rane et al., 2023), challenging conventional notions of its invasion timeline and suggesting a more intricate, independent, and earlier spread than previously documented.

In 2015, research aimed at exploring entomopathogenic fungi in maize (Fitriana et al., 2021; Semenguk, 2016) led to a curious discovery of various *Spodoptera* species that co-existed in maize in Lampung, Indonesia. An unusual *Spodoptera* species was identified, differing from the known *Spodoptera* species reported in the region. Subsequent identification, done as part of the current study revealed this unusual species to be *S. frugiperda*. This finding indicates the presence of FAW in Indonesia as early as 2015, prompting speculation that FAW may have been accidentally introduced to Indonesia in 2015 or even earlier, before its formal documentation.

Keys to common *Spodoptera* larvae in Indonesia

Various *Spodoptera* species occur in Indonesia. Of the 10 species so far reported, at least five are

economically important. These include *S. exigua* (Hübner 1808), *S. litura* (Fabricius 1775), *S. mauritia* (Boisduval 1833), *S. exempta* (Walker 1857), and *S. frugiperda* (Smith 1797) (Franssen, 1930; Kalshoven, 1981; Sartiami et al., 2020; Trisyono et al., 2019; Viette, 1963). The different phases of *Spodoptera*, such as solitaria or gregaria, are known to exhibit variations in larval coloring and other characteristics, posing challenges for accurate species identification (Brown & Dewhurst, 1975). Notably, distinguishing between species can be particularly tricky due to these variations. For instance, the green morphotype of *S. frugiperda* is often mistaken for *S. exigua* (Passoa, 1991; Swezey, 1938).

Furthermore, in 1985, researchers identified two distinct strains of *S. frugiperda* based on the host plants from which they were isolated: the corn and rice strains (Pashley, 1986; Pashley et al., 1985). Although evidence suggests that the host plant environment influences wing morphology (Cañas-Hoyos et al., 2014, 2016), both strains remain morphologically identical. Recent studies by Herlinda et al. (2022) have identified two genetic strains of *S. frugiperda* (the rice and maize strains) established in maize in Indonesia. Therefore, given the complexity of species identification, below are revised keys to identifying common *Spodoptera* larvae in Indonesia (modified after Brown & Dewhurst, 1975; Gilligan & Passoa, 2014; Oliver & Chapin, 1981; Passoa, 1991).

1. Adfrontal sutures reaching epicranial suture near vertical triangle (epicranial notch); cuticular granulose.....genera like *Agrotis*/*Feltia* complex
 - Adfrontal sutures reaching epicranial suture well below vertical triangle (epicranial notch).....genera like *Spodoptera*/*Helicoverpa*
2. Cuticle smooth (except in *Spodoptera frugiperda*); Adfrontal area outlined in white forming an inverted "Y" *Spodoptera* spp. (3)
 - Cuticle conspicuously spinose; Adfrontal area outlined not like above *Helicoverpa* spp.
3. Mandible lacks scissorial teeth resulting in a smooth cutting edge.....0.4

- Mandible with scissorial teeth resulting in a serrate cutting edge (Fig. 1I)..... 5
- 4. Colour largely black, the dorso-lateral and spiracular bands with narrow whitish or yellow longitudinal stripes; Head black..... *Spodoptera exempta* (Walker)
 - Black color absent except for, in some cases, segmental spots, with brown dorso-lateral band and green lateral band; Head brownish or greenish, the front not usually paler than the epicranial plates..... *Spodoptera mauritia* (Boisduval)
- 5. Dorsal pinacula usually conspicuous but sometimes pale in the green morphotype, as large as or larger than the diameter of the abdominal spiracles; Dorsum of abdominal segments granulated *Spodoptera frugiperda* (J.E. Smith) (Fig. 2)
 - Dorsal pinacula minute, inconspicuous no more than a half of the diameter of the abdominal spiracles; Dorsum of abdominal segments smooth 6
- 6. Abdominal segments never with dorsal triangular markings, the pattern consists of a series of dorsal dashes or, more commonly, an irregular series

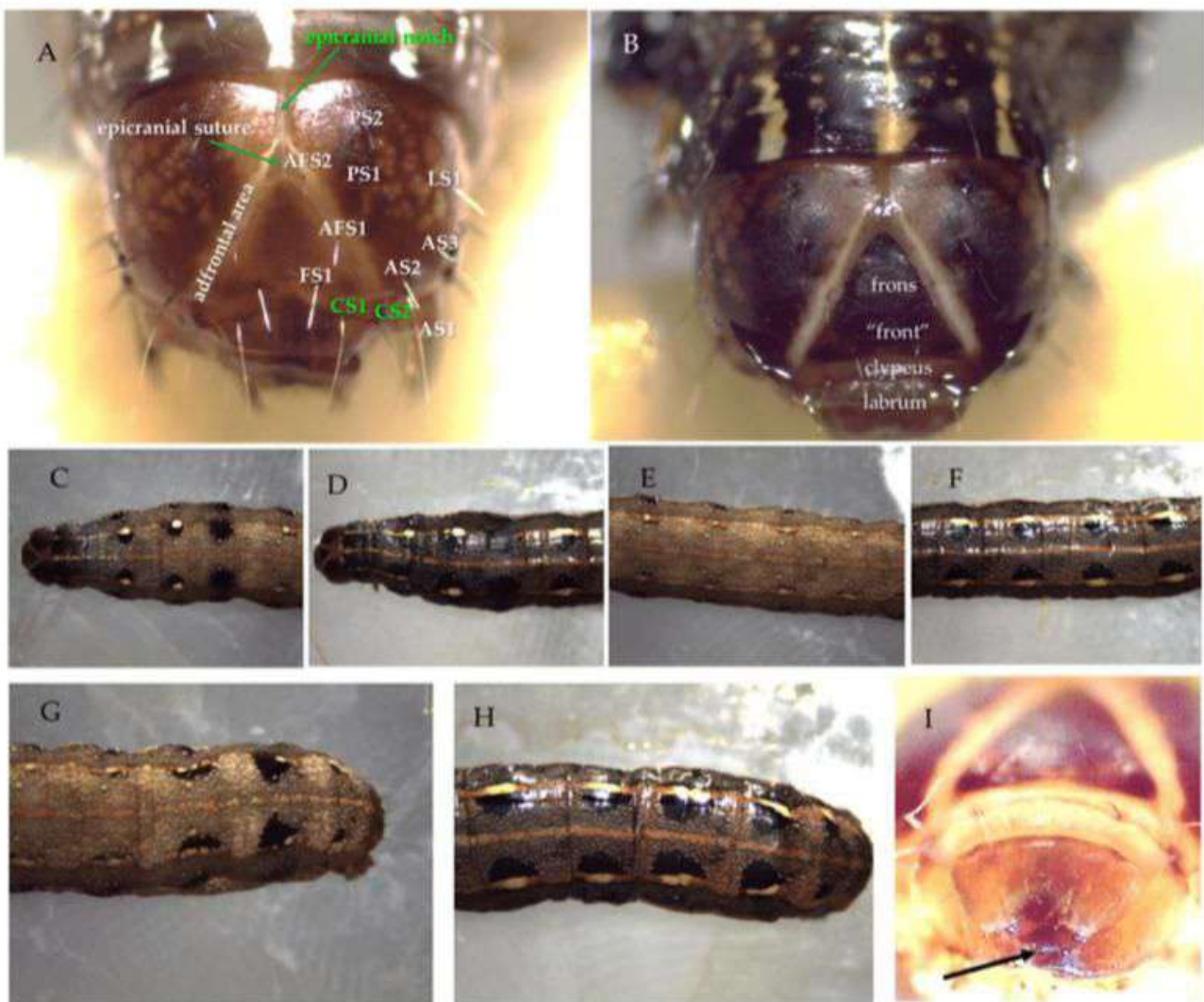


Fig. 1 Polymorphism in *Spodoptera litura*. (A–B) Head and chaetotaxy, Setae, and structures are labeled according to Stehr, 1987 (AS: anterior setae; AFS: adfrontal setae; CS: clypeal setae; FS: frontal setae; LS: lateral setae; PS: posterior-dorsal setae); (C–D) Dorsal view of head, thorax, and abdo-

men segment 1 (A1), middorsal line often present and conspicuous; (E–H) Dorsal view of abdomen, dorsal triangles are on all abdominal segments; (I) mandible with four scissorial teeth. Photographed using Leica EZ4 HD stereo microscope (Leica Microsystems (Schweiz) AG)

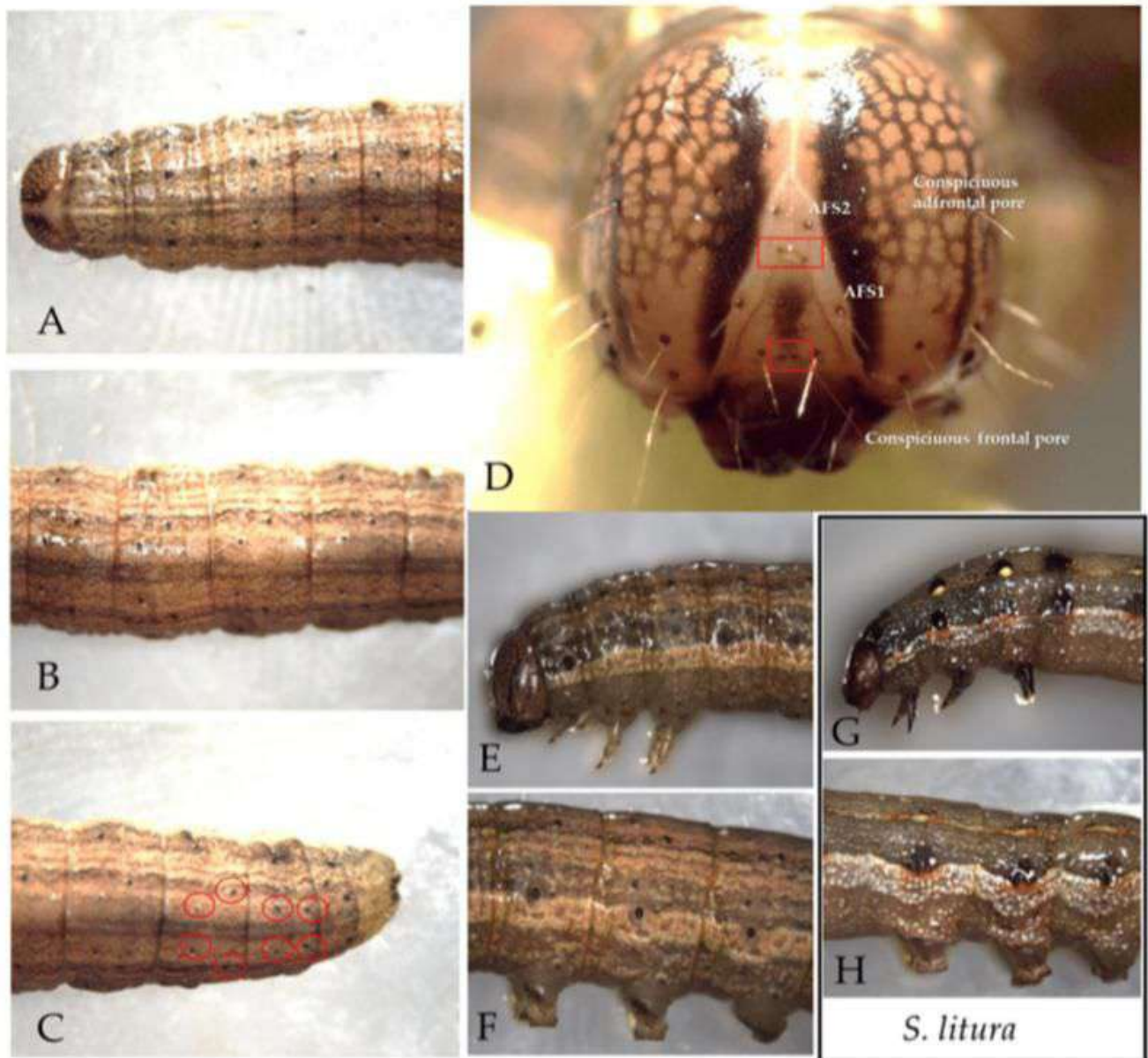


Fig. 2 Morphological comparison of *S. frugiperda* and *S. litura*. (A–F) *S. frugiperda*; (G–H) *S. litura*. Photographed using Leica EZ4 HD stereo microscope (Leica Microsystems (Schweiz) AG)

of white dots and lines; lateral spot, if present, is on the mesothorax; subdorsal area often contrasting with paler dorsum.....
 *Spodoptera exigua* (Hübner)

- Abdominal segments with dorsal triangular markings, middorsal line often present and conspicuous; spiracular stripe often interrupted on A1 by a black band or spot; dorsal triangles, if present, are on all abdominal segments, A1 and A8, A7, and A8 or just

A8 and most of them usually have an apical white dot; subdorsal area often not contrasting with paler dorsum..... *Spodoptera litura* (Fabricius) (Fig. 1)

A list of other, less common species found in the Indo-Australian region, including Java, Borneo, and Sulawesi is provided in Table 1. Information on their taxonomy, synonyms, and identification of the *Spodoptera* species examined are provided below.

Table 1 Rare and non-economically important species of *Spodoptera* in Indonesia (adapted from Holloway, 1989)

No	Species	Distribution (Indonesia)	Habitat preference
1	<i>Spodoptera pecten</i> Guenee, 1852	Indo-Australian tropics to New Guinea. (Borneo)	The species is abundant in open, cultivated, or disturbed habitats in the lowlands
2	<i>Spodoptera cilium</i> Guenee, 1852	Old World tropics (Borneo)	The species is much rarer than <i>S. mauritia</i> and <i>S. pecten</i> but is found in similar habitats
3	<i>Spodoptera pectinicornis</i> (Hampson 1895) Syn <i>Xanthoptera pectinicornis</i> Hampson, 1895 <i>Caradrina hennia</i> Swinhoe, 1901	N.E. Himalaya to Sundaland, also in New Guinea. (Java)	The species is associated with sluggish waterways and other bodies of freshwater where its host plant grows
4	<i>Spodoptera apertura</i> (Walker, 1856) Syn <i>Prodenia apertura</i> Walker, 1856, <i>Prodenia synstictis</i> Hampson, 1896, <i>Prodenia leucophlebia</i> Hampson, 1902 <i>Spodoptera apertura</i> Walker; Brown & Dewhurst, 1975	Old World tropics (Sulawesi)	The species has been reared from <i>Nicotiana</i> (Solanaceae) in Africa (Brown & Dewhurst, 1975)
5	<i>Spodoptera picta</i> (Guerin-Meneville 1830) Syn <i>Phalaena (Noctua) festiva</i> Donovan, 1805 <i>Polia picta</i> Guerin-Meneville, 1830	Indo-Australian tropics (Borneo)	This is the largest of Bornean <i>Spodoptera</i> . Prefer the coastal area. The host plants are Liliaceae, particularly the <i>Crinum</i> species

Identification larva *Spodoptera* collected in 2015 in Lampung, Indonesia

Spodoptera litura (Fabricius, 1775)

Syn. *Noctua litura* Fabricius, 1775.
Noctua histrionica Fabricius, 1775.
Noctua elata Fabricius, 1781.
Prodenia ciligera Guenée, 1852.
Prodenia tasmanica Guenée, 1852.
Prodenia subterminalis Walker, 1856
Prodenia glaucistriga Walker, 1856
Prodenia declinata Walker, 1857.
Mamestra albisparsa Walker, 1862.
Prodenia evanescens Butler, 1884.
Orthosia conjuncta Rebel, 1921.

Material examined 2 larvae on 20 photographs taken by Andrianto, E.; South Lampung-Lampung, Indonesia, 5.38°S, 105.22°E, 5.III.2016. Specimens were collected during November- December 2015 by

B. Semenguk, a part of a study conducted by Fitriana et al. (2021). Photographs were documented in the Laboratory of Plant Pest Science, Department of Plant Protection, Faculty of Agriculture, University of Lampung (UNILA).

Host plant Maize (*Zea mays*).

Diagnosis Head with adfrontal area outlined in white forming an inverted "Y" (Fig. 1A–D). This character however is most likely to be generic characters of *Spodoptera*, not specific to a particular species. *S. litura* could be recognized by combinations of characteristics such as the ground color green to yellow–brown (Fig. 1A, C, E, and G) to the dark blue gray (Fig. 1B, D, F, and H); subdorsal area often not contrasting with paler dorsum (Fig. 2G–H); middorsal line often present and conspicuous (Fig. 1C–H); spiracular stripe often interrupted on A1 by a black band or spot (Fig. 2G–H); dorsal triangles, if present, are on all abdominal segments (Fig. 1D, F, and H), A1 and A8, A7 and A8 or just A8 (Fig. 1C, E, and G) and most of them usually have an apical white dot.

Remarks Two morphotypes of the *Spodoptera* species—*S. litura*, and *Spodoptera* sp. 1—have been identified from the specimens obtained. *Spodoptera* sp.1 (dark blue-gray) specimen was identified as *S. litura* in this case.

Spodoptera frugiperda (J.E. Smith, 1797)

Syn. *Phaleana frugiperda* J.E.Smith 1797.

Noctua frugiperda J. E.Smith.

Trigonophora frugiperda Geyer, 1832.

Laphygma frugiperda Guenee, 1852.

Caradrina frugiperda

Laphygma macra Guenee, 1852.

Laphygma inepta Walker, 1856

Prodenia plagiata Walker, 1856

Prodenia signifera Walker, 1856

Prodenia autumnalis Riley, 1870.

Laphygma frugiperda var. *fulvosa* Riley, 1876.

Laphygma frugiperda var. *obscura* Riley, 1876.

Material examined 1 larva on 13 photographs taken by Andrianto, E.; South Lampung-Lampung, Indonesia, 5.18°S, 105.20°E; 5.III.2016; 1 larva on 1 photograph; South Lampung-Lampung, Indonesia, 5.34°S, 105.23°E, 13.I.2016. Specimens were collected during November- December 2015 by B. Semenguk, a part of study conducted by Fitriana et al. (2021). Photographs were documented in the Laboratory of Plant Pest Science, Department of Plant Protection, Faculty of Agriculture, University of Lampung (UNILA).

Host plant Maize (*Zea mays*).

Diagnosis Dorsal setigerous tubercles (pinacula) are often noticeable but can occasionally be pale (Fig. 2A–C) in the green form, and their diameter is the same as or greater than that of the abdomen spiracles. Typically, the huge pinacula of *S. frugiperda* makes it easy to identify (Supplementary Fig. 1). However, due to its pale pinacula, *S. frugiperda*'s green form can be mistaken for *S. exigua* which also already exists in Indonesia. These two species can also be separated using cuticular texture. The cuticular texture of *S. frugiperda* is granular. The lateral spot of *S. frugiperda*, when present, is on the first

abdominal segment. However, the lateral spot of the current specimen is absent (Fig. 2E) and not in the mesothorax as is the case with *S. exigua*.

Remarks The specimens referenced in this study are from photographic documentation in Semenguk (2016), which is part of the Fitriana et al. (2021) study. We have re-identified the specimen labeled *Spodoptera* sp. 2 as *S. frugiperda*. A photograph taken by Semenguk on January 13, 2016 (Supplementary Fig. 1), was also identified as *S. frugiperda* based on morphological characteristics. While we are confident in this identification, the photographic specimens are not available for molecular diagnostics like whole genome sequencing, as they were not preserved for such analyses. However, FAW populations in Lampung have been confirmed by Lestari et al. (2020) using mitochondrial COI barcodes.

Discussion

Spodoptera frugiperda poses a significant global threat to agriculture. In Indonesia, the initial detection of FAW was documented in late March 2019 (Sartiami et al., 2020) in maize fields. The infestation began in West Sumatra and swiftly spread across the archipelago, causing varying degrees of damage from mild to severe, and these impacts have persisted over time (Lestari et al., 2024). By 2021, a mere two years following the initial report, FAW had established itself in numerous regions of Indonesia, including Sumatra, Java, Bali, Kalimantan (Borneo), Sulawesi, and Papua (BBPOPT, 2022). Despite the rapid spread, the precise factors driving this phenomenon remain shrouded in uncertainty. One potential contributing factor could be the lack of awareness among farmers regarding the presence of FAW prior to their first report in 2019.

This situation mirrors events in Uganda, where farmers observed FAW damage in maize as early as 2014, predating formal reports of FAW presence in Africa. However, at that time, farmers lacked awareness of this highly invasive exotic armyworm species infiltrating their fields (Otim et al., 2018; Kalyebi et al. 2023). The parallels between these experiences underscore the critical importance of early detection and proactive management strategies to mitigate the impact of invasive species.

The invasion of FAW is likely to be less straightforward than initially thought. Recent genetic and genomic studies challenge the west-to-east timeline of FAW invasion, suggesting a more complex pattern, including independent introductions in China (Jiang et al., 2022). Evidence indicates that FAW populations in Africa may have originated from Asia and Southeast Asia, such as Malaysia, implying that FAW was present in these regions before 2016 (Rane et al., 2023; Tay et al., 2022). Supporting this, FAW was reported as a pest in turf grass in Vietnam in 2008, indicating its earlier presence in Southeast Asia prior to major maize outbreaks (Vu, 2008, and Nguyen & Vu, 2009, as reported in Tay et al., 2022). These findings emphasized the need for more extensive research on FAW populations in Southeast Asia and Oceania (Kenis et al., 2023; Tay et al., 2023b). Additionally, our findings suggest that FAW was present in Indonesia by 2015, and possibly even earlier, before 2014 (Gilligan & Passoa, 2014; Tay et al., 2023b).

Understanding the global distribution of FAW highlights the pivotal role of international trade in facilitating the spread of invasive species (Tay et al., 2022). The global movement of fresh commodities contaminated with FAW significantly contributes to their introduction into non-native regions. Historical records indicate FAW interceptions through plant materials outside the New World dating back to before 1984 in England and Wales (Seymour et al., 1985). Even earlier, FAW was first detected in Israel in 1967, believed to have potentially originated from the Caribbean (Wiltshire, 1977). However, this detection was later questioned, being considered either a misidentification or a transient population that never established (CIE, 1985; EFSA Panel on Plant Health (PLH) et al., 2017).

Brown and Dewhurst (1975) highlighted that reports of *S. frugiperda* in Ethiopia, Uganda, and islands on Lake Victoria are more accurately attributed to *S. exempta*. Despite this uncertainty, interceptions of FAW from Israel as well as Indonesia to the US have been well recorded since 2014 (Gilligan & Passoa, 2014; Kenis et al., 2023). Moreover, European countries, particularly the Netherlands, have documented numerous FAW interceptions in recent years. Between January 1995 and May 2017, at least 46 interceptions were recorded, with the earliest instance in May 2005. Most of these interceptions in the Netherlands involved shipments from Suriname

containing *Capsicum*, *Solanum melongena*, and *Solanum macrocarpon* (EFSA Panel on Plant Health (PLH) et al., 2017). This persistent issue highlights the significant role of global trade in the spread of FAW.

The historical presence of FAW in Southeast Asia, particularly in Indonesia, may be connected to its movement from Suriname. Between 1890 and 1939, Indonesia and Suriname had a relationship involving the migration of people and commodities. Approximately 33,000 Javanese immigrants, alongside individuals from China and India, migrated to Suriname to work on sugar cane plantations. Before World War II, around 20–25 percent of these migrants returned to Java (Allen, 2011). In 1954, an additional 1,200 Javanese returned to Indonesia to establish an agricultural cooperative in Tongar, western Sumatra (Djasmadi et al., 2010; Hoefte, 1998). This migration likely involved some movement of plants between Java and Suriname. For example, Suriname maize varieties developed by the Agricultural Experiment Station, which began experiments in 1917, had roots from Java and the Near East (Lata, 1978). While there is no direct evidence of FAW introduction through these migrations, it is worth noting that FAW was recognized as a major pest in Suriname during that era (Segeren & Sharma, 1978).

Another potential route for the dispersal of FAW to Southeast Asia could be through its association with Para grass, *Brachiaria mutica* (Forssk.) Stapf, an alternative host for FAW in Suriname and America (USDA, 1975; van Dinther, 1955). Para grass, originally from western and northern Africa or South America, has been cultivated as a pasture plant since at least 1849 and introduced to many tropical nations (Cameron & Kelly, 1970; Parsons, 1972; Smith, 1979). It has subsequently naturalized in most parts of Southeast Asia, India, and Australia (PIER, 2024; Holm et al., 1977). In Indonesia, it is considered an alien invasive species (Holm et al., 1977; Setyawati et al., 2015). While these historical connections suggest possible routes for FAW's introduction to Southeast Asia, it is important to consider that many historical records and accounts could result from species misidentification.

Review of historical literature therefore indicated that *S. frugiperda*, previously known as *Laphygma frugiperda*, could potentially have established in Indonesia since at least the nineteenth century (Mabille,

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