

First insights into the genetic diversity of *Spodoptera* spp. (Lepidoptera: Noctuidae) affecting vegetable crops in Jamaica

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Abstract

Spodoptera spp. (Lepidoptera: Noctuidae) are economically important insect pests of cereal and vegetable crops in Tropical and Subtropical regions of the Americas, but little is known of their distribution and diversity in countries of the Caribbean, in particular, Jamaica. In this study, larvae collected from hosts in the three major vegetable producing regions of Jamaica were characterized based on morphological characters and mitochondrial cytochrome *c* oxidase I (COI) sequence data. Three species were identified; *S. exigua*, *S. latifascia* and *S. frugiperda*. All three species were prevalent on bunching onions (*Allium fistulosum*); while bell pepper (*Capsicum annum*) and corn (*Zea mays*) were also hosts for *S. exigua* and *S. frugiperda*, respectively. Species clades at 99% confidence were obtained in phylogenetic analyses with Jamaican COI sequences and those from different geographical locations. Separate clustering occurred with native *S. latifascia* and invasive *S. exigua* populations of the Americas. *S. frugiperda* corn and rice strain groupings that were closely related to native accessions of the Americas and invasives in Africa and Asia, including populations with recorded insecticide resistance, were distinguished. Based on this sampling, the Jamaican populations are consistent with those previously reported in the Americas and elsewhere. Low intraspecific genetic distances of $\leq 0.6\%$ were obtained with the three species and apart from two exceptions, interspecific distances ranged from zero to 1.4%. The results provide new information about the population dynamics of *Spodoptera* species affecting vegetable crops in Jamaica and establish a baseline for further studies.

Introduction

Armyworm larvae of *Spodoptera* (Lepidoptera: Noctuidae) are important insect pests of agricultural crops (Pogue, 2002; 2011). They feed in large numbers on the leaves, stems and reproductive tissues of a wide range of grain, row, forage, vegetable, and ornamental crops (Kergoat et al., 2012). Armyworms are mainly a tropical group, but they are also found in warmer subtropical and temperate climates. *Spodoptera* species that cause economic and food losses in South America include *S. albula*, *S. androgea*, *S. cosmiodes*, *S. dolichos*, *S. eridania*, *S. frugiperda*, *S. ochrea* and *S. ornithogalli*. These and two other species, *S. exigua* and *S. latifascia*, are important in Central America, the United States and Canada. *S. littoralis* ranges in Africa, southern Europe and the Middle East, while *S. litura* is also present throughout the Middle East and Asia and extends southward to Australia and the Pacific Ocean.

Many *Spodoptera* species are highly polyphagous, fecund, exhibit long range migratory behaviors and a long adult life span of *ca.* 10 days. Two are well known invaders that have been detected outside of their native range. *S. exigua*, the beet armyworm, is presumed to have been introduced into North America from Southeast Asia in the 1800s, and established across the Americas and Europe by the 1900s (Capinera, 1999). The fall armyworm, *S. frugiperda* which is native to the Americas and migrates from Central America up North to Canada and South to Argentina during warm periods every year, has quickly moved through Africa, Asia and Australia (FAO, 2022) in the last six years, most likely via human-assisted migration. The species poses an eminent threat to the Middle East and Europe. Conversely, *S. littoralis* and *S. litura* in Europe are regarded as invasive threats to the Americas (Ellis, 2005; Pogue, 2002).

Accumulating evidence using DNA barcodes, such as those derived from segments of the mitochondrial cytochrome oxidase subunit I (COI), show low genetic heterogeneity within and between *Spodoptera* populations such as *S. exigua* (Shashank et al., 2015; Wang et al., 2020) and *frugiperda* (Nagoshi et al., 2006). Two strains of the latter, that exhibit different host plant preferences, are recognized across the native geographical range in the Americas (Nagoshi et al., 2015; 2017). Little is known about the population genetics of *Spodoptera* spp. in the Caribbean which has been considered as a link and possible migration pathway between the two continents of the Americas (Nagoshi et al., 2010). Jamaica is one such territory located between the mainland territories of North and South America. Occurrence reports based on morphological systematics document armyworms in Jamaica as far back as the 1940s

(CABI, 2019; EPPO, 2020). One species, *S. exigua*, that is traditionally recognized as a sporadic pest confined to the southwestern region of the island, attracted national attention in the early 2000s after increasingly frequent and serious outbreaks in other major vegetable growing regions (Lopez et al., 2014). These infestations of more crops in new regions further west threaten the livelihoods of vulnerable farmers and food security. In this study, we clarify the status of armyworm species in major economically important vegetable producing regions of the island by examining morphological characters along with COI gene sequence analysis, and compare their genetic diversity and phylogenetic relationships with other populations.

Materials And Methods

Seven locations in three regions of Jamaica (St. Elizabeth, Clarendon, and St. Thomas) that are known for armyworm outbreaks were surveyed between June and December 2015 (Fig. 1). Using indicators of fresh frass, leaf funnels or feeding damage, specimens were collected and tentatively named to species based on descriptions by Passoa (1991). Sample collection sites and codes are given in Fig. 1 and Table 1.

Table 1
Sample information on armyworms collected in this study.

Genus/species	Armyworm sample code	Origin	Host	Latitude	Longitude	Accession number
<i>Spodoptera latifascia</i>	CSE001, CSE003, CSE005, CSE007, CSE008, CSE010	Clarkmount, St Elizabeth	Bunching onion	17° 56' 12.948" N	77° 40' 19.056" W	MT881743.1 – MT881753.1
	BSE001, BSE010, BSE018, BSE021, BSE025	Bull Savanna, St Elizabeth	Bunching onion	17° 54' 0.036" N	77° 46' 6.996" W	
<i>Spodoptera frugiperda</i>	BHB001, BHB003, BHB007, BHB008, BHB010, BHB014, BHB021	Brown's Hall, Clarendon	Corn	18° 10' 46.02" N	77° 15' 21.06" W	MT881754.1 – MT881762.1
	BSE002, BSE004	Bull Savanna, St Elizabeth	Bunching onion	17° 54' 0.036" N	77° 46' 6.996" W	
<i>Spodoptera exigua</i>	BSE008, BSE013, BSE031, BSE034	Bull Savanna, St Elizabeth	Bunching onion	17° 54' 0.036" N	77° 46' 6.996" W	MT881720.1 – MT881742.1
	MB001, MB002, MB005, MB016, MB017, MB021, MB026, MB033, MB039, MB043	Morant Bay, St Thomas	Bell pepper	17° 53' 54.744" N	76° 25' 31.908" W	
	SPE001, SPE004, SPE009, SPE013, SPE018, SPE020, SPE024, SPE025, SPE026	Small Park, St Elizabeth	Bunching onion	17° 59' 1.644" N	77° 40' 9.804" W	

Total genomic DNA was extracted using a modified CTAB method of Kondidie (2011). Following the removal of digestive tracts, larval tissues (100 mg) were homogenised in 500 µL CTAB buffer (100 mM Tris-HCl pH 8.0, 1.4 M NaCl, 0.02 M EDTA, 2% CTAB and 0.2% β-mercaptoethanol). DNA, precipitated with 500 µL isopropanol after phenol

chloroform extraction, was washed with 70% chilled ethanol, dried and resuspended in 50 µL TE buffer (200 mM Tris-HCl pH 8.0, 1 mM EDTA). DNA was analyzed by 1% agarose gel electrophoresis.

Partial fragments of the COI gene were amplified following Vidigal et al. (2002) and Folmer et al. (1994). Reaction volumes of 20 µL contained 0.1 µM each primer, 4 ng of DNA template, 1 unit *Taq* polymerase (New England BioLabs), 2 mM MgCl₂, 100 µM dNTPs and 2 µL of 10X PCR buffer. Cycling conditions consisted of an initial denaturation of 95°C for 3 min, followed by 25 cycles of 95°C for 1 min, 50°C for 1 min, 72°C for 1.5 min, and a final extension of 72°C for 7 min. PCR products, verified by electrophoresis on a 1% agarose gel, were purified using QIAquick spin columns (Qiagen Inc., Valencia, CA) and bidirectional sequencing performed by the Center for Functional Genomics (University of Albany, Rensselaer, NY).

COI sequences were edited and aligned using BioEdit and ClustalW (Hall, 1999; Thompson et al., 1997). Resulting sequences were compared to sequences by query of the GenBank database using BLASTn. Aligned sequences and those from 17 countries were used to generate a neighbor-joining (NJ) tree in MEGA 7.0 (Kumar et al. 2016) with the K-2 parameter (K2P) model and 1000 bootstrap replications. The same data set was used to construct a phylogenetic tree based on Maximum-Likelihood (ML) with 1000 bootstrap replications and the Tamura-3 parameter. Outgroup sequences were those of *Psychomorpha epimenis* (Drury) (Insecta:Lepidoptera:Noctuidae) and *Helicoverpa zea* (Boddie) (Insecta:Lepidoptera:Noctuidae). Pairwise genetic distances among sequences were calculated using MEGA 7.0 (Kumar et al., 2016). Genetic diversity indices, haplotype diversity (*H_d*) and nucleotide diversity (π) were calculated using DnaSP v.5 (Librado & Rozas, 2009).

Results And Discussion

A total of 186 noctuid larvae, ranging from the third to sixth instar, were collected from 70% of the survey area. Based on features of the head capsule and body markings, larvae comprised a mixture of three *Spodoptera* species; *S. exigua* was the most common species (49%) followed by *S. latifascia* (22%) and *S. frugiperda* (13%). The remaining larvae (16%) were identified as corn earworm (*Helicoverpa zea*).

All three *Spodoptera* species occurred on the farms surveyed in St. Elizabeth, whereas only *S. frugiperda* was observed in Clarendon and *S. exigua* in St. Thomas. Larvae of these two species were found on corn (*Zea mays*) and bell pepper (*Capsicum annum*) hosts, respectively. Leaves of pepper plants infested with *S. exigua* exhibited large irregular holes. Similarly, *S. frugiperda*, along with *H. zea*, caused irregular holes on corn leaves and whorls and all three species caused comparable damage on bunching onion (*Allium fistulosum*). Larvae of *S. exigua* and *S. frugiperda* were often found within the tubular leaves of these plants, while those of *S. latifascia* occurred on outer leaf surfaces. Bell pepper and corn are known hosts for *S. exigua* and *S. frugiperda* armyworms (Greenberg et al., 2001; Montezano et al., 2018). Bunching onion was not found in host lists published for *S. latifascia* (EPPO, 2015; Robinson, 2010).

Barcode sequences, consisting of the 5' end of the COI gene (681 bp), were generated with armyworms collected from five locations. Sample localities, source information and Genbank accession numbers are given in Table 1. BLASTn analysis confirmed the molecular identities of three *Spodoptera* species. Based on sequence alignments, *S. exigua* represented 53% of the larvae surveyed, *S. latifascia* 26%, and *S. frugiperda* 21%. Samples were assigned similarity scores of 99 to 100% to sequences of *S. exigua* from India (JQ64572), *S. latifascia* from Costa Rica (GU159445) and *S. frugiperda* from the United States, including the US territory, Puerto Rico (U72974, U72975, MW666000). Low and some differences in genetic diversities were observed among the sampled species. *S. latifascia* exhibited a haplotype diversity (*H_d*) of 0.691±0.128, and nucleotide diversity (π) 0.00138±0.00037, *S.*

frugiperda 0.389 ± 0.164 and 0.00631 ± 0.00267 and *S. exigua* showed an H_d of 0.577 ± 0.069 and a π of 0.00124 ± 0.00031 .

Neighbor joining (Fig. 2) and Maximum likelihood (data not shown) analyses gave well supported, congruent phylogenies. Clades, consistent with the three *Spodoptera* species, separated into two primary branches with *S. exigua* species forming one clade and *S. frugiperda* and *S. latifascia* another, albeit separated with 99 and 97% confidence on the NJ and ML trees, respectively. Jamaican sequences in the *S. latifascia* cluster were more closely aligned with those of indigenous populations derived from North and Central America (Table 2) than with those from South America (Brazil). The latter separated from the Jamaican samples and samples from other countries with K2P genetic distances > 2 (Table 2). *S. latifascia*, the lesser known of the armyworms and not as well characterized, occurs in the Americas at low densities (EPPO, 2015). Unlike its invasive counterparts, there appears to be limited movement about the region.

Shared genetic similarities between indigenous and invasive populations were observed within the *S. frugiperda* cluster which resolved into two distinct groups (Fig. 2), corresponding to corn (C) and rice (R) strain sequences. Most *S. frugiperda* specimens from Jamaica grouped with the C strain associated with the native range of the United States, Puerto Rico and Mexico along with an invasive population from India. The remaining sequences grouped with the R strain also of the United States and those from invasive populations of China, Nigeria and Thailand. The clusters were well supported in both NJ and ML analyses at 99% confidence (Fig. 2). Sequences in each group were identical, and sequences between groups differed by 1.42% (Table 2). To our knowledge, this is the first report of these strains in Jamaica. Larvae from which the C strain sequences were derived, were found feeding on corn, which is typical, and the R strain was found on bunching onion, a new recently reported host (Montezano et al., 2018).

Table 2 Pairwise Kimura two-parameter distances of armyworm species based on COI sequences from Jamaica and specimens from other geographical locations

Species	Origin	Mean distance
<i>S. latisfascia</i>	Within Jamaica	0-0.60
	Between Jamaica & Northern Caribbean	0-0.40
	Between Jamaica & Central America	0-0.40
	Between Jamaica & North America	0-0.40
	Between Jamaica & South America	2.50-2.90
<i>S. frugiperda</i>	Within Jamaica-C	0
	Within Jamaica-R	0
	Between Jamaica-C and Jamaica-R	1.40
	Between Jamaica-C & Northern Caribbean	0
	Between Jamaica-C & Central America	0
	Between Jamaica-C & North America	0
	Between Jamaica-C & Asia	0
	Between Jamaica-R & North America	0
	Between Jamaica-R & Asia	0
	Between Jamaica-R & Africa	0
<i>S. exigua</i>	Within Jamaica	0-0.40
	Between Jamaica & North America	0-0.60
	Between Jamaica & Europe	0-0.80
	Between Jamaica & Asia	0.40-1.00
	Between Jamaica & Oceania	4.50-4.80

Sequences from previous studies were obtained from the NCBI GenBank or BOLD: Northern Caribbean- Cuba GWOST423-11, Puerto Rico MK318377.1; Central America- Costa Rica GU159445.1, JQ554807.1, JQ577384.1, Mexico HQ961255.1, MK318311.1, Panama MT357872.1, North America- Georgia USA EU779856.1, Florida USA HM756078.1, U72977.1, U7274.1, BBLOB1534-11; Europe- Germany GU707393.1, Spain FN908004.1, United Kingdom FN907975.1, Asia- China MK860939.1, KM670453.1, Japan AB733675.1, India MN541574.1, JQ064572.1, Pakistan MT449730.1, Thailand MW387604.1, South America- Brazil INCATA523-10, Oceania- Australia HQ950505.1,

KF522650.1; Africa-Nigeria MK492940.1 C: sequences derived from *S. frugiperda* collected from corn plant hosts, respectively. R: sequences derived from *S. frugiperda* collected from bunching onion plant hosts.

While studies on populations of the Americas and South Africa record both C and R types (CABI, 2019; Jacobs et al., 2018; Kondide, 2011) or the prevalence of only one strain, recent studies have shown that invasive populations are mostly hybrids (Nagoshi et al., 2019; Tay et al., 2022). Notwithstanding, the propensity to migrate combined with the results of whole genome sequence analyses, suggest that *S. frugiperda* is a single breeding population across its native geographical range, with limited regional genetic heterogeneity (Tay et al., 2022). Besides native and invasive populations to which the Jamaican populations show genetic similarities, have acquired resistance to a number of insecticides including Bt products (Gutiérrez-Moreno et al., 2019; Storer et al., 2010). Similar resistance has been reported with *S. exigua* (Moulton et al., 2000).

Consistent with previous studies (e.g. Dumas et al., 2015), clear discriminant clusters between *S. exigua* of the Americas, Asia, and Australia were observed (Fig. 2). The latter separated from Jamaican and other samples with K2P genetic distances of 4.5 to 4.8% (Table 2). Jamaican *S. exigua* mostly grouped with invasive populations of North America and Europe and not with populations of *S. exigua* native to Asia. Further, a separate cluster contained one sample from Jamaica and Spain at 99% confidence, which suggests different and more than one incursion of *S. exigua* into the country.

Our study represents the first attempted genetic description of three species of *Spodoptera* armyworms infesting vegetable crops in Jamaica. Taken together, low within-population genetic diversity was found, and the Jamaican COI sequences perfectly matched or closely matched those of neighbouring as well as distant regions and in some instances non-native populations. The findings indicate mixing among populations of various locations and that Jamaica continues to be at risk for introductions of non-native armyworms, which could complicate mitigation efforts. A close relationship of Jamaican populations to *S. frugiperda* and *S. exigua* populations reporting field-evolved resistance to synthetic insecticides and Bt products was noted. Investigations into the distribution of resistance genes relative to the genetic structure of armyworm populations and assessments of the threat that armyworms present to other crops in the country are warranted.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Availability of data and material

Sequence data that support the findings of this study have been deposited in GenBank. Accession codes are listed in Table 1.

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

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Authors' contributions

Conceptualization, Damion Neath and Dwight Robinson; methodology, Damion Neath and Paula Tennant; formal analysis, Damion Neath and Paula Tennant; resources, Damion Neath, Dwight Robinson and Paula Tennant; writing-original draft preparation, Damion Neath and Paula Tennant; writing- review and editing, Damion Neath, Dwight Robinson and Paula Tennant.

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Figures

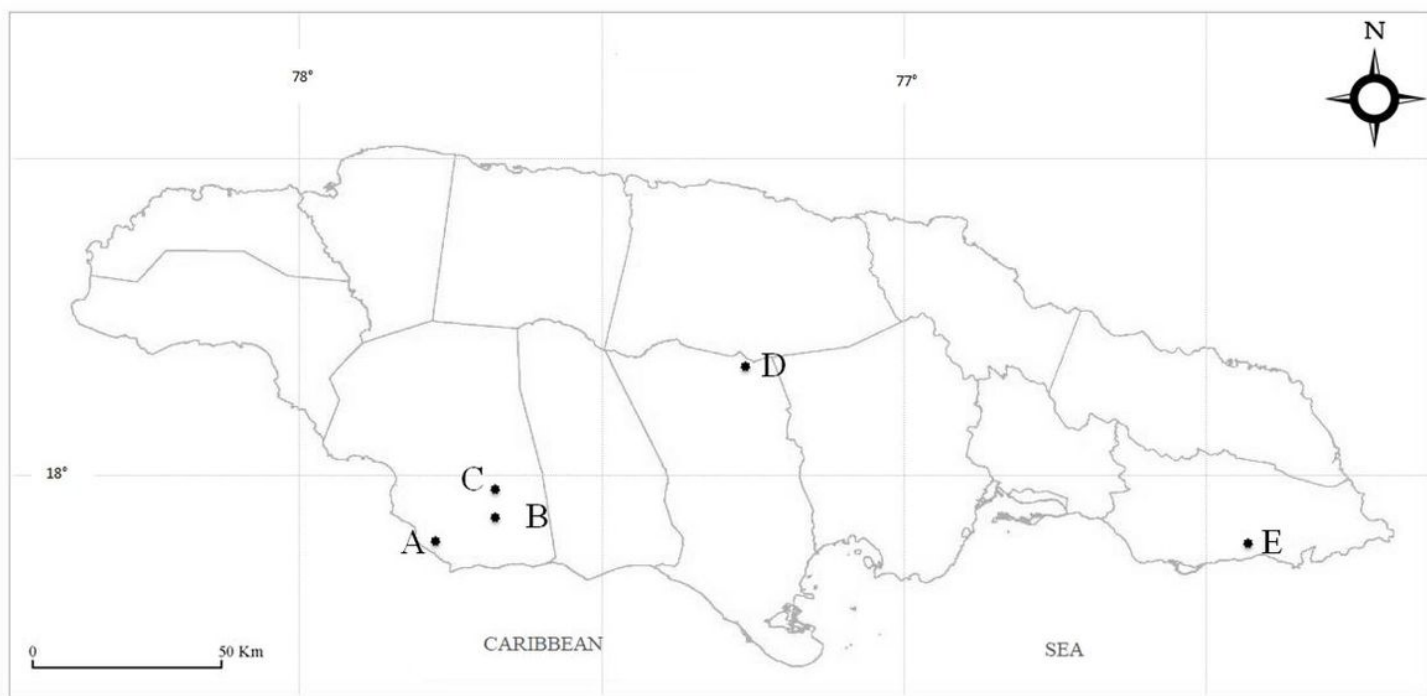


Figure 1

Spodoptera collection sites in Jamaica. A – St. Elizabeth (Bull Savanna), B – St. Elizabeth (Clarkmount), C – St. Elizabeth (Small Park), D – Clarendon (Brown’s Hall), E – St. Thomas (Morant Bay). Sample codes are given in Table 1.

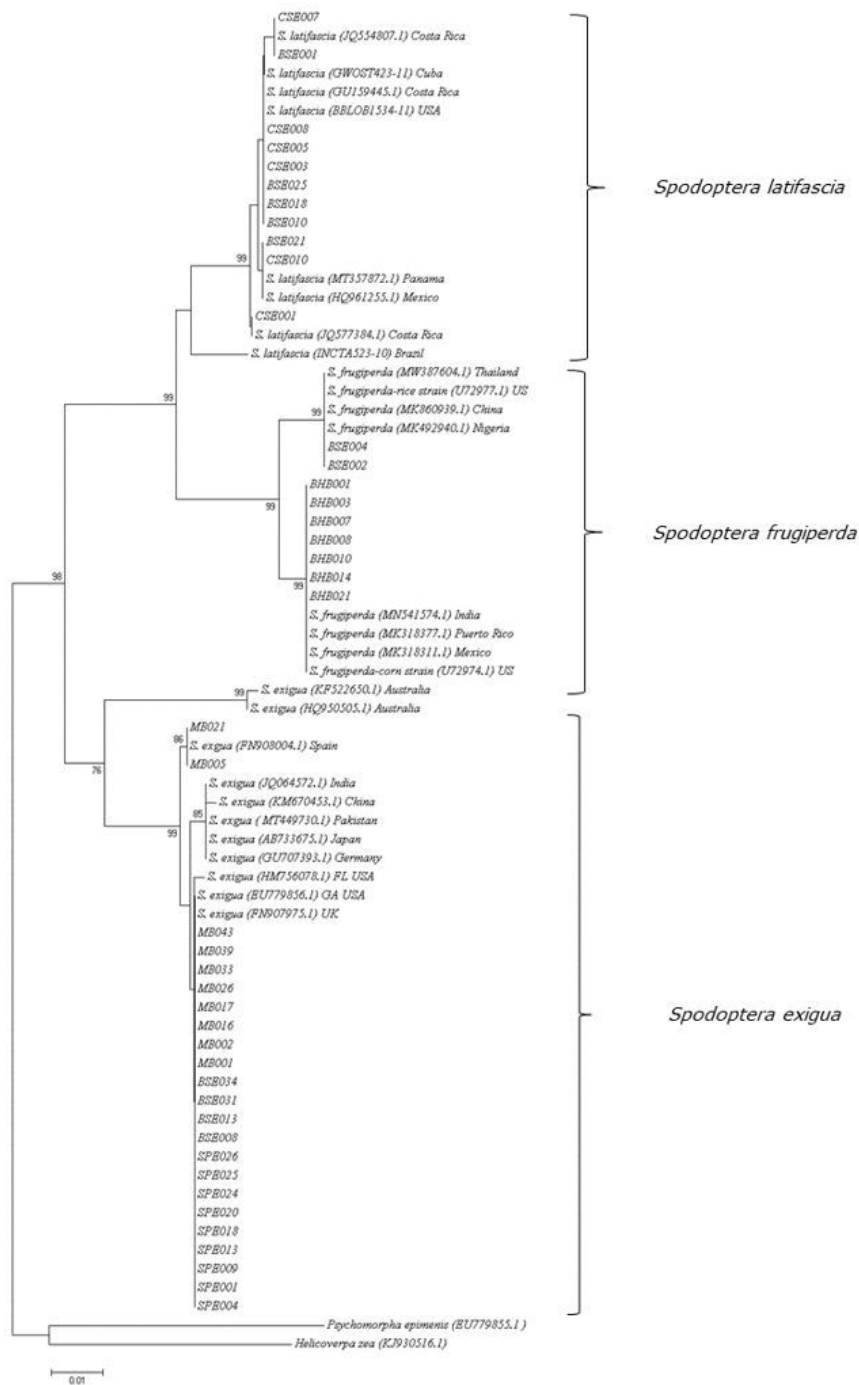


Figure 2

Neighbour-joining tree based COI sequences of *Spodoptera* sp from Jamaica and 27 specimens from other geographical locations. Node support was estimated from 1,000 bootstrap replications. The genetic distance is shown in the scale below. Sample descriptions are provided in Tables 1 and 2.