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# COI HAPLOTYPE ANALYSIS REVEALS PREDOMINANCE OF CORN-ASSOCIATED LINEAGES OF *Spodoptera frugiperda* IN SARAWAK, EAST MALAYSIA

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## ABSTRACT

The fall armyworm (*Spodoptera frugiperda* (J.E. Smith, 1797)) is a highly invasive agricultural pest of global economic importance, comprising two host-associated strains, the corn (C-strain) and rice (R-strain) that differ in ecology and management responses. Since its first detection in Malaysia in 2019, this species has become a persistent threat to corn production; however, information on its strain composition in Sarawak remains limited. This study characterised the strain structure and distribution of fall armyworm populations from major corn-growing regions in Sarawak using mitochondrial cytochrome oxidase I (COI) DNA barcoding. A total of 39 specimens collected from five localities were analysed through PCR amplification, sequencing, and phylogenetic comparison with global reference haplotypes. The results revealed a strong predominance of C-strain-associated COI haplotypes (89.7%) across all sampling sites, consistent with host-associated patterns reported throughout Southeast Asia. In contrast, R-strain haplotypes were detected at low frequency and were restricted to Bintulu and Samarahan. Haplotype clustering analyses showed close genetic affinity between Sarawak populations and previously reported invasive lineages, consistent with previously reported COI haplotypes from invaded regions. The coexistence of strain-associated haplotypes in localized populations may indicate ecological overlap or potential interstrain mixing; however, interpretation is constrained by the maternal inheritance of mitochondrial markers. Consequently, COI-based strain assignments should be treated cautiously and do not necessarily reflect biologically distinct host-associated populations. Despite these limitations, this study provides baseline molecular evidence of FAW strain composition in Sarawak and highlights the need for continued multi-marker surveillance to support strain-informed integrated pest management strategies for corn and other susceptible crops.

**Keywords:** *Spodoptera frugiperda*; Borneo; DNA barcoding; mitochondrial; strain typing

## ABSTRAK

Ulat ratus tentera (*Spodoptera frugiperda* (J.E. Smith, 1797)) merupakan perosak pertanian invasif yang berkepentingan dari segi ekonomi global, terdiri daripada dua strain yang berasosiasi dengan perumah, iaitu strain jagung (C-strain) dan strain padi (R-strain) yang berbeza dari segi ekologi dan tindak balas pengurusan. Sejak pengesanan pertamanya di Malaysia pada tahun 2019, spesies ini telah menjadi ancaman berterusan kepada pengeluaran jagung; namun, maklumat mengenai komposisi strainnya di Sarawak masih terhad. Kajian ini mencirikan struktur dan taburan strain populasi ulat ratus tentera dari kawasan utama penanaman jagung di Sarawak menggunakan barkod DNA bagi gen mitokondria cytochrome oxidase I (COI). Sebanyak 39 spesimen yang dikumpul dari lima lokaliti dianalisis melalui amplifikasi PCR, penjujukan dan perbandingan filogenetik dengan haplotip rujukan global. Hasil kajian menunjukkan dominasi kuat haplotip COI yang berkaitan dengan C-strain (89.7%) di semua tapak persampelan, selaras dengan corak berkaitan perumah yang dilaporkan di seluruh Asia Tenggara. Sebaliknya, haplotip R-strain dikesan pada frekuensi rendah dan hanya terhad di Bintulu dan Samarahan. Analisis pengelompokan haplotip menunjukkan pertalian genetik yang rapat antara populasi di Sarawak dengan susur galur invasif yang dilaporkan sebelum ini, selaras dengan haplotip COI dari kawasan pencerobohan yang telah dilaporkan. Kewujudan bersama haplotip berkaitan strain dalam populasi setempat mungkin menunjukkan pertindihan ekologi atau potensi pencampuran antara strain; walau bagaimanapun, tafsiran ini terhad oleh pewarisan maternal penanda mitokondria. Oleh itu, penentuan strain berasaskan COI perlu ditafsir dengan berhati-hati dan tidak semestinya mencerminkan populasi berkaitan perumah yang benar-benar berbeza secara biologi. Walaupun terdapat kekangan ini, kajian ini menyediakan bukti molekul asas mengenai komposisi strain FAW di Sarawak dan menekankan keperluan pemantauan berterusan menggunakan pelbagai penanda bagi menyokong strategi pengurusan perosak bersepadu yang mengambil kira strain untuk tanaman jagung dan tanaman lain yang rentan.

**Kata kunci:** *Spodoptera frugiperda*; Borneo; barkod DNA; mitokondria; penentuan strain

## INTRODUCTION

The fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is an invasive lepidopteran pest that has become a serious constraint to agricultural production worldwide. Native to the tropical and subtropical regions of the Americas, FAW has historically been a major pest of corn and other graminaceous crops (Tay et al. 2023). Since its first detection outside the Americas in Africa in 2016, FAW has rapidly expanded its geographical range across Africa, the Middle East, South Asia, and Southeast Asia (Goergen et al. 2016; Kenis et al. 2023). This rapid spread has been driven by the species' strong migratory capacity, high reproductive potential, and ability to exploit a wide range of host plants under diverse environmental conditions (Tay et al. 2023).

Corn is consistently reported as the crop most severely affected by FAW infestations (Montezano et al. 2018). Larval feeding causes extensive damage to leaves, whorls, and reproductive structures, often leading to significant yield losses when infestations occur at early growth stages (Hruska 2019). In newly invaded regions, FAW outbreaks have placed considerable pressure on farming systems, particularly smallholder agriculture, through increased crop losses and reliance on chemical insecticides. These challenges are further exacerbated by the pest's capacity to develop resistance to several commonly used insecticide classes, raising concerns about the long-term sustainability of chemical-based control strategies (Bird et al. 2022).

An important biological characteristic of FAW that complicates its management is the existence of two genetically distinct but morphologically indistinguishable host-associated strains, commonly referred to as the corn strain (C-strain) and the rice strain (R-strain). The strains were initially differentiated based on host plant associations, with the C-strain predominantly associated with corn and sorghum, and the R-strain more frequently linked to rice and pasture grasses (Nagoshi 2022). Subsequent research has demonstrated that these strains also differ in aspects of mating behaviour, migratory patterns, and responses to insecticides and biological control agents. Although overlap in host use has been reported, strain identity remains an important factor influencing FAW ecology and management outcomes (Nagoshi & Meagher 2004).

The presence of cryptic strains may have implications for pest risk assessment and Integrated Pest Management (IPM) (Day et al. 2017). Differences in host preference raise concerns regarding the potential expansion of FAW populations from corn into other economically important crops, particularly rice. In addition, mixed-strain populations may exhibit greater ecological flexibility, potentially enhancing their ability to adapt to new environments and management practices (Hruska 2019). Understanding strain composition is therefore useful for informing predictions of pest behaviour, assessing risks to multiple cropping systems, and improving the effectiveness of control strategies.

Studies conducted in Africa and Asia following FAW invasions have revealed considerable variation in strain composition across regions and cropping systems (Goergen et al. 2016). In corn-dominated agroecosystems, the COI haplotypes associated with the corn strain generally predominate, consistent with its reported host preference (Nagoshi & Meagher 2004). However, R-strain haplotypes have also been detected at low frequencies in several countries, sometimes occurring alongside the C-strain within corn fields (Sarr et al. 2021). These findings suggest that FAW populations in invaded regions may consist of mixed strain-associated haplotypes, highlighting the need for continued genetic surveillance to better understand population dynamics and potential host range expansion (Early et al. 2018).

In Malaysia, FAW was first reported in 2019 and has since been established across major corn-growing regions, including East Malaysia. Sarawak (Mohammed et al. 2021), located on the island of Borneo, has experienced increasing FAW infestations in recent years, coinciding with the expansion of corn cultivation and favourable climatic conditions for pest development. Despite the growing importance of FAW as an agricultural pest in Sarawak, information on the genetic structure and strain composition of local populations remains limited. Most existing reports have focused on pest occurrence and field damage, with little molecular evidence available to clarify strain identity and distribution (Kueh et al. 2023).

Strain-level information is particularly relevant in Sarawak due to the region's diverse agricultural landscape, which includes corn, rice, and other potential FAW host plants. The presence of R-strain haplotypes within corn fields could indicate an increased risk of FAW spillover into rice-based systems, with implications for food security and pest management planning. Establishing baseline molecular data is therefore essential for improving surveillance, supporting early detection of shifts in strain composition, and informing future evaluation of strain-specific IPM strategies.

The present study aims to characterise the strain composition of FAW populations collected from major corn cultivation areas in Sarawak using COI DNA barcoding. Specifically, this study seeks to determine the prevalence of corn and rice strain haplotypes among sampled populations, examine their geographical distribution, and provide baseline genetic information to support future monitoring and management efforts in East Malaysia. By addressing a key knowledge gap in an under-studied region, this study contributes to a broader understanding of FAW invasion dynamics and supports the development of evidence-based approaches for sustainable FAW management.

## MATERIALS AND METHODS

### Sample Collection

Field sampling was carried out in five major corn-producing areas of Sarawak, East Malaysia, namely Miri, Bintulu, Mukah, Samarahan, and Lundu. These sites were selected to represent key corn-growing regions across different geographical zones of the state. Sampling was conducted between January 2024 and March 2025. Fall armyworm specimens were collected from corn fields during routine field inspections, targeting plants exhibiting typical feeding symptoms such as leaf windowing, ragged whorl damage, and frass accumulation. All specimens were collected at the larval stage from multiple plants per field. One to three fields were sampled per locality, depending on accessibility and crop availability. From the available material, 39 FAW specimens were selected and processed for molecular analysis in this study. Individual specimens were handled using clean forceps to avoid cross-contamination and were immediately preserved in 85% molecular-grade ethanol in the field. Samples were subsequently transported to the laboratory and stored at -20 °C until DNA extraction.

### DNA Extraction, PCR Amplification and Sequencing

Genomic DNA was extracted from individual FAW specimens using PrimeWay Genomic DNA Extraction Kit (1st BASE, Singapore), following the manufacturer's recommended protocol. DNA quality was assessed based on amplification success and visualization of PCR products using agarose gel electrophoresis. A partial fragment (~658 bp) of the mitochondrial cytochrome c oxidase subunit I (COI) gene was amplified using the universal primers LCO1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAAAATCA-3′), following Folmer et al. (1994) and Mohammed et al. (2023). Polymerase chain reaction (PCR) amplifications were performed in a 25 µL reaction volume containing 12.5 µL of PCR master mix, 0.5 µM of each primer, 1-2 µL of template DNA, and nuclease-free water to volume. Negative controls were included in each PCR run to monitor potential contamination. The thermal cycling profile consisted of an initial denaturation at 95°C for 3 min, followed by 30 cycles of 95°C for 30 s, 47°C for 1 min, and 72°C for 30 s, with a final extension at 72°C for 10 min.

PCR products were examined by electrophoresis on agarose gels stained with a nucleic acid dye to confirm successful amplification and expected fragment size. Successfully amplified products were purified to remove residual primers and nucleotides and subsequently submitted for bidirectional Sanger sequencing by Apical Scientific Sdn. Bhd. (Serdang, Selangor).

**Sequence Analysis and Phylogenetic Reconstruction**

Raw sequence chromatograms were inspected, edited, and assembled into consensus sequences using BioEdit ver.7.2.5 (Hall 1999). Low-quality regions at the sequence ends were trimmed prior to further analysis. The resulting consensus sequences were aligned and compared against reference sequences available in the NCBI GenBank and Barcode of Life Data System (BOLD) databases to confirm species identity.

Phylogenetic relationships among the sampled fall armyworm (FAW) individuals were inferred using the Neighbor-Joining (NJ) method implemented in PAUP* version 4.0 (Swofford 2002). Genetic distances were calculated using the Kimura 2-parameter (K2P) substitution model (Kimura 1980), and nodal support was evaluated with 1,000 bootstrap replicates. To facilitate strain assignment and interpretation of clustering patterns, published mitochondrial cytochrome oxidase I (COI) reference sequences representing the corn-associated COI haplotypes (C-strain; GenBank accession numbers U72976.1, MT933361.1, and MT933057.1) and the rice-associated COI haplotypes (R-strain; GenBank accession numbers HM136602.1, MT103344.1, and MT103334.1) were included in the NJ tree construction. The NJ approach was selected as a standard method for DNA barcoding-based clustering rather than for robust phylogenetic inference.

## RESULTS

All 39 fall armyworm (FAW) specimens were successfully amplified at the mitochondrial cytochrome oxidase I (COI) locus, yielding high-quality sequences suitable for downstream analyses. BLAST searches against the GenBank and Barcode of Life Data Systems (BOLD) databases confirmed all samples as *Spodoptera frugiperda*, with 100% sequence identity to reference sequences (Table 1).

Table 1. COI sequence identity of fall armyworm (*Spodoptera frugiperda*) specimens from different sampling localities in Sarawak, Malaysia, based on BLAST searches against GenBank and the Barcode of Life Data Systems (BOLD)

| Sampling Locality | No. of Specimens (N) | Genbank Identity (%) | BOLD Identity (%) |
|---|---|---|---|
| Miri | 7 | 100 | 100 |
| Bintulu | 7 | 100 | 100 |
| Mukah | 12 | 100 | 100 |
| Samarahan | 7 | 100 | 100 |
| Lundu | 6 | 100 | 100 |
| Total | 39 | | |

Strain differentiation based on COI sequence variation revealed clear diagnostic nucleotide differences between the corn strain (C-strain) and rice strain (R-strain). These strain-specific base substitutions were consistent with previously reported COI markers and are summarized in Table 2 which presents representative reference sequences used to support molecular strain assignment.

Phylogenetic relationships inferred using a Neighbor-Joining (NJ) approach further supported the presence of two genetically distinct FAW lineages in Sarawak. The NJ tree, constructed using the Kimura 2-parameter model with 1,000 bootstrap replicates, separated all Sarawak samples into two well-defined clades corresponding to the C-strain and R-strain (Figure 1). Reference sequences representing established C-strain haplotypes from the USA, Vietnam, and Tanzania clustered together with the majority of Sarawak specimens, forming a single, well-supported C-strain clade. In contrast, R-strain reference sequences formed a distinct clade that included only a small subset of Sarawak samples. Bootstrap support values for the separation between the two clades were consistently moderate (≥50%), indicating clear genetic differentiation based on the COI dataset. The NJ tree is presented primarily to illustrate haplotype clustering and should not be interpreted as robust phylogenetic or phylogeographic inference.

Of the 39 individuals analysed, 35 specimens (89.7%) grouped with COI haplotypes associated with the corn strain. These included all samples collected from Miri, Mukah, and Lundu, as well as most individuals from Bintulu and Samarahan. Only four specimens (10.3%) clustered with the R-strain reference sequences, with R-strain individuals detected exclusively in Bintulu (n = 2) and Samarahan (n = 2).

The geographic distribution of FAW COI haplotypes across Sarawak is illustrated in Figure 2. COI haplotypes associated with the corn strain were detected at all sampled localities, indicating its widespread distribution across the study area. In contrast, rice strain-associated haplotypes showed a more restricted distribution and were recorded only in Bintulu and Samarahan, where both strains co-occurred. This spatial pattern is consistent with phylogenetic and sequence-based assignments, indicating the predominance of COI haplotypes associated with the corn strain across Sarawak corn agroecosystems, with rice strain-associated haplotypes occurring at low frequency and restricted to specific localities.

Table 2. Summary of unique COI haplotypes of *Spodoptera frugiperda* identified from Sarawak, East Malaysia, showing diagnostic nucleotide positions, associated strain-related haplotype group, and frequency of occurrence

| **Haplotype** | **Diagnostic Nucleotides** | **Associated Strain** | **No. of Samples** |
|---|---|---|---|
| Hap1 | G T C T C C T | Corn | 35 |
| Hap2 | A A T C T T C | Rice | 4 |

Full nucleotide profiles of all individual samples are provided in Supplementary Table S1

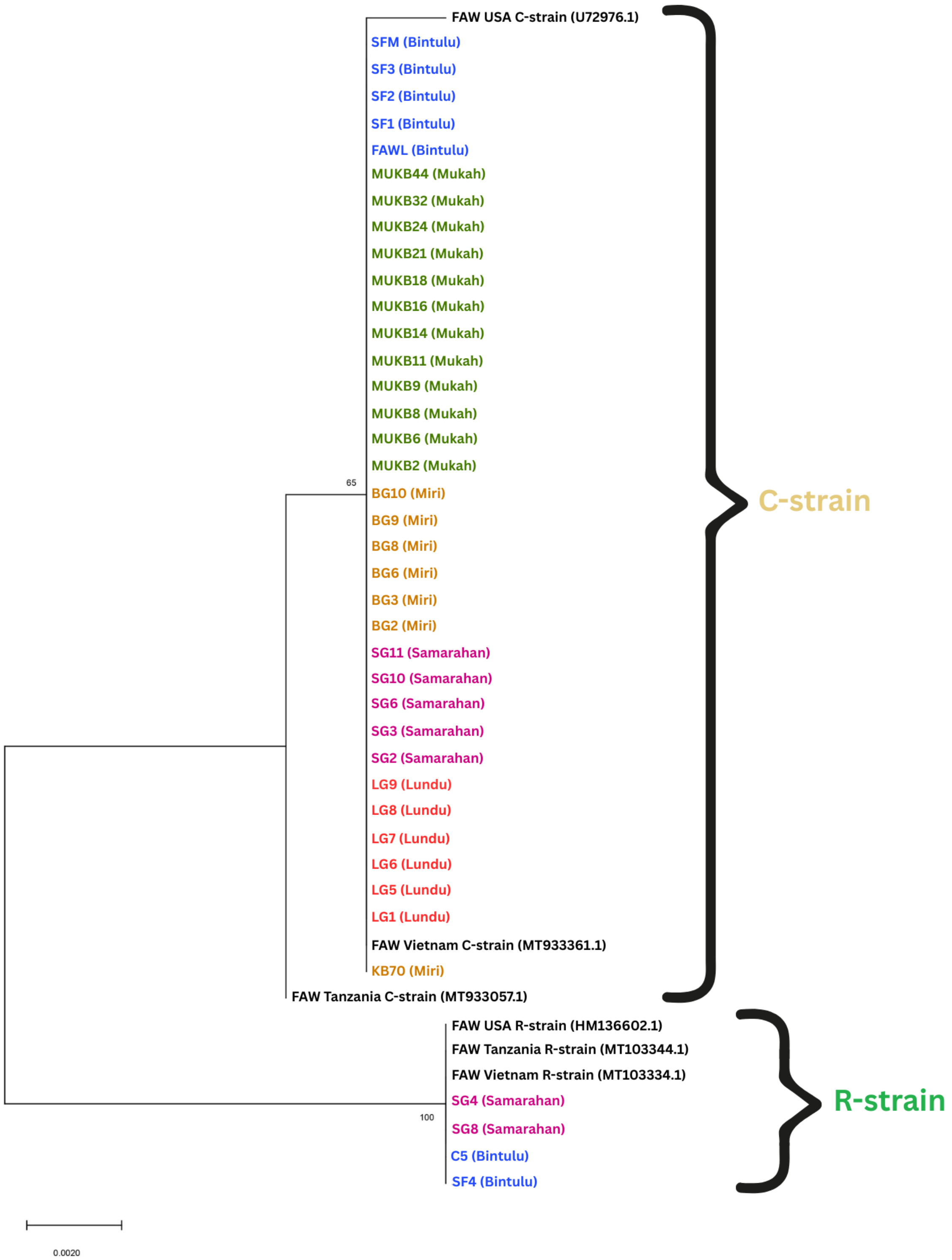


Figure 1. Neighbor-Joining (NJ) tree based on mitochondrial cytochrome oxidase I (COI) sequences of fall armyworm (*Spodoptera frugiperda*) from Sarawak, Malaysia, and selected reference sequences. The tree was constructed using the Kimura 2-parameter (K2P) model with 1,000 bootstrap replicates. Reference sequences representing corn- and rice-associated haplotypes are included for comparison. Bootstrap values ≥50% are shown for reference. The scale bar indicates the number of substitutions per site

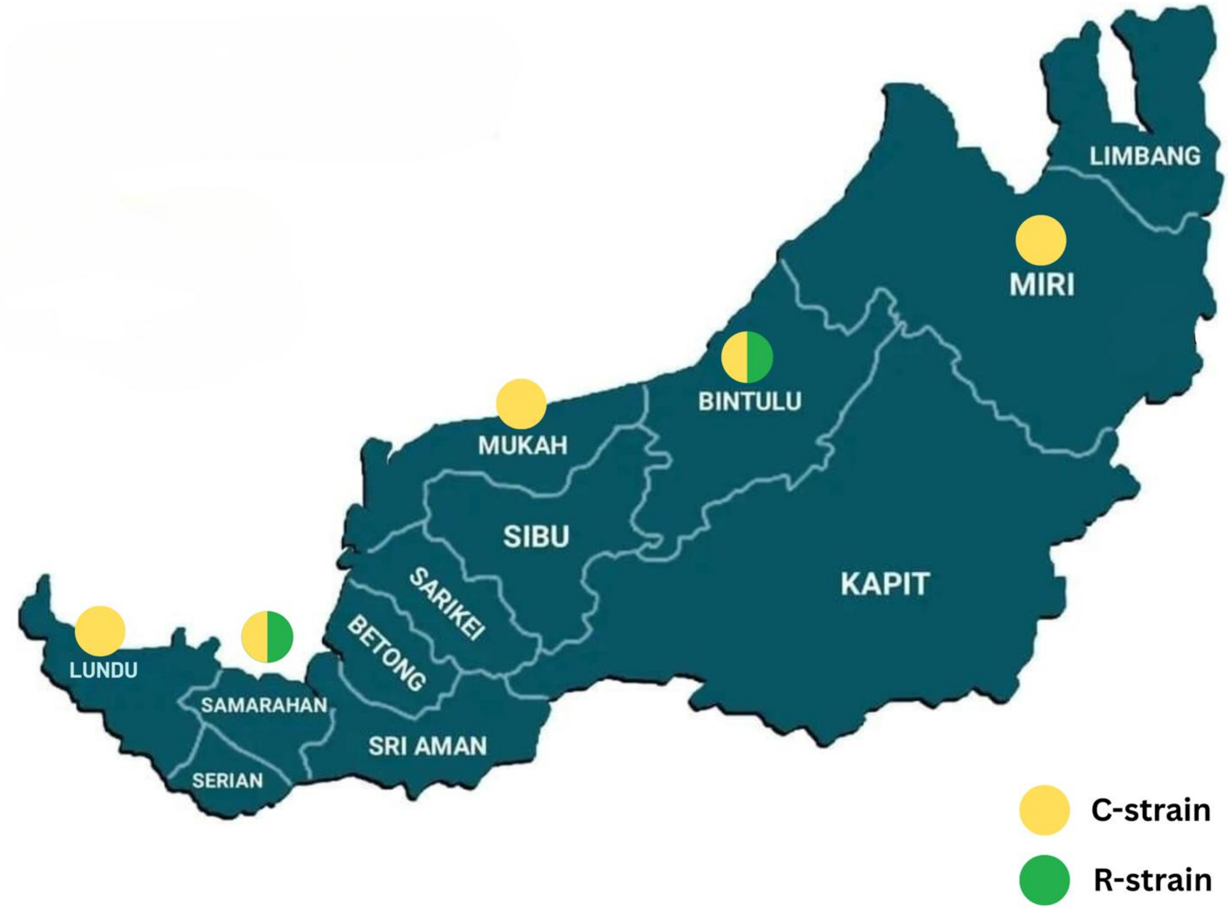


Figure 2. Geographic distribution of fall armyworm (*Spodoptera frugiperda*) COI haplotypes across sampled localities in Sarawak, Malaysia. Yellow circles represent individuals with COI haplotypes associated with the corn strain, while green circles represent individuals with haplotypes associated with the rice strain. Mixed symbols indicate localities where both haplotype groups were detected

## DISCUSSION

The predominance of COI haplotypes associated with the corn strain in FAW populations from Sarawak is generally consistent with reports from other parts of Southeast Asia, where FAW infestations are closely associated with corn cultivation (Hong et al. 2022; Navasero et al. 2019). Since FAW was first reported attacking corn in Bintulu in 2019, the pest has become established in several corn-growing areas across the state. As all specimens examined in the present study were collected from corn fields, the high proportion of C-strain individuals observed is therefore not unexpected and reflects the host association commonly reported for this strain.

The clustering of Sarawak samples with reference C-strain haplotypes from Africa, the United States, and other parts of Asia is consistent with previously reported COI haplotype patterns from invaded regions (Zhang et al. 2023). However, given the short mitochondrial fragment analysed, the neighbour-joining (NJ) tree provides limited resolution for robust inference of invasion pathways or fine-scale population structure. Previous studies have suggested that FAW populations spreading into Asia were largely derived from African source populations dominated by the C-strain, followed by progressive eastward expansion (Yainna et al. 2022; Zhang et al. 2023). The phylogenetic patterns observed here are consistent with COI haplotype patterns previously reported from other invaded regions.

Although the corn strain (C-strain) was clearly dominant, a small number of rice strain (R-strain) individuals were detected in Bintulu and Samarahan. Earlier molecular studies in Sarawak, which focused mainly on Serian and Samarahan, also reported the presence of both strains in corn fields based on mitochondrial COI markers (Kueh et al. 2023). By including additional sampling localities, the present study indicates that mixed strain-associated haplotype signatures are not restricted to the areas previously studied but can also be detected elsewhere in Sarawak, albeit at low frequencies, a pattern that has similarly been reported from other invaded regions in Asia (Acharya et al. 2021; Herlinda et al. 2022).

The presence of rice strain (R-strain) haplotypes in corn fields may be influenced by several factors, including local landscape structure, availability of alternative host plants, and movement of individuals between adjacent habitats (Day et al. 2017; Nagoshi 2012). In Sarawak, corn cultivation often occurs alongside other crops and semi-natural vegetation, which may facilitate the persistence of different FAW lineages within the same area. Although the R-strain is more commonly associated with rice and pasture grasses, its occurrence in corn fields has been reported from several invaded regions, indicating a degree of ecological overlap between strains under certain conditions (Acharya et al. 2021; Herlinda et al. 2022).

Although differences between fall armyworm (FAW) strains in terms of insecticide susceptibility and biological control responses have been reported in other regions, such differences have not yet been validated under Sarawak conditions. Therefore, current pest management strategies should not be adjusted based solely on COI-defined strain composition. Instead, the observed mitochondrial lineage diversity should be considered as a potential factor warranting further investigation using more robust genetic markers.

Strain assignments in this study were supported by phylogenetic analysis and diagnostic nucleotide differences in the mitochondrial cytochrome oxidase I (COI) sequences. Individuals assigned to the corn strain (C-strain) showed nucleotide patterns consistent with published C-strain reference haplotypes, whereas those grouped with the rice strain (R-strain) exhibited the corresponding strain-specific substitutions (Nagoshi 2012). These findings are in agreement with earlier molecular reports from Sarawak and neighbouring regions and indicate that COI remains useful for preliminary strain identification, particularly for broad-scale population surveys (Herlinda et al. 2022; Kueh et al. 2023).

It is important to note that strain assignments in this study are based solely on mitochondrial COI markers, which reflect maternal lineage rather than nuclear genetic structure. Recent genomic studies have demonstrated that COI-defined "R-strain" haplotypes detected in corn fields often represent hybrid or introgressed individuals rather than true rice-associated populations. Therefore, the occurrence of R-strain haplotypes in the present study should be interpreted as evidence of mitochondrial lineage diversity rather than definitive indication of host-associated strain differentiation. In this context, the term "strain" is used operationally, and further validation using nuclear markers such as the triosephosphate isomerase (Tpi) gene is required to resolve biological strain identity.

Nevertheless, some limitations should be acknowledged. The relatively small sample size, particularly the low number of individuals assigned to R-strain haplotypes (n = 4), limits the strength of conclusions regarding strain coexistence. The apparent absence of R-strain haplotypes in some localities may reflect sampling limitations rather than true absence in the field. The mitochondrial *cytochrome oxidase I* (*COI*) gene is maternally inherited and, when used alone, may not fully resolve strain identity in areas where interstrain hybridisation occurs (Malekera et al. 2023). Previous molecular studies from Sarawak have highlighted this limitation and suggested that rice strain (R-strain) COI haplotypes detected in corn fields may represent hybrid individuals rather than distinct R-strain populations (Kueh et al. 2023). Therefore, the low-frequency occurrence of R-strain haplotypes observed in the present study should be interpreted with caution.

In addition, earlier molecular studies in Sarawak were largely limited to Serian, Samarahan, and Bintulu. Although the present study extends strain characterisation to additional localities, sampling was still restricted to corn fields and a relatively limited number of sites. Broader geographic coverage across Sarawak, inclusion of other potential host plants, and the incorporation of nuclear markers such as the sex-linked triosephosphate isomerase (Tpi) gene, together with other strain-informative nuclear loci or population genetic markers, would provide a more comprehensive understanding of fall armyworm strain distribution and population structure in the region.

## CONCLUSION

This study provides molecular insight into the strain composition of fall armyworm (FAW) populations in Sarawak, East Malaysia, based on COI DNA barcoding. The results indicate that FAW populations in corn-growing areas are largely dominated by COI haplotypes associated with the corn strain, with rice strain-associated haplotypes detected at low frequencies in Bintulu and Samarahan. The presence of mixed COI haplotypes associated with different strain lineages in these areas suggests the possibility of strain intermixing and warrants attention, particularly in landscapes where multiple host plants are cultivated. Overall, the findings highlight the value of continued molecular monitoring and the need to further evaluate the potential role of variation in strain-associated haplotypes when developing integrated pest management strategies to protect corn and other susceptible crops in Sarawak.

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## AUTHORS DECLARATIONS

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**Conflict of Interest**

The authors declare that they have no conflict of interest.

**Ethics Declarations**
No ethical issues are associated with this study.

**Data Availability Statements**
All data generated or analyzed during this study are included in this published article.

**Author's Contributions**
The authors' contributions are as follows: MAM: conceptualization, funding acquisition, project administration, supervision, validation, and writing-original draft and editing; MGB, VGR, AH, NA, FJJ, and NJM: data curation, investigation, methodology, and formal analysis; AAZ: conceptualization, methodology, supervision, validation, and writing-review and editing; SY: conceptualization, validation, and editing.

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