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RESEARCH PAPER

Distribution of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) strains and their association with different landscape structures in Bali, Indonesia

Dheya Cintya Monica, Yayi Munara Kusumah, & I Wayan Winasa

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ABSTRACT

Spodoptera frugiperda, commonly known as the Fall Armyworm (FAW), is an invasive pest originating from the Americas that poses a serious threat to maize production in Bali, with potential crop losses reaching up to 50%. To monitor its genetic distribution, this study employed molecular identification using the mitochondrial cytochrome oxidase subunit I (mt*COI*) and triosephosphate isomerase (*Tpi*) gene markers. The research aimed to identify FAW strains present in Bali and to assess their distribution across different landscape structures. The study consisted of four main stages: (1) sample and coordinate collection, (2) DNA extraction, amplification, and sequencing, (3) molecular data analysis, and (4) spatial analysis using QGIS, Google Earth Pro, and RStudio 4.3.1 with a generalized linear model (GLM). showed that the *COI*-R/*Tpi*-C strain was dominant in the central (Badung and Tabanan) and eastern (Klungkung) regions of Bali, whereas the *COI*-C/*Tpi*-C strain was found in the northern (Buleleng), southern (Denpasar), and western (Jembrana) regions. FAW haplotypes were relatively evenly distributed across all sampling locations. No significant association was detected between FAW strain distribution and landscape structure, leaving unclear which vegetation types act as ecological corridors or barriers. The low strain and haplotype diversity observed across both gene markers suggests that genetic variation is largely confined within, rather than between, regions, resulting in a relatively uniform distribution of FAW haplotypes across Indonesia, including Bali.

Keywords: *Spodoptera frugiperda,* invasive pest, mtCOI, *Tpi,* corridor, landscape genetic

INTRODUCTION

Spodoptera frugiperda, commonly referred to as the fall armyworm (FAW), poses a significant threat to maize cultivation, causing substantial crop losses. This invasive species, originally from the Americas, was first reported in Indonesia in 2019 and detected in Bali in 2020, where infestations led to yield reductions of up to 50% (Sartiami et al., 2020; Supartha et al., 2021). The pest initially appeared in lowland areas and subsequently spread across the entire province (Supartha et al., 2021). Similar patterns of spread have also been reported in other provinces of Indonesia. Lestari et al. (2024) observed a rapid increase in S. frugiperda populations following its initial invasion in Lampung, influenced by climatic variation and host availability. Likewise, Ginting et al. (2024) found that infestation intensity in Bengkulu varied across elevations, indicating that agroecological conditions strongly affect FAW establishment and damage levels. Accurate identification of FAW at the strain or haplotype level is essential to understand its distribution and dispersal mechanisms, thereby facilitating the development of effective management strategies.

Molecular markers such as *mtCOI* (mitochondrial cytochrome oxidase subunit I) and *Tpi* (triosephosphate isomerase, a Z-linked gene) are commonly employed to differentiate between FAW strains. These markers enable the identification of strain types, inference of life-history traits, and determination of host plant preferences through the analysis of single nucleotide polymorphisms (SNPs) (Nagoshi, 2010; Nagoshi & Meagher, 2022). Strain and haplotype identification enhances our understanding of FAW distribution and dispersal through comprehensive strain mapping, which is fundamental to designing targeted control strategies. In particular, implementing pheromone-based control measures can benefit substantially from detailed knowledge of the specific strains and haplotypes present (Nagoshi et al., 2007; Meagher et al., 2019; Akinbuluma et al., 2024). Furthermore, analysing the proportions of different strains or haplotypes provides valuable insights into dispersal and gene flow dynamics, supporting the estimation of

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Corresponding author:
Dheya Cintya Monica (cintyamonica008@gmail.com)

Department of Plant Protection, Faculty of Agriculture, IPB University. Jl. Kamper, Kampus IPB Dramaga, Bogor, Indonesia 16680

appropriate control measures (Lebody et al., 2024).

FAW dispersal is influenced by both internal dynamics (e.g., individual mobility) and external conditions, including biotic factors (such as food availability) and abiotic factors (such as climatic and environmental conditions). Landscape structure plays a pivotal role in shaping FAW distribution, functioning either as a corridor that facilitates movement or as a barrier that restricts gene flow. Studies have shown that dense vegetation barriers can reduce genetic similarity within populations, while high landscape connectivity promotes genetic exchange (Holderegger & Wagner, 2006; Dong et al., 2021; Sataral et al., 2023). Certain genotypes may also be confined to specific vegetation structures, influencing their spread and population dynamics.

However, previous studies have shown that the relationship between landscape structure and genetic diversity may take considerable time to become evident. This occurs particularly when vegetation changes occur more rapidly than gene flow (Holzhauer et al., 2006). Similar findings were reported in Bogor, Indonesia (Fahmi et al., 2023), highlighting the complexity of discerning clear patterns in this relationship. Therefore, this study seeks to evaluate whether the association between vegetation structure and FAW strain or haplotype is readily observable or remains difficult to detect.

Currently, there is limited research on the diversity of FAW strains in Bali using *COI* and *Tpi* markers. Understanding the haplotype composition of FAW in Bali is crucial to completing its dispersal mapping across Indonesia. Moreover, examining the association between FAW strains and landscape structure will provide valuable insights into how environmental factors influence its distribution. Consequently, this study aims to identify FAW strains and haplotypes in Bali and analyse their relationship with landscape structure to improve our understanding of FAW dispersal dynamics in the region.

MATERIALS AND METHODS

Research Site. Samples were collected from 12 locations across one city and five districts in Bali: Denpasar, Buleleng, Badung, Klungkung, Jembrana, and Tabanan (Table 1). Sampling was conducted purposively by collecting specimens from maize plants infested with FAW. The research was carried out at the Insect Pathology Laboratory, Department of Plant Protection, IPB University, from December 2023 to July 2024.

Sample Collection and Location Coordinates. FAW larvae obtained from the sampling sites were preserved in glass vials containing 70% ethanol. Each vial was labeled with the collection site and date, then stored at –20 °C until further analysis. Environmental parameters were recorded by documenting the geographic coordinates of each sampling point using a GPS device.

The surrounding landscape within a 300-m radius of each site was categorized into three classes: 1) Rice paddies (wetland), 2) Seasonal agricultural land (including maize fields and other dryland crops), 3) Semi-natural land (shrubs and tree stands).

Table 1. Sampling location in Bali

Location		Elevation (masl)*	Code	Coordinate	
City/District	Sub-district			Latitude	Longitude
Klungkung	Klungkung 1	31	K1	8°33'49.8"S	115°24'33.2"E
	Klungkung 2	18	K2	8°34'08.3"S	115°24'08.8"E
	Klungkung 3	16	K3	8°34'11.3"S	115°24'09.7"E
Badung	Abiansemal	132	Ba	8°32'58.9"S	115°13'29.0"E
Denpasar	Denpasar Timur 1	26	D1	8°39'13.1"S	115°15'07.2"E
	Denpasar Timur 2	19	D2	8°39'56.5"S	115°15'02.3"E
	Denpasar Timur 3	22	D3	8°39'28.7"S	115°15'26.3"E
Buleleng	Seririt	15	Bu	8°12'21.9"S	114°52'35.9"E
Jembrana	Medoyo 1	13	J1	8°23'57.8"S	114°45'57.7"E
	Medoyo 2	22	J2	8°22'51.0"S	114°43'36.4"E
Tabanan	Denbatas 1	172	T1	8°30'46.5"S	115°08'30.3"E
	Denbatas 2	180	T2	8°30'33.8"S	115°08'35.9"E

*masl= meter above sea level.

DNA Extraction. Genomic DNA was extracted using the cetyltrimethylammonium bromide (CTAB) method as described by Marín et al. (2021), with minor modifications. The centrifugation speed was adjusted to 12,000–13,000 rpm, and the final DNA was dissolved in TE buffer (pH 8.0; 1st Base, Singapore) according to laboratory availability.

DNA Amplification, Visualization, and Sequencing. Two primers sets, *COI*B and *Tpi*, were used for DNA amplification following Nagoshi et al. (2007) and Nagoshi et al. (2017) (Table 2). PCR amplification was performed using MyTaq™ HS RedMix with standard buffer under the cycling conditions described by Nagoshi (2010) and Nagoshi et al. (2017).

Amplified products were visualized on a 0.8% agarose gel under UV illumination and sequenced commercially (PT Genetika Science Indonesia) using the Sanger method.

Data Analysis. Raw sequences were edited using GeneStudio and aligned with ClustalW in BioEdit. FAW populations were classified into corn (C) and rice (R) strains. For the rice strain, identification was based on SNPs at *COI*1164 (T) and *COI*1287 (A) in the *COI*B region. For the corn strain, haplotypes were divided into four subgroups (C-h1, C-h2, C-h3, and C-h4) following Nagoshi et al. (2007; 2017). These were further grouped into three categories: FAW[TX] from Texas ($x \leq -0.3$), FAW[FL] from Florida ($x \geq 0.1$), and FAW[M] (mix) ($-0.3 < x < 0.1$), based on the haplotype ratio C = (h4-h2/h4+h2).

For the *Tpi* gene, strain determination was based on polymorphisms at g*Tpi*183Y in exon-4, resulting in three categories: *Tpi*-C (corn strain), *Tpi*-R (rice strain), and hybrid strains between Tpi-C and *Tpi*-R (*Tpi*-int/*Tpi*-H) with overlapping bases due to heterozygosity (Nagoshi et al., 2007; Nagoshi et al., 2017). Two unique corn-strain haplotypes, *Tpi*-Ca1 and *Tpi*-Ca2, were identified based on polymorphisms at g*Tpi*192 and g*Tpi*198 in exon 4.

Landscape Structure and Spatial Analysis. Landscape maps within a 300-m radius of each site were generated using QGIS and Google Earth Pro. Quantitative landscape metrics—including number of patches (NumP), class area (CA), total edge (TE), mean patch size (MPS), mean shape index (MSI), and mean patch fractal dimension (MPFD)—were analyzed using logistic regression (glm). Spatial distribution patterns were visualized using principal coordinates analysis (PCoA) in RStudio version 4.3.1.

RESULTS AND DISCUSSION

These findings are consistent with reports from other regions of Indonesia. Lestari et al. (2024) demonstrated that *S. frugiperda* population growth in Lampung followed seasonal patterns, with peaks corresponding to maize cropping cycles, whereas Ginting et al. (2024) highlighted that infestation intensity in Bengkulu varied across elevations, influenced by temperature and agroecological conditions. Such environmental heterogeneity may also explain the relatively even haplotype distribution observed in Bali.

***Spodoptera frugiperda* Strain Diversity and Distribution in Bali.** Based on analyses of the *COI* and *Tpi* genes, the distribution of FAW strains in Bali revealed distinct spatial patterns. The *COI*-R/*Tpi*-C strain combination was primarily found in the central region of the island (Badung and Tabanan districts) and on the eastern edge, specifically at two locations in Klungkung district. In contrast, the *COI*-C/*Tpi*-C strain was detected in the northern region (Buleleng district), southern region (Denpasar district), and western region (Jembrana district) of Bali.

The presence of corn-strain haplotypes, identified by both *COI* (*COI*-Ch4) and *Tpi* (*Tpi*-Ca1 and *Tpi*-Ca2), markers, appeared to be evenly distributed across all sampling sites (Figure 1). Although *COI*-R exhibited a tendency for geographic isolation, it is important to emphasize that studies examining the invasion ecology of FAW should not rely exclusively on the *COI* gene. This caution arises from observed inconsistencies between strain identification and host

Table 2. Primers used for amplifying *COI*B and *Tpi* in *S. frugiperda*

Targeted gene		Primer sequence (5′ - 3′)	Amplicon (pb)
*COI*B	891F	TAC ACG AGC ATA TTT TAC ATC	± 603
	1472R	GCT GGT GGT AAA TTT TGA TAT C	
Tpi	282F	GGT GAA ATC TCC CCT GCT ATG	± 500
	850R	AAT TTT ATT ACC TGC TGT GG	

plant associations, as seen in several locations across Bali.

In this study, six samples identified as the rice strain based on the *COI* gene were collected from maize host plants. This finding indicates that the *COI* gene marker alone may not serve as a reliable indicator for assessing the environmental habitat or host preference of FAW (Monica et al., 2025). Similarly, Yudha et al. (2024) reported that samples from Jembrana were classified as rice strain (*COI*-R), despite being collected from maize, the first report of FAW occurrence in Bali. These inconsistencies underscore the limitations of relying solely on *COI*-based identification for determining FAW strain composition, particularly when correlating strain type with host plant (Durand et al., 2024).

As FAW populations expanded into the Eastern Hemisphere, including Southeast Asia, several studies have demonstrated that the *Tpi* gene marker provides a more accurate representation of host-associated strain identity. The Tpi gene, located on the Z chromosome, reflects host preference more consistently than the maternally inherited mitochondrial *COI* gene (Nagoshi & Meagher, 2022). The present study further supports this conclusion, confirming that *Tpi* is the more appropriate molecular marker for distinguishing FAW host strains in Asia, including Indonesia. All FAW samples collected from maize in this study were accurately identified as the corn strain based on the *Tpi* marker (Monica et al., 2025). This finding demonstrates that, in Indonesia—including Bali—the *Tpi* gene marker is a reliable indicator of the association between FAW strain type (corn strain) and its primary host plant (maize).

The dominant FAW strain infesting maize in Indonesia is *COI*-R/*Tpi*-C (Herlinda et al., 2022; Fahmi et al., 2023). This genotype likely represents a hybrid population resulting from interstrain mating between rice-strain females and corn-strain males. The limited migration ability of the *COI*-R strain from the Americas and Africa has contributed to the predominance of *COI*-C populations in the invaded regions. The rice strain (*COI-R*) exhibits relatively low natural dispersal capacity, and its spread is largely facilitated by human activities. Consequently, it is hypothesized that *COI-R* females mate with the more widespread *COI-C* males, leading to a high proportion of *COI-R*/Tpi-C hybrids (RC type) across Asia, including Indonesia (Nagoshi et al., 2022; Nagoshi & Meagher, 2022; Tay et al., 2023).

The Relationship Between Landscape Structure and FAW Strains. Within 300-m radius, the sampling sites exhibited distinct landscape characteristics. The Klungkung site was predominantly surrounded by dry seasonal agricultural crops, whereas Jembrana was characterized mainly by wetland rice paddies. In contrast, the Buleleng site consisted largely of semi-natural vegetation, including shrubs and tree stands. The sites in Denpasar, Badung, and Tabanan showed a more balanced land composition with smaller patch sizes (Figure 2). Because only the *COI* gene marker differentiated between the two distinct strains, statistical analyses were conducted solely based on *COI*-derived strain data.

Logistic regression analysis revealed that all landscape parameters yielded p-values greater than 0.05, indicating that landscape structure did not significantly influence the occurrence of FAW strains based on the *COI* gene marker (Table 3). However, there was a tendency, although only marginally significant ($0.05 \le p < 0.1$), for an increase of one unit in the number of patches (NumP), mean patch size (MPS), and mean shape index (MSI) to reduce the likelihood of the rice strain (*COI*-R) being present. Conversely,

Figure 1. Distribution map of FAW strains in Bali based on *COI* and *Tpi* gene markers. K1-K3 = Klungkung; D1-D3 = Denpasar Timur; Ba = Badung; T1-T2. = Tabanan; J1-J2 = Jembrana; Bu = Buleleng.

increases in total edge (TE) and mean patch fractal dimension (MPFD) tended to elevate the probability of *COI*-R occurrence. The opposite pattern was observed for the corn strain (*COI*-C).

The number of patches (NumP) in a landscape serves as an indicator of fragmentation. A highly fragmented environment can impede organismal dispersal and the ability to locate preferred habitats (McGarigal & Marks, 1995; Manel et al., 2003; Phillipsen et al., 2015). According to the MSI results, the likelihood of *COI*-R occurrence decreased in areas with larger mean patch sizes, whereas *COI-C* occurrence increased. This suggests that *COI*-C is less negatively affected by larger patch sizes. Landscapes with large patch sizes generally exhibit greater structural heterogeneity (McGarigal & Marks, 1995), which may create more stable habitats. Conversely, increased total edge length (TE) was associated with a higher likelihood of *COI*-R occurrence, suggesting that more edge-rich environments facilitate dispersal for this strain.

Similarly, the MPFD value, which measures the geometric complexity of patch edges, was positively correlated with the presence of *COI*-R. Higher MPFD values indicate more irregular and complex patch boundaries that can function as natural dispersal corridors. Additionally, higher MSI values denote more complex patch shapes, which may increase internal fragmentation within the landscape (McGarigal & Marks, 1995).

These results align with the findings of Holzhauer et al. (2006), who reported that landscape configuration from 50 years prior significantly influenced bush-cricket population genetics. This indicates that detecting clear associations between landscape structure and genetic composition requires a long temporal scale. Continuous changes in agricultural land use, especially those driven by human activities, can delay the establishment of such associations between habitat structure and genotype distribution.

Indications of FAW Strains and Haplotype Distribution Patterns in Bali. The association between landscape structure and FAW strains did not

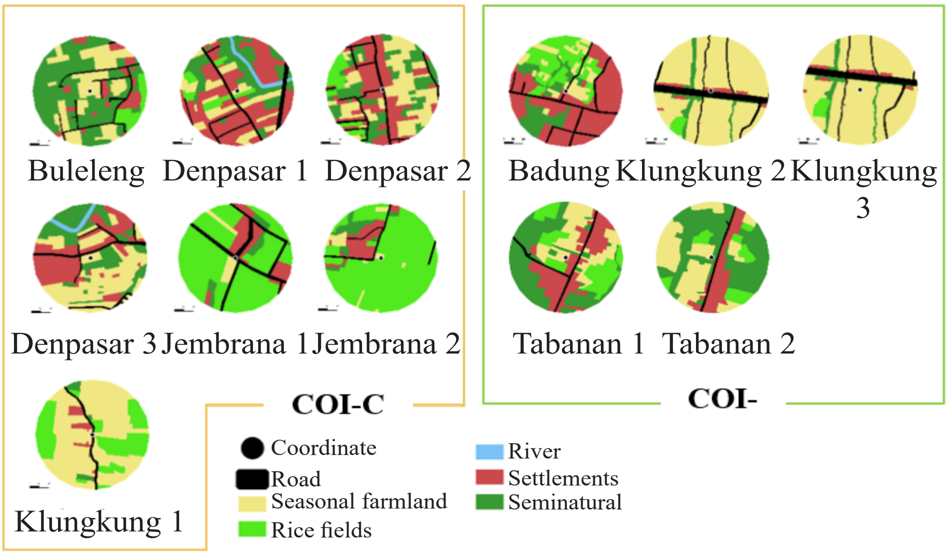

Figure 2. Distribution map of the FAW strain based on the *COI* gene across different landscape structures in Bali, categorized by land class within a 300 m radius. *COI*-C: corn strain; *COI*-R: rice strain.

Table 3. Regression coefficients and p-values from the logistic analysis of landscape metrics in relation to the presence of the FAW strain, as identified by the *COI*B gene

Variable dependent	Coefficient (x103)	P-value	Interpratation
NumP*	-0.014	0.99	Ns*
MPS* (ha)	-2.04	0.99	Ns*
TE* (m)	0.008	0.99	Ns*
MSI*	-0.61	1.00	Ns*
MPFD*	4.22	0.99	Ns*

* NumP)= Number of Patches ; TE= Total Edges; MPS= Mean Patch Size; MSI= Mean Shape Index; MPFD= Mean Patch Fractal Dimension; Ns= Not Significant.

yield statistically significant results ($p > 0.05$). This suggests that the two strains identified through the *COI* marker do not exhibit distinct preferences for specific landscape types. Principal coordinates analysis (PCoA) further supported this finding, showing a broad dispersion of both strains without distinct clustering based on the evaluated landscape metrics (Figure 3). These results indicate that landscape structure is not a determining factor in the distribution of FAW strains. The absence of clear landscape preferences implies that both strains can adapt and thrive across a wide range of environments. This ecological flexibility, combined with FAW's strong dispersal capacity, likely contributes to its widespread success in diverse landscapes.

Based on these findings, it remains uncertain which vegetation types act as ecological corridors or barriers for the two *COI*-identified strains. The PCoA results showed no distinct clustering, reinforcing that the two strains do not demonstrate specific affinities toward particular landscape structures. Across the twelve sampled locations with varying land-use compositions, none showed a consistent pattern indicative of either corridor or barrier effects. This absence of association helps explain the lack of strain differentiation in the PCoA plot.

Moreover, the observed discrepancy between *COI*-based strain identification and host plant type supports this interpretation. The *COI* marker does not reliably distinguish between FAW strains associated with specific host plants, which complicates analyses of ecological interactions between strains and their surrounding vegetation. These results align with the hypothesis proposed by Nagoshi & Meagher (2022), which posits that genomic mixing within hybrid (RC-type) FAW populations results in overlapping ecological niches and similar habitat preferences (Juárez et al., 2012).

The low genetic and haplotype diversity detected in both gene markers further suggests that genetic variation is concentrated within, rather than between, regional populations (Belay et al., 2012; Cabusas et al., 2024). The relatively homogeneous haplotype distribution across Indonesia, including Bali, can be attributed to the high flight capability of FAW, which enhances gene flow and dispersal. This strong mobility promotes genetic homogenization, thereby limiting the formation of localized genetic differentiation driven by landscape features (Phillipsen et al., 2015).

Although no distinct landscape preference was identified, these findings provide valuable implications for FAW management in Bali. Understanding the genetic distribution of FAW in relation to landscape characteristics is essential for designing targeted pest control strategies. One promising approach involves identifying alternative host plants that can serve as trap crops (Nurkomar et al., 2023), thereby helping regulate FAW populations across various land-use types. Integrating trap crops could facilitate the simultaneous management of multiple FAW strains and haplotypes, including *COI*-h4 and *Tpi*-Ca1 and *Tpi*-Ca2.

Furthermore, knowledge of FAW strain distribution can inform the development of strain-specific, pheromone-based control strategies. Previous studies have shown that different FAW strains respond differently to pheromone compositions (Nagoshi et al., 2007; Meagher et al., 2019; Akinbuluma et al.,

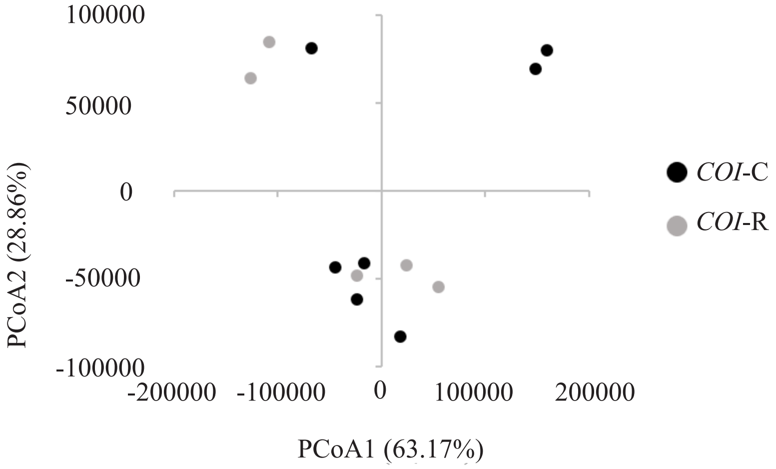

Figure 3. Principal Coordinates Analysis (PCoA) was performed using landscape metric values to examine their relationship with the presence of the FAW strain, as determined by the *COI*B gene. A larger value on either PCoA axis indicates a stronger influence of landscape metrics on strain presence, with PCoA1 explaining more variance in strain distribution.

2024). Therefore, tailoring pheromone formulations to match the dominant strain composition in each region could improve the effectiveness of pest management. By integrating molecular strain data with pheromone-based techniques, FAW population suppression could be optimized through mating disruption, ultimately reducing population densities more effectively across Bali's diverse agroecosystems.

CONCLUSION

The *COI* gene analysis identified two strains of *Spodoptera frugiperda* (*COI*-R and *COI*-C) and one haplotype (*COI*-Ch4) that closely corresponds to the FAW[FL] profile originating from Florida. The rice strain (*COI*-R) was predominantly distributed in central and eastern Bali, while the corn strain (*COI*-C) was more frequently found along the island's periphery, including Klungkung, Denpasar, and Jembrana districts. In contrast, analysis using the Tpi gene marker detected only the corn strain (*Tpi*-C), along with two haplotypes—*Tpi*-Ca1 and *Tpi*-Ca2—that were evenly distributed across all sampling sites. Statistical analyses showed that all landscape parameters yielded p-values greater than 0.05, indicating that landscape structure does not significantly influence the presence or distribution of FAW strains as determined by the *COI* gene. Establishing a definitive relationship between landscape configuration and specific genotypes requires long-term observation and may be further complicated by dynamic agricultural conditions and continuous human intervention.

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AUTHORS' CONTRIBUTIONS

DCM considered and planned the experiment, collecting sampel and environment data, carried out molecular and non molecular work, also done the data analysis. DCM, YMK, and IWW prepared the manuscript. The authors provided feedback on the research flow, data analysis, and interpretation, as well as the structure of the manuscript. All authors have read and approved the final version.

COMPETING INTEREST

We confirm that regarding the publication of our work, we have no competing interests to declare.

REFERENCES

Akinbuluma MD, van Schaijk RAH, Roessingh P, & Groot AT. 2024. Region-specific variation in the electrophysiological responses of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) to synthetic sex pheromone compounds. *J. Chem Ecol*. 50: 631–642. https://doi.org/10.1007/s10886-024-01479-w

Belay DK, Clark PL, Skoda SR, Isenhour DJ, Molina-Ochoa J, Gianni C, & Foster JE. 2012. Spatial genetic variation among *Spodoptera frugiperda* (Lepidoptera: Noctuidae) sampled from the United States, Puerto Rico, Panama, and Argentina. *Ann. Entomol. Soc. Am*. 105(2): 359–367. https://doi.org/10.1603/AN11111

Cabusas JVB, Latina RA, & Caoili BL. 2024. Genetic diversity and population structure of the fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) in the Philippines. *J. Appl. Entomol*. 148(8): 983–995. https://doi.org/10.1111/jen.13307

Dong Z, Li C, Zhang Q, Li L, Lu Z, Ouyang F, Song Y, Yu Y, & Men X. 2021. Landscape genetic analyses reveal host association of mitochondrial haplotypes in the Asian corn borer, *Ostrinia furnacalis. Insect Sci*. 28(4): 1169–1178. https://doi.org/10.1111/1744-7917.12798

Durand K, An H, & Nam K. 2024. Invasive fall armyworms are corn strain. *Sci. Rep*. 14: 5696. https://doi.org/10.1038/s41598-024-56301-0

Fahmi F, Kusumah RYM, & Buchori D. 2023. Genetic variation of pest fall armyworm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) in different landscapes in Bogor. *J Entomol Indones.* 20(1): 1–9. https://doi.org/10.5994/jei.20.1.1

Ginting S, Chozin M, & Sudjatmiko S. 2024. Infestation of *Spodoptera frugiperda* on corn in Bengkulu at different elevations. *J. Trop. Plant Pests Dis*. 24(1): 38–47. https://doi.org/10.23960/jhptt.12438-47

Herlinda S, Suharjo R, Elbi Sinaga M, Fawwazi F, & Suwandi S. 2022. First report of occurrence of corn and rice strains of fall armyworm, *Spodoptera frugiperda* in South Sumatra, Indonesia and its damage in maize. *J. Saudi Soc. Agric. Sci.* 21(6): 412–419. https://doi.org/10.1016/j.jssas.2021.11.003

Holderegger R & Wagner HH. 2006. A brief guide to landscape genetics. *Landsc Ecol*. 21(6): 793–796. https://doi.org/10.1007/s10980-005-6058-6

Holzhauer SIJ, Ekschmitt K, Sander AC, Dauber J, & Wolters V. 2006. Effect of historic landscape change on the genetic structure of the bush-cricket *Metrioptera roeseli*. *Landscape Ecol.* 21(6): 891–899. https://doi.org/10.1007/s10980-005-0438-9

Juárez ML, Murúa MG, García MG, Ontivero M, Vera MT, Vilardi JC, Groot AT, Castagnaro AP, Gastaminza G, & Willink E. 2012. Host association of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) corn and rice strains in Argentina, Brazil, and Paraguay. *J. Econ. Entomol*. 105(2): 573–582. https://doi.org/10.1603/EC11184

Lebody KAE, Salim RG, El-Sayed GM, & Mahmoud SH. 2024. Identification and genetic diversity of *Spodoptera frugiperda* J. E. Smith (Lepidoptera: Noctuidae) in Egypt. *Agronomy*. 14(4): 809. https://doi.org/10.3390/agronomy14040809

Lestari P, Swibawa IG, Fitriana Y, Suharjo R, Utomo SD, & Hartaman M. 2024. The population dynamics of *Spodoptera frugiperda* after its invasion in Lampung Province, Indonesia. *J. Trop. Plant Pests Dis*. 24(1): 98–108. https://doi.org/10.23960/jhptt.12498-108

Manel S, Schwartz MK, Luikart G, & Taberlet P. 2003. Landscape genetics: Combining landscape ecology and population genetics. *Trends Ecol. Evol.* 18(4): 189–197. https://doi.org/10.1016/S0169-5347(03)00008-9

Marín DV, Castillo DK, López-Lavalle LAB, Chalarca JR, & Pérez CR. 2021. An optimized high-quality DNA isolation protocol for *Spodoptera frugiperda* J. E. Smith (Lepidoptera: Noctuidae). *MethodsX*. 8: 101255. https://doi.org/10.1016/j.mex.2021.101255

McGarigal K & Marks BJ. 1995. *FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure*. Portland. Department of Agriculture, Forest Service, Pacific Northwest Research Station. https://doi.org/10.2737/PNW-GTR-351

Meagher Jr RL, Agboka K, Tounou AK, Koffi D, Agbevohia KA, Amouze TR, Adjévi KM, & Nagoshi RN. 2019. Comparison of pheromone trap design and lures for *Spodoptera frugiperda* in Togo and genetic characterization of moths caught. *Entomol. Exp. Appl.* 167(6): 507–516. https://doi.org/10.1111/eea.12795

Monica DC, Kusumah YM, & Winasa IW. Keanekaragaman strain ulat grayak jagung *Spodoptera frugiperda* (Smith) berdasarkan marker *COI* dan *Tpi* dengan kajian kepadatan populasi di Bali [Genetic diversity of fall armyworm *Spodoptera frugiperda* (Smith) strains based on *COI* and *Tpi* markers with population density analysis in Bali]. *Jurnal Entomologi Indonesia*. 22(1): 41–51. https://doi.org/10.5994/jei.22.1.41

Nagoshi RN. 2010. The fall armyworm triose phosphate isomerase (*Tpi*) gene as a marker of strain identity and interstrain mating. *Ann. Entomol. Soc. Am.* 103(2): 283–292. https://doi.org/10.1603/AN09046

Nagoshi RN, Goergen G, Koffi D, Agboka K, Adjevi AKM, Du Plessis H, Van den Berg J, Tepa-Yotto GT, Winsou JK, Meagher RL, & Brévault T. 2022. Genetic studies of fall armyworm indicate a new introduction into Africa and identify limits to its migratory behavior. *Sci. Rep.* 12: 1941. https://doi.org/10.1038/s41598-022-05781-z

Nagoshi RN, Koffi D, Agboka K, Tounou KA, Banerjee R, Jurat-Fuentes JL, & Meagher RL. 2017. Comparative molecular analyses of invasive fall armyworm in Togo reveal strong similarities to populations from the eastern United States and the Greater Antilles. *PLoS One*. 12(7): e0181982. https://doi.org/10.1371/journal.pone.0181982

Nagoshi RN & Meagher RL. 2022. The *Spodoptera frugiperda* host strains: What they are and why they matter for understanding and controlling this global agricultural pest. *J. Econ. Entomol*. 115(6): 1729–1743. https://doi.org/10.1093/jee/toac050

Nagoshi RN, Silvie P, & Meagher RL. 2007. Comparison of haplotype frequencies differentiate fall armyworm (Lepidoptera: Noctuidae) corn-strain populations from Florida and Brazil. *J. Econ Entomol.* 100(3): 954–961. https://doi.org/10.1603/0022-0493(2007)100[954:COHFDF]2.0.CO;2

Nurkomar I, Trisnawati DW, Fahmi F, & Buchori D. 2023. Survival, development, and fecundity of *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) on various host plant species and their implication for pest management. *Insects.* 14(7): 629. https://doi.org/10.3390/insects14070629

Phillipsen IC, Kirk EH, Bogan MT, Mims MC, Olden JD, & Lytle DA. 2015. Dispersal ability and habitat requirements determine landscape-level genetic patterns in desert aquatic insects. *Mol. Ecol.* 24(1): 54–69. https://doi.org/10.1111/mec.13003

Sartiami D, Dadang, Harahap IS, Kusumah YM, & Anwar R. 2020. First record of fall armyworm (*Spodoptera frugiperda*) in Indonesia and its occurence in three provinces. *IOP Conf. Ser.: Earth Environ. Sci.* 468: 012021. https://doi.org/10.1088/1755-1315/468/1/012021

Sataral M, Amrulloh R, Megasari D, Khoiri S, & Zulfajrin M. 2023. Leveraging environmental and landscape effects on the *Spodoptera frugiperda* abundance and attack rates' spatial distribution. *Nat. Sci.: J. Sci. Technol.* 12(1): 17–28. https://doi.org/10.22487/25411969.2023.v12.i1.16182

Supartha IW, Sunari AAAAS, Krisna IGPB, Yudha IKW, Mahaputra IGF, & Wiradana PA. 2021. Invasion, population development, and attack intensity of the fall armyworm (*Spodoptera frugiperda*) J.E Smith (Lepidoptera: Noctuidae) on two varieties corn in Serongga Village, Gianyar Regency, Bali-Indonesia. *Technol. Rep. Kansai Univ*. 63(01): 6945–6954.

Tay WT, Meagher Jr RL, Czepak C, & Groot AT. 2023. *Spodoptera frugiperda*: Ecology, evolution, and management options of an invasive species. *Annu. Rev. Entomol.* 68: 299–317. https://doi.org/10.1146/annurev-ento-120220

Yudha IKW, Supartha IW, Susila IW, Sudiarta P, Wijaya IN, & Wiradana PA. 2024. New occurrence of corn and rice strains of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Bali and Lesser Sunda (Indonesia): Genetic diversity, distribution, and damage. *Biodiversitas*. 25(5): 1890–1900. https://doi.org/10.13057/biodiv/d250505