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Adaptive evolution of invasive fall armyworms to maize with potential involvement of Cytochrome P450 genes

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Abstract

Background An invasion occurs when introduced species establish and maintain stable populations in areas outside of their native habitat. Adaptive evolution has been proposed to contribute to this process. The fall armyworm (*Spodoptera frugiperda*) is one of the major pest insects infesting maize in both invaded and native areas. The invasion of this species was reported from West Africa in 2016, followed by spreading across the Old World. We tested adaptive evolution to maize using 56 native samples from the USA and 59 invasive samples from Senegal, based on genomic and transcriptomic analyses.

Results Principal component analysis revealed that the Senegalese population originated from corn strain. Three genetic loci were identified as targets of selective sweeps in the Senegalese population. These loci include four Cytochrome P450 genes (CYP321B1, CYP321B3, CYP321B4, and CYP337B5), as well as 12 genes of which the function is unclear. Transcriptomic analysis showed an overexpression of CYP321B1 and CYP321B3 genes in sfC samples compared to sfR samples. Additionally, these two genes were overexpressed when corn strain samples were exposed to maize. In larval feeding assays, the Senegalese population exhibited higher survival rates than a Floridan population across all four tested maize varieties.

Conclusions These results suggest that the analyzed Senegalese population experienced adaptive evolution involving loci containing CYP genes, potentially associated with an increase in the survival rates on maize. We argue that the invasive success of the fall armyworm is contributed by stabilizing selection to maize.

Keywords Cytochrome P450, Fall armyworm, Host-plant adaptation, Invasive success, *Spodoptera frugiperda*

Introduction

Invasion occurs when introduced species establish a stable population in a non-native area [1]. Introduced species often face challenges for survival posed by the new environment or experience inbreeding depression [2]. The number of invasion cases has rapidly increased, especially in insects [3], probably due to the rise in human trade [4]. As invasion is one of the main causes of losses in biodiversity [5] and agricultural production [6], there is an increasing need to identify evolutionary forces potentially responsible for invasive success to manage each case of invasionctively. Adaptive evolution

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has been proposed as an evolutionary force enabling invasive success through the generation of a stable population [1]. Genomic analysis is now a popular approach for identifying adaptive evolutionary forces associated with invasive success through bottom-up approaches without pre-selection of candidate genes [7] that could introduce human bias. In particular, population genomics approaches have been used for this purpose [8] because polymorphism data provide ample information on recent adaptive evolutionary forces [9].

The fall armyworm (FAW, *Spodoptera frugiperda*; Lepidoptera; Noctuoidea) is one of the major pest insects of diverse crops, including cotton, maize, rice, and sorghum. In particular, occasional outbreaks cause severe losses in maize crops in both native and invaded areas [10–12]. FAW is native to North and South America, and its invasion was first reported in West Africa in 2016 [13]. Since then, invasive FAWs have spread rapidly across Sub-Saharan Africa, the Middle East, Asia, Oceania, Egypt, Cyprus, and Greece [14]. The damaging effect is particularly severe in Sub-Saharan Africa, where FAWs have caused maize yield losses upto 58% [15]. Since maize provides at least 30% of caloric intake in Sub-Saharan Africa [16], controlling FAW is of utmost importance in this region.

FAW is composed of two strains with differentiated ranges of host plants [17, 18]. As their names indicate, the corn strain (sfC) primarily colonizes maize, cotton, and sorghum crops, while the rice strain (sfR) prefers pasture grasses and rice crops. In addition to host plants, sfC and sfR exhibit allochronic mating times [19–21] and differences in female sex pheromone blends [22, 23]. Hybrids generated from the cross-breeding of sfC and sfR exhibit decreased fertility [24]. These studies imply the possibility of incipient speciation between sfC and sfR [25, 26]. Population genomics analysis demonstrated that the whole genome sequences of native FAWs are clearly separated into two groups: one group consists of FAWs collected from maize (sfC-preferred host-plants), and the other group consists of FAWs collected from grasses (sfR-preferred host plants) [27]. This separation implies that differential usage of host plants has driven the differentiation in whole genome sequences between sfC and sfR [28]. While sfC and sfR are observed sympatrically across their entire native ranges, invasive FAW populations originated from sfC [29] without detectable gene flow from sfR [30].

Population genomics studies suggested that the invasive success of FAW was influenced by invasive FAW-specific adaptive evolution. Yainna et al. [29] showed four loci that were targeted by selective sweeps specific to invasive populations. These loci include genes belonging to the CYP (cytochrome P450) gene family, which is responsible for the detoxification of plant secondary metabolites or insecticides [31, 32]. Yainna et al. [33] reported that invasive FAW populations had increased gene copy numbers of CYP genes compared to native ones, implying that invasive populations might have increased capacity for detoxifications. Gui et al. [34] also identified CYP genes within selectively swept loci in a Chinese population and reported the response of CYP genes to insecticides. They interpreted this result as a selective pressure on the Chinese population. However, it is unclear whether the same CYP genes are involved in both insecticide response and selective sweeps. Notably, the conclusion of Gui et al. on CYP genes should be considered carefully because they reported an unrealistically high number of CYP genes. While all the other studies have revealed CYP gene numbers ranging from 117 to 200 [35–37], Gui et al. reported a surprisingly higher count of 425 CYP genes.

If invasive populations indeed experienced evolutionary changes of CYP genes, it is tempting to hypothesize that invasive populations experienced adaptive evolution to host plants with the involvement of CYP genes because in insects CYPs genes are well known for the detoxification of plant secondary metabolites [38]. In this study, we aimed to test this hypothesis by conducting population genomics and transcriptomics analyses between invasive and native populations. To minimize the potential influence of geographic variations, we analyzed invasive FAW samples only from Senegal. In addition, we conducted larval feeding assays to compare survival rates of invasive and native FAW larvae on maize plants.

Results

Genomic differentiation between native and invasive populations

This study includes 45 samples collected from maize fields and 11 samples collected from grasses in Florida, USA (Table 1), which is a native area of FAW. A previous population genomics study using these samples demonstrated a clear separation of whole genome sequences into two groups based on host plants, which was used to identify strains [27]. Specifically, samples from maize fields were classified as the sfC strain, while those from grasses corresponded to the sfR strain in this dataset. This strain identification aligns perfectly with the TPI genes, which are widely used to identify strains in FAW [39]. Additionally, 59 samples from Senegal, an invaded area, were included, totalling 104 samples in the resequencing dataset. In total, 24,263,666 single nucleotide variants (SNVs) were identified from this dataset.

Principal component analysis was performed to infer the population structure of the analyzed populations. The first principal component revealed three distinct groups;

Table 1 The samples analyzed in this study. sfC and sfR indicate corn and rice strains, respectively

Strain	Host plants	Geographic locations	Sample number	Source
sfC—mtA	maize	Mississippi (Stoneville)	9	Nam et al. [40]
sfC- mtB	maize	Mississippi (Stoneville)	8	
sfC—mtA	maize	Puerto Rico (Santa Isabel)	11	Gimenez et al. [32]
sfC- mtB	maize	Puerto Rico (Santa Isabel)	4	
sfC -mtA	maize	Florida (Citra)	13	Fiteni et al. [27]
Hybrid between sfC and sfR	grass	Florida (Jacksonville)	1	
sfR	grass	Florida (Jacksonville)	10	
Invasive population	maize	Senegal (Casamance and Kaolack)	59	This study

sfR, sfC, and the invasive Senegalese population, in that order (Fig. 1). This result indicates that the Senegalese population has a closer genetic distance to sfC than sfR, suggesting that the Senegalese population originated from the sfC strain, as observed in a previous study [29].

Senegalese population-specific adaptive evolution involving CYP genes

Next, we used the composite likelihood approach to identify selective sweeps specific to the Senegalese population to identify candidate genes under natural selection. Four outliers of composite likelihood were identified in the Senegalese population (Fig. 2A). One of these outliers also exhibited relatively high composite likelihood in the native sfC populations compared to the rest of the genomic sequences. Consequently, three loci were identified as Senegalese population-specific outliers of selective sweeps. In total, 16 genes were identified from these loci (Table S1), including four CYP genes and eight genes of which the function is unclear. A randomization test was performed to test if four CYP genes could be observed by chance by counting the number of cases where the observed CYP copy number equaled or exceeded four with 10^5 replications. No random group exhibited such a

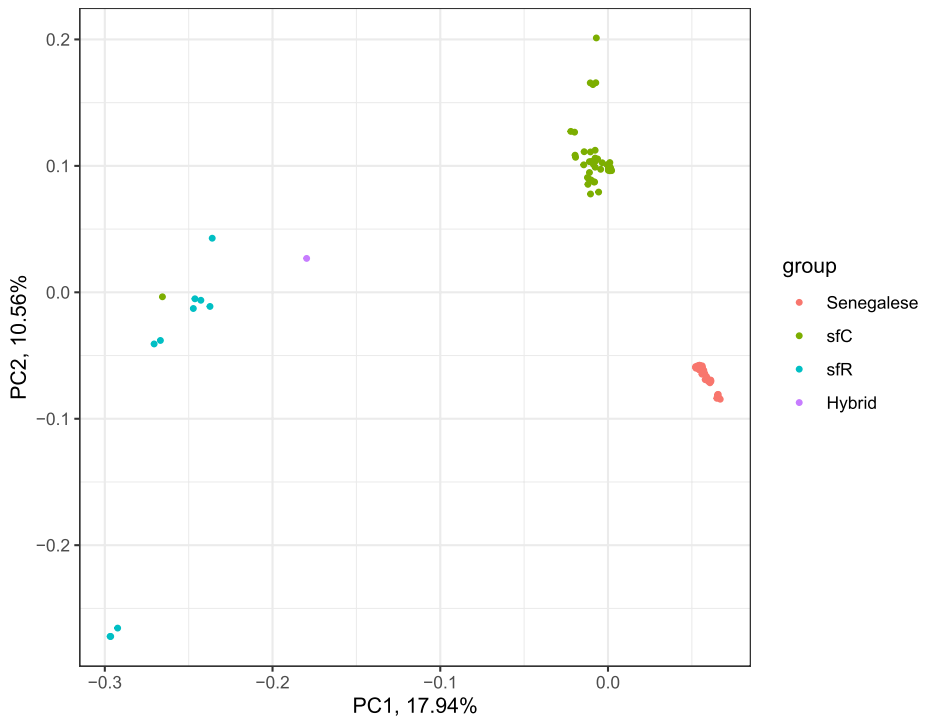

Fig. 1 Population structure of the analyzed samples The principal component analysis reveals the presence of three distinct groups: native sfC, native sfR, and invasive Senegalese populations. The genetic similarity between the Senegalese population and native sfC is higher than with native sfR. This observation indicates that the invasive Senegalese population likely originated from the native sfC strain

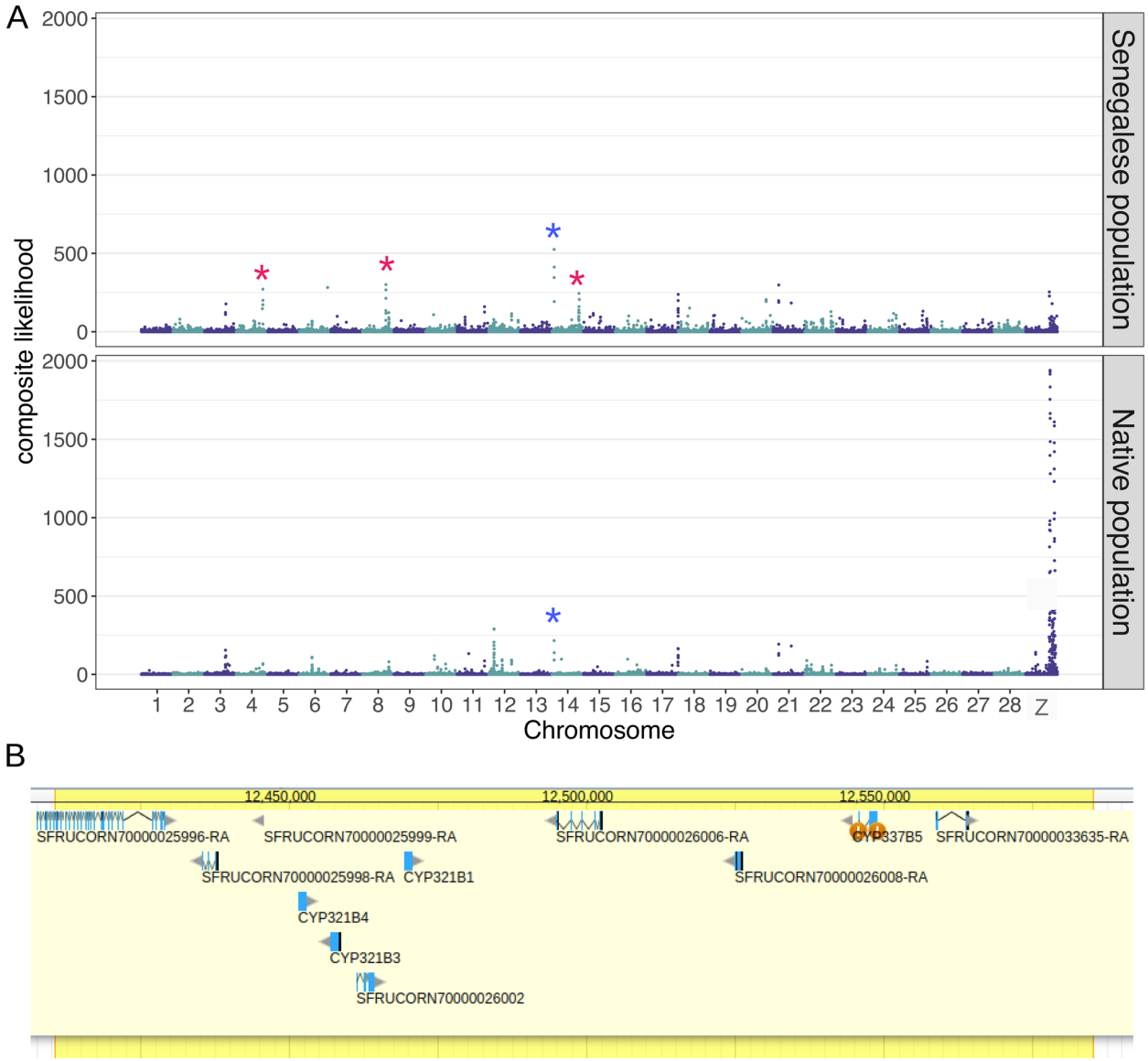

Fig. 2 Loci under selective sweeps (**A**) The outliers of the composite likelihood of selective sweeps are visually represented using asterisks. Invasive Senegalese-specific outliers are indicated with red color, while common outliers shared with native populations are denoted with blue color. **B** Genes within the target of selective sweeps on chromosome 14. The arrows of each gene indicate the orientation of transcription. This locus includes four CYP genes, including CYP321B1, CYP321B3, CYP321B4, and CYP337B5 genes

case, indicating the overrepresentation of CYP genes with statistical significance (random expectation = 0.0068, p-value < 0.00001). Notably, these four CYP genes were found from one locus as a cluster. According to expert annotation, these CYP genes included three CYP321B genes (CYP321B1-B3-B4) and CYP337B5 (Fig. 2B).

We tested the possibility that genes associated with maize plants are included in the putative targets of selective sweeps. Genes associated with maize plants were identified by comparing gene expression levels in sfC and sfR using a publicly available dataset, which was generated from sfC samples collected from maize fields and sfR samples collected from grasses in Florida [41]. In total, 526 out of 10,673 genes were found to be overexpressed in sfC (Fig. 3A, Table S2). Among them, two genes were included in the outliers of composite likelihood (Fig. 2). Randomization test revealed that the observed overlap of two genes between the selective sweep and host-plant genes is statistically significant (random expectation = 0.23684; p-value = 0.03829), indicating that this overlap cannot be explained by chance. Interestingly, these two genes were CYP321B1 (5.31

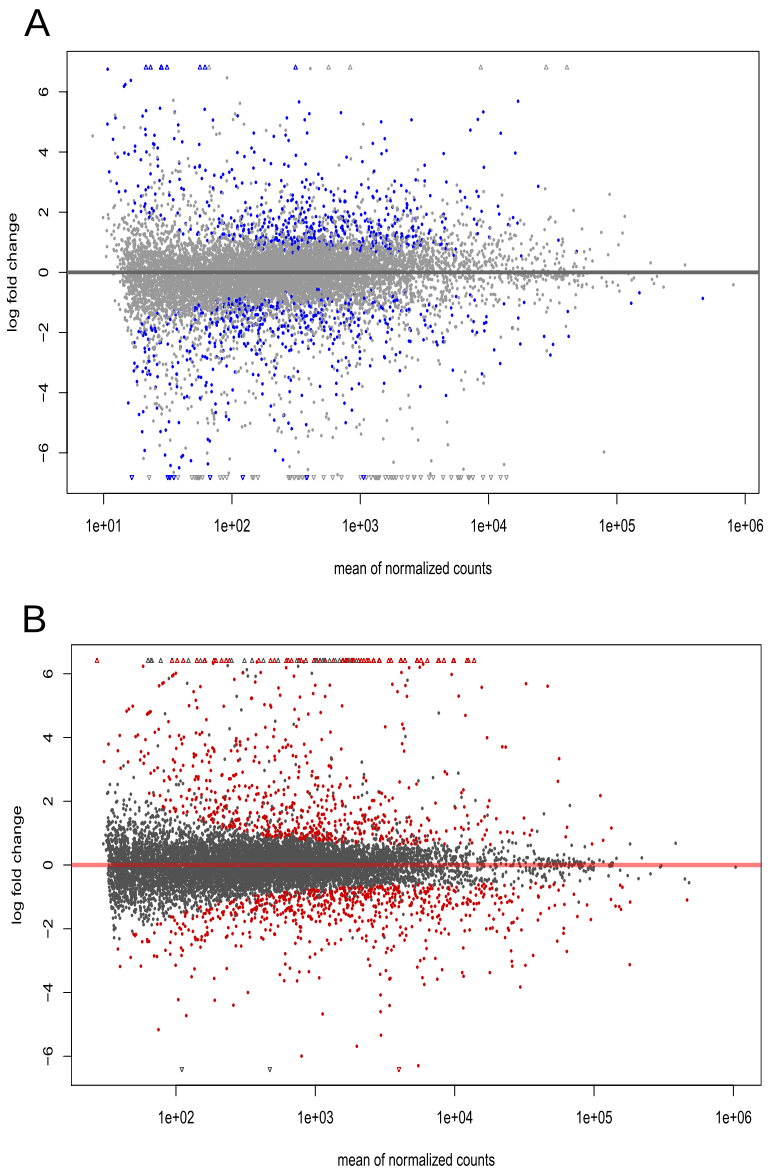

Fig. 3 Host-plant genes of the corn strain. The log-transformed ratio of gene expression (**A**) between the corn strain and the rice strain and (**B**) between corn strain insects treated with maize and another corn strain insect treated with rice is plotted against the number of mapped counts for each gene. The blue points above the solid lines indicate genes that are overexpressed and blue points below the solid lines represent genes that are underexpressed (**A**) in sfC or (**B**) upon maize treatment

fold difference; FDR-corrected p-value $= 3.80 \times 10^{-6}$) and CYP321B3 (5.3 fold difference; FDR-corrected p-value $= 4.46 \times 10^{-9}$).

To further examine the association between selectively swept genes and host-plant genes, we used a different transcriptome dataset from the same study. In this case, host-plant genes were identified by comparing gene expression levels in sfC samples raised on maize and rice plants. In total, 709 out of 11,131 genes were found to be overexpressed in response to maize in sfC (Fig. 3B, Table S3). Two CYP genes that were identified as selectively swept genes were also found among the host-plant genes. These two genes were, again, CYP321B1 (5.28 fold difference; FDR-corrected p value $= 6.08 \times 10^{-25}$) and CYP321B3 (3.05 fold difference; FDR-corrected p value $= 1.68 \times 10^{-11}$).

A phylogenetic tree was reconstructed using lepidopteran CYP321B genes. The resulting tree revealed that the phylogenetic pattern of CYP321B1 is fully congruent with the known phylogenetic relationship among the

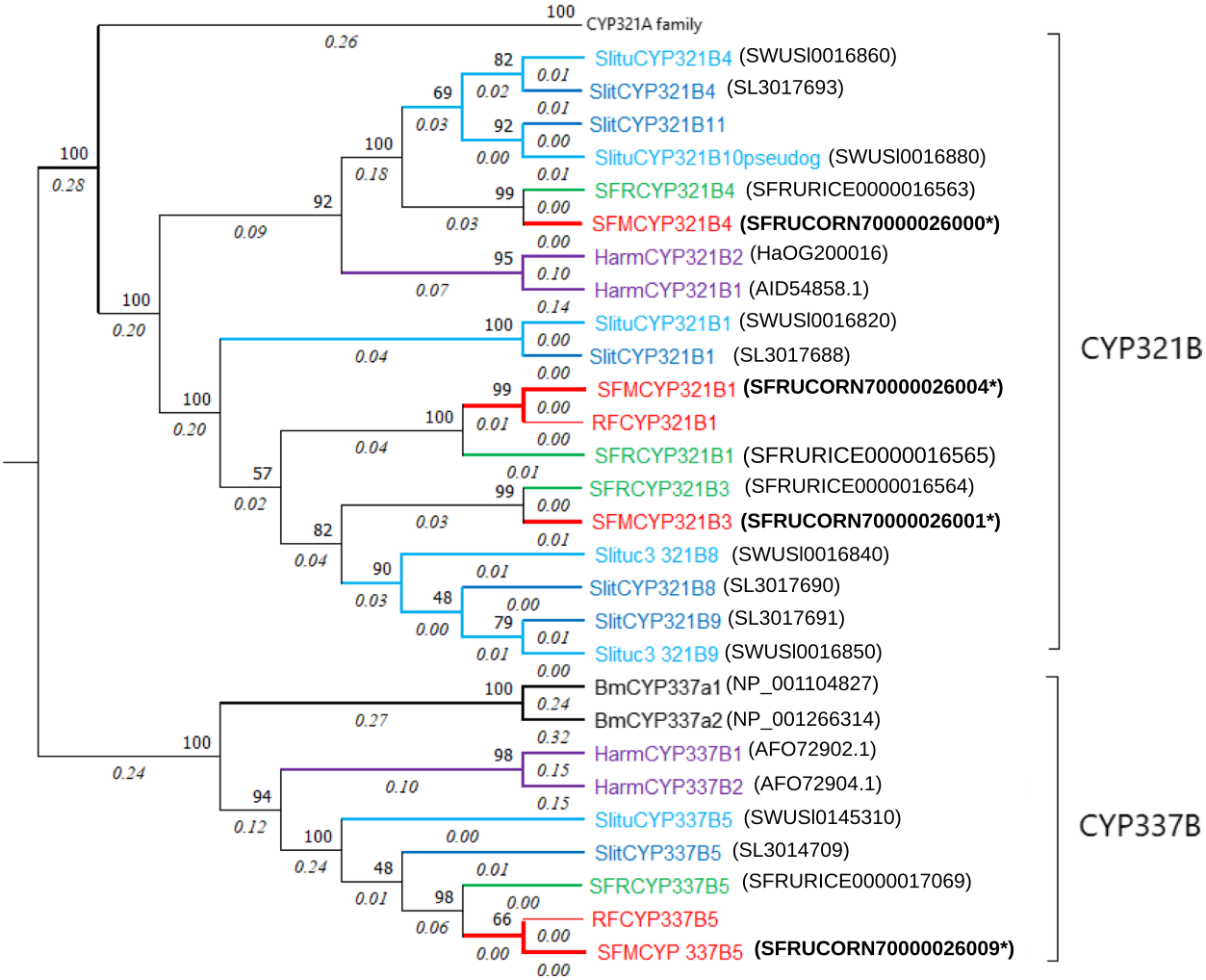

Fig. 4 Maximum likelihood phylogeny of CYP321B genes The red-colored genes represent the CYP321B genes identified through putative selective sweeps. We used the CYP337B family and CYP321A family as outgroups for comparison. The numbers above the branches indicate the bootstrapping support value. Notably, the following abbreviations denote the species: SFR for *S. frugiperda* rice strain, SFM for *S. frugiperda* corn strain, Slit for *S. littoralis*, Slitu for *S. litura*, and Harm for *Helicoverpa armigera*. Specifically, RFc3 321B1 is a gene observed in the rice strain (NCBI ID: AGO62009.1)

species in the *Spodoptera* genus [42]. FAW CYP321B3 and CYP321B1 were derived from a common ancestral CYP321B gene in the *Spodoptera* genus while the bootstrapping support is low (57%) (Fig. 4). Interestingly, CYP321B4 in the fall armyworm as well as its orthologs from *S. litura* and *S littoralis* grouped with *Helicoverpa armigera* CYP321B1 and CYP321B2.

Increased survival rate on maize plants

We compared survival rates on maize between native FAWs from Florida and invasive ones from Senegal using two maize varieties from each of the native and invaded areas. The survival rates were calculated based on the relative survival rate until the L5 larval stage on maize compared to the artificial diet. The Senegalese populations consistently exhibited higher survival rates than the native population across all four maize varieties (Fig. 5). Notably, while the Senegalese FAWs had a survival rate of nearly 54% until the L5 stage on the variety from Puerto Rico, only 14% of the native FAWs were able to develop until the L5 stage within a lifespan of the maize plants without the existence of obvious stressors or pathogens (Fig. 6).

Discussion

Since the first report of the FAW invasion in West Africa, FAWs have spread very rapidly across the Old World. In this paper, we studied an invasive population in Senegal

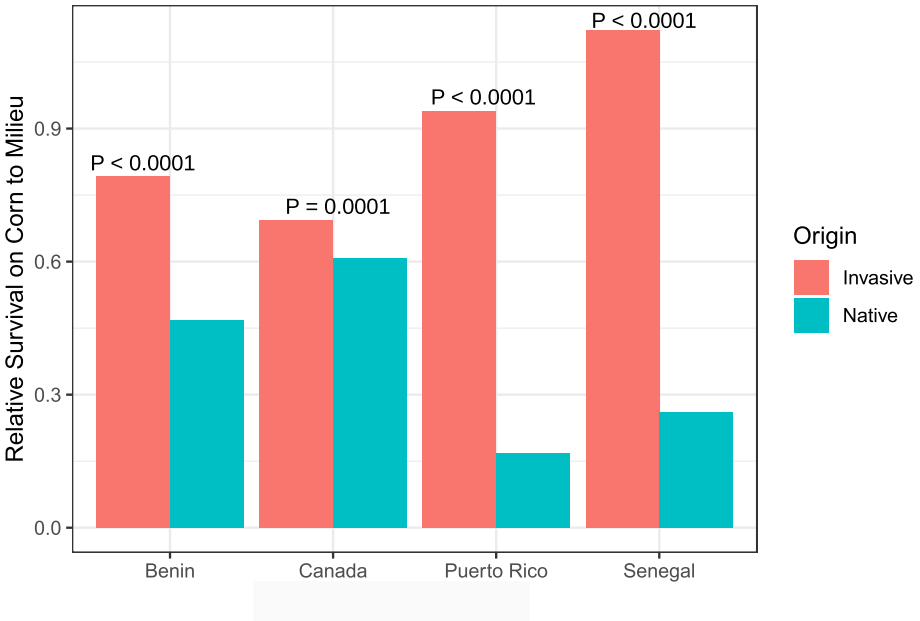

Fig. 5 Increased survival rates of invasive fall armyworms on maize varieties. The survival rates were calculated by dividing the proportion of survived larvae until the fifth instar (L5) stage on maize by the proportion on artificial diets. This comparison was made between an invasive fall armyworm population from Senegal and a native fall armyworm population from Florida, USA. A bootstrapping test was conducted to assess the statistical significance of the observed differences with 10^4 replications

Fig. 6 Sampling locations where fall armyworms were collected in Senegal

to test adaptive evolution to maize plants, which potentially contributed to the invasive success. We conducted an evolutionary genomics analysis using 56 native samples from the USA, which displayed a clear pattern of whole genome differentiation between sfC and sfR strains [27], and 59 invasive samples from Senegal, as well as larval feeding assays. Principal component analysis showed that the Senegalese population is genomically more similar to the native sfC than sfR populations, suggesting that the invasive population originated from sfC, as proposed by Yainna et al. [29] and Durand et al. [30]. We identified three loci that were specifically targeted by selective sweeps in the Senegalese population. One of the loci included four CYP genes including CYP321B1, CYP321B3, CYP321B4, and CYP337B5. Transcriptomic analysis revealed that CYP321B1 and CYP321B3 genes were overexpressed in sfC samples compared to sfR samples. When sfC samples were reared on maize, these two CYP genes were also overexpressed. These results indicate the involvement of the CYP321B1 and CYP321B3 genes in the interaction with maize. CYP321B1 gene is known to increase susceptibility to chlorantraniliprole when this gene is knocked down by RNAi in FAW [43]. In *S. litura*, a closely related species of FAW, the CYP321B1 gene is known to confer insecticide resistance to chlorpyrifos, β-cypermethrin, and methomyl [44] and detoxify plant tannins [45], which are known to have insecticidal effects [46]. Therefore, CYP321B1 may play a role in detoxifying certain insecticides or insecticidal phytochemicals in the investigated Senegalese population. The larval feeding assays showed that the Senegalese population has increased survival rates compared to native sfC populations, further supporting that invasive FAW experienced additional adaptive evolution to maize. Taken together, these results suggest that the investigated invasive Senegalese population experienced adaptive evolution to maize with the involvement of CYP genes.

We also propose the possibility that the difference in pest management is one of the most critical environmental challenges for the establishment of invasive FAW populations. In native areas, pest management is largely carried out using *Bt* (*Bacillus thuringiensis*) genetically engineered maize. Thus, native sfC is likely under selective pressure for alternative plants to maize or for *Bt* resistance. On the other hand, in invaded areas, pest management primarily relies on the application of synthetic chemical insecticides, leading to invasive FAW populations being subjected to selective pressure for resistance to these synthetic insecticides, as shown in our previous study [33]. If the same set of CYP genes is responsible for the detoxification of both insecticides and plant toxins, as suggested for a long time [47, 48], natural selection involving CYP321B1 gene and possibly CYP321B3 could have increased the survival rates of invasive FAWs by providing resistance to insecticides while simultaneously experiencing stabilizing natural selection to the maize plants. If this hypothesis is true, invasive FAWs might have a narrower range of host plants than native sfC by stabilizing selection. Indeed, the damage caused by invasive FAWs appears to be almost exclusively reported in maize. Future studies may compare the host plant ranges between invasive and native FAW populations. It is also possible that the CYP337B5 gene may be involved in interactions with host plants, as observed in the Glanville fritillary butterfly [49].

We also suggest that future studies should prioritize three aspects to gain a better understanding of host-plant adaptive evolution in invasive FAWs. First, we should perform functional comparative studies to test if the adaptive evolution of CYP321B genes confers increased survival rates in invasive populations using knock-out or knock-down experiments. Second, we could analyze regulatory elements, such as promoters, of CYP321B genes to test if the regulation of CYP gene expression plays a role in the adaptation. Third, potential variation in selective pressure across invaded areas should be investigated. In East Asian countries, where the usage of synthetic insecticides is the highest in the world [50], there might be particularly strong selective pressure for insecticide resistance in FAW. This expectation aligns with the frequent observation of insecticide resistance in Chinese FAW populations [34, 43, 51–54]. Conducting comparative studies among different invaded areas could be useful for testing differential selective pressure.

In this paper, we performed a comparative study between invasive and native populations of FAW to investigate whether the invasive FAWs experienced adaptive evolution specific to maize plants. We showed that an invasive population from Senegal had higher survival rates to maize than native populations from the USA with footprints of selective sweeps with involvement of natural selection on host-plant CYP genes including CYP321B1 and CYP321B3. It should be noted that we do not argue that the natural selection of CYP genes is the exclusive driver of adaptive evolution to maize. Instead, we posit that CYP genes play a significant role in this evolution.

The observed adaptive evolution to maize underscores the importance of developing new approaches and strategies that effectively control invasive FAW populations. For example, the unequal level of survival rates to maize between invasive and native FAWs highlights the need for distinct strategies to develop resistant maize. For instance, the analyzed maize variety from Puerto Rico could be considered to be resistant to native populations while fully susceptible to invasive ones. Thus, if a new variety is developed using native FAW populations,

it might not be resistant to invasive FAWs. The unique characteristics and adaptations of invasive FAWs could be pieces of information that should be considered when developing pest management strategies.

Materials and methods

Sequencing and variant calling

The larvae of FAW were handpicked from maize fields in the Velingara and Sédhiou villages of the Casamance, and the Nioro village of Kaolack of Senegal in September 2021. Larvae at the fourth to sixth larval stages were randomly collected from the field, ensuring that only one larva was taken from each plant to avoid sampling kin. The collected larvae were transferred into cups containing artificial diets upon delivery to the BIOPASS lab in Dakar. Genomic DNA was extracted using the Promega Wizard Genomic DNA kit or the Qiagen DNeasy Blood and Tissue kit from these samples according to the the instructions of the manufacturer. The quality of the extracted genomic DNA was then assessed using gel electrophoresis. Samples with degraded genomic DNA were excluded from further analysis. Libraries for whole genome resequencing were prepared by utilizing 1.0 μg of DNA per sample with the NEBNext DNA Library Preparation Kit. Whole genome resequencing was performed using paired-end 150 bp sequencing with the Illumina NovaSeq S6000 platform with 30X coverage for each sample. Adapter sequences and low-quality base pairs were removed using AdapterRemoval v2.1.7 [55]. We also used publicly available raw whole genome resequencing datasets of native populations from Mississippi [40] (NCBI: PRJNA494340), Florida [27] (PRJNA639296), and Puerto Rico [32] (PRJNA577869). Adapter sequences and low-quality base pairs within these reads were discarded in the same way.

The filtered reads were mapped against the ver7 reference genome (https://bipaa.genouest.org/sp/spodoptera_frugiperda_pub/download) [27] using bowtie2 v2.3.4.1 with the –very-sensitive-local preset [56]. Variant calling was performed using the GATK v4.1.2.0 [57] with HaplotypeCaller [57]. If a called SNV has QD lower than 2.0, FS higher than 60.0, MQ lower than 40.0, MQRakSum lower than -12.5, or ReadPosRankSum lower than -8.0, this SNV was discarded.

Transcriptome analysis

We identified maize-interacting genes from those overexpressed in sfC insects compared to sfR using a publicly available RNA-seq dataset generated from FAWs in Florida (European Nucleotide Archive, Project ID: PRJEB25159) [41]. The sfC and sfR colonies used in the experiment have been isogenized in the laboratory for approximately 20 years prior to the study [35]. Therefore, gene expression variation under controlled laboratory conditions is believed to be minimized. This dataset includes three samples from sfC and three samples from sfR, which we analyzed. Adapter sequences or low-quality reads from these six samples were filtered using AdapterRemoval v2.1.7 [55]. The filtered reads were mapped against the transcript sequences (OGS 7.0) using bowtie2 v2.4.4 [56] with the –very-sensitive preset. The mapped reads at resulting bam files were counted using salmon v1.4.0 [58]. Genes overexpressed in sfC compared with sfR were identified using DEseq2 [59], with FDR-corrected *p*-values below 0.05. Since the differences in gene expression between sfC and sfR may be due to strain-specific factors that might not be unrelated to host plants, we also identified host-plant genes from a list of genes overexpressed in sfC insects treated with maize compared to rice plants using the same RNA-seq dataset. For this analysis, two sfC samples treated with maize and one sfC sample treated with rice were used. Overexpressed genes by maize were identified using the same approach.

Population genomics and CYP gene analysis

Principal component analysis was conducted using plink v1.9 [60]. Genetic loci targeted by selective sweeps were identified using the composite likelihood of selective sweeps from the site frequency spectrum, utilizing SweeD v3.2.1 [61]. The composite likelihood was calculated from 1,000 grids for each of the largest 29 chromosome-sized scaffolds for each of the Senegal population and the native sfC group. Apparent Senegal population-specific outliers of composite likelihood were identified through careful examination with eyeballing. F_{ST} and nucleotide diversity were calculated using VCFtools v0.1.15 [62].

Maximum likelihood approach was used to reconstruct a phylogenetic tree of CYP321B genes. Members of the CYP321B, CYP321A and CYP337B families from sfC and sfR were collected from Hilliou [63] and Hilliou [64], respectively. Furthermore, sequences belonging to these families in *S. litura*, *S. littoralis*, and *H. armigera* were obtained from Dermauw et al. [65]. The multiple sequence alignment was generated utilizing MAFFT v7 with the E-INS-i option [66, 67]. Subsequently, the alignment underwent manual inspection and editing, wherein non-conserved regions were discarded. ProTest 3.0 [68] was used to determine the best amino acid replacement model, and the LG model [69] was chosen. A maximum likelihood phylogenetic tree was generated using RaxML ver4 [70] with non-parametric bootstraping with 1,000 replications.

Larval feeding assays

Larval feeding assays were conducted to compare survival rates in maize between native and invasive FAWs using maize seeds from Benin, Canada, Puerto Rico, and Senegal, representing two native and two invaded areas. The seeds from Benin, Canada, and Puerto Rico were obtained from the germplasm bank of the International Maize and Wheat Improvement Center, with accession IDs CIMMYTMA 30389, CIMMYTMA 24086, and CIMMYTMA 29014, respectively. Maize seeds from Senegal were obtained from Institut Sénégalais de Recherche Agricole. For this experiment, native FAW samples from Belle Glade in Florida were handpicked from maize fields between October and November 2021. Alive FAW samples were sent to the DGIMI lab, and reared on artificial diets. The FAW colony has been maintained over multiple generations through sibling matings. Larval feeding assays was performed using this colony in 2022. An invasive laboratory colony was established from FAW samples collected in Senegal in 2019 for larval feeding assays. After maintaining these laboratory colonies for about a year, we conducted the following larval feeding assays. Each L1 larvae was transferred to an individual plant, which was covered with gauze to prevent the FAW larvae from escaping. The photoperiod for both experiments was set to 11 h, from 8:00 AM to 7:00 PM, and the temperature ranged from 24 °C to 27 °C, within the FAW's active temperature range. Thirty insect-plant pairs were established for each type of maize, and the proportion of larvae surviving until L5 was recorded. As a control, L1 larvae were reared on artificial diets and raised under the same conditions. This proportion was normalized by dividing it by the proportion of larvae that survived from L1 to L5 when raised on an artificial diet. A comparison of survival rates between invasive and native populations was performed using a bootstrapping test with 10,000 replications. The experiment was conducted at the DGIMI lab in France for native populations and at the BIOPASS lab in Senegal for invasive populations with the same photoperiod and temperature. The number of replications was two for the Floridan population and four for the Senegalese population. For statistical analyses, the counts from these replications were pooled according to the origin of the FAWs to increase statistical power.

Abbreviations

CYP	Cytochrome P450
FAW	Fall armyworm
FDR	False Discovery Rate
L5	Fifth larval stage
sfC	Spodoptera frugiperda Corn strain
sfR	Spodoptera frugiperda Rice strain

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12864-024-10845-7.

Supplementary Material 1.

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Authors' contributions

SY, SH, EA, TB, and KN performed sampling. FH performed CYP gene annotation. SY and KN performed bioinformatics analysis. SY, EA, and TB performed insect breeding experiments. KN and TB conceived and designed the analysis.

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Availability of data and materials

The resequencing data from the Senegalese population is available at NCBI SRA (PRJNA1015028). The scripts used in this study are available at https://github.com/kiwoong-nam/sfrugi_SenegalHostPlant.

Declarations

Ethics approval and consent to participate

The authors state that experimental research using maize seeds was approved by CIMMYT with Standard Material Transfer Agreement (No. 1943970) and by Ministère de l'Agriculture in Senegal (No. 000060).

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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