

Research Article

GENETIC DIVERSITY AND POPULATION STRUCTURE OF *BACTROCERA DORSALIS* FROM MANGO (*MANGIFERA INDICA*), CITRUS (*CITRUS RETICULATA*), AND CASHEW APPLE (*ANACARDIUM OCCIDENTALE*)

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ABSTRACT

Tropical fruit production plays a crucial role in food security and rural livelihoods through export-driven income generation. However, this sector is severely threatened by invasive insect pests, particularly the Oriental fruit fly, *Bactrocera dorsalis* (Diptera: Tephritidae), a highly polyphagous quarantine species responsible for substantial economic losses in fruit crops. This study aimed to assess the genetic diversity and population structure of three *Bactrocera dorsalis* populations from different host plants in Niayes area in Senegal. Three host-associated populations were defined: *Bactrocera dorsalis* from citrus, *Bactrocera dorsalis* from mango, and *Bactrocera dorsalis* from cashew apple. The DNA was extracted individually, and the mitochondrial gene *cytochrome oxidase* subunit I (*COI*) was amplified. Nucleotide composition analysis revealed a higher A+T content relative to G+C across all populations. The mutation rate was comparatively lower in the population from cashew than in the population from mango. Genetic variability among populations was linked to amino acid substitutions involving isoleucine, asparagine, glutamine, and tryptophan residues. Overall genetic differentiation was low, indicating weak population structuring. Analysis of Molecular Variance (AMOVA) suggested that most of the observed variation occurred within populations rather than among host plants groups. Haplotype network reconstruction revealed shared haplotypes among individuals, supporting the existence of gene flow between populations. These findings indicate limited host-driven genetic structuring in *B. dorsalis* within the Niayes area, despite ecological differences among fruit hosts.

Keywords: AMOVA, *COI*, Genetic structure, Genetic variability, Niayes area, Oriental fruit fly.

INTRODUCTION

Biological invasions facilitated by international and regional trade are shaped by geographic, climatic, and ecological factors that influence species establishment and adaptation. Invasive species capable of surviving under diverse environmental conditions often exhibit genetic adjustments that enhance their adaptive potential (Dia, 2019). Understanding population genetic structure is therefore fundamental to elucidating evolutionary dynamics and invasion success. This is particularly relevant for polyphagous phytophagous insects associated with multiple host plants. Host-associated differentiation has been documented in several insect species, including *Caryedon serratus* (Sembène, 1997). The Oriental fruit fly, *B. dorsalis*, represents a model organism for investigating

such processes. Recognized as a species complex (Aketarawong *et al.*, 2014), *B. dorsalis* was first reported in Senegal in 2004 (Vayssières *et al.*, 2011) and rapidly expanded its host range. It has been recorded on at least 17 fruit species, including mango, citrus, cashew apple, and various wild plants with successive ripening periods (Boinahadji *et al.*, 2019). The temporal availability of multiple hosts enhances its reproductive capacity and population growth (Vayssières *et al.*, 2011). Previous multilocus, *COI*, and microsatellite analyses, combined with reproductive compatibility studies, demonstrated that *B. dorsalis* encompasses taxa formerly described as *Bactrocera papayae*, *Bactrocera philippinensis*, and *Bactrocera invadens* (Clarke *et al.*, 2014). More recently, resistance to organophosphate insecticides has been

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reported (Li *et al.*, 2023), raising concerns about its adaptive potential.

Given its broad host range and adaptive capacity, it is essential to determine whether host plant association contributes to genetic structuring within local populations. The present study therefore investigates the genetic diversity and population structure of *B. dorsalis* associated with three economically important fruit species in the Niayes zone of Senegal using the mitochondrial COI marker.

MATERIAL AND METHODS

Study Area and Sampling

Specimens were collected from three localities in the Niayes agro-ecological zone of Senegal: Sangalkam (14°47'58"N, 17°14'17"W), Sébikotane (14°44'17"N,

17°00'15"W), and Notto (14°57'56.8"N, 17°00'25"W). Sampling was conducted between November 2021 and July 2022 across multiple orchards, irrespective of orchard size, to maximize genetic heterogeneity and reduce the likelihood of sampling related individuals. Infested fruits of mango (*Mangifera indica*), citrus (*Citrus reticulata*), and cashew apple (*Anacardium occidentale*) were collected based on their economic importance, infestation levels, and successive ripening periods. Fruits were transported to the laboratory and incubated at room temperature until adult emergence. Three host-associated populations were defined: BdA (citrus-associated population), BdM (mango-associated population), BdP (cashew-associated population). Each population consisted of 15 randomly selected adults, yielding a total of 45 individuals for molecular analysis.

Table 1. Summary of the studied populations and sampling codes.

Populations	Sample Codes	Number of Sequenced Individuals
Citrus-associated <i>B. dorsalis</i>	BdA	15
Mango-associated <i>B. dorsalis</i>	BdM	15
Cashew-associated <i>B. dorsalis</i>	BdP	15

Mass breeding

Infested mango, citrus, and cashew apple fruits were incubated in 5- or 20-liter plastic containers containing a layer of sterilized sand at the bottom to allow pupation. After 8–10 days of incubation, the sand was sieved every two days to recover pupae, which were subsequently transferred to Petri dishes until adult emergence. Newly emerged adults (≤ 24 hours old) that had not been fed were collected and preserved individually in 7 mL tubes containing 96% ethanol for subsequent genetic analyses.

Genetic Study

The mitochondrial cytochrome c oxidase subunit I (COI) gene was selected for genetic characterization due to its high intraspecific specificity and strong interspecific variability (Le Borgne & Bouchet, 2024). The COI marker is widely used in molecular systematics and population genetics studies of insects.

DNA Extraction and PCR Amplification

This study was done in the Genomic laboratory of the Department of Animal Biology (FST/UCAD). Genomic DNA was extracted using the Zymo Research standard extraction kit following the manufacturer’s protocol. For each specimen, the abdomen and wings were removed to minimize contamination, and the remaining body tissue was homogenized prior to extraction. PCR amplification of the COI gene was performed using the following primers: Forward: 5'-CCAGGTAATTAATAATATAAACTTC-3'. Reverse : 5'-GGATCACCTGATATAGCATTC-3'. Each PCR reaction was carried out in a total volume of 25 μ L containing : 18.3 μ L Milli-Q water, 2.5 μ L 10 $\times$ PCR

buffer, 0.5 μ L dNTP mix, 0.25 μ L of each primer, 0.2 μ L Taq DNA polymerase, 1 μ L MgCl₂, DNA template (adjusted to final volume). Thermal cycling conditions consisted of an initial denaturation at 94°C for 3 minutes, followed by 35 cycles of: Denaturation at 94°C for 1 minute, Annealing at 48°C for 1 minute, Extension at 72°C for 1 minute. A final extension was performed at 72°C for 10 minutes. PCR products were separated on a 2% agarose gel stained with SafeView. Electrophoresis was performed at 100 V for 35 minutes using 7 μ L of PCR product mixed with 2 μ L loading dye to verify successful amplification.

Genetic and Statistical Analyses

Sequence Alignment and Editing

Raw sequences were aligned, inspected, and manually corrected using BioEdit v7.2.5 (Hall, 1999). This software allowed identification of base similarities and differences across sites, gap correction, and verification of sequence quality prior to downstream analyses.

Genetic Diversity

Polymorphism Analysis

Genetic polymorphism parameters were estimated using DnaSP v5.10.1 (Rozas *et al.*, 2010), including: Number of invariant sites (Si), Number of polymorphic sites (Sp), Singleton variable sites (Svs), Parsimony-informative sites (Sip). These indices describe the level of biological variation at the gene level.

Genetic Diversity Indices

The following parameters were calculated: Nucleotide frequencies, Number of polymorphic sites (Sp), Transition (Ts) and transversion (Tv) rates, Transition/transversion ratio (R). These indices were estimated using MEGA v7 (Kumar *et al.*, 2016). The transition/transversion ratio (R) was calculated as:

$$R = [A * G * k_1 + T * C * k_2] / [(A + G) * (T + C)]$$

where *k*₁ represents the transition/transversion ratio among purines and *k*₂ among pyrimidines.

Nucleotide diversity (π), mean number of nucleotide differences (K), number of haplotypes (H), and haplotype diversity (Hd) were estimated using DnaSP v5.10.1 (Rozas *et al.*, 2010) following Nei (1987). Synonymous (Ks) and non-synonymous (Ka or Kns) substitution rates were calculated using MEGA v7 to assess selection pressure: Ka = Ks → neutral evolution, Ka > Ks → positive selection, Ka < Ks → purifying (negative) selection.

Mean nucleotide and amino acid frequencies were also estimated using MEGA v7. Statistical analyses were conducted in R v3.6.1 (R Core Team, 2019). Normality of amino acid frequencies was first assessed. Depending on distribution: Student’s t-test was applied for normally distributed data. Kruskal Wallis test was used for non-parametric comparisons. Statistical significance was assessed at *p* < 0.05.

Population Genetic Structure

Genetic Differentiation

Population genetic differentiation was assessed using: Wright’s fixation index (F_{ST}) (Wright, 1951). Nei’s genetic distance (D) (Nei, 1987). F_{ST} values were calculated in Arlequin v3.1.0.2 (Excoffier *et al.*, 2005) to estimate the degree of genetic differentiation and infer gene flow among populations. F_{ST} was computed based on genetic distances among haplotypes, treating each nucleotide site as a distinct locus (Hudson *et al.*, 1992). Nei’s genetic distance (D) was calculated within and between populations using MEGA v7, including standard errors.

Analysis of Molecular Variance (AMOVA)

Analysis of Molecular Variance (AMOVA) was performed using Arlequin v3.5.2.2 (Excoffier & Lischer, 2015) to partition genetic variation: Among host-associated populations. Within populations. This analysis allowed evaluation of the extent to which host plant association contributes to population genetic structure.

RESULTS AND DISCUSSION

A total of 45 mitochondrial COI sequences were analyzed, each consisting of 444 base pairs (bp). Out of the 444 bp examined, 422 sites (95.04%) were conserved, whereas 22 sites (4.96%) were polymorphic. Among the polymorphic sites : 5 sites (3.38%) were singleton variable sites. 7 sites (1.58%) were parsimony-informative sites. The detailed distribution of conserved and polymorphic sites is presented in Table 2.

Table 2. Summary of conserved and polymorphic sites in the COI sequences (444 bp).

Site Category		Percentage (%)	Number of Sites
Conserved sites		95.04%	422
Polymorphic sites	Singleton variable sites	3.38%	15
	Parsimony-informative sites	1.58%	7 (2 variants)

The overall *B. dorsalis* population exhibited high haplotype diversity (Hd = 0.65 ± 0.06) and low nucleotide diversity (π = 0.005 ± 0.001), with a mean number of nucleotide differences between sequence pairs (K) of 2.32 (Table 3). The citrus-associated population (BdA) showed high haplotype diversity (Hd = 0.59 ± 0.08), low nucleotide diversity (π = 0.004 ± 0.002), and a mean number of nucleotide differences (K) of 1.96. Similarly, the mango-associated population (BdM) exhibited high haplotype

diversity (Hd = 0.76 ± 0.10), low nucleotide diversity (π = 0.008 ± 0.002), and a mean number of nucleotide differences (K) of 3.39. The cashew-associated population (BdP) presented lower haplotype diversity (Hd = 0.48 ± 0.15), low nucleotide diversity (π = 0.003 ± 0.001), and a mean number of nucleotide differences (K) of 1.29. Across all populations, the transition rate (Ts) was higher than the transversion rate (Tv).

Table 3. Standard genetic diversity indices of *B. dorsalis* populations.

Populations	N	Sp	H	Hd	π	Ts	Tv	R	K
Total Pop	45	22	9	0.65 ±0.06	0.005 ±0.001	83.82	16.18	5.244	2.32
BdA	15	9	3	0.59 ±0.08	0.004 ±0.002	90.95	9.04	9.92	1.96

BdM	15	16	6	0.76 ±0.10	0.008 ±0.002	89.93	10.07	8	3.39
BdP	15	8	5	0.48 ±0.15	0.003 ±0.001	81.4	18.6	4.185	1.29

Notes: BdA: Citrus-associated *B. dorsalis*; BdM: Mango-associated *B. dorsalis*; BdP: cashew-associated *B. dorsalis*; N: number of sequences; Sp: number of polymorphic sites; H: number of haplotypes; Hd: haplotype diversity; π : nucleotide diversity; Ts: number of transitions; Tv: number of transversions; R: transition/transversion ratio; K: mean number of nucleotide differences between sequence pairs.

The most frequent haplotype was H1, comprising 24 individuals distributed across the three populations: 6 individuals from the citrus-associated population (BdA), 7 from the mango-associated population (BdM), and 11 from the cashew-associated population (BdP). Haplotype H2 included 12 individuals and was predominantly represented by individuals from the citrus population (7), followed by mango (3), and one individual from the cashew population. Haplotype H7 was detected in three individuals: two from the mango population (BdM13 and BdM15) and one from

the cashew population (BdP6). Haplotypes H3 (BdA9), H4 (BdM1), H5 (BdM2), H6 (BdM3), H8 (BdP2), and H9 (BdP9) were unique haplotypes, each represented by a single individual. The citrus-associated population exhibited three haplotypes (H1, H2, and H3), whereas the mango-associated population showed six haplotypes (H1, H2, H4, H5, H6, and H7). The cashew-associated population displayed five haplotypes (H1, H2, H7, H8, and H9). Details of haplotype distribution are presented in Table 4.

Table 4. Summary of haplotype distribution among *B. dorsalis* populations.

Haplotypes	Number of Individuals	BdA	BdM	BdP
H1	24	BdA1, BdA2, BdA6, BdA7, BdA13, BdA15	BdM4, BdM5, BdM7, BdM9, BdM10, BdM11, BdM12	BdP1, BdP3, BdP4, BdP5, BdP7, BdP8, BdP10, BdP11, BdP12, BdP14, BdP15
H2	12	BdA3, BdA4, BdA5, BdA8, BdA10, BdA11, BdA12, BdA14	BdM6, BdM8, BdM14	BdP13
H3	1	BdA9		
H4	1		BdM1	
H5	1		BdM2	
H6	1		BdM3	
H7	3		BdM13, BdM15	BdP6
H8	1			BdP2
H9	1			BdP9

Notes: BdA: Citrus-associated *B. dorsalis*; BdM: Mango-associated *B. dorsalis*; BdP: cashew-associated *B. dorsalis*.

Table 5. Nucleotide frequencies and mutation parameters (transitions and transversions) of *Bactrocera dorsalis* populations.

Populations	T/U (%)	C (%)	A (%)	G (%)	R(%)	A-T(%)	C-G(%)	Ts(%)	Tv(%)
BdA	29.40	15.63	34.82	20.15	9.92	64.22	35.78	90.95	9.04
BdM	29.26	15.72	34.83	20.18	8	64.09	35.91	89.93	10.07
BdP	29.23	15.77	34.74	20.26	4.185	63.97	36.03	81.4	18.6
Total	29.30	15.71	34.80	20.20	5.244	64.1	35.9	83.82	16.18

Notes: BdA: Citrus-associated *B. dorsalis*; BdM: Mango-associated *B. dorsalis*; BdP: cashew-associated *B. dorsalis*; Ts: number of transitions; Tv: number of transversions; R: transition/transversion ratio.

The overall nucleotide composition across all populations was as follows: T (29.3%), C (15.7%), A (34.8%), and G (20.2%) (Table 5). The mean nucleotide frequencies of the total population showed that the A+T content (64.1%) was higher than the G+C content (35.9%). A similar pattern was observed in each population analyzed separately. The

mutation rate in the cashew-associated population (BdP) was approximately half that observed in the mango-associated (BdM) and citrus-associated (BdA) populations. Conversely, the transversion rate in BdP was nearly twice that recorded for BdA and BdM (Table 5).

The overall *B. dorsalis* population contained a total of 19 amino acids, which was consistent across each population analyzed. The distribution of mean amino acid frequencies did not follow a normal distribution; overall, no significant differences were observed among most amino acids. Significant differences in amino acid frequencies were observed for alanine, cysteine, aspartate, phenylalanine, isoleucine, proline, glutamine, threonine, tryptophan and tyrosine between the cashew-associated population (BdP)

and the citrus-associated population (BdA). However, there is no significant difference between populations derived from mangoes and those derived from mandarins, nor between populations derived from mangoes and those derived from cashews. No significant differences were found for glutamine, glycine, lysine, leucine, methionine, arginine, serine, and valine between the three populations (Table 6).

Table 6. Amino acid frequencies and statistical significance across *B. dorsalis* populations.

Pop	Ala	Cys	Asp	Glu	Phe	Gly	Ile	Lys	Leu	
BdA	5.26 ^a ±0.21	2.23 ^a ±0.01	2.98 ^a ±0.01	5.16 ^a ±0.18	2.98 ^a ±0.01	3.77 ^a ±0.21	4.91 ^a ±0.40	9.73 ^a ±0.22	6.65 ^a ±0.18	
BdM	5.20 ^{ab} ±0.02	2.23 ^{ba} ±0.01	2.97 ^{ab} ±0.01	5.10 ^a ±0.26	2.97 ^{ab} ±0.01	3.81 ^a ±0.26	4.85 ^{ab} ±0.40	9.76 ^a ±0.27	6.59 ^a ±0.27	
BdP	5.19 ^b ±0.01	2.18 ^b ±0.019	2.97 ^b ±0.01	5.14 ^a ±0.19	2.97 ^b ±0.01	3.76 ^a ±0.19	4.55 ^b 0.27±	9.69 ^a ±0.19	6.62 ^a ±0.19	
Pop	Met	Asn	Pro	Gln	Arg	Ser	Thr	Val	Trp	Tyr
BdA	8.93 ^a ±0.04	2.98 ^a ±0.01	6.70 ^a ±0.03	3.27 ^a ±0.36	1.49 ^a ±0.01	11.07 ^a ±0.36	5.21 ^a ±0.02	12.16 ^a ±0.40	2.28 ^a ±0.20	2.23 ^a ±0.01
BdM	8.87 ^a ±0.20	3.02 ^{ab} ±0.19	6.69 ^{ab} ±0.02	3.37 ^{ab} ±0.37	1.49 ^a ±0.01	11.24 ^a ±0.25	5.20 ^{ab} ±0.02	12.13 ^a ±0.51	2.28 ^{ab} ±0.19	2.23 ^{ab} ±0.01
BdP	8.95 ^a ±0.19	2.97 ^b ±0.01	6.67 ^b ±0.02	3.61 ^b ±0.25	1.53 ^a ±0.19	11.12 ^a ±0.03	5.19 ^b ±0.01	12.46 ^a ±0.28	2.22 ^b ±0.01	2.22 ^b ±0.01

Notes: BdA: Citrus-associated *B. dorsalis*; BdM: Mango-associated *B. dorsalis*; BdP: cashew-associated *B. dorsalis*; Statistical significance is indicated by letters (a, b, c). Means sharing the same letter are not significantly different, whereas means with different letters indicate significant differences ($p < 0.05$).

Genetic differentiation within populations varied according to host origin. The mango-associated population exhibited the lowest level of genetic differentiation ($F_{ST} = 0.032$). The overall population of *B. dorsalis* showed a moderately low genetic differentiation ($F_{ST} = 0.065$) (Table 7). Pairwise population comparisons revealed a null and non-significant genetic differentiation between the mango- and

citrus-associated populations ($F_{ST} = 0$). A low and non-significant genetic differentiation was observed between the mango- and cashew-associated populations. In contrast, genetic differentiation between the citrus- and cashew-associated populations was high and statistically significant ($F_{ST} = 0.184$) (Table 8).

Table 7. Genetic differentiation within *B. dorsalis* populations.

Populations	F_{ST}
BdA	0.072
BdM	0.032
BdP	0.091
Total Populations	0.065

Note: BdA: Citrus-associated *B. dorsalis*; BdM: Mango-associated *B. dorsalis*; BdP: cashew-associated *B. dorsalis*.

Table 8. Genetic differentiation between *B. dorsalis* populations.

Populations	BdA	BdM	BdP
BdA	0		
BdM	-0.012 NS	0	
BdP	0.184 *	0.052 NS	0

Note: BdA: Citrus-associated *B. dorsalis*; BdM: Mango-associated *B. dorsalis*; BdP: cashew-associated *B. dorsalis*; NS = not significant ($p > 0.05$); * = significant ($p < 0.05$).

The genetic distance among individuals within the citrus-associated population (BdA) was very low (0.003), with a low standard deviation (0.001). Similarly, the cashew-associated population (BdP) showed a very low genetic distance (0.002) with a low standard deviation (0.001). The overall population exhibited a moderately low genetic distance (0.005), with a low standard deviation (0.002). The mango-associated population (BdM) showed the highest

genetic distance (0.007), and it also had the highest standard error (0.003) (Table 9). The genetic distance between the citrus-associated and cashew-associated populations was the lowest (0.002), with a low standard deviation (0.001). A moderately low genetic distance was observed between the citrus-associated and mango-associated populations (Table 10).

Table 9. Genetic distance and standard deviation within populations.

Population	Genetic distance	Standard deviation
BdA	0.003	0.001
BdM	0.007	0.003
BdP	0.002	0.001
Totale	0.005	0.002

Note: BdA: Citrus-associated *B. dorsalis*; BdM: Mango-associated *B. dorsalis*; BdP: cashew-associated *B. dorsalis*.

Table 10. Genetic distance and standard error between populations.

Population 1	Population 2	Genetic distance	Standard error
BdA	BdM	0.005	0.002
BdA	BdP	0.002	0.001
BdM	BdP	0.004	0.002

Note: BdA: Citrus-associated *B. dorsalis*; BdM: Mango-associated *B. dorsalis*; BdP: cashew-associated *B. dorsalis*.

Table 11. Molecular variance of *B. dorsalis* populations

Source of variation	Degrees of freedom (df)	Sum of squares (SS)	Variance components	Percentage of variation (%)	Fixation index (F_{ST})	P-value
Entre populations	2	4.533	0.077 va	6.52%		
Intra-populations	42	46.533	1.108 vb	93.48%		
Total	44	51.067	1.185	100%	0.065	0.04±0.01

Significance tests were performed using 1.023 permutations.

The analysis of molecular variance (AMOVA) showed a low percentage of variation among populations (6.52%) and a high percentage of variation within populations (93.48%). Among populations, the degrees of freedom (2), sum of squares (4.533), and variance components (0.077) were low. Within populations, these values were higher, with degrees of freedom of 42, a sum of squares of 46.533, and variance components of 1.108. The overall fixation

index (F_{ST}) was 0.065 and was at the limit of statistical significance (Table 11).

The objective of this study was to genetically characterize three populations of *B. dorsalis* associated with three different host plants (mango, citrus, and cashew) using the mitochondrial COI gene. The overall genetic polymorphism observed in the total population was low. This reduced variability may be partly explained by the

predominance of transition mutations (83.82%) compared to transversions (16.18%). Transition mutations are generally more frequent in mitochondrial DNA and are less likely to induce amino acid substitutions, thereby contributing to limited functional divergence. The nucleotide composition showed a marked bias toward A+T (64.1%) compared to G+C (35.9%), a pattern commonly reported in insect mitochondrial DNA. The lower proportion of G+C nucleotides, which are linked by three hydrogen bonds, compared to A+T nucleotides, which are linked by two hydrogen bonds, may influence molecular stability and mutation dynamics. Notably, the transversion rate in the cashew-associated population (18.6%) was markedly higher than in the mango-associated (10.7%) and citrus-associated populations (9.4%). Conversely, the transition rate was lower in the cashew population, resulting in an overall reduced mutation rate (4.185%) compared to mango (8%) and citrus populations (9.92%). The reduced mutation rate observed in the cashew-associated population may be related to limited gene flow. Cashew fruits are generally less suitable for long-term storage and long-distance commercialization, potentially restricting the dispersal of associated fruit fly populations. Reduced dispersal may consequently limit genetic exchange among populations. In contrast, mangoes and citrus fruits are more easily transported and commercialized in fresh form, which may facilitate the spread of *B. dorsalis* and promote gene flow among geographic locations. These findings are consistent with previous studies reporting gene flow among populations of other insect species, such as *Sitophilus zeamais* (Sarr, 2019) and *Callosobruchus maculatus* (Barry, 2023). Additionally, the nutritional composition of cashew fruits differs from that of mangoes and citrus. Cashew apples contain higher levels of calcium, vitamin A, magnesium, and potassium (Ciquel-Anses, 2020; Dossou, 2014). However, their high astringency (Lautié *et al.*, 2001) may affect larval development. Such host-specific characteristics could influence selective pressures, potentially contributing to genetic differentiation through local adaptation processes.

The analysis of haplotype distribution revealed that the mango-associated population exhibited the highest number of haplotypes (6), followed by the cashew-associated population (5), whereas the citrus-associated population displayed only three haplotypes. This pattern suggests greater genetic diversification within the mango-associated population. This higher haplotype richness may be linked to the historical and commercial importance of mango as a primary host of *B. dorsalis*. In Senegal, mangoes are widely imported from neighboring countries such as Guinea and Mali and distributed through major markets, including Sandaga in Pikine, which serves as a central redistribution hub for fruits across the country. The large-scale movement of mangoes may facilitate the passive dispersal of infested fruits, thereby promote gene flow and increase genetic variability within mango-associated populations. Because mango is considered a preferred host for *B. dorsalis*, populations adapted to alternative hosts may recolonize mango during its fruiting season. Moreover, the mango season partially overlaps with that of cashew. At the end of

the mango season (early varieties), flies may shift to cashew fruits, which could explain the presence of shared or closely related haplotypes between mango- and cashew-associated populations. Despite the relatively high number of haplotypes in the cashew-associated population, its haplotype diversity ($H_d = 0.48 \pm 0.15$) and nucleotide diversity ($\pi = 0.003 \pm 0.001$) were low. In contrast, the mango-associated population showed the highest haplotype diversity ($H_d = 0.76 \pm 0.10$) and nucleotide diversity ($\pi = 0.008 \pm 0.002$). The citrus-associated population presented intermediate values ($H_d = 0.59 \pm 0.08$; $\pi = 0.004 \pm 0.002$). These patterns are consistent with the mean number of nucleotide differences (K), which was highest in mango-associated individuals ($K = 3.39$), followed by citrus ($K = 1.96$) and cashew ($K = 1.29$). Such results are consistent with previous studies. Sarr (2019) reported that high haplotype diversity in *S. zeamais* populations was associated with international trade and repeated introductions. Similarly, Ndiaye (2018) observed elevated haplotype and nucleotide diversity in older infestations of *S. zeamais*, suggesting that long-term establishment may increase genetic variability. This may explain the higher diversity observed in mango-associated populations, possibly reflecting a longer or more intense infestation history. In addition, Dia (2019) suggested that haplotype diversification may occur when insect lineages emerging from one host subsequently exploit another host plant, contributing to genetic structuring across host types.

The genetic variability observed between citrus and cashew-associated populations could be attributed to significant differences in amino acid concentrations, particularly involving alanine, cysteine, aspartate, phenylalanine, isoleucine, asparagine, proline, glutamine, threonine, tryptophan and tyrosine. These variations are likely associated with differences in the biochemical composition of the fruits and their environmental conditions. According to Sarr (2019), fruits contain distinct organoleptic compounds (amino acids, proteins, sugars, vitamins etc.) that influence their taste, flavour, and colour. Consequently, species infesting these fruits are feeding on different diets may develop long-term genetic variability influenced by both nutritional and environmental factors. However, the mango-associated population exhibited amino acid levels that were nearly similar to those recorded in citrus and cashew apple populations. These levels were intermediate between those of two other populations, which could be explained by the fact that *B. dorsalis* originally developed on mangoes before colonizing citrus fruits and cashew apples.

Genetic differentiation between citrus- and cashew-associated individuals was highly significant ($F_{ST} = 0.184$) compared to other population pairs. In contrast, differentiation between citrus- and mango-associated populations was negligible, while the differentiation between mango- and cashew-associated populations was moderate and not significant ($F_{ST} = 0.052$). The lack of differentiation between citrus- and mango-associated populations may be partly explained by the similar pH values of these fruits (Boinahadjji, 2020). Conversely,

several organoleptic compounds in cashew fruits are substantially higher than those in oranges (Dossou, 2014), which could drive the observed genetic divergence between cashew- and citrus-associated individuals. These findings are consistent with Sembène (2000), who demonstrated that differences in fruit chemical composition can contribute to host-associated genetic differentiation. Additionally, the pronounced astringency of cashew apples, due to their high acidity, may further contribute to this genetic divergence. Notably, climatic conditions are unlikely to explain these patterns, as mango and cashew fruits mature during the rainy season under similar optimal temperatures, whereas citrus fruits ripen in December during the dry and cooler season. Moreover, geographic distance does not account for the observed differentiation, since all populations were sampled from the same localities.

The lowest genetic distance was observed between cashew- and citrus-associated populations, and it was also low within the cashew-associated population. The values of these distances do not differ substantially, as their standard deviations are small, indicating that the number of mutations is relatively low compared to the other populations, which is reflected in the smaller number of haplotypes. In contrast, the mango-associated population shows higher genetic distances with larger standard deviations, reflecting greater individual variation within this population, which accounts for its higher haplotype number. AMOVA results indicate that most of the molecular variance occurs within populations, suggesting that the genetic structuring of *B. dorsalis* populations is largely influenced by variation among individuals associated with the same host plant. The global F_{ST} is low (6.5%) and close to the significance threshold ($P = 0.04$), indicating weak differentiation and limited structuring at the population level, likely influenced by environmental parameters. These findings are further supported by the sums of squares, degrees of freedom, and variance components, which are low between populations and high within populations. Overall, there appears to be gene flow between individuals from different host fruits, facilitated by the sequential ripening periods of mangoes, cashew apples, and citrus fruits, which allow *B. dorsalis* to move and reproduce across host species.

The free movement of people and goods within the country likely facilitates gene flow through the transport of fruits infested with *B. dorsalis*. This is supported by Diome *et al.* (2013), who reported that the cultivation and transport of insect-infested seeds can lead to the establishment and spread of insects across multiple areas. Additionally, adult flies are capable of covering long distances in search of mates or host plants, further promoting gene flow among populations. Our findings are consistent with Diome *et al.* (2013), who demonstrated gene flow among co-existing host plants, Ndiaye (2018), who emphasized the role of human activities, agricultural systems, and trade intensification in promoting gene flow, and Barry (2023), who highlighted the influence of increased commercial

exchanges. According to Ndiaye (2018), this partitioning of molecular variation suggests that anthropogenic activities may have a stronger effect on pest population genetic structure than ecological parameters. Furthermore, our results align with Dia (2019), who reported that individual- and population-level characteristics explain the majority of genetic variability.

CONCLUSION

This study revealed that the overall genetic diversity of *B. dorsalis* populations is characterized by a higher A+T content compared to G+C, indicating a less rigid DNA backbone. Mutation rates were lower in the cashew-associated population compared to the mango-associated population. Genetic differentiation at the population level was weak, resulting in limited population structuring. However, there is significant genetic differentiation between populations derived from cashew apples and those derived from citrus fruits. AMOVA results indicated that the observed variability is influenced by organoleptic differences among host plants. Haplotype network analysis confirmed the presence of gene flow among individuals, highlighting the dynamic connectivity of these populations across host species.

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CONFLICT OF INTERESTS

The authors declare no conflict of interest

ETHICS APPROVAL

Not applicable

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AI TOOL DECLARATION

The authors declare that no AI and related tools are used to write the scientific content of this manuscript.

DATA AVAILABILITY

Data will be available on request

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