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Ibrahima Diallo

1. Centre pour le Développement de l'Horticulture/ Institut Sénégalais de Recherches Agricoles (CDH-ISRA), 3120 Rte des hydrocarbures, Bel Air, Dakar- Sénégal
2. Département de Biologie Animale, Faculté des Sciences et Techniques Université Cheikh Anta Diop (UCAD), Dakar BP 5005, Senegal
3. Génétique et Gestion des Populations, Gengespop, Senegal

Awa Ndiaye

Centre pour le Développement de l'Horticulture/ Institut Sénégalais de Recherches Agricoles (CDH-ISRA), 3120 Rte des hydrocarbures, Bel Air, Dakar- Sénégal

Emile Faye

1. CIRAD, UPR HortSys, F-34398 Montpellier, France
2. HortSys, Univ Montpellier, CIRAD, Montpellier, France

Mariama Faye

1. Centre pour le Développement de l'Horticulture/ Institut Sénégalais de Recherches Agricoles (CDH-ISRA), 3120 Rte des hydrocarbures, Bel Air, Dakar- Sénégal
2. Département de Biologie Animale, Faculté des Sciences et Techniques Université Cheikh Anta Diop (UCAD), Dakar BP 5005, Senegal
3. Génétique et Gestion des Populations, Gengespop, Senegal

Mbacke Sembene

1. Département de Biologie Animale, Faculté des Sciences et Techniques Université Cheikh Anta Diop (UCAD), Dakar BP 5005, Senegal
2. Génétique et Gestion Des Populations, Gengespop, Senegal

Corresponding Author:**Ibrahima Diallo**

1. Centre pour le Développement de l'Horticulture/ Institut Sénégalais de Recherches Agricoles (CDH-ISRA), 3120 Rte des hydrocarbures, Bel Air, Dakar- Sénégal
2. Département de Biologie Animale, Faculté des Sciences et Techniques Université Cheikh Anta Diop (UCAD), Dakar BP 5005, Senegal
3. Génétique et Gestion des Populations, Gengespop, Senegal

Does landscape factors drive the genetic diversity and structure of populations of fruit flies, Senegal? Exploratory study of the case of *Bactrocera dorsalis* (Hendel, 1912) in the Niayes, Senegal

Ibrahima Diallo, Awa Ndiaye, Emile Faye, Mariama Faye and Mbacke Sembene

Abstract

Objectives: This present study aims to understand the landscape structures as well as the environmental (climatic) factors influencing the genetic diversity of fly populations in the agroecological area of Niayes.

Methodology and results: Landscape composition of different mango orchards of different typologies were determined after drone mapping and fly samples carried out on Kent mangoes. The molecular biology process carried out on about fifty individuals made it possible to obtain sequences of the Cytochrome oxidase I. The results revealed a high genetic diversity and structuring in the populations of flies dependent on single-variety orchards and in contrast a very low diversity in diversified orchards. The genetic diversity appears closely linked to the landscape composition of orchards. Orchards with the most diverse landscapes have populations of *B. dorsalis* with lower diversity and genetic structure.

Conclusions and application of findings: The results made it possible to objectively understand the diversity of the landscape associated with the different mango production systems in relation to the genetic variability of the populations of *B. dorsalis* in the Niayes area. Genetic analyses revealed a low level of polymorphism, diversity and genetic structuring of the fly population subservient to the diversified orchard of Carmel and a greater diversity and polymorphism in the population of Notto (monovarietal orchard). A strong negative correlation is noted between the landscape diversity and the genetic diversity of the populations of *B. dorsalis* underpinning a maintenance of the populations at the level of the orchards diversified in low numbers from one mango production season to another and seasonal appearances in single-variety industrial orchards with populations from elsewhere. This study provides new elements which, if confirmed by larger-scale studies, would make it possible to refine the fly control techniques currently applied.

Keywords: *Bactrocera dorsalis*, landscape, diversity, genetic, barcoding, Niayes

Introduction

The mango sector occupies 60% of the horticultural production of Senegal [1]. The export sector has developed over the years. The management of the plantations and especially the harvesting and packaging of the fruits maintains a number of jobs, particularly for women. Therefore the mango sector became a provider of significant income in rural areas, these are estimated at around 800 Million FCFA for 3,800 T of mangoes exported, it also actively participates in the fight against food insecurity in rural areas during the lean season [2]. However, this sector still faces many constraints, including phytophagous pests such as *Bactrocera dorsalis* (Hendel, 1912). The oriental fruit fly is one of the most devastating for the mango sector³. Since it was first reported in Senegal in 2003, the integrated control of *B. dorsalis* has been a major issue for the development of the mango sector [4]. Each year, between 30 to 40% of mango production in Africa is destroyed by this invasive species [5]. Economic losses due to *B. dorsalis* are estimated at US \$ 42 million each year [3]. Moreover, *B. dorsalis* is classified as a quarantine pest by European countries that increases the negative impact of this pest on the mango sector in Senegal. In the last decade, many studies have been carried out on to improve knowledge about this pest of major economic importance. These studies focused in particular on: the inventory of different species of Tephritidae in orchards [4], fly parasitoids [6], the dynamics of Tephritidae populations [7], fly-host plant interactions [8], etc.

However, very few studies have been so far devoted to the landscape genetics of this invasive pest. Landscape genetics could address various issues, particularly, landscape genetics would allow to study the interactions between genetic populations and gene flows with the landscape structure experienced by *B. dorsalis*. These elements which are essential to understand the processes underlying the dynamics and genetic structuring of *B. dorsalis* populations of this fly but also to provide evidences on the origins of the seasonal infestations by identifying the landscapes that are likely to shelter these populations between the mango production seasons.

This study aims to understand the landscape structures influencing the genetic variability of *B. dorsalis* populations in the agroecological area of Niayes in Senegal. After a brief presentation of the methodology adopted, the main results obtained will be discussed before concluding with a conclusion and the perspectives opened up by these results.

Materials and Methods

Study area: The study was carried out in the Niayes area, the main horticultural production area of Senegal. It concerned five (5) orchards located in five different localities (Sébikotane, Notto, Gorom, Carmel and Sangalkam)

distributed in the regions of Dakar and Thiès. These orchards belong to the three (3) typologies of mango production encountered in the Niayes area as described previously by Sarron *et al.*, 2018 namely: traditional orchards (extensive), diversified orchards (intermediate) and industrial orchards (intensive). Traditional (extensive) orchards: the case of Sangalkam, they are made up of small family farms with great varietal and specific diversity. The plants are mostly left in the wild with little or no maintenance, no irrigation or inputs. Diversified orchards (Carmel and Gorom2) are intermediate types characterized by an association of mango cultivation with other fruit plants (citrus, papaya, cashew trees, etc.) but also market gardening. The mango trees benefit from irrigation and inputs, particularly from market gardening. Industrial orchards (Notto and Sébikotane): These are intensive type farms with a monovarietal culture (mainly Kent), mainly intended for export. These orchards benefit from maintenance (irrigation, input of inputs, etc.) but also from phytosanitary protection measures. The mango trees are very homogeneous in size because they are cut regularly and arranged in rows. The figure 1 and table 1 show respectively the localisation and the characteristics of these different orchards.

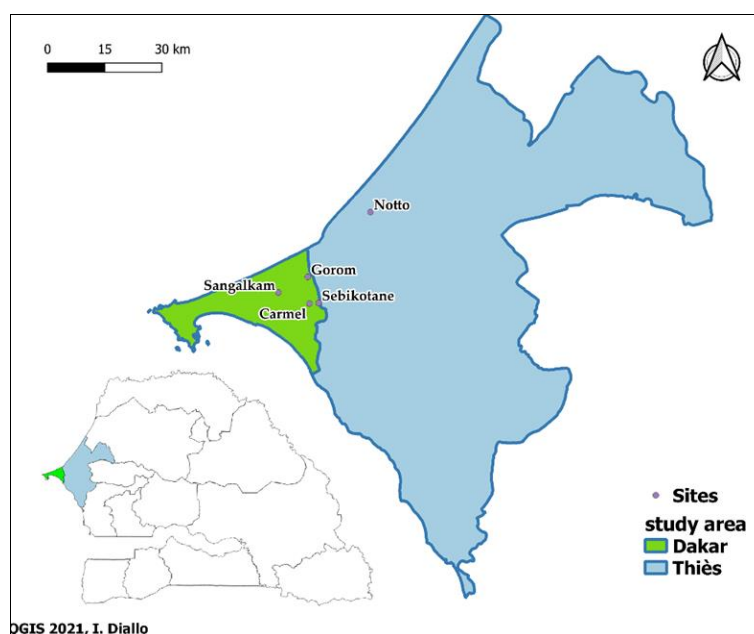


Fig 1: Localisation of the sampling sites

Table 1: Description of the different orchards

Orchard	Typology	Coordinates	Area (ha)	Cultivated mangoes varieties	Edge
Sébikotane	Intensive	14°45'50.55"N 17° 7'47.40"W	8,7	KENT	Hedge
Notto	Intensive	14°59'1.01"N 17° 0'13.57"W	1,7	KENT	None
Carmel	Diversified	14°45'44.73"N 17° 9'6.63"W	1,5	BDH, KENT, KEITT, others	Hedge
Gorom	Diversified	14°49'36.68"N 17° 9'21.58"W	1,7	KENT, KEITT	Wall
Sangalkam	Traditional	14°47'21.01"N 17°13'37.76"W	0,7	BDH, KENT, KEITT	None

Landscape characterization of orchards

Drone mapping of the orchards was done using a DJI Mavic Pro Quadcopter generating Very High Resolution and georeferenced images. These images were processed in

Pix4Dmapper Pro 1.3 software (Pix4D SA, Lausanne, Switzerland) to generate an Orthomosaic RGB (georeferenced image whose geometry has been corrected), a digital terrain model (DTM), and a digital surface model (DSM) for each

orchard. These RGB maps were then used to create land cover maps following a GEOBIA procedure [9] achieved with eCognition Developer 9 software (Trimble Geospatial, Munich, Germany). Objects of these landscapes were classified between bare soil, shrubs, building, vegetable crop, and “citrus”, “mimosae”, “cashew” and “mango trees, or other trees. The resulting maps were loaded, corrected and processed on the ArcGIS 10.3 software ((ESRI, Redlands, CA, USA). The figure 2 shows the orchard yield mapping outputs.

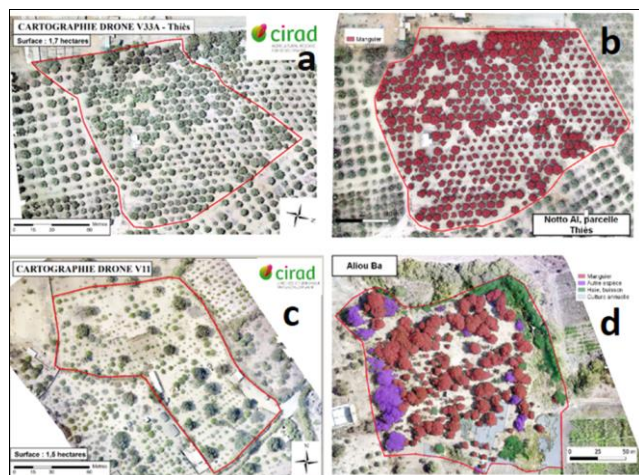


Fig 2: Orchard yield mapping outputs: UAV-acquired RGB Orthomosaic of an Industrial orchard (a) & diversified orchard (c) and corresponding GEOBIA land cover map (b) & (d)

Landscape statistics at the landscape level were then computed using the Fragstat version 4.2.1 program. The landscape indices used in this study are composition indices for each orchard. These different parameters make it possible to understand the richness / diversity of composition of the orchard landscapes.

NP: Number of patches or spots in the orchard

PD: Patch Density is the number of spots per unit area (ha)

PR: Richness patch which gives the number of types of spots on the landscape

PRD: Patch Richness Density looks at the number of types of spots per unit area (ha)

SHDI (Shannon Diversity Index) and SIDI (Simpson Diversity Index), respectively Shannon Diversity Index and Simpson Diversity Index, are used to assess the diversity of the landscape (plant species) for each orchard.

Flies sampling

The samples was collected in each studied orchard indicated (Fig. 1). Sampling was carried out in the period from July 17 to August 29. About 30-50 fruits of the Kent cultivars showing signs of pitting from at least 10 fruiting and fruit ripening trees were collected from each orchard. These fruits were incubated in laboratory in 5L pots, the bottom of which is previously filled with sand. After 10 days, the pupae of the flies were recovered from the sand and placed in breeding cages until the emergence of adults occurs. After checking the specie identification, 632 individuals emerged and were kept in 90° alcohol.

Molecular biology processes

Total DNA from 52 flies was extracted with the Zymo Quick-DNA™ Miniprep Plus Kit according to the manufacturer's

protocol. The sequences of the subunit I of Cytochrome Oxidase (COI) and Cytochrome B (CytB) were amplified by Polymerase Chain Reaction (PCR) using respectively the universal primers pair: LCO1490/HCO2198 [10] and CB-J-10933/CB-N-11328 [11]. The reactions were performed according to the reagents protocol of the Taq PCR Kit (New England Biolabs). For the two genes, amplification is carried out in a reaction volume of 25 µl containing 5 µl of Buffer (10X), 0.5 µl of dNTP, 0.5 µl of each primer, 1 µl of MgCl₂, 0.125 µl of Taq polymerase and 2 µl of DNA extract diluted to the 10th, the whole supplemented with 15.375 µl of MilliQ water. PCR takes place in a thermal cycler (Bioer XP Thermal Cycler). Table 2 shows the PCR amplification conditions. The PCR products of the 52 samples were sequenced by MacroGen Europe Amsterdam and focused on the Forward sequences with the primers HCO2198 (F) and CB-J-10933 (F) respectively.

Table 2: PCR amplification conditions

Steps		Cytochrome oxidase I	Cytochrome B
35 cycles	Initial denaturation	94 °C -2 minutes	94 °C -2 minutes
	Denaturation	94 °C-30 seconds	94 °C-1 minute
	Hybridization	48 °C-30 seconds	48 °C-1 minute
	Elongation	72 °C-1 minute	72 °C-1 minute
Final elongation		72 °C-10 minutes	72 °C-10 minutes

Data analysis

The sequences obtained after sequencing are checked, corrected and aligned with the Bio Edit program version 7.2.5 [12]. The parameters of genetic diversity (Number of sites N, Number of Polymorphic sites S, Number of mutations Eta, Number of haplotypes, Average number of nucleotide difference k, Nucleotidic diversity Pi and Haplotypic diversity Hd) and structure (Genetic distance D and Percentage of variation) were released by MEGA version 7.0.14 [13], DnaSP version 5.10.01 [14] and Arlequin version 3.5 software [15]. The landscape data as well as the genetic diversity indices were recorded in an Excel spreadsheet and were later used for statistical analyses (Shapiro-Wilk normality test & Kendall correlation between genetic and landscape diversity parameters) on Rstudio version 1.2.5033 [16].

Results

Orchard diversity: Table 3 presents the metrics of the landscape composition computed in the 5 studied orchards.

Table 3: Orchards metrics parameters

Site	TA	PR	PRD	SHDI	SIDI
Sébikotane	8,514	4	46,9818	0,9776	0,5657
Notto	2,094	3	143,2726	0,6811	0,474
Carmel	1,312	10	762,1423	1,2827	0,6053
Gorom	1,524	9	590,2681	1,5054	0,72
Sangalkam	0,862	8	927,8213	1,6101	0,7732

TA: Total area (Ha); PR: Patch Richness; PRD: Patch Richness Density; SHDI: Shannon Index of Diversity; SIDI: Simpson Index of Diversity

The size of the orchards varies from less than 1 ha (0.862, Sangalkam) to more than 8 ha (Sébikotane). The richness of the patches is markedly lower in the Notto and Sébikotane orchards (single-variety industrial orchards PR equal 3 and 4 respectively) compared to diversified and traditional orchards (PR ≥ 8). The latter present a greater landscape diversity SHDI ≥ 1).

Genetic polymorphism and diversity

After extraction and PCR, a batch of 52 samples of PCR products including 8 of Cytochrome B (CytB) and 44 of Cytochrome oxidase I (COI) from the 5 sites was sent for sequencing, 14 sequences returned usable including 13 of COI (8 from Carmel, 3 from Notto, 1 from Sébikotane and 1 from Gorom) and one from CytB. The individual sequences

(Sébikotane and Gorom) are eliminated because they cannot constitute a population. The remaining 11 sequences (Carmel and Notto) aligned to a length of 184 bp and constituted our dataset for the analyses. Table 4 presents the basic parameters of genetic diversity as well as the indices of genetic diversity (Pi and Hd).

Table 4: Index of polymorphism and genetic diversity

Parameters	Carmel Population	Notto Population	Global Population
Sample size	8	3	11
Number of sites N	184	184	184
Polymorphic sites S	2	13	14
Number of mutations Eta	2	13	15
Number of haplotypes	2	3	4
Average number of nucleotide difference k	0,5	8,667	2,855
Nucleotidic diversity Pi	0,00272±0,00196	0,04710±0,01896	0,01551±0,009
Haplotypic diversity Hd	0,250±0,180	1±0,272	0,491±0,175

The number of polymorphic sites on the total population is 14, the population of Notto is more polymorphic (13 sites) than that of Carmel (2 sites), just as the total number of mutations and the average number of nucleotide differences. There is also a low nucleotide diversity over the entire population, however it is higher in the Notto population. A very large haplotypic diversity is noted in the Notto population (1 ± 0.272) as well as in the overall population (0.491 ± 0.175), it is less strong for the Carmel population (0.250 ± 0.180)^[19].

Genetic structuration

The parameters of genetic structuring within and between populations obtained with the AMOVA test are presented in table 5.

Table 5: Genetic structuration parameters

Parameters	Carmel	Notto	Inter population
Genetic distance D	0,002±0,0019	0,041±0,0165	0,023
Percentage of variation	65,17%		34,83%

The genetic distance within populations is greater in the Notto population (0.041) and significantly higher in absolute value than the distance between populations. The observed variation is due more to variation between individuals (65.17%) than between populations (34.83%).

Correlations between parameters of genetic and landscape diversity

The results of the correlation test by the Kendall (Tau) method carried out between the parameters of genetic diversity and landscape diversity are presented in table 6.

Table 6: Correlation between genetic and landscape diversity parameters

	Eta	K	Pi	Hd	D
SHDI	Tau= -1*	Tau= -1*	Tau=-1*	Tau=-1*	Tau=-1**
SIDI	Tau= -1*	Tau= -1*	Tau=-1*	Tau=-1*	Tau=-1*

Tau: Kendall's correlation coefficient; * P-value = 0, 02535; ** P-value = 2.2e-16

Correlation tests between the parameters of genetic diversity (Pi, Hd and D) and those of landscape diversity (SHDI and SIDI) give a strong negative and significant correlation coefficient (Tau = -1) (p-value = 0, 02535; p-value = 2.2e-16).

Discussion

The general objective of this study was to identify the landscape and environmental factors influencing the genetic variability of populations of the oriental fruit fly *B. dorsalis* in the Niayes area in Senegal.

The orchards of Notto and Sébikotane (industrial, monovarietal orchards) only produce mango, often the Kent cultivar, the only other plant species found in these orchards are boundary plants and defensive species (border hedges)^[17]. This explains the observed low values of landscape diversity (SHDI and SIDI) and specific richness (PR and PRD). On the other hand, the three other sites which are diversified orchards for Carmel and Gorom and traditional for Sangalkam, are orchards with a predominance of mangoes but associated with other fruit crops (such as citrus, papaya, cashew...) and sometimes with vegetable crops, hence the great landscape diversity noted. As shown by Diatta^[18], the typology as well as the production systems have a great influence on the dynamics of the populations of *B. dorsalis* and therefore on the genetics of the populations thereof.

The polymorphism and genetic diversity indices indicate a low level of diversity in the general population with only 4 haplotypes even though the Notto population appears to be more polymorphic than the general population. The Carmel population is relatively more homogeneous, only two polymorphic sites and two haplotypes, one of which is predominant. The low values of Hd and Pi (0.491 and 0.01551 respectively) also support the low genetic diversity obtained. The hypothesis of a recent Bottleneck (sharp reduction in the size of the population) according to Grant (1998) could explain this. The population of Notto, on the other hand, has a weak Hd and a strong Pi, which could indicate secondary contact between isolated populations^[19]. Previous studies carried out with large-scale trap sampling^[20, 21, 22] have shown high genetic diversity (Hd from 0.636 to 0.984 and Pi up to > 0.01) of *B. dorsalis* populations mainly in Asia. In addition, a study also carried out in Senegal in the Niayes area and in Lower Casamance on various host plants^[23] reported high genetic diversity (Hd = 0.972 and Pi = 0.1563). The low diversity noted in our study could be explained by the more targeted sampling method (on a single variety of mango), the proximity of the two sites (less than 50 km) but also the small size of the population and the number low of exploitable sequences.

The genetic distances observed suggest a higher level of

genetic structuring within the population of Notto ($D = 0.05$) compared to the one of Carmel ($D = 0.003$). What is in adequacy with the genetic diversity observed within these two populations previously and could find explanation in the different systems of production of these orchards. A previous study carried out in the Niayes area ^[23] reported a greater genetic distance within these populations in the Niayes area ($D = 0.092 \pm 0.016$). Barr *et al.* ^[24] described a weak genetic structure within populations of *B. dorsalis* on the island of Taiwan, while Qin *et al.* ^[22] in a global trapping study report significant genetic structuring between different sampling sites. The size of the population of this study as well as the selectivity of the samples (a single variety of host plant) considered here could explain the weak structuring observed. Correlation tests between parameters of diversity and genetic structure and those of landscape diversity show a strong negative correlation ($\text{Tau} = -1$ and $p\text{-value} = 0.02535$) between these two types of parameters. In other words, the more specifically an orchard is rich and diversified, the weaker the genetic diversity and structure of its population. This could be explained in particular by the seasonality of mango (from May to October in Senegal) ^[25] and the large polyphagia of the fly ^[8]. In fact, from one mango season to another, in diversified orchards (case of Carmel), the fly subsists on other host plants (such as pomelo, papaya, lemon...) present in the orchards. Residual populations could be the cause of re-infestation of mangoes the following season. The population would therefore remain relatively the same and very homogeneous from a genetic point of view as suggested by our results. In the industrial type of orchards (Notto's case) which are often monovarietal, the absence of refuge plants means that at the end of the mango season, the population would disappear locally and would not reappear until the following season from other sites. This explains the diversity observed as supported by the percentages of variations observed (variations due to 65.17% variability between individuals). A study of the fly population by trapping on various types of orchards carried out over three years (between 2011 and 2014) by Diatta¹⁸ shows that in monovarietal orchards, the fly was only present from June to September, which corresponds to the period of mango production. While in multispecies (diversified) orchards the fly is present throughout the year with population peaks during the mango production season and residual population during the non-mango period. This could explain the relative homogeneity noted within the population of Carmel and the high level of polymorphism and diversity of the population of Notto which, moreover, according to the values of P_i and H_d would be the result of a contact between once isolated populations ^[19].

Conclusion

The results of this study made it possible to objectively understand the diversity of the landscape (diversity indices) associated with the different mango production systems in the Niayes area. Genetic analyses revealed a low level of polymorphism, diversity and genetic structuring of the fly population subservient to the diverse Carmel orchard and a greater diversity and polymorphism in the Notto population (monovarietal orchard). A strong negative correlation has been revealed between the landscape diversity metrics and the genetic diversity of the populations of *B. dorsalis* underpinning a maintenance of the populations at the level of the orchards diversified in low numbers from one mango

production season to another and seasonal appearances in monovarietal industrial orchards with populations from elsewhere. This study provides new elements which, if confirmed by larger-scale studies, would make it possible to refine the fly control techniques applied.

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