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Agroecological Factors Determining Occurrence and Abundance of the Fall Armyworm (*Spodoptera frugiperda*) on the Outlooks of Maize Production in Benin

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Abstract

The fall armyworm (*Spodoptera frugiperda* J.E. Smith) is one of the most notorious pests of maize crops worldwide. However, few studies have shown the influence of agroecological factors and future distribution patterns of the *FAW* in Benin. This study assessed the abundance of the FAW in the Territorial Agricultural Development Agency Division 4, with extrapolation of the data in relation to environmental variables in the study areas leading to future *FAW* distributions in these regions. For this purpose, *FAW* surveys were carried out in

80 maize fields at three stages of maize development (sowing, flowering and maturity). Magurren's formula and Shannon's diversity index were used to assess species abundance. Mixed effects Poisson and MaxEnt models were developed to investigate the distribution patterns of *FAW* and the relative influence of agroecological factors on *FAW* presence and abundance. Results showed that *FAW* abundance varied from one region to another, depending on the stage of maize development and the areas. All model parameters were statistically significant at the 5% level (p-value < 0.05) except sowing stage (p-value > 0.05). Flowering stage showed a significant negative effect on *FAW* abundance, with an IRR ≈ 0.31, indicating that *FAW* abundance at maturity is reduced by about 69% compared to flowering. In contrast, the effect of sowing stage was not significant (IRR ≈ 1.30). These results also suggest that pest management strategies can be adapted to new climatic conditions. This would allow a proactive rather than a reactive approach.

Keywords: fall armyworm, environmental variables, spatial variability, predict, maize, MaxEnt

1. Introduction

The fall armyworm (FAW), *Spodoptera frugiperda* is a lepidopteran pest native to tropical and subtropical regions of the Americas and its first successful invasion outside the native region was reported in Africa, more precisely in Nigeria, Togo, and Benin in 2016 (Goergen *et al*., 2016). This quick spread across continents might have been speeded up by the high natural wind-assisted flight capability of FAW allowing it to reach several hundreds of kilometers in a single day (Early *et al*., 2018). The *FAW* is an extremely destructive omnivorous pest of subtropical and tropical origin with higher viabilities over a wide range of temperatures and distributions (Fonseca *et al*.,2018). Its strong fertility ability, high migratory capacity and ecological plasticity contribute to the *FAW*'s major economic damage by voraciously infiltrating key growing areas of at least 353 known different host plant species belonging to 76 botanical families, e.g., maize (Zea mays L.), rice, sorghum, sugarcane, cotton and varieties of vegetables (Montezano *et al*.,2019). The pest is known to have high dispersal abilities. After the first report on its outbreak in Africa (Goergen *et al*.,2016), farm areas of nearly 25 million hectares of its main host plant (maize) production have been severely compromised within only two years post detection of this pest on the continent. Without any control measures, maize yield losses due to FAW can exceed 50% of the total annual production of the affected countries, especially in the low and medium maize producing areas (De Groote *et al*., 2020), leading to serious economic and social implications. Hence, with its extensive spread, FAW has the potential to negatively impact the food security of billions of people, which calls for a collective and holistic approach for its global management (Molo *et al*., 2020). However, early outbreaks of *FAW* were quite devastating, and in some cases, maize crops were totally lost. Thus, whether further vast *FAW* management campaigns contributed to successful reduction of pest populations, the new associations of natural enemies contributed to *FAW* population regulation, or the initial impact assessments were overestimates is unclear. Although offering fast curative action, the health risks associated with synthetic insecticides and resistance patterns (Muraro *et al*.,2021) continue to point to the need for alternative pest management methods, particularly in the

African context where the use of the chemicals does not always comply with standards. Indeed, field data collected from several countries from 2016 to 2020 appeared to show an almost total absence of stem borers from maize fields (P.Chinwada, unpublished data; S. Nyamutukwa, unpublished data). However, recent field studies are starting to show increased incidence of some stemborer species in maize fields infested by FAW, thus pointing to a putative partitioning of the niche permitting coexistence of both (Sokame *et al*.,2022). The diversity of plant species and habitats in a landscape can also influence the availability of natural enemies, such as predators and parasites, which can help control fall armyworm populations (Harrison *et al*., 2019). However, the exact mechanisms through which landscape structure influences fall armyworm populations and crop loss were not well understood, and further research is needed to elucidate this complex relationship in diffrents agroecosystems of Benin. It is important to point out that, in the absence of location specific data on FAW incidence and temporal dynamics (as influenced by planting dates and season), extrapolating this recommendation on Ampligo application schedules to other regions should be avoided.

Furthermore, the occurrence of *S. frugiperda* infestations can be influenced by bioclimatic factors, including temperature, rainfall and humidity. Fall armyworms thrive under moderate temperatures and high relative humidity, which supports their moisture needs for survival and reproduction (Yan *et al*., 2022). On the other hand, areas with low rainfallor prolonged drought conditions may experience fewer infestations due to limited soil moisture and reduced host plant vigor (Paudel *et al*.,2022). Notably, the changing environmental conditions associated with climate change would also have a direct impact on the life cycle of crop pests and diseases. Globally, there is a large body of literature linking the occurrence and distribution of crop pests and diseases to climate variability (Goergen *et al*., 2016, Osunga *et al*., 2017, Day *et al*., 2017, Timilsena *et al*., 2022, Ibrahim *et al*., 2023). Temperature and rainfall have been shown to be the most important factors influencing the occurrence and development of many pests and crop diseases (Goergen *et al*., 2016, Day *et al*., 2017, Timilsena *et al*., 2022, Ibrahim *et al*., 2023). To gain a comprehensive understanding of the abundance and impact of *S. frugiperda*, it is essential to survey not only FAW populations but also landscape features, alternate hosts, and management strategies. Inland planning and management, reliable data sources, such as land use maps, are crucial. As the distribution range of the pest is expanding worldwide, the need for designing long-term management strategies based on right decision guidance becomes crucial. However, cropping systems, farming practices, and the agroecosystems in Benin are different from those of north, central and south. Therefore, the FAW temporal and spatial infestation spread in different parts of Benin could be influenced by these factors which are yet to be established. Many models have been developed worldwide to help understand the dynamics and behavior of FAW using different frameworks and modeling techniques. A wide range of sophisticated crop models exist worldwide (Jones *et al., 2017*). In recent times, scientists have become increasingly interested in using crop models (Donatelli *et al*., 2017) and biophysical models to directly assess the impact of climate change on the distribution of pests, including FAW. However, one of the most common tools for predicting pests and diseases is the species distribution modelling (SDM) approach, also referred to as "environmental niche modelling" (Early *et al*., 2018, Timilsena *et al*., 2022, Ramasamy *et al*., 2022, Wang *et al*., 2023). For example, Early *et al*. (2018) integrated observed FAW data with historical temperature and precipitation data to project future global FAW risks using SDM. Estimating the density level of a pest insect in a crop is complex but can be addressed using empirical and mechanistic modeling approaches such as rule-based modeling (Liebhold and Tobin, 2008; Bell *et al*., 2013).

Thus, the present study aims to use scientific data and the rule-based modeling approach to adjust, predict and map the level of *FAW* density on maize crops across Benin using the following data collected in the Territorial Agency for Agricultural Development Pole 4, which covers a region of southern, central, eastern, western and northern Benin: *FAW* larvae field collection, meteorological data (temperature, rainfall) were downloaded, data on the altitude of the data collection site. The proposed approach aims to provide the first step towards information and knowledge on where to prioritize and implement effective agroecological *FAW* control strategies in Benin.

2. Material and Methods

2.1 Study Framework on Species Occurrence Data

The occurrence data of *S. frugiperda* are projected and shown in **Fig. 1.** We collected data from fieldwork carried out in Benin Republic. All recorded data has been carefully checked, the false and duplicate points have been removed. In all, 80 georeferenced occurrences were used as input data for the presence of the species. The data included only the longitude and latitude of the species. The study was conducted across seven distinct administrative districts located in the central-southern region of Benin (**Fig. 1**). These districts include N'Dali and Borgou in the northern part of the study area, Donga and Bassila in the west, Ouèssè in the center, Glazoué (Collines) in the southwest, Djidja and Zou in the south. The map illustrates the spatial distribution of these administrative zones, intersected by multiple watercourses and connected through a network of main and paved roads. The region's climate varies along a north-south gradient. The northern districts (N'Dali, Borgou, and Donga) are characterized by a Sudanian climate with distinct rainy and dry seasons (Adomou *et al*., 2017). The central zone (Bassila, Ouèssè, and Glazoué) experiences a transitional Sudanian-Guinean climate, while the southern part (Djidja and Zou) benefits from a subequatorial climate with two rainy seasons (Yabi & Afouda, 2012). These districts also exhibit significant differences in agricultural production systems. According to Tovignan *et al*. (2020), large-scale cotton and cereal production dominates the northern regions, whereas central and southern zones are characterized by more diversified agriculture, including subsistence crops (maize, cassava, yam) and plantations (cashew, oil palm). The average farm size ranges from 5–10 hectares in the north to 1–3 hectares in the south (Honlonkou, 2019). From a socio-economic perspective, population density generally increases from north to south, with the highest concentrations observed in Glazoué and Zou (INSAE, 2023). Access to development infrastructure (health centers, schools, markets) is more limited in the northern districts, particularly in N'Dali and Donga, compared to the better-served southern districts (Adégbola *et al*., 2016). These regional disparities in climate, agricultural systems, and socio-economic development are crucial factors to consider when analyzing and interpreting the study results. The **table 1** shows the characteristic features of Benin's climates.

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Table 1. Characteristics of Benin's climatic zones (Mensah *et al*.,2014)

Parameters	Sudanian Zone	Sudano-Guinean Zone	Guinean Zone
Annual rainfall range (mm)	1200	900–1110	<1000
Temperature range (_C)	25-29	25-29	24-31
Relative humidity range (%)	69-97	31-98	18-99

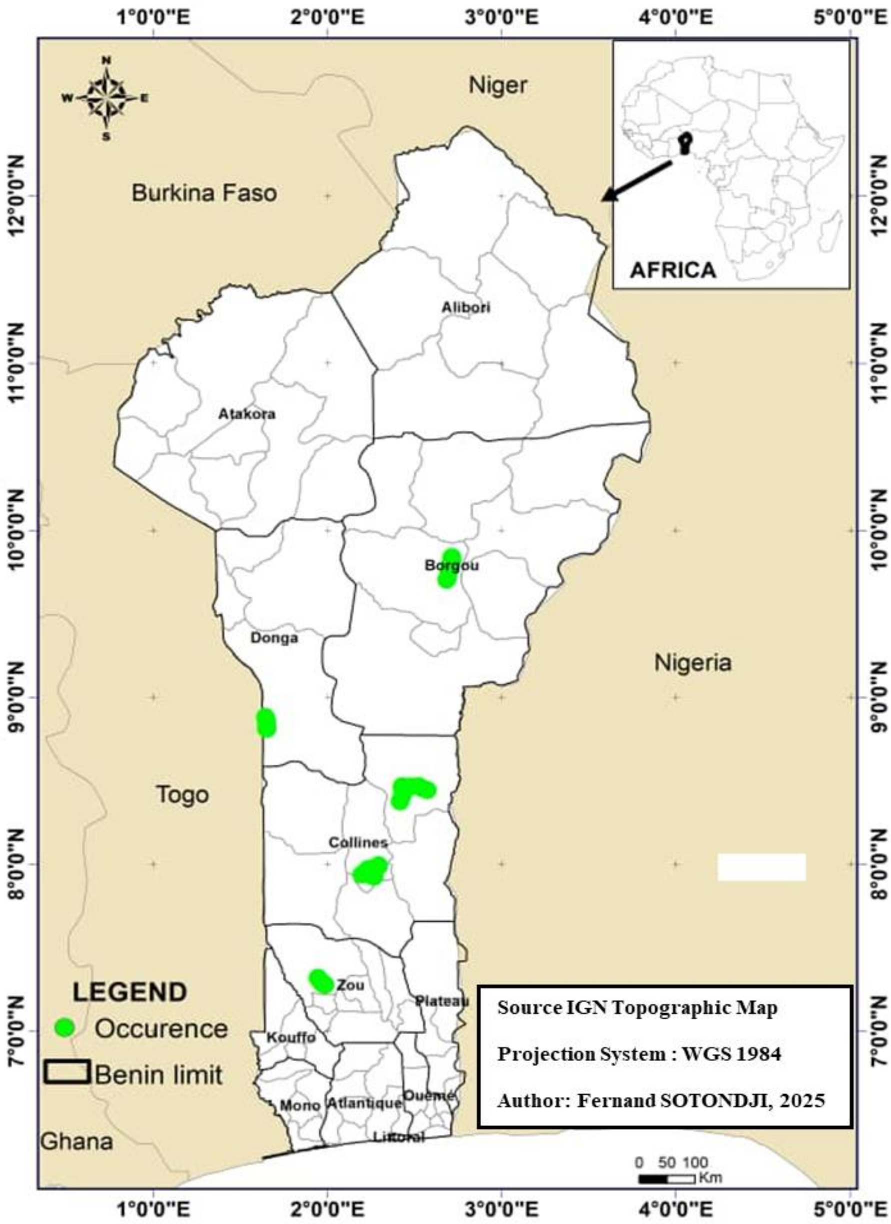

Fig. 1. Map of the study area in the five districts showing the presence of *S. frugiperda* in Benin

2.2 Environmental Data

Bioclimatic and soil data were considered as environmental data to predict suitable habitat for the conservation of *S. frugiperda.* The ISRIC database (www.isric.org) was used to obtain the soil variable. Past bioclimatic data (From 1950–2000) and futures data were downloaded from the database WorldClim (Hijmans *et al*., 2005, www.worldclim.org) at 30 seconds spatial resolution (1 km × 1 km). This dataset includes 19 bioclimatic variables derived from interpolated means of minimum and maximum temperatures as well as precipitation (Hijmans *et al*., 2005). For future climate projections, four global climate models (GCMs: CanESM5, CNRM-CM6-1, HadGEM3-GC31-LL and MIROC6) were selected. Two climate scenarios, titled Shared Socio-Economic Development Pathways (SSPs) were considered: SSP 245 representing an optimistic scenario and SSP 585 representing a pessimistic scenario. These scenarios were considered for three time horizons: 2041–2060 (2050s), 2061–2080 (2070s) and 2081–2100 (2090s) (O'Neill *et al*., 2017; Riahi *et al*., 2017; Jingyun Guan *et al*., 2021).

2.3 Sampling Method for S. Frugiperda in Maize Fields of Five Districts in Benin

During the 2024 rainy season, the occurrence and larval density of the fall armyworm were studied in five districts (Djidja, Glazoué, Bassila, Ouèssè and N'Dali) described (Fig. 1). Based on the sampling plan developed by Overholt *et al*. (1994) and the proportion of cultivated land (Guihe'neuf 2004, Goux 2005), 80 maize fields were selected for assessment of *FAW* prevalence sampled, with 16 maize fields per district mentioned above. To cover the vegetative, reproductive and maturity stages, all selected fields were visited thrice, three weeks after planting (sowing, flowering and maturity stages) to check for the presence of *S. frugiperda* caterpillars. In each field, a 0.5-hectare area was designated untreated, from which 50 maize plants were randomly selected on each observation date. The number of *FAW* larvae on the selected plants was counted in order to estimate *FAW* abundance per field

2.4 Data Analysis

2.4.1 Estimation of Relative Abundance and Diversity of Insect Families - Assessment of Pest Diversity Relative Abundance (F) Was Determined After Counting Individuals Per Family

$$.F(\%) = n_i \times \frac{100}{N} ;$$

To assess family diversity, the Shannon index (H^'), which evaluates the diversity of taxa (in this case families) in each environment considered, was determined using the formula of Magurran (2004): H^'=-∑p_i ln(p_i); p_i=n_i/N where n_i is the abundance of the ith species and N is the total abundance. Next, the equitability (E) associated with the Shannon index was calculated. It is defined by E=H^'/ (H^' max) where H^' max=ln(S) (maximum Shannon diversity) and S is the total number of families. E is between 0 and 1. If it tends to 0, it means that almost all numbers are concentrated in one family. On the other hand, if all families have the same abundance, E tends to 1. Finally, the Simpson's index (D), which measures the probability that two randomly selected individuals belong to the same taxonomic level, was also calculated as follows:

$$D = 1 - \frac{\sum n_i(n_i - 1)}{N(N - 1)}$$

where n_i is the number of individuals in the given family and N is the total number of individuals in all families considered. This index varies between 0 (minimum diversity) and 1 (maximum diversity).

2.4.2 Data Processing and Model Evaluation

For the modeling process, the Jackknife test was first carried out on the initially selected environmental variables to check the contribution of each variable to the distribution of *S. frugiperda*. Variables with a higher percentage contribution were then retained for further analysis (Wang *et al*., 2019; Rodriguez *et al*., 2020). The Variance Inflation Factor (VIF) was then used to assess multicollinearity among the environmental variables (Dormann *et al*., 2013; Moraitis *et al*., 2019). This test was performed using the "SDM" package in R software (R Core Team, 2022). For this test, we adopted a default threshold (VIF < 10) to select important non-collinear variables for the distribution of the species (Naimi and Araújo, 2016; Biaou *et al*., 2023). A VIF greater than 10 indicates collinearity problems in the model (Chatterjee and Hadi, 2006). A total of six environmental variables were selected for prediction using the Maximum Entropy (MaxEnt) algorithm (Phillips *et al.*, 2006). The MaxEnt algorithm has frequently been used in species distribution modeling (Dimobe *et al*., 2022).

To assess the accuracy of the model, the Area Under Curve (AUC), the Correlation statistic (COR), and the True Skill Statistic (TSS) were used (Allouche *et al*., 2006). AUC values > 0.9 indicate excellent performance, while values between 0.8 and 0.9 indicate good performance, values between 0.7 and 0.8 indicate fair performance, values between 0.6 and 0.7 indicate poor performance, and values between 0.5 and 0.6 indicate failure (Swets, 1988).

The TSS ranges from -1 to +1, with +1 indicating sensitivity (detection of true presence) and -1 indicating specificity (detection of true absence). A model with a TSS ≤ 0.5 is considered a random prediction, while a model with a TSS > 0.5 has good predictive power (Landis and Koch, 1977).

Correlation (COR) was performed to assess the variation between predictions and observations. Deviance is essentially a measure of variation unexplained in the logistic regression model; the higher the value, the less accurate the model. Seventy-five percent of the occurrences were used as a random subset for model calibration, and 25% were used for model evaluation. Current and future distribution maps of *S. frugiperda* were produced using ArcGIS 10.4 software. An overview map for each horizon was displayed, showing the areas potentially high suitable by combining the results of the four General Atmospheric Circulation Models (GCMs).

2.4.3 Mixed Effects Poisson Model

Two generalized linear mixed effects models were fitted, including the Poisson model using the glmer function from the lme4 package (Douglas *et al.*, 2015) and the negative binomial model using the glmer.nb function from the MASS package (Venables & Ripley, 2002) of the R 4.1.3 software (R Core Team, 2022). The developmental stage factor was considered a fixed factor and the locality factor was considered a random factor.

2.4.4 Evolution of FAW Abundance During the Three Developmental Stages of the Maize Plant (Sowing, Flowering and Maturity)

The analysis of spatial variability in FAW abundance during the three developmental stages of maize (sowing, flowering and maturity) was carried out using geostatistical approaches, which are widely recognized for their effectiveness in modeling natural phenomena (Goovaerts, 1997; Gongnet, 2017). In order to capture spatial dependencies, semi-variograms were calculated for each phenological stage, allowing to quantify the correlation between observations as a function of the distance separating them (Jafari *et al.*,2011). Among the commonly used theoretical models (exponential, spherical, Gaussian), the Gaussian model was chosen to fit the semivariograms due to its ability to capture smooth continuities in ecological data, especially when there is a gradual transition in insect abundance within the agricultural space (Goovaerts, 1998; Qingmin *et al.*, 2013). Variogram parameters (nugget, range, threshold) were estimated to characterize the spatial structure of larvae abundance at each stage. Prediction of FAW abundance across the study area was then performed using ordinary kriging, an interpolation method that minimizes prediction error by weighting observations according to their distance and the modeled spatial variability structure (Fereydoon *et al*., 2010; Sajid *et al*., 2013). This approach produces continuous maps of *FAW* abundance, facilitating the identification of areas at high risk of infestation at different stages of maize development. Spatial analysis and mapping were performed using ArcGIS 10.4 and R software, two tools widely used for geostatistical modeling and agroecological systems analysis (Gongnet, 2017).

2.4.5 Climatic Factors Affecting Fall Armyworm Abundance

To assess the effect of climatic variables on FAW abundance at different stages of plant development, we followed a rigorous approach combining spatial analysis and statistical modeling, as recommended by Elith and Leathwick (2009). Our methodology included several key steps to ensure a robust analysis of the interactions between climate and insect populations. Climate data were downloaded online as rasters with a resolution of 30 arc seconds, using the RCP 4.5 emissions scenario, following the protocol established by van Vuuren *et al*. (2011). The selected climate variables included key parameters such as precipitation, temperature, and various bioclimatic indices identified as relevant by Deutsch *et al*. (2018). The geographic coordinates of the study fields, which were spread across different district, were collected in the field using the methodology of Fick and Hijmans (2017). Using the "Extraction" function of the Spatial Analyst Tools package in ArcGIS 10.8 software, we extracted the climatic values corresponding to each georeferenced point, according to the recommendations of ESRI (2020). To study the relationship between climatic variables and insect abundance at the sowing, flowering and maturity stages of maize plants, we fitted regression models multiple Poisson, following the approach developed by Zuur *et al*. (2009). This method, which is particularly well suited to count data, as demonstrated by O'Hara and Kotze (2010), allows us to model the discrete nature of *FAW* abundance. The response variable was *FAW* abundance, while the explanatory variables included extracted climatic indices, in line with the analytical framework proposed by Guisan and Thuiller (2005). The estimated coefficients of the model were interpreted to determine the direction and statistical significance of each climatic factor on insect abundance, following the approach of Bolker *et al*. (2009). The p-values associated with the coefficients were used to identify variables with a significant effect at different thresholds (0.05; 0.01; 0.001), following the statistical conventions established by Crawley (2013). This approach, combining spatial analysis and statistical modeling, allowed us to identify the most influential climatic factors at each stage of plant development, providing valuable insights for pest management in the context of climate change, as suggested by Bebber *et al.* (2014).

3. Results

3.1 Distribution of Spodoptera Frugiperda by District According to the Three Stages of Plant Development (Sowing, Flowering and Maturity)

The Fig. 2 shows the distribution of the number of *S. frugiperda* found in the 81 sampled maize fields according to the stages of plant development (sowing, flowering, maturity) in five communes of Benin: Bassila, Djidja, Glazoué, N'Dali and Ouèssè. Significant differences were observed in larval infestation depending on the district and the stage of development. In Bassila, infestation was mainly observed on the hundred maize plants sampled per field in the size fields at the sowing stage (281 larvae), followed by the flowering stage (270 larvae), with a notable absence of *S. frugiperda* caterpillars at the mature stage. In Djidja, the maximum infestation occurred in the flowering stage (350 larvae), followed by an intermediate level in the seedling stage (201 larvae) and a low level in the mature stage (38 larvae) of *S. frugiperda*. In Glazoué, a similar trend of larvae was recorded, with an increasing infestation (43 caterpillars) at the maturity stage of the maize plant, (239 caterpillars) at the seedling stage and (279 caterpillars) at the flowering stage. N'Dali has a maximum infestation at flowering (320 caterpillars), followed by a decrease during flowering (299 larvae) and a low level at plant maturity (64 caterpillars). Finally, Ouèssè shows a relatively stable infestation at the flowering and seedling stages (301 and 266 caterpillars, respectively), with a low level of FAW at the maturity stage (51 larvae).

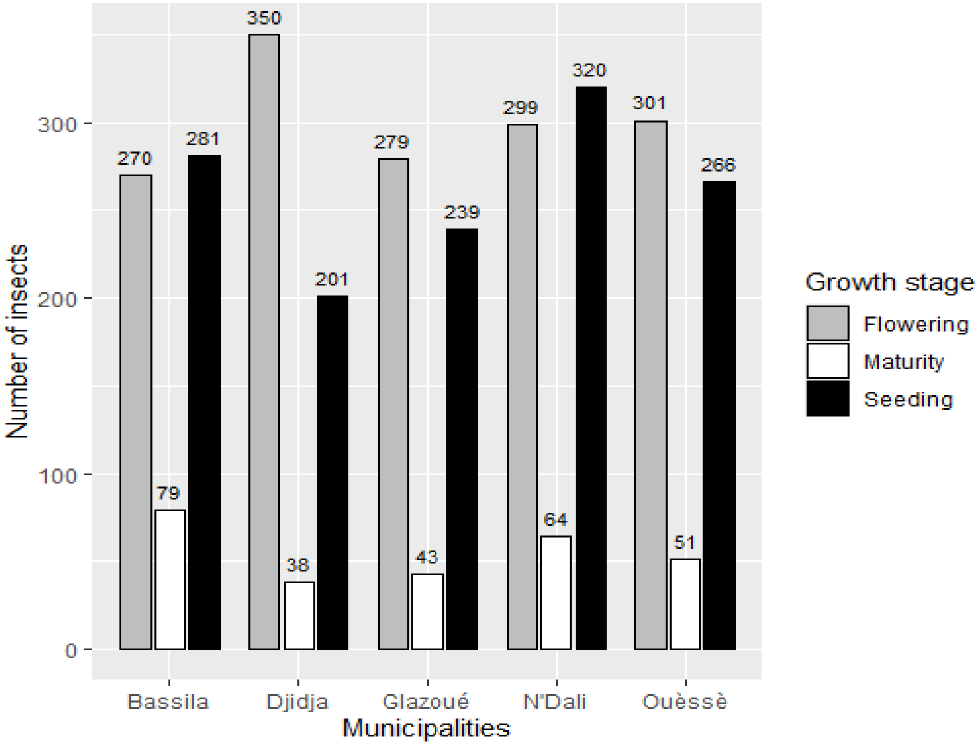

Fig. 2. Number of fall armyworm per maize plant development phase in five districts of Benin

3.2 Comparison of FAW Abundance Between Different Districts

Poisson and negative binomial Poisson regression models were used to analyze caterpillar abundance among districts. Comparison of Akaike Information Criteria (AIC) indicated that the negative binomial model was the best model to describe the data (AIC = 214.449 vs. 835.906 for the Poisson model). This difference indicates that the negative binomial model better captures the variability of the data, probably due to overdispersion.

The following Table 2 and Fig. 3. shows the results of the models. The results in the table indicate that all model parameters are statistically significant at the 5% level (p-value < 0.05) except sowing stage (p-value > 0.05). These differences can be seen in the figure below:

Table 2. Comparison of FAW abundance between different districts

Source	**Coefficients (se)**	**Valeur Z**	**Pr(>|z|)**
Intercept	6.39 (0,26)	24.470	<2e-16***
Flowering stage	-1,17 (0,30)	-3.931	8.47e-05***
Sowing stage	0.26 (0,29)	0.904	0.366
Variance of random locality effect		0.13	
R^2 marginal (%)		0,59	
R^2 conditional (%)		0,82	
Meaning codes P-values: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1			

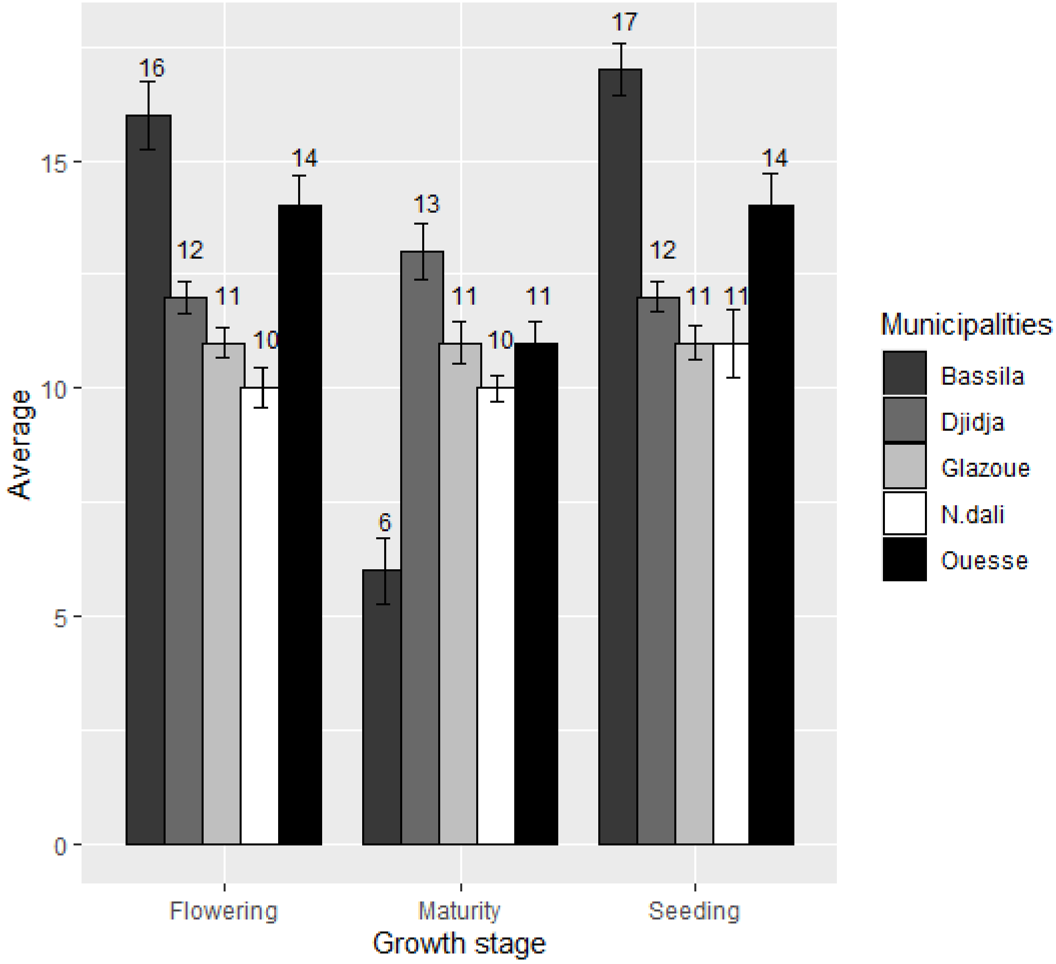

Fig. 3. Comparison of FAW abundance between different districts

3.3 Diversity of FAW Collected Together with S. frugiperda in the Five Study Districts

The following Table 3 shows the distribution of insect species in the different districts. The data showed that *S. litoralis* is the most abundant species in all localities, with numbers ranging from 44 larvae in Ouèssè to 30 caterpillars in Bassila. This species dominates the others, with high numbers also in N'dali (32 larvae) and a gradual decrease of *S. littoralis* in Glazoué (19 caterpillars) and Djidja (12 larvae). *Helicoverpa armigera* is the second most abundant species with more moderate numbers ranging from 6 larvae in Djidja, 14 in Ouèssè, 22 in Glazoué, 31 in Bassila and 33 in N'dali. *Sesamia calamistis*, on the other hand, displayed a more heterogeneous abundance, with peaks in Djidja (15 larvae) but very low numbers in the other localities (11 in Bassila, 8 in Ouèssè, 7 in N'dali and 4 in Glazoué). Finally, *Eldana saccharina* was the least abundant species, with numbers ranging from 2 larvae in Bassila to 9 in Ouèssè. Overall, Bassila recorded the highest total abundance (84 larvae), followed by Ouèsse (76 larvae), N'Dali (75 larvae), Glazoué (44 larvae) and Djidja (41 larvae) in the five districts surveyed. Six (06) *Marasmia trapezalis* larvae were found on maize plants in Djidja and one (01) in Glazoué.

Table 3. Diversity of *FAW* Collected Together with S. Frugiperda in the Five Study Districts

Species	Bassila	Djidja	Glazoué	N'Dali	Ouèssè
Eldana saccharina	2	8	5	4	9
Helicoverpa armigera	31	6	22	33	14
Sesamia calamistis	11	15	4	7	8
Sopodoptera littoralis	40	12	13	32	44
Marasmia trapezalis	0	06	01	0	0
Total	**84**	**48**	**45**	**76**	**75**

3.4 Diversity of Species Collected According to the Shannon Index in the District Studied

The Shannon indices observed in the study districts Fig. 4 showed great variability, with the highest values recorded in Djidja (0.98) and Glazoué (0.79), suggesting a potentially greater diversity of species in these localities compared to Ouèssè (0.71), Bassila (0.66) and N'Dali (0.62). Equitability, on the other hand, varied significantly between district, with higher values observed in Djidja (0.71) and Glazoué (0.57), indicating a more even distribution of species abundance in these localities. On the contrary, Bassila (0.48) and N'Dali (0.45) had lower values of equity, indicating a possible dominance of certain species. Simpson's index followed a similar trend as equitability, with higher values in Djidja (0.71) and Glazoué (0.57) and lower values in Bassila (0.41) and N'Dali (0.45), reinforcing the idea of greater species diversity in the former and possible dominance in the latter.

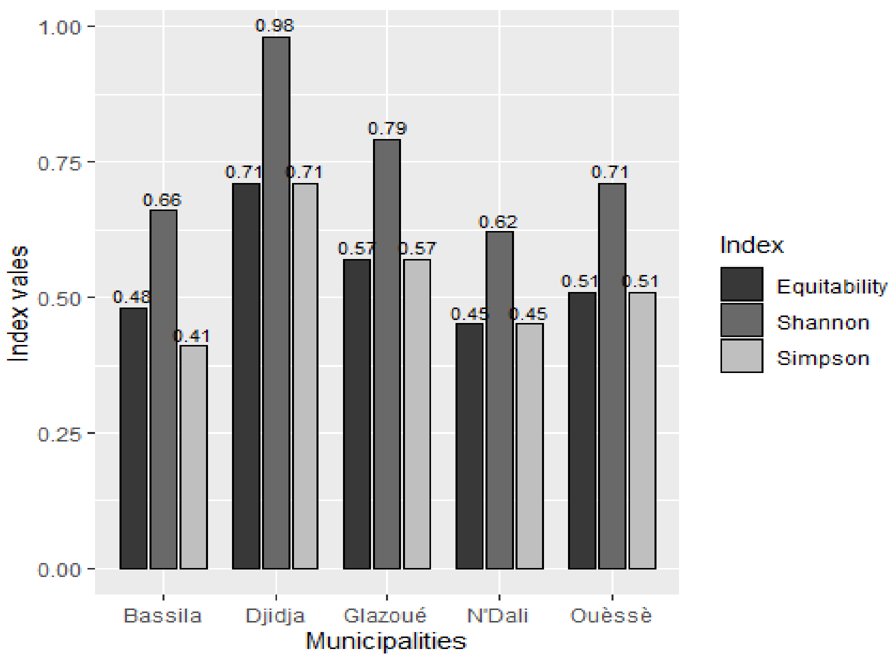

Fig. 4. Shannon index of larvae *FAW* diversity collected in the study areas.

3.5 Spatial Variability of FAW Abundance During Three Stages of Maize Plant Development (Sowing, Flowering, and Maturity)

- **Sowing stage of maize**

The sowing stage map **Fig. 5** shows a high concentration of *FAW* in the northern districts, particularly in N'Dali and Bassila, with very high densities (53-56 larvae). There is a decreasing gradient from north to south, with the lowest values (32-39 larvae) recorded in the districts of Glazoué and Djidja.

- **Flowering stage of maize**

During the flowering stage, the spatial distribution of FAW showed a significant change. Infestations moved mainly towards Djidja in the south (54-82 larvae) and partly towards N'Dali in the north. Central areas (Ouessé, parts of Bassila) show medium densities (20-37 larvae), while Glazoué shows variable densities.

- **Maturity stage of maize**

In the mature stage, there has been a noticeable reorganization of the FAW distribution. The Djidja district maintains a high density (21-30 larvae), while N'Dali in the north now has the lowest densities (4-6 larvae). Ouessé shows a variable density gradient.

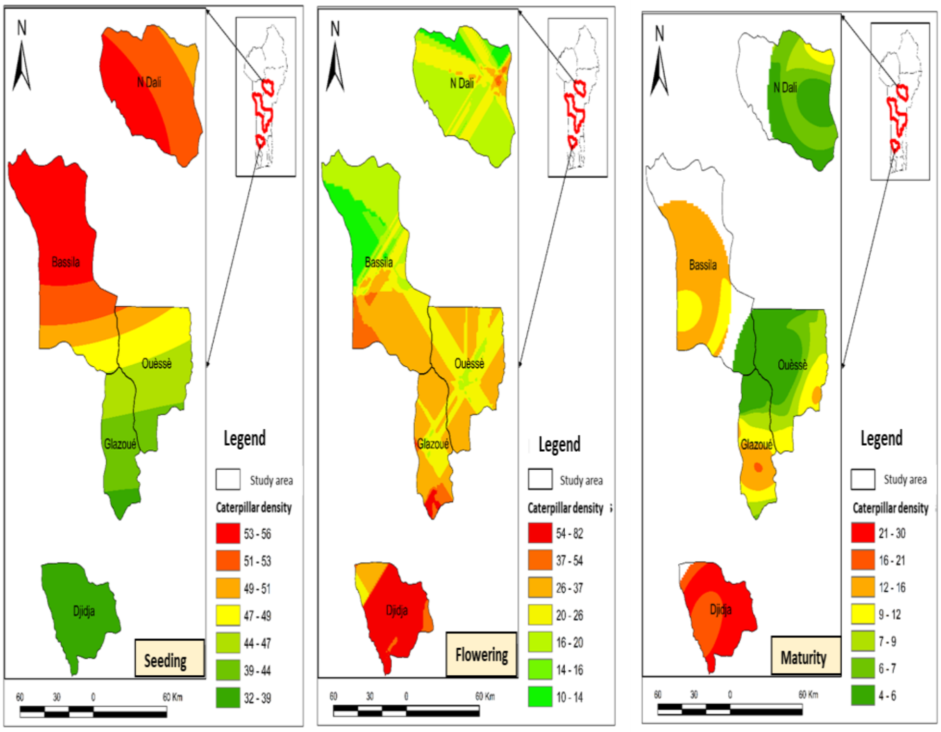

Fig. 5: Spatial Variability in FAW Abundance During the Three Stages of Maize Plant Development (Sowing, Flowering and Maturity)

3.6 Climatic Factors Influencing Fall Armyworm Abundance

This analysis evaluated the effect of climatic variables on FAW abundance at different stages of plant development (Table 4). The variables considered were: annual precipitation (bio12), precipitation in the wettest month (bio13), precipitation in the driest month (bio14), interannual variability in precipitation (bio15), precipitation in the wettest quarter (bio16) and in the driest quarter (bio17), as well as environmental indices such as vegetation density (dm), moisture index (mi) and air quality indices (miaq and mimq). The aim was to identify climatic factors with a significant impact, either positive or negative, on insect population dynamics at the sowing, flowering and maturity plant stages.

At the sowing stage, several climatic variables showed significant effects on FAW abundance. Rainfall in the wettest month (bio13) showed a significant negative effect ($p = 0.023$), indicating that higher rainfall reduced FAW abundance. However, rainfall in the driest quarter (bio17) had a significant positive effect ($p = 0.017$).

During the flowering stage, *S. frugiperda* abundance appears to be more responsive to precipitation and environmental stress indices. Annual precipitation (bio12) showed a highly significant positive effect (p < 0.001), indicating that higher total precipitation favors FAW proliferation. On the other hand, precipitation variability (bio15) had a significant negative effect ($p = 0.007$), showing that strong climatic fluctuations can disrupt FAW populations. In addition, vegetation density (dm) had a very strong positive effect (p < 0.001), while moisture index (mi) had a negative effect ($p = 0.012$), indicating that wetter environments without high climatic variability are more conducive to FAW abundance.

Table 4. Climatic factors influencing fall armyworm abundance in Benin

Variations	Sowing stage				Flowering stage				Maturity stage			
	Coefficient	SE	Z value	Pr(>|z|)	Coefficient	SE	Z value	Pr(>|z|)	Coefficient	SE	Z value	Pr(>|z|)
Intercept	9.063e+00	3.184e+00	2.847	0.00441**	-15.968103	4.555005	-3.506	0.000456***	1.367017	7.100664	0.193	0.8473
bio12	-2.691e-03	5.380e-03	-0.500	0.61693	0.030332	0.006542	4.637	3.54e-06***	-0.004361	0.011568	-0.377	0.7062
bio13	-5.636e-02	2.478e-02	-2.274	0.02296*	0.052629	0.031702	1.660	0.096891.	0.090414	0.055572	1.627	0.1037
bio14	-5.098e-03	1.164e-01	-0.044	0.96508	0.068284	0.134323	0.508	0.611202	-0.150958	0.232913	-0.648	0.5169
bio15	1.741e-01	9.934e-02	1.752	0.07976.	-0.285441	0.105739	-2.699	0.006945**	-0.389401	0.194427	-2.003	0.0452*
bio16	8.498e-05	1.958e-02	0.004	0.99654	0.018385	0.025077	0.733	0.463465	0.022446	0.043441	0.517	0.6054
bio17	1.325e-01	5.533e-02	2.394	0.01667*	-0.037063	0.066868	-0.554	0.579392	-0.135250	0.123150	-1.098	0.2721
dm	-3.125e-01	1.241e-01	-2.518	0.01181*	0.984001	0.252808	3.892	9.93e-05***	-0.248225	0.336717	-0.737	0.4610
llds	2.058e-02	5.865e-01	0.035	0.97201	0.567913	0.729991	0.778	0.436585	-0.410730	1.360972	-0.302	0.7628
mi	-1.232e-01	9.990e-02	-1.233	0.21746	-0.300381	0.119758	-2.508	0.012133*	0.230605	0.214763	1.074	0.2829
miaq	-2.844e-01	1.337e-01	-2.128	0.03337*	0.387373	0.182009	2.128	0.033311*	0.215273	0.305813	0.704	0.4815
mimq	2.829e-02	4.585e-02	0.617	0.53724	-0.032242	0.048793	-0.661	0.508751	-0.037909	0.088204	-0.430	0.6673

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

3.7 Model Performance

The MaxEnt algorithm meets the requirements for good performance based on statistical parameters: AUC (0.99), COR (0.72), TSS (0.96), and deviance (0.29). The results showed AUC values greater than 0.9 and TSS values greater than 0.5 (Table 5, Fig. 6). This result suggests that the algorithm used for modeling is an effective predictive model capable of predicting the spatial distribution of *S. frugiperda* under current and future climate conditions. This highlights the robustest of the MaxEnt algorithm to accurately model the distribution of the species.

Table 5. Evaluation of the MaxEnt algorithm

Performance criteria	AUC	COR	TSS	Deviance
MaxEnt Algorithm	0.99	0.72	0.96	0.29

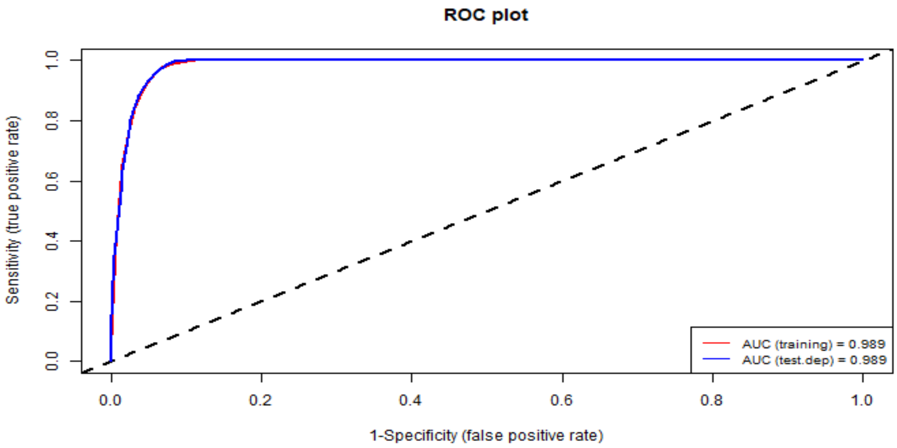

Fig. 6. Area under the ROC curve (AUC) of the MaxEnt prediction model (AUC=0.99)

3.8 Influential FAW Predictor Variables

Table 6 gives the contribution of environmental variables, with Bio3 being the most influential (21.1%), followed by Bio14 (20.7%), Bio13 (19.6%), Bio8 (8.7%), Bio2 (7.5%) and Soil (6.1%).

Table 6. Contribution of environmental variables fall armyworm influential predictor

Variable	Contribution percentage
Bio3	21.1
Bio14	20.7
Bio13	19.6
Bio8	8.7
Bio2	7.5
Soil	6.1

The Jackknife analysis presented in Fig. 7 showed that the bioclimatic variable that increases the information gain when used in isolation is Bio4. On the other hand, the variable Bio3, when not used, results in a loss of information regarding the distribution of *S. frugiperda*. The Bio8 and Soil variables, which present contribution percentages greater than six (6), respectively 8.7 and 6.1, do not result in any significant gain or loss of information when used in isolation or not in the model. Therefore, they will be excluded from the variables. In total, four bioclimatic variables were retained for the model: Bio2, Bio3, Bio14, and Bio13.

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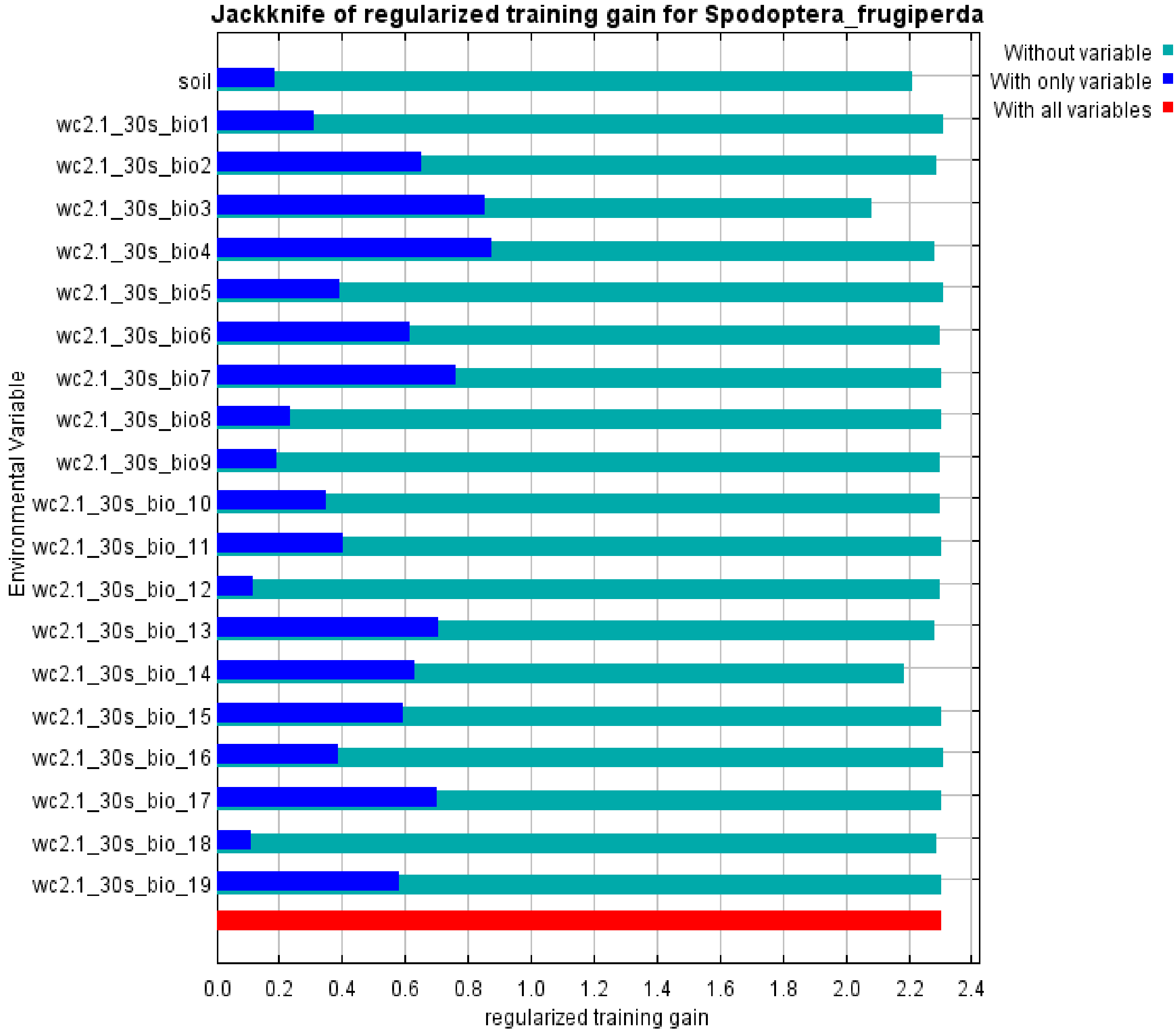

Fig. 7. Jackknife test of environmental variables in the studies area of Benin

Table 7 presents the VIF of environmental variables. A VIF value less than 5 indicates a weak correlation of the predictor compared with other predictors. A value between 5 and 10 indicates a moderate correlation, while VIF values greater than 10 indicate a high and unacceptably high correlation between the predictors of the model. The results show that none of the four input variables presents any collinearity problem (Bio2 = 8.36, Bio3 = 4.82, Bio13 = 1.67, Bio14 = 1.67). The linear correlation coefficients are as follows: minimum correlation (Bio13 ~ Bio2): 0.509504; maximum correlation (Bio14 ~ Bio2): -0.8878778.

Table 7. VIF of environmental variables on FAW in studies area in Benin

N	Variables	VIF
1	Bio2	8.36
2	Bio3	4.82
3	Bio13	1.67
4	Bio14	5.28

3.8.1 Impact of Climate Variability On the Potential Distribution of *S. frugiperda* in Benin

Current and future potential distributions, according to the different horizons, were depicted in Fig. 8, 9, and 10. The dynamics of areas high suitable to *S. frugiperda* are presented in Table 8. Habitat potentially suitable refers to areas where environmental conditions (such as temperature, humidity, availability of resources, etc.) are conducive to the survival and reproduction of *S. frugiperda*.

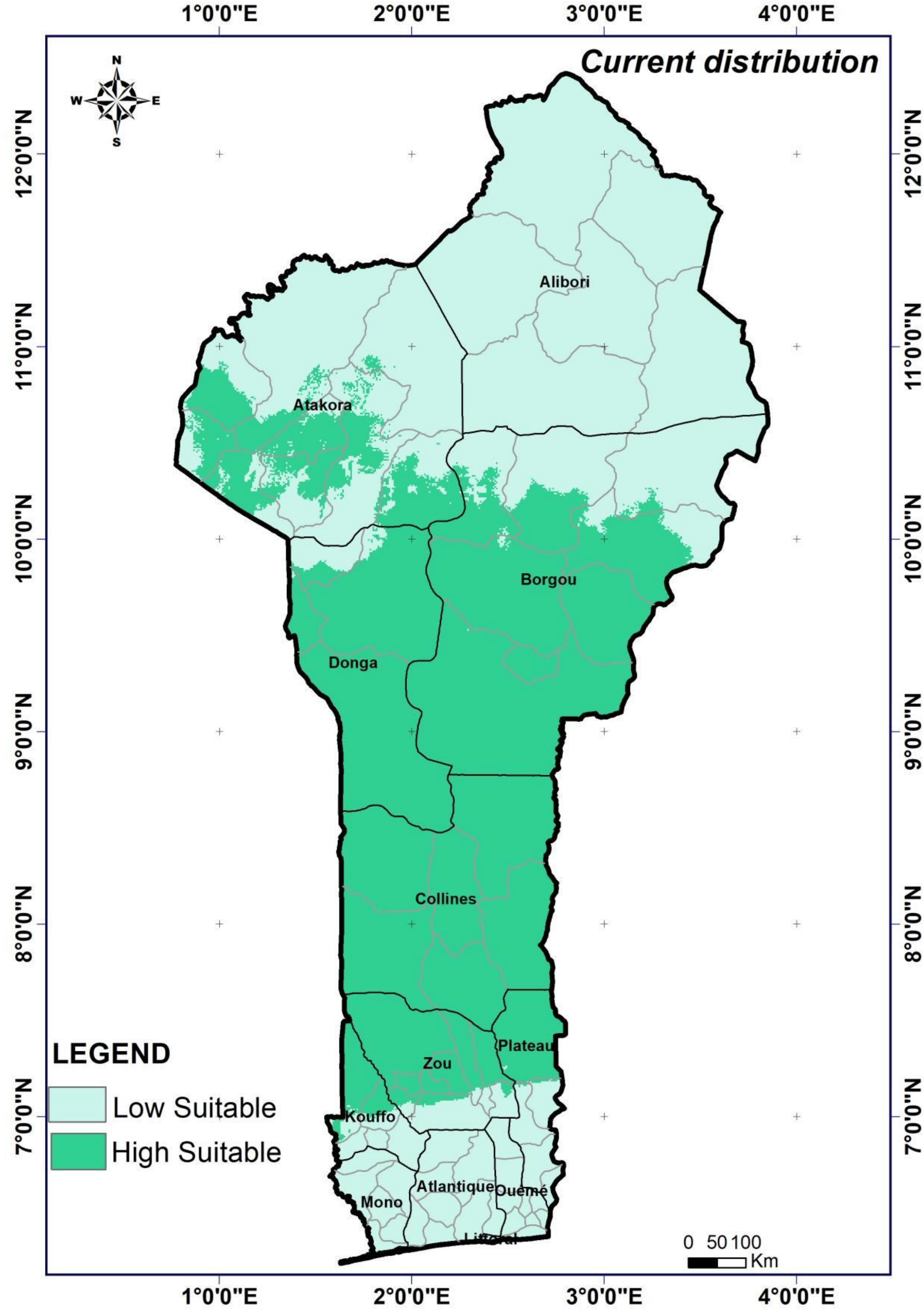

Fig 8. Current potential distribution of S. frugiperda in studie areas

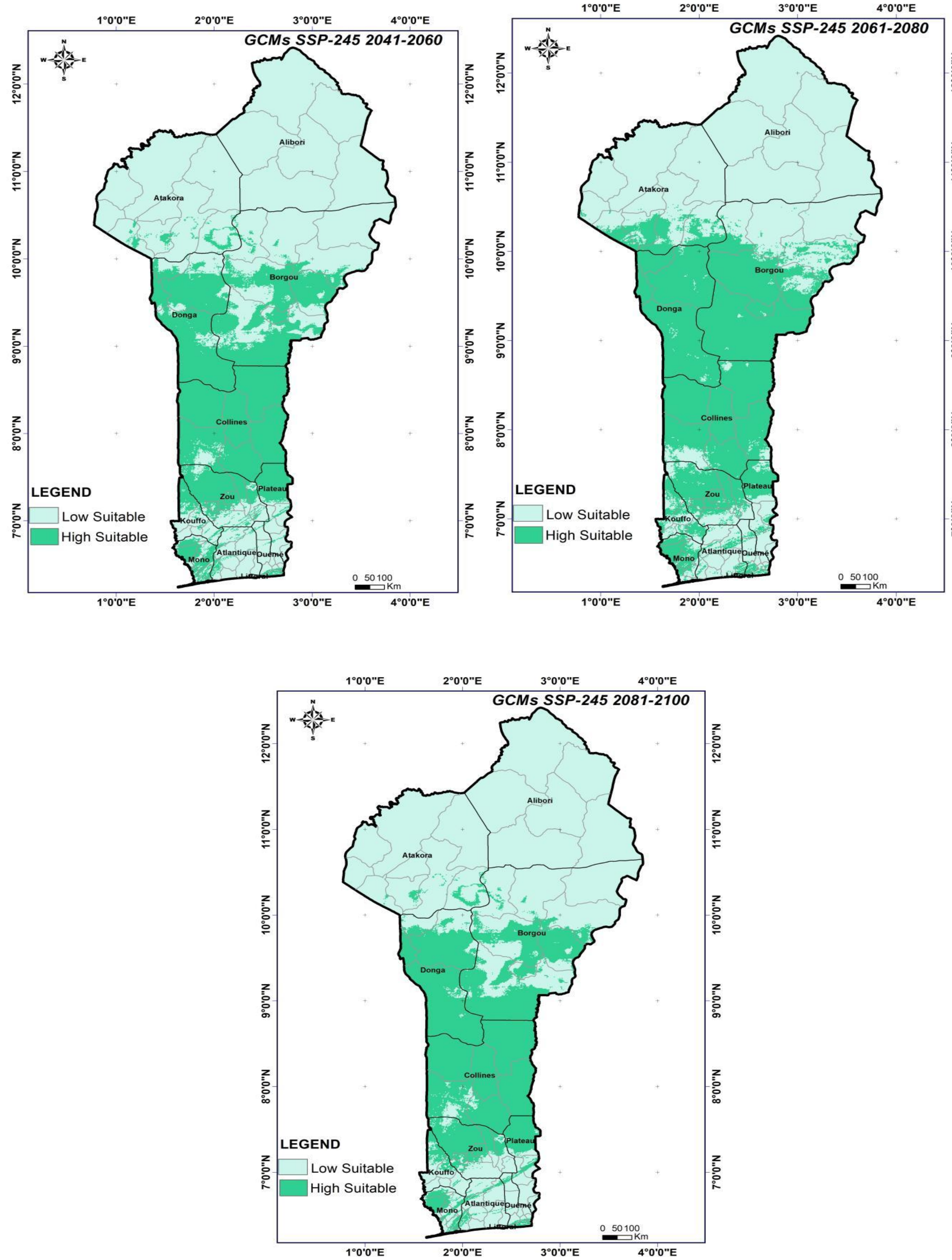

Fig 9. Map showing the future distribution of *S. frugiperda* under the SSP 245 scenario (A: Horizon 2041-2060, B: Horizon 2061-2080

C: Horizon 2081-2100) according to the General Atmospheric Circulation Models GCMs (GCMs = CanESM5 + CNRM-CM6-1 + HadGEM3-GC31-LL + MIROC6) in Benin

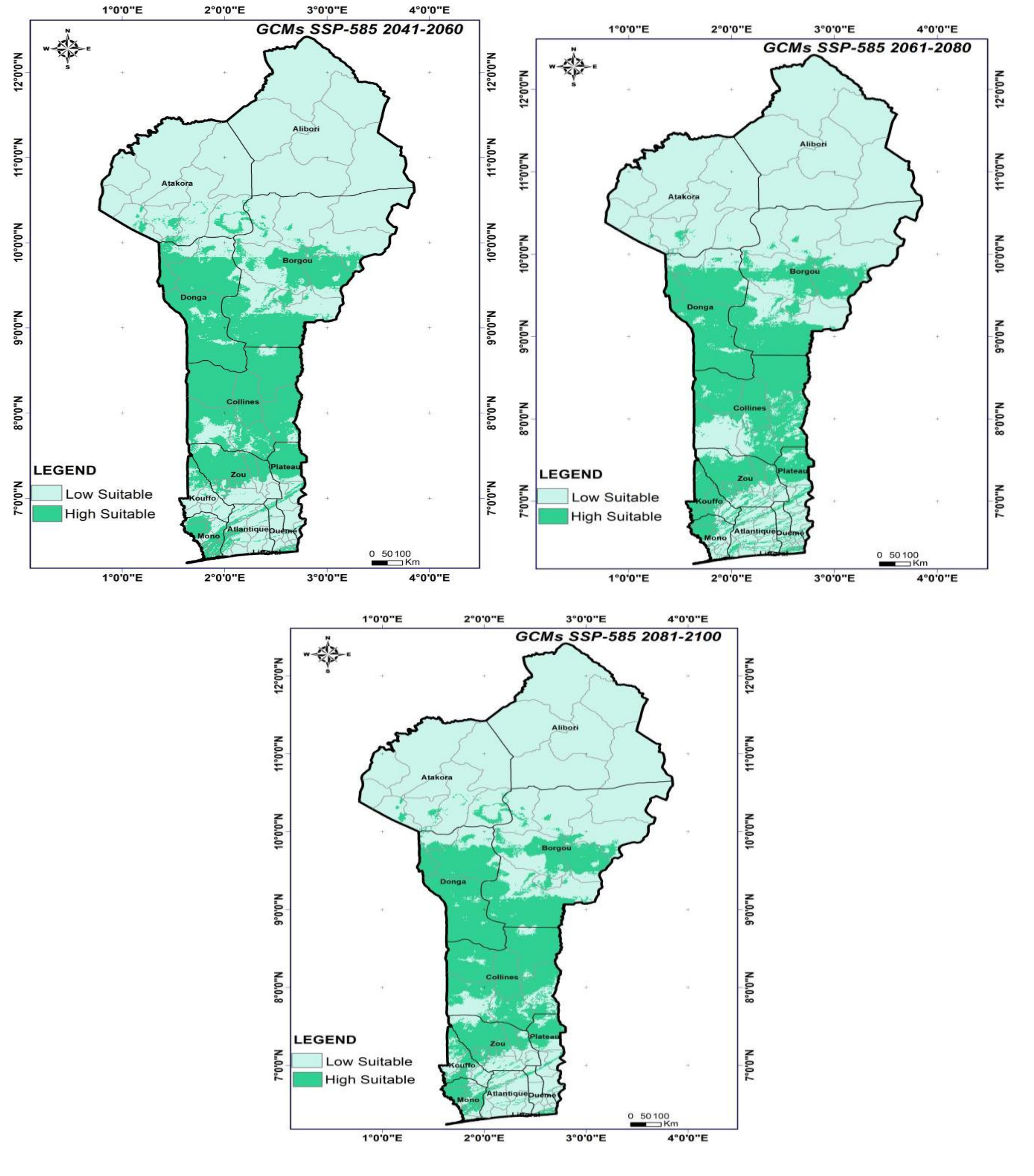

Fig. 10. Map showing the future distribution of *S. frugiperda* under the SSP 585 scenario (A: Horizon 2041-2060, B: Horizon 2061-2080

C: Horizon 2081-2100) in Benin according to the General Atmospheric Circulation Models GCMs (GCMs = CanESM5 + CNRM-CM6-1 + HadGEM3-GC31-LL + MIROC6) in Benin.

Results of modeling the current potential distribution of *S. frugiperda* revealed a distribution in high suitable habitats of 58,964.33 km² and low suitable habitats of 55,798.67 km² (**Fig. 8, Table 8**). Regarding the bioclimatic projection under the SSP 245 scenario for 2041-2060, it showed a distribution in low suitable habitats of 74,275.61 km² and high suitable habitats of 40,487.39 km² (**Fig. 9, Table 8**).

In addition, the bioclimatic projection under the SSP 245 scenario for the horizon 2061-2080 revealed a distribution of 64,638.71 km² in low suitable habitats and 50,124.29 km² in high suitable habitats (**Fig. 9, Table 8**). For the period 2081-2100, this projection showed a distribution of 75,224.98 km² in low suitable habitats and 39,538.02 km² in high suitable habitats (**Fig. 9, Table 8**).

Regarding the SSP 585 scenario, the bioclimatic projection for the horizon 2041-2060 revealed a distribution of 75,665.72 km² in low suitable habitats and 39,097.30 km² in high suitable habitats (**Fig. 10, Table 8**).

In addition, the bioclimatic projection under the SSP 585 scenario for the horizon 2061-2080 also showed a distribution of 77,354.96 km² in low suitable habitats and 37,408.04 km² in high suitable habitats (**Fig. 10, Table 8**). These scenarios projected a reduction in high suitable habitats of 37.82%, 11.32%, 41.13%, 42.72%, 47.71%, and 49.16%, followed by an extension of low suitable habitats of 20.61%, 8.78%, 21.62%, 22.07%, 22.07%, 23.41%, and 23.77%.

Table 8. Dynamics of potential distribution areas for *S. frugiperda* in Benin

Characteristics		Low Suitable Habitat		High Suitable Habitat	
		Area (Km^2)	Trend (%)	Area (Km^2)	Trend (%)
Current distribution		58964.33		55798,67	
CanESM5	**SSP_245_2041-2060**	74275.61	**+20.61**	40487.39	**-37.82**
	SSP_245_2061-2080	64638.71	**+8.78**	50124.29	**-11.32**
CNRM-CM6-1	**SSP_245_2081-2100**	75224.98	**+21.62**	39538.02	**-41.13**
HadGEM3-GC31-LL	**SSP_585_2041-2060**	75665.72	**+22.07**	39097.30	**-42.72**
	SSP_585_2081-2100	76987.12	**+23.41**	37775.88	**-47.71**
MIROC6	**SSP_585_2061-2080**	77354.96	**+23.77**	37408.04	**-49.16**

4. Discussion

Today, it is important to monitor the spread of the fall armyworm in order to contribute to maintaining global food security, and more specifically in Benin, a West African country, where this pest species has a major impact on maize production and a high capacity for dispersal. In order to regulate and/or prevent FAW spread, it is necessary to understand its potential distribution and factors limiting it under current and future conditions. It is also important to identify regions with a high invasion potential through surveys in areas of high maize production, so that strict preventive measures could be taken now and in the future. Marian *et al*. (2025) confirm the Fall armyworm (FAW), *S. frugiperda* has emerged as a significant pest in agricultural landscapes, particularly in Africa, where its impact is profound given the continent's dependency on agriculture. To manage this pest effectively, understanding the environmental and terrestrial drivers behind its spread is imperative (Marian *et al*., 2025).

Our study was carried out in five districts of Benin to assess the current abundance of armyworm in maize fields. The analysis of the relationship between plant development stages and *FAW* abundance was therefore carried out using a negative binomial regression model. To facilitate the interpretation of the results, the coefficients of the model were exponentiated to express them as incidence ratios (IRR), allowing the effect of developmental stages on FAW abundance to be quantified directly. Flowering stage shows a significant negative effect on larvae abundance, with an IRR ≈ 0.31, indicating that *FAW* abundance at maturity is reduced by about 69% compared to flowering. In contrast, the effect of sowing stage is not significant (IRR ≈ 1.30), suggesting that *FAW* abundance at sowing stage is not significantly different from that observed at flowering stage. We also note that the marginal R^2 is lower than the conditional R^2 for this model, reflecting that this significant variation in *FAW* abundance at the three (03) developmental stages considered in the study is due to both the fixed effect of host plant developmental stage and the random effect of location. A more recent field trial reported *FAW* yield losses of 5–20 % at the whorl stage (Capinera, 2017). Occasionally, they resow maize when pests have eaten the first plants, sometimes even after the optimum sowing date (Rose *et al.*, 2000) or apply chemicals weekly to avoid pest and disease outbreaks (Ibrahim *et al.*, 2023). The diversity of Lepidoptera collected with *S. frugiperda* in the five districts studied shows that the other Lepidoptera are reduced to trace levels in the maize fields. This distribution *FAW* during sowing stage can be explained by the drier, warmer climatic conditions in the north at the beginning of the maize season, which favored the emergence of the first larval stages of maize lepidopteran pests, probably those of *FAW*. This redistribution could be related to the attractiveness of flowering plants, which are particularly rich in nutrients and attract more adult lepidoptera for oviposition. The overall increase in densities at this stage was consistent with the life cycle of the pests, which multiply and often reach their peak abundance during miaze flowering stage. This general decline in *FAW* abundance, particularly in the northern areas, can be explained by: (1) the effect of control measures that may have been applied after infestations were detected at earlier stages, (2) the development of crops that are less palatable, (3) the natural cycle of pests completing their development, and (4) possibly less favorable climatic conditions at this stage. Furthermore, the FAW may benefit from drier conditions. In addition, plant density (dm) and mean annual air quality index (miaq) had a significant negative effect ($p = 0.012$ and $p = 0.033$, respectively), highlighting that denser habitats or atmospheric variations may limit FAW presence during this initial phase.

Map of habitat suitability reveals that *FAW* infestations have been reported in nearly all sub-Saharan African countries, with varying levels of incidence and severity depending on the agroecological zone and period of the year (Yan *et al.*, 2022). Countries with a suitable climate and vegetation for the survival, reproduction, and migration of *FAW*s in Africa are those that support the pest's presence. *FAW* thrives under warm, humid, and wet conditions, but it can also persist under drier conditions if alternative host plants or refuges are available (Du *et al.*, 2020). It is essential to note that the distribution and severity of *FAW* can vary within and between countries based on climate, seasonality, agroecology, crop management practices, pest control strategies and socioeconomic conditions (Harrison *et al.*, 2019). Consequently, a country's suitability for *FAW* occurrence should be evaluated based on local conditions and data, and appropriate measures should be taken to monitor and manage the FAW in order to minimize its impact on food security and livelihoods. Finally, at the maturity stage, the significant effects were more limited. Rainfall variability (bio15) maintained a significant negative effect ($p = 0.045$), suggesting that persistent climatic variability can slow down fall armyworm population dynamics at this late stage of plant development.

The MaxEnt model performance showed **Fig. 6** that this result suggests that the algorithm used for modeling was an effective predictive model capable of predicting the spatial distribution of *S. frugiperda* under current and future climate conditions. This highlights the robust capacity of the MaxEnt algorithm to accurately model the distribution of the species. Our research fills this gap by integrating these overlooked variables in the MaxEnt modelling, presenting a more detailed landscape of the factors influencing *FAW*'s spread, providing a more holistic understanding of *FAW* dynamics. Further accentuating our study's uniqueness is the comparison of four different MaxEnt models, an endeavor seldom undertaken in previous research in Benin. While several past studies, like Baudron *et al*. (2019), Durocher *et al*. (2021), and Ramasamy *et al*. (2022), have explored bioclimatic variables, and some like Huang *et al*. (2020) in Asia exclusively relied on these variables, they often overlooked the potential influence of factors such as *FAW* phenology, soil nitrogen, or soil pH. Based on the contribution of variables, the Jackknife test, and the VIF analysis, four bioclimatic variables were found to be the most significant factors associated with the predicted distribution of the species: annual precipitation (**Bio2**), temperature seasonality (**Bio3**), isotherm (**Bio13**), precipitation in the driest month (**Bio14**) and soil. Species distributions could be significantly modified by topography, which might regulate the influences of climate and land-use changes (Chardon *et al*., 2015; Oldfather & Ackerly, 2019). In other words, the suitability of climate and land-use might be reduced when suitable topographical conditions are lacking (Suz *et al*., 2015; Oldfather & Ackerly, 2019). Therefore, according to the data and models used in our study, these areas could theoretically support the species in question. However, the fact that an area is identified as "weakly suitable" in a spatio-temporal prediction does not necessarily mean that the species would not develop properly there. This situation can be explained by a number of factors, including the unavailability or lack of data collected in these areas. In conclusion, climatic variations will reduce the area of distribution of *S. frugiperda*, regardless of the horizon considered. Thus, future climatic conditions will not be conducive to the expansion of the habitat of *S. frugiperda*. The results of modeling *S. frugiperda* reveal that future climatic conditions will not favor the expansion of its habitat. Indeed, the non-expansion of the habitat of this insect pest could mean greater stability for crops in the regions concerned, which is good news for farmers. Furthermore, these results suggest that pest management strategies can be adapted to new climatic conditions. This would allow for a proactive approach rather than a reactive approach.

5. Conclusion

The fall armyworm is a major threat to maize production in Benin, influenced by several agroecological factors. Our study shows that the seasonal and spatial distribution of this pest varies according to agro-ecological zones, with higher infestations observed in some regions during the dry season and the development stage of the maize plant. The diversity of other lepidoptera also varies according to region and crop development stage, which influences fall armyworm population dynamics through the complex of natural enemies in the environment. Environmental predictors of FAW occurrence in the study area were identified using Maxent modelling. Agro-ecological approaches, such as sustainable soil fertility management and intercropping, offer low-cost management solutions that can be incorporated into integrated FAW management programmes. However, the effectiveness of these measures needs to be evaluated in different ecological and socio-economic contexts before large-scale implementation. Annual precipitation (Bio2), temperature seasonality (Bio3), isotherm (Bio13), precipitation in the coldest quarter (Bio14) and soil have a positive influence on fall armyworm distribution its presence and abundance. Additionel vegetation density (dm) had a very strong positive effect. Integrating agroecological strategies into farming practices could provide sustainable solutions to reduce the impact of this pest on maize production, while protecting the environment and human health.

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Authors contributions

Conceptualization, F.A.S.; methodology, F.A.S; K.K.G; D.C.C and E.D.; data collection and analysis, F.A.S. and K.B.C.; writing—original draft preparation, F.A.S.; writing—review and editing, E.D.; K.K.G.; C.D. and D.C.C. All authors have read and agreed to the published version of the manuscript.

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Competing interests

Sample: The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Informed consent

Obtained.

Ethics approval

The Publication Ethics Committee of the Macrothink Institute.

The journal's policies adhere to the Core Practices established by the Committee on Publication Ethics (COPE).

Provenance and peer review

Not commissioned; externally double-blind peer reviewed.

Data availability statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Data sharing statement

No additional data are available.

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