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Diversity and seasonal abundance of tephritid fruit flies in three agro-ecosystems in Benin, West Africa

D. Gnanvossou[1] (iD) | R. Hanna[1,2] | G. Goergen[1] (iD) | D. Salifu[3] | C. M. Tanga[3] |
S. A. Mohamed[3] | S. Ekesi[3] (iD)

[1]International Institute of Tropical Agriculture (IITA) Benin Station, Cotonou, Benin

[2]International Institute of Tropical Agriculture (IITA) Cameroun Station, Yaounde, Cameroun

[3]International Centre for Insect Physiology and Ecology (ICIPE), Nairobi, Kenya

Correspondence
Désiré Gnanvossou, International Institute of Tropical Agriculture (IITA) Benin Station, Cotonou, Benin.
Email: d.gnanvossou@cgiar.org

Abstract

The horticulture industry in Benin is under threat due to fruit fly infestation on important crops such as cucurbits and mango. Given the economic losses due to fruit fly infestations, population dynamics of fruit flies on these crops were monitored over 6 years (2004–2010) using three parapheromones—cuelure, methyl eugenol and terpinyl acetate. A total of 2,714,186 specimens belonging to 14 species in four genera (*Bactrocera*, *Ceratitis*, *Dacus* and *Zeugodacus*) were collected. *Bactrocera dorsalis* was the dominant species that accounted for 89%, 89.6% and 77.2% of captures in the Forest Savannah Mosaic (FSM), Southern Guinea Savannah (SGS) and Northern Guinea Savannah (NGS) agro-ecosystems, respectively. Shannon index values of species diversity differed significantly among agro-ecosystems, with highest diversity in FSM followed by SGS and NGS. Temperature, rainfall and relative humidity (RH) positively influenced the abundance of *Dacus* species and *Zeugodacus cucurbitae* across the three agro-ecosystems. Monthly mean temperatures were in a range suitable for development and reproduction of fruit flies, although minimum temperatures could be below such range, which may explain the lower abundance of fruit fly populations during this period of the year. The abundance of *B. dorsalis* was negatively correlated with maximum temperature and positively correlated with RH and rainfall. *Ceratitis* species assemblages were significantly affected by minimum temperatures, rainfall and agro-ecosystem. Populations of *B. dorsalis* and *Ceratitis cosyra* dropped drastically in August, while those of *Z. cucurbitae* and *Dacus punctatifrons* increased sharply from August. Results of this study provide a platform for developing a comprehensive and sustainable management strategy for *B. dorsalis* and other fruit flies in the three agro-ecosystems to protect the horticulture industry in Benin.

KEYWORDS
Bactrocera dorsalis, *Ceratitis* spp., *Dacus* spp., parapheromones, *Zeugodacus* spp.

1 | INTRODUCTION

Tephritid fruit flies are among the most economically important group of fruit flies attacking horticultural crops (Billah et al., 2008; Goergen, Vayssières, Gnanvossou, & Tindo, 2011; Mau, Martin-Kessing, & Diez, 2007; Vayssières, Kori, Coulibaly, Temple, & Boueyi, 2008; Wharton, 1989). There are approximately 4,000 known/described species of fruit flies in tropical, subtropical and temperate regions of the world, out of which 200 species are the most damaging on fruit and vegetable crops (Bharathi, Sathiyanandam, & David, 2004; Clarke et al., 2005; Ekesi, De Meyer, Mohamed, Virgilio, & Borgemeister, 2016; Gnanvossou et al., 2008; Goergen et al., 2011; Roessler, 1989; White & Elson-Harris, 1992). Many of the species that occur in Africa are indigenous to the continent while others are of Asian origin (Billah et al., 2008; Ekesi et al., 2016; Goergen et al., 2011; Lux, Copeland, White, Manrakhan, & Billah, 2003; Mwatawala, De Meyer, White, Maerere, & Makundi, 2007; Papadopoulos, 2014; Vayssières et al., 2008; White, 2006).

The extent of damage caused by tephritid fruit flies ranges between 30% and 100% on cucurbit crops (Dhillon, Singh, Naresh, & Sharma, 2005; Gnanvossou et al., 2008) and 40%–75% on mango and other fruit crops (Ekesi, Nderitu, & Rwomushana, 2006; Ekesi et al., 2016; Goergen et al., 2011; Hanna, Goergen, Gnanvossou, Tindo, & Vayssières, 2005; Hanna, Goergen, Vayssières, & Tindo, 2004; Vayssières, Korie, & Ayegnon, 2009; Vayssières, Sinzogan, Korie, Ouagoussounon, & Odjo, 2009), which depends largely on the environmental conditions, cultivar, host species and the season. Environmental factors such as temperature, rainfall and relative humidity are key biotic parameters regulating insect populations, such as tephritid fruit flies (Brévault & Quilici, 2000; Duyck, David, & Quilici, 2004; Duyck & Quilici, 2002; Fletcher, 1989; Grout & Stoltz, 2007; Rwomushana, Ekesi, Ogol, & Gordon, 2008; Vargas, Walsh, Kanehisa, Stark, & Nishida, 2000; Vayssières et al., 2008). Changes in climate have been reported to influence the geographical distribution of species, their density and seasonality (Aidoo, Kyerematen, Akotsen-Mensah, & Kwame Afreh-Nuamah, 2014; Hodkinson, 2005; Mwatawala, De Meyer, Makundi, & Maerere, 2006a). The availability and suitability of host plants have been found to exert a strong impact on fruit fly population dynamics (Mwatawala, De Meyer, Makundi, & Maerere, 2006b; Rwomushana et al., 2008; Vayssières et al., 2008) and occurrence patterns.

In Benin, the horticultural sector is permanently under threat of fruits flies, but there is limited knowledge on their population dynamics to guide intervention. Wild host plants play an important role in maintaining fruit fly populations, especially during periods when cultivated fruit and vegetable crops are scarce and out of season. To reduce their threat to fruit and vegetable production, much emphasis has been placed on early detection, monitoring and suppression on cultivated crops (Hall et al., 2005; Navarro-Llopis, Alfaro, Domínguez, Sanchis, & Primo, 2008; Thomas, Holler, Heath, Salinas, & Moses, 2001).

The use of commercially available parapheromones, which can either be in liquid form and/or polymeric plugs, is one of the fast and convenient methods for detecting fruit flies and monitoring their populations (Manrakhan, 2006). Fly captures by parapheromone baited traps help in identifying, delimiting and keeping track of changes in population levels of fruit fly pests (Manrakhan, 2006; Simpson, 1993). A diverse group of commonly used male fruit fly attractants includes methyl eugenol (ME), cuelure, alpha-ionol and cade oil, spiroketal, trimedlure, terpinyl acetate (TA), ceratitislure and vertlure (Manrakhan, 2006). This study focused on the diversity, abundance and seasonal patterns of both indigenous and invasive fruit fly species in addition to identifying the factors influencing their abundance and distribution across three agro-ecosystems in Benin. The study sought to provide necessary data for practical management strategies of fruit fly infestations.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted in three agro-ecosystems in the Republic of Benin, West Africa, namely Forest Savannah Mosaic (FSM), Southern Guinea Savannah (SGS) and Northern Guinea Savannah (SGS) (Figure 1). The FSM is a transitory ecotone between the tropical rain forest, interspersed with open drier savannahs to woodlands for both tree and herb layer from the north and south of the forest belt (Bassett, Bi, & Ouattara, 2003), thus a convergence zone for savannah and forest species. Southern Guinea Savannah is a band of interlaced forest, savannah and grassland running east to west and dividing the tropical moist forest near the coast (White, 1983). The Northern Guinea Savannah is dominated by moist woodlands and savannahs, separating the northern and the southern zones where most of the vegetation has been replaced by secondary grasslands or savannahs due to human impact (Bohlinger, 1998). Benin has a tropical climate (hot and humid) with two rainy seasons in the FSM: long rainy season (March–July) and a short rainy season with less intense rains (late September to November). The SGS and the NGS have unimodal rainy season that runs from April to October. Average temperatures increase when moving from south towards the north. Harmattan, a dry, dusty wind originating from the Sahara desert, blows into Benin during the months of December–March (Akoègninou, van der Burg, & van der Maesen, 2006). During this period, average relative humidity and temperature decrease sharply. The period of harmattan in NGS is generally longer than in the SGS and FSM. The mean monthly temperature and relative humidity range between 24.2 and 32.0°C and 23.0%–88.5%, respectively, across regions.

2.2 | Fruit fly population monitoring

Male fruit fly populations were monitored in cucurbit farms and mango orchards (Figure 1) using three trapping methods as described below. Data on temperature (°C), relative humidity (%) and rainfall (mm) were provided by the nearest Agency for Aerial Navigation Safety in Africa and Madagascar (ASECNA) stations.
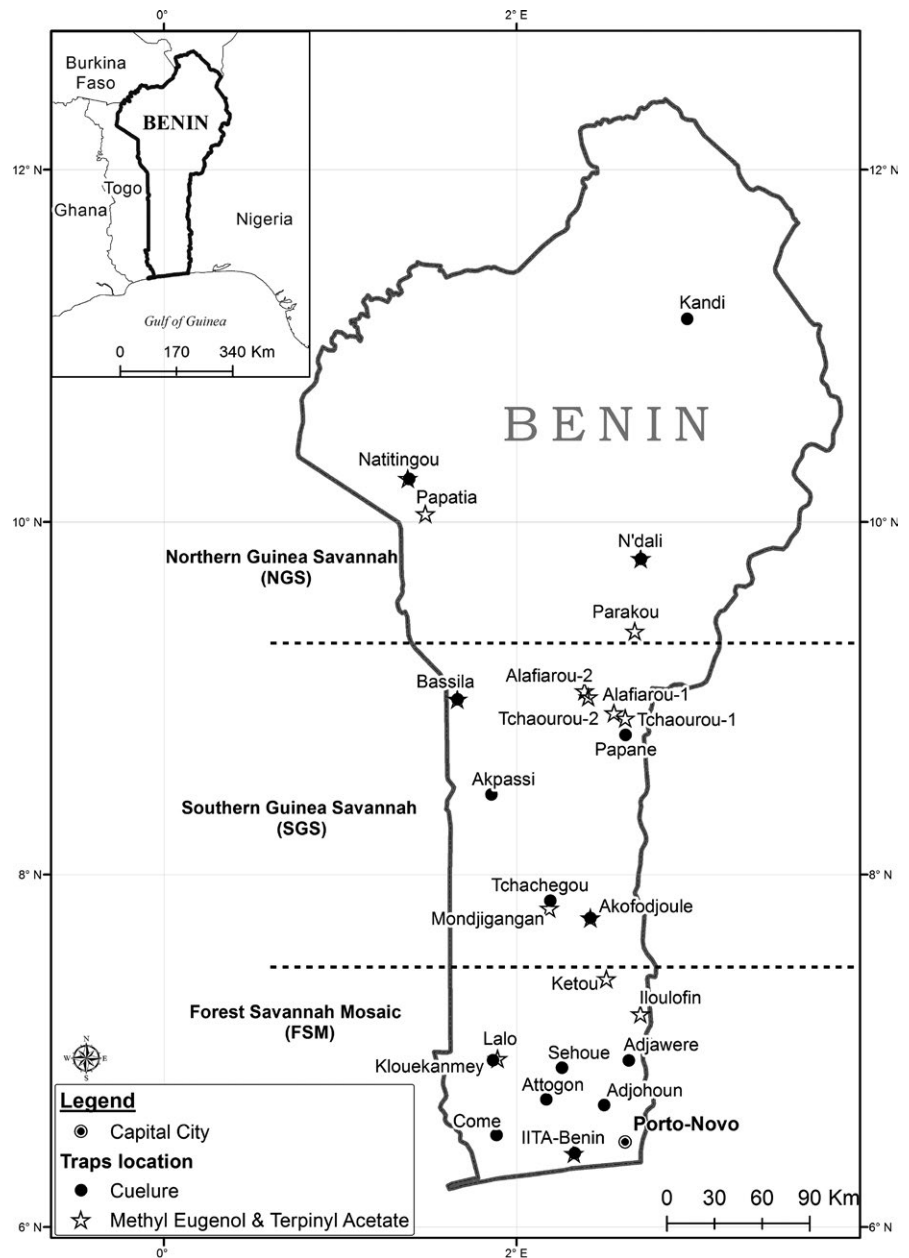
FIGURE 1 Study sites and agro-ecosystems of the Republic of Benin, West Africa—full black circle represents cuelure trap locations; hollow stars are methyl eugenol and terpinyl acetate trap locations. Dash lines are boundaries between agro-ecosystems

2.3 | Parapheromones and trapping system

Three commercially available parapheromones (liquid form) were used for monitoring, namely cuelure (CL) (Better World MFG Inc., USA), ME (Jian Hairui Natural Plant Co., Ltd., USA) and TA (Dalian Sinobio Chemistry Co., Ltd., USA). At each study site, 2–3 traps per parapheromone were installed. Cuelure captures fruit flies of *Dacus* and *Zeugodacus* genera, while ME and TA capture fruit fly species that belong to *Bactrocera* and *Ceratitis* genus, respectively. Cotton wicks baited with 2 ml of either CL, ME or TA (attractant) and a strip of the killing agent DDVP (Hercon® Environmental Corporation, P O Box 435, Emigsville, PA, 17318, USA, Trade Names: DDVP, Vapona, etc.) = Dimethyl 2,2-dichlorovinyl phosphate) were suspended inside 1.5 L perforated transparent plastic bucket trap, manufactured in Nigeria. The traps were distributed across the three

agro-ecosystems (Table 1). Methyl eugenol and TA traps were placed in mango orchards. Traps were placed on mango tree branches at a height of 1.5–2 m above the ground. In cucurbit farms, traps were held on wooden stands and were shielded from direct exposure to sunlight. Traps were 30–40 m apart from each other. Sticky glue (The Tanglefoot Company, Grand Rapids, Michigan 49504, USA) was applied on branches to protect caught specimens from ants.

2.4 | Data collection

The catches in the traps were counted and recorded at 2-week intervals in the morning hours in all the study sites. The attractants and insecticide were replaced every month. Fruit flies caught in the traps were preserved in 70% alcohol in 70-ml or 600-ml plastic containers prior to sorting and identification to the species level in the laboratory

TABLE 1 Description of fruit fly male trapping study sites, in three agro-ecosystems in Benin: Forest Savannah Mosaic (FSM), Southern Guinea Savannah (SGS) and Northern Guinea Savannah (NGS) for the study period March 2004–August 2010

Agro-ecosystem	Lure	Orchard/garden type	No. of sites with traps	Duration of deployment of traps	
				Start	End
FSM	Cuelure	Open area—wild and cultivated cucurbits	7	March 2004	December 2007
	Methyl eugenol	Mango	3	April 2007	August 2010
	Terpinyl acetate	Mango	3	February 2008	August 2010
SGS	Cuelure	Open area—wild and cultivated cucurbits	5	December 2004	August 2007
	Methyl eugenol	Mango	6	May 2005	August 2010
	Terpinyl acetate	Mango	5	February 2008	August 2010
NGS	Cuelure	Open area—wild and cultivated cucurbits	3	May 2005	August 2007
	Methyl eugenol	Mango	4	May 2005	August 2010
	Terpinyl acetate	Mango	4	February 2008	August 2010

with the aid of a binocular stereomicroscope and using keys by White and Elson-Harris (1992) and Billah, Masell, De Myer, and Goergen (2006). Some specimens were sent to the Royal Museum for Central Africa for further identification and confirmation.

2.5 | Statistical analyses

Species abundance data were ranked in ascending order using the *Biodiversity R* package (Kindt & Coe, 2005). Species richness was estimated using nonparametric extrapolation estimates; Chao (Chao, 1987; Chiu, Wang, Walther, & Chao, 2014), first-order jackknife estimates (Smith & van Belle, 1984) and Bootstrap estimates (Smith & van Belle, 1984) alongside the total number of species present, implemented using *vegan* package (Oksanen et al., 2017). Diversity of species was estimated using the Shannon's index and Inverse Simpson's index. These diversity indices account for both abundance and evenness of the species present. Evenness refers to how close is in numbers each species in an environment. Analysis of variance was used to analyse the Shannon's and Inverse Simpson's indices of the three agro-ecosystems, and means were separated using Tukey's HSD test ($\alpha = 0.05$). Canonical correspondence analysis (CCA), a multivariate ordination method, was used to examine the amount of variation in fruit fly species abundance data accounted for by the environmental variables, namely minimum temperature (TempMini), maximum temperature (TempMaxi), minimum relative humidity (RHMini), maximum relative humidity (RHMaxi) and agro-ecosystem (Muylaert, Sabbe, & Vyverman, 2000; Pires-Vanin, 2001). Mean temperature and mean RH were strongly correlated with minimum and maximum temperature and minimum and maximum RH, respectively, and hence, mean RH and mean temperature were not included as explanatory terms in the CCA. The species abundance matrix was log-transformed before CCA to reduce variability and the effect of outliers. The CCA was done for each of the lure species assemblages. The significance of the environmental variables was tested by means of Monte Carlo

permutation tests (999 unrestricted permutations), and Type III tests for significance of terms were obtained using *anova.cca* function of *vegan* package. Variance inflation factor (VIF) was calculated for each of the environmental variables in the model. The general rule is that VIF should not exceed 10, values >10 may indicate a collinearity problem (Robinson & Schumacker, 2009), and hence, such variables should not be included in the CCA model. The CCA was implemented using *vegan* package (Oksanen et al., 2017) of R. Monthly catches used for the analyses were generated by averaging two biweekly catches per trap over total number of traps by region for specific attractant. All analyses were performed using R version 3.3.3 (R Core Team 2017).

3 | RESULTS

3.1 | Fruit fly species abundance across agro-ecosystems

In total, 2,714,186 fruit fly specimens were collected during the entire study period across the three agro-ecosystems. Specimens belonged to four genera: *Dacus*, *Zeugodacus*, *Bactrocera* and *Ceratitis*. Of the total specimens collected, 24% were collected from FSM, 44% from SGS and 32% from NGS. *Bactrocera dorsalis* (Hendel) was the most dominant across the three agro-ecosystems and accounted for 89% of the total specimens collected in FSM, 89.6% in SGS and 77.2% in NGS. *Ceratitis cosyra* (Walker) ranked second in SGS (7.6%) and NGS (21.1%), while *Dacus punctatifrons* ranked second (7.4%) in FSM (Table 2).

3.2 | Fruit fly species richness and diversity

All fruit flies collected during this study belonged to the four genera—*Dacus*, *Zeugodacus*, *Bactrocera* and *Ceratitis*. Fourteen species were recorded across the three agro-ecosystems: *B. dorsalis*, *C. bremii* (Guérin-Méneville), *C. capitata* (Wiedemann), *C. cosyra*,

TABLE 2 Fruit fly species abundance recorded in all agro-ecosystems for all years of study

Forest Savannah Mosaic		Southern Guinea Savannah		Northern Guinea Savannah	
Species	Abundance	Species	Abundance	Species	Abundance
B. dorsalis	**569,071**	**B. dorsalis**	**1,072,915**	**B. dorsalis**	**676,367**
D. punctatifrons	**47,074**	**C. cosyra**	**91,127**	**C. cosyra**	**184,536**
Z. cucurbitae	**13,929**	**D. humeralis**	**10,952**	**C. quinaria**	**8,451**
D. bivittatus	6,024	C. bremii	5,613	C. silvestrii	5,218
C. cosyra	1,852	C. quinaria	5,391	C. fasciventris	1,319
D. armatus	556	Z. cucurbitae	4,408	C. bremii	351
D. humeralis	453	C. silvestrii	3,315	Z. cucurbitae	157
C. bremii	221	D. bivittatus	2,602	D. bivittatus	126
D. mediovittatus	129	D. punctatifrons	599	D. humeralis	40
D. vertebratus	125	C. fasciventris	400	D. punctatifrons	28
C. capitata	66	D. diastatus	280	D. diastatus	8
D. diastatus	38	C. anonae	122	D. congoensis	2
C. anonae	30	D. armatus	70	C. capitata	1
D. langi	30	D. vertebratus	32	D. xanthaspis	1
C. fasciventris	25	D. congoensis	17	D. langi	1
D. pleuralis	19	D. mediovittatus	16		
D. taurus	18	C. capitata	4		
C. silvestrii	12	D. langi	2		
C. neostictica	11	D. pleuralis	2		
D. congoensis	11	C. ditissima	1		
D. xanthaspis	9	C. neostictica	1		
C. quinaria	6				
C. ditissima	2				
Total	639,711		1,197,869		876,606

B., Bactrocera; C., Ceratitis; Z., Zeugodacus; D., Dacus.
In bold are the first three dominant species in each agro-ecosystem.

C. fasciventris (Bezzi), *C. quinaria* (Bezzi), *C. silvestrii* (Bezzi), *D. bivittatus* (Bigot), *D. congoensis* (White), *D. diastatus* (Munro), *D. humeralis* (Bezzi), *D. langi* (Curran), *D. punctatifrons*, *Z. cucurbitae* (Coquillett). Furthermore, *D. armatus* (Fabricius), *D. congoensis* (White), *D. mediovittatus* (White), *D. vertebratus* (Bezzi), *D. pleuralis* (Collart), *C. anonae* (Graham), *C. neostictica* (De Meyer) and *C. ditissima* (Munro) occurred in both FSM and SGS. *Dacus xanthaspis* (Munro) was recorded in FSM and the NGS, while *D. taurus* (Munro) was recorded in FSM only (Table 2). The FSM and NGS had the highest and the lowest number of species, respectively, according to extrapolated Chao estimates for species richness, first-order Jackknife estimates and Bootstrap estimates for species richness (Table 3). Shannon diversity index ($F_{2,2224}$ = 92.15, p < .001) and Inverse Simpson's diversity index ($F_{2,2224}$ = 73.68, p < .001) were significantly higher in FSM agro-ecosystem than in SGS and NGS agro-ecosystems, respectively (Table 4).

TABLE 3 Fruit fly species richness; total and extrapolated for the three agro-ecosystems over the years the species were sampled

Agro-ecosystem	Total richness	Extrapolated estimates		
		Chao	Jackknife (1st order)	Bootstrap
Forest Savannah Mosaic	23	23.5 (1.3)	24.0 (1.0)	23.6 (0.7)
Northern Guinea Savannah	15	19.5 (7.2)	18.0 (1.7)	16.2 (0.9)
Southern Guinea Savannah	21	22.0 (1.9)	23.0 (2.0)	22.0 (1.1)

Figures in parenthesis are standard error of estimate.

TABLE 4 Fruit fly species mean diversity indices estimated for the three agro-ecosystems over the years the species were sampled

Agro-ecosystem	Shannon	Inverse Simpson
Forest Savannah Mosaic	0.39 ± 0.02a	1.54 ± 0.04a
Northern Guinea Savannah	0.14 ± 0.01b	1.17 ± 0.02b
Southern Guinea Savannah	0.17 ± 0.01b	1.18 ± 0.02b

Values (mean ± SE) followed by the same letter in the same column are not significantly different, Tukey HSD test, α = 0.05.

3.3 | Seasonal fluctuation and abundance of dominant fruit flies

For the sake of brevity and clarity, we determined seasonal fluctuation of the first three dominant species in each agro-ecosystem (Table 2). *Bactrocera dorsalis* dominated the FSM throughout the year and peaked twice in May and August (first and second rainy seasons), while *Z. cucurbitae* and *D. punctatifrons* peaked in October and November (beginning of dry season), respectively (Figure 2). The abundance of *C. cosyra* in SGS increased from February to June and peaked in May and June (start of rainy season), respectively, in SGS (Figure 3). The abundance of *B. dorsalis* in NGS peaked in July (rainy season), while the abundance of *C. cosyra* peaked in May (start of rainy season). Population of *C. quinaria* in NGS peaked in March (end of the dry season) (Figure 4).

3.4 | Effect of environmental factors on species assemblages

The CCA marginal test results of the environmental variables on species assemblages for CL, ME and TA are presented in Table 6. There was significant variation in the abundance of *Dacus* species and *Z. cucurbitae* (in CL traps) across the three agro-ecosystems.

Temperature and RH also significantly affected the abundance of the species attracted to CL (Table 6). Temperature and RH significantly affected the abundance of *B. dorsalis* and *C. bremii*, across the three agro-ecosystems (Table 6). *Bactrocera dorsalis*, which was the dominant across the three agro-ecosystems, on its own, was negatively correlated with temperature but positively correlated with RH and rainfall (Table 5). Abundance of species in the genus *Ceratitis*, in TA traps, was significantly affected by temperature, rainfall and agro-ecosystem (Table 6).

The effect of variation in environmental factors on species assemblage abundance was further illustrated in the ordination plots (Figures 5 and 6).

The first two axes of Figure 5 accounted for about 85% of the total variance in species abundance, with the first axis explaining 67%. Abundance of *D. punctatifrons* was positively affected by maximum RH, minimum RH and inversely affected by minimum and maximum temperatures. Abundance of *Z. cucurbitae* was negatively associated with minimum temperature but positively associated with maximum relative humidity. Abundance of *D. humeralis* was positively associated with minimum temperature and negatively associated with maximum temperature (Figure 5).

The first two axes of Figure 6 explained about 88% of the total variance in species abundance, with the first axis explaining 68%. Abundance of *C. cosyra* was negatively affected by RH and positively affected by temperatures (Table 5). The response of *C. quinaria* to weather variables was similar to that of *C. cosyra* as the abundance of these two species were significantly correlated (Table 5).

4 | DISCUSSION

The results of our study indicate that the SGS had the highest mean record of flies/trap/week, while FSM had the lowest. In the SGS, more than a million *B. dorsalis* were caught. This is not surprising because most
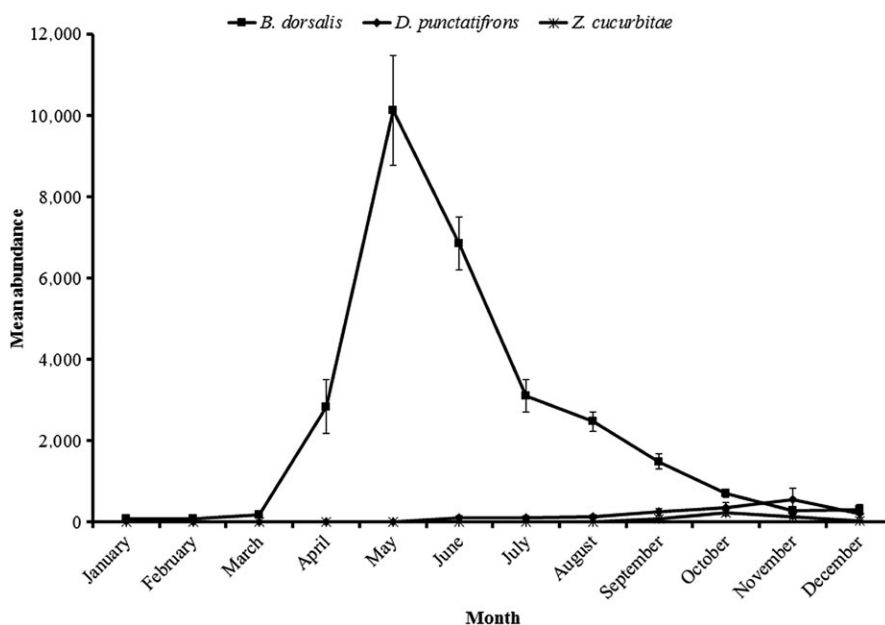
FIGURE 2 Seasonal fluctuation (mean abundance ± *SE*) of dominant species in Forest Savannah Mosaic, during the trapping period from March 2004 to August 2010—with two rainy seasons from March to late July and September to November and two dry seasons from December to February and August
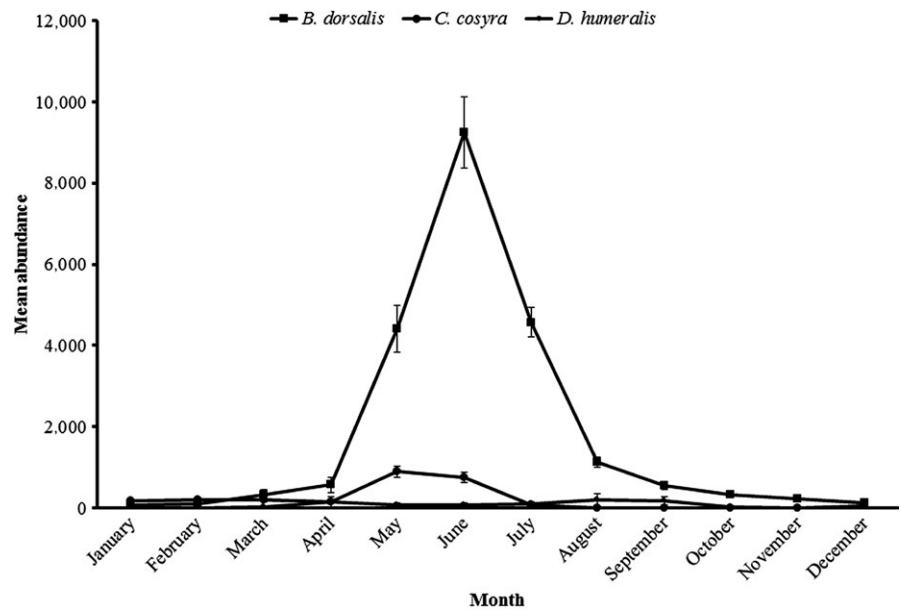
FIGURE 3 Seasonal fluctuation (mean abundance ± *SE*) of dominant species in Southern Guinea Savannah, during the trapping period from December 2004 to August 2010. May–October corresponds to the mango fruiting period and November–April to the dry season
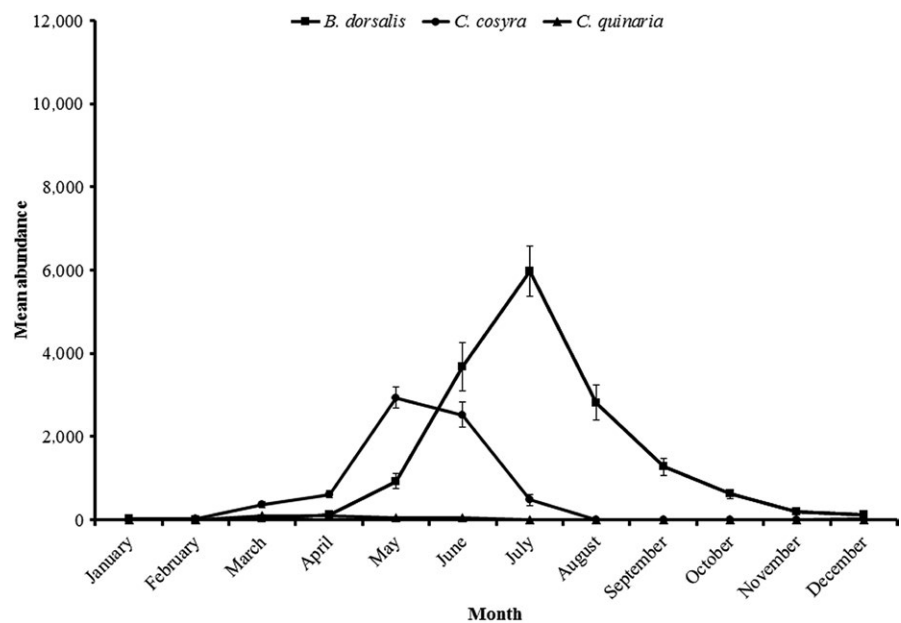

FIGURE 4 Seasonal fluctuation (mean abundance ± *SE*) of dominant species in Northern Guinea Savannah, during the trapping period from May 2005 to August 2010. May–October corresponds to the mango fruiting period and November–April to the dry season

TABLE 5 Spearman's correlation coefficient between weather variables and fruit fly species that were dominant in the three agro-ecosystems

Weather variables	Fruit fly species					
	B. dorsalis	C. cosyra	D. punctatifrons	Z. cucurbitae	C. quinaria	D. humeralis
TempMaxi	−0.662***	0.181***	−0.274***	−0.003 ns	0.244***	−0.085 ns
TempMini	−0.045 ns	0.149***	−0.185***	−0.236***	0.294***	0.020 ns
TempMean	−0.548***	0.185***	−0.301***	−0.130**	0.303***	−0.042 ns
RHMaxi	0.593***	−0.213***	0.450***	0.306***	−0.214***	−0.060 ns
RHMini	0.640***	−0.159***	0.213***	−0.091 ns	−0.190***	0.029 ns
RHMean	0.635***	−0.173***	0.327***	−0.001 ns	−0.182***	−0.018 ns
Rainfall	0.549***	0.048 ns	0.043 ns	−0.061 ns	0.051 ns	−0.008 ns

Significant codes for correlation: **$p \leq .01$ and ***$p \leq .001$; ns = correlation not significant, $p > .05$.

Lure/species assemblage	Environmental variable	F_{pseudo}	p-Value
Cuelure (species: *Dacus, Z. cucurbitae*)	**TempMaxi**	**2.68**	**.031**
	TempMini	**9.37**	**.001**
	RHMaxi	**2.73**	**.034**
	RHMini	1.24	.306
	Rainfall	2.02	.077
	Agro-ecosystem	**25.45**	**.001**
Methyl eugenol (species: *B. dorsalis, C. bremii*)	**TempMaxi**	**19.01**	**.001**
	TempMini	0.10	.797
	RHMaxi	2.32	.209
	RHMini	**20.90**	**.001**
	Rainfall	0.57	.532
	Agro-ecosystem	**81.11**	**.001**
Terpinyl acetate (species: *Ceratitis*)	TempMaxi	2.43	.067
	TempMini	**17.79**	**.001**
	RHMaxi	1.77	.190
	RHMini	0.69	.643
	Rainfall	**6.56**	**.001**
	Agro-ecosystem	**42.10**	**.001**

TABLE 6 Canonical correspondence analysis results evaluating the effect of weather variables on species assemblages abundance for male traps; cuelure, methyl eugenol and terpinyl acetate

The environmental variables in bold significantly affected the abundance of species assemplages.

Bactrocera species, including *B. dorsalis* are known predominantly as lowland resident (Ekesi et al., 2006; Vargas, Nishida, & Beardsley, 1983), enabling it to successfully displace other native fruit fly species. The presence of host fruits clearly influenced the abundance of *B. dorsalis* in SGS. Higher numbers of *B. dorsalis* were previously linked to availability of mango (Mwatawala et al., 2006a; Vayssières, Goergen, Lokossou, Dossa, & Akponon, 2005), which is the most suitable and preferred host plant of the highly competitive invasive species (Ambele, Billah, Afreh-Nuamah, & Obeng-Ofori, 2012; Goergen et al., 2011; Rattanapun, Amornsak, & Clarke, 2009; Rwomushana et al., 2008; Duyck, David, Pavoine, & Quilici, 2008; Wigunda, Weerawan, & Clarke, 2009). The current study on the diversity and seasonality of fruit flies captured in cuelure traps in cucurbit farms across the three agro-ecosystems of Benin was the first extensive fruit fly research study undertaken in Benin in terms of time and geographical coverage. Traps were baited with attractants that targeted specific fruit fly groups—cuelure, mostly trapped fruit fly species that belong to *Dacus* and *Zeugodacus* genera, while ME and TA in mango orchards trapped fruit fly species that belong to *Bactrocera* and *Ceratitis* genus, respectively. Methyl eugenol was the most potent attractant acting particularly on *B. dorsalis*.

A total of 12 *Dacus* species were captured in the FSM, 10 species in the SGS and 7 species in the NGS. *Zeugodacus cucurbitae* was the only exotic species recorded in CL and dominated cucurbit infesting tephritid species in the three agro-ecosystems, and accounted for 41.8% of catches in FSM, 32.9% in SGS and 25.4% in NGS. The dominance of *Z. cucurbitae* over indigenous *Dacus* species was reported in other cucurbit growing regions in Africa (Mwatawala, Maerere, Makundi, & De Meyer, 2010). Similar results were reported in other countries where *Z. cucurbitae* displaced *D. vertebratus*, *Dacus ciliatus* (Loew) on

watermelon, cucumber and zucchini respectively (Gnanvossou et al., 2008). Studies by Mwatawala et al. (2006a) and Gnanvossou et al. (2008) showed that *Dacus* and *Zeugodacus* mainly infested fruit species from the Cucurbitaceae, Passifloraceae and Asclepiadaceae families. *Dacus* species (except *D. humeralis*) and *Z. cucurbitae* were more active and peaked from October to January (warmer period of the year) in the three agro-ecosystems. In contrast, *D. humeralis* peaked from May to August, which coincided with the rainy season when cucurbit crop production was high (see also Laskar & Chatterjee, 2010).

Bactrocera dorsalis accounted for more than 77% of all the fruit fly species collected across all the agro-ecosystems. Previous studies showed that the highly aggressive *B. dorsalis* competitively displaced and dominated *C. cosyra* in Kenya, East Africa (Ekesi, Billah, Nderitu, Lux, & Rwomushana, 2009), and in Benin, West Africa (Vayssières et al., 2005; Goergen et al., 2011). During our investigations, the levels of population peaks of *B. dorsalis* were variable across years of sampling, with relatively higher abundance in 2007 compared with 2008 and 2010 in SGS and NGS. In the SGS and NGS agro-ecosystems, the abundance of fruit flies was lower in 2008 and 2010 possibly because of the implementation of fruit fly management programs with the use of GF-120 (Vayssières, Sinzogan, et al., 2009), male annihilation (Hanna, Gnanvossou, & Grout, 2008), application of various food baits (Vayssières, Sinzogan, et al., 2009; R. Hanna, D. Gnanvossou, S. Ekesi & A.H. Bokonon-Ganta, unpublished data) and the release of the parasitoid, *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae) (Gnanvossou, Hanna, Bokonon-Ganta, Ekesi, & Mohamed, 2016). In addition to being related to season, fluctuations of the populations of *B. dorsalis* and *C. cosyra* were also related to relative availability and suitability of host species in each of the study sites, which is in agreement with
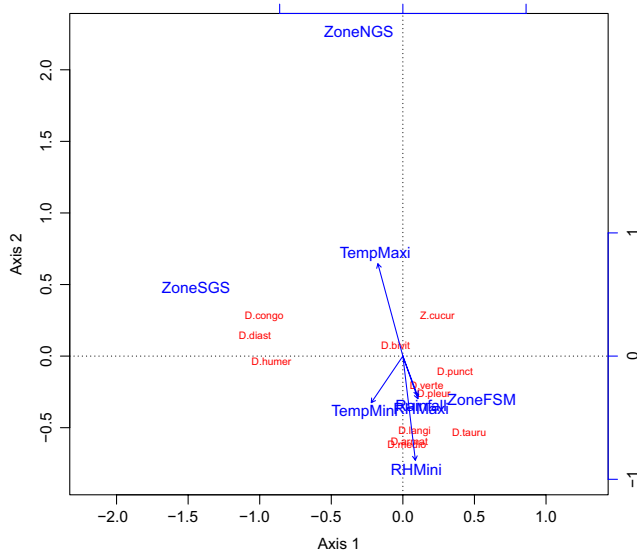
FIGURE 5 Ordination plot illustrating the variation in abundance of fruit fly taxa captured in cuelure traps as influenced by weather variables indicated by arrows. The qualitative explanatory variable, zone (Agro-ecological system), is indicated as a centroid. Zone NGS, Northern Guinea Savannah; Zone SGS, Southern Guinea Savannah; Zone FSM, Forest Savannah Mosaic

previous reports by De Meyer et al. (2002), Raghu, Drew, and Clarke (2004) and Goergen et al. (2011).

In this study, *B. dorsalis* was exclusively captured in ME traps and was the dominant species in all the three agro-ecosystems representing over 75% of the total number of flies captured. This species was particularly abundant in the FSM zone, with its bimodal rainfall, has a large diversity of host plants (Goergen et al., 2011) that were available nearly year around, compared with SGS and NGS where host plant diversity was lower than FSM and fruit hosts were available for a shorter duration.

Bactrocera dorsalis first colonized the FSM and the SGS in 2004 (Hanna et al., 2005; Vayssières et al., 2005) and became the most abundant fruit fly species from May to June during the first rainy season. Low populations of *B. dorsalis* were later reported in the drier agro-ecosystem in NGS during the first mango season, but became the dominant species in subsequent seasons particularly after the onset of rains and replaced *C. cosyra* as the primary pest of mango in Benin. Similar patterns of displacement of *C. cosyra* by *B. dorsalis* have been reported in the rest of sub-Saharan Africa (Ekesi et al., 2006; Goergen et al., 2011; Vayssières, Korie, et al., 2009). *Ceratitis cosyra* was the dominant among several other *Ceratitis* species in SGS and NGS but least abundant in the FSM, regardless of the sampling year. Its population followed temporal abundance patterns different to that of *B. dorsalis* in the NGS and peaked earlier, that is, at the end of the dry season.

Among the weather variables used in this study, *C. cosyra* and *C. quinaria* populations were significantly and positively correlated with minimum, maximum and mean temperature, while populations of *B. dorsalis*, *D. punctatifrons* and *Z. cucurbiatae* were negatively

correlated with the same variables. Laskar and Chatterjee (2010) showed that *Z. cucurbitae* populations increased with increasing temperatures, especially during the hotter months of the year, while populations dropped at lower temperatures coinciding with the colder months. *Bactrocera dorsalis* and *D. punctatifrons* trap captures were significantly and positively correlated with minimum, maximum and mean relative humidity, while trap captures of *C. cosyra* and *C. quinaria* were negatively correlated with the same weather variables. Several authors have demonstrated that temperature can affect abundance of *B. dorsalis* and *Ceratitis* in different agro-ecosystems (Duyck, David, & Quilici, 2006; Rwomushana et al., 2008; Tanga et al., 2015; Vayssières, Korie, et al., 2009; Vera, Rodriguez, Segura, Cladera, & Sutherst, 2002). *Zeugodacus cucurbitae* abundance was significantly correlated with maximum RH. Abundance of *B. dorsalis* was significantly positively correlated with rainfall, while those of *D. punctatifrons*, *C. cosyra* and *C. quinaria* were positively but not significantly correlated with the same weather variable. Trap catches of *Z. cucurbitae* and *D. humeralis* were negatively but not significantly correlated with rainfall, and similar findings have been reported by Gupta, Verma, and Bhalla (1990) and Gajalakshmi, Revathi, Sithanantham, and Anbuselvi (2011). The positive impact of rainfall on fruit fly abundance is corroborated with that of earlier findings of Mahmood, Hussain, Khokhar, and Hidayatullah (2002) and Vargas, Stark, and Nishida (1989). The possible reason explaining this positive correlation of minimum humidity with fly abundance may be due to higher rainfall that indirectly leads to increase in relative humidity of the environment.

Our results showed that the abundance and richness of fruit fly species varied considerably among agro-ecosystems. The most abundant species in increasing order were *B. dorsalis* > *C. cosyra* > *Z. cucurbitae* > *D. punctatifrons* > *D. humeralis* > *C. quinaria*. The diversity of species
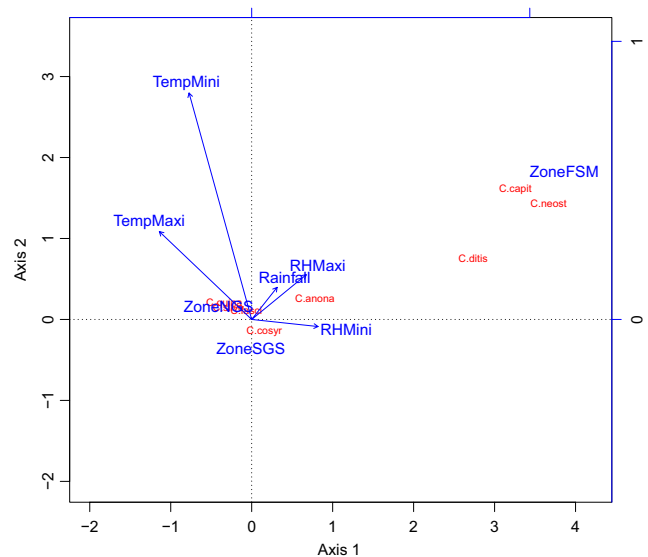

FIGURE 6 Ordination plot illustrating the variation in abundance of fruit fly taxa captured in terpinyl acetate traps as influenced by weather variables indicated by arrows. The qualitative explanatory variable, zone (Agro-ecosystem), is indicated as centroids. Zone NGS, Northern Guinea Savannah; Zone SGS, Southern Guinea Savannah; Zone FSM, Forest Savannah Mosaic

in FSM was significantly higher compared with that of SGS and NGS. Temperature, rainfall and relative humidity were special factors that played a significant role in regulating tephritid fruit fly populations in diverse agro-ecosystems (Duyck et al., 2006; Rwomushana et al., 2008; Tanga et al., 2015; Vayssières, Korie, et al., 2009; Vera et al., 2002). The absence of *D. frontalis*, *D. ciliatus* and *D. vertebratus* (Gnanvossou et al., 2008) in traps during the surveys further confirmed that they were not attracted to male lures in the present study. This highlights the need for future studies focusing on intensive fruit collection and processing to provide additional information on host plants of rare fruit fly species that might actually have been occurring at low population levels or alternatively went undetected by the trapping systems. Results of the present investigation provide information useful for the development of a comprehensive and sustainable management tool of *B. dorsalis* and other fruit flies in Benin.

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AUTHOR CONTRIBUTION

DG, Study conception and design, Data collection, Data interpretation & Drafting of manuscript; RH, Study conception, design, supervision, drafting of manuscript & Critical review; GG, Fruit fly species identification & Critical review; DS, Data analysis and interpretation, Drafting of manuscript & Critical review; CMT, Data interpretation, Drafting of manuscript & Critical review; SAM, Critical review; SE, Critical review.

ORCID

D. Gnanvossou (iD) http://orcid.org/0000-0003-1790-368X

G. Goergen (iD) http://orcid.org/0000-0003-4496-0495

S. Ekesi (iD) http://orcid.org/0000-0001-9787-1360

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