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Spatio-temporal partitioning and sharing of parasitoids by fall armyworm and maize stemborers in Cameroon

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Abstract

Biological invasion is a global concern with species deployed out of native range, the most recent in Africa being the invasion by fall armyworm (FAW) *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae). One of the most mentioned ecological consequences is the capacity of invaders to change native communities' structure. *Busseola fusca* Fuller (Lepidoptera: Noctuidae) has long been the most destructive pests of maize in Africa. Few or no studies have attempted to look at the interaction between FAW and native maize pests over a cropping cycle for sustainable management. Maize trials were established over two cropping cycles in Cameroon to investigate the nature of such interactions and eventual sharing of parasitoids. FAW incidence decreased with maize growth, while the reverse was observed for stemborers. Few cases of co-occurrence were recorded at the later maize growth stage. There was a clear indication that FAW infestation was associated with vegetative stages, while stemborers were associated with reproductive stages. Only FAW eggs were found on abaxial and adaxial leaf surfaces, while only stemborer eggs were inside leaf sheaths. Similarly, while larvae of both groups were found in maize whorl and on ears, only FAW larvae were found in closed tassels, while only stemborers were found inside stems. These results are in favour of segregation in time and space in plant colonization by native and invasive pests, which may limit competition and exacerbates damage if no control is provided. The same egg, larval and pupal parasitoids respectively *Telenomus remus*, *Cotesia icipe* and *Procerochasmias nigromaculatus* emerged from isolated FAW and *B. fusca* eggs, larvae, and pupae. The sharing of parasitoids by both species provides a unique opportunity for augmentative biocontrol.

KEYWORDS

competition, co-occurrence, displacement, natural enemies, *Spodoptera frugiperda*, stemborers

1 | INTRODUCTION

Biological invasions are commonly defined as the establishment of non-native organisms outside their natural geographical range, which causes, or has the potential to cause, environmental, social or economic change (Didham et al., 2007). There are numerous examples

of the ecological consequences and the impact of the intentional or accidental introduction of alien species to a new environment structure of arthropod communities (Chapman & Bourke, 2001; Holway et al., 2002; O'Dowd et al., 2003; Snyder & Evans, 2006; Tobin, 2015). Species that thrive outside their historic geographical range may also introduce new traits and alter ecosystem functioning through

biological interactions with native species. For instance, the case of six Lithocolletinae leaf mining species invasions in Europe had both positive (e.g. increase in species diversity) and negative impacts (e.g. possible damages on the host plant; CSoka, 2001; Šefrová, 2003). Invasive species are thought to possess some special preconditions that allow them to successfully invade and establish in their new environments (Šefrová, 2003). A well-known example from Africa is the displacement of native stemborer *Chilo orichalcociliellus* (Strand; Lepidoptera: Crambidae) by the invasive stemborer, *Chilo partellus* (Swinhoe; Lepidoptera: Crambidae), which was reported in eastern and Southern Africa, with the invader becoming the most injurious stemborer (Mutamiswa et al., 2017).

Until recently, several species of stemborers were the most important pests of maize on the African continent (Calatayud et al., 2014; Cardwell et al., 1997; Ebenebe et al., 1999; Kfir et al., 2002; Van Den Berg et al., 1991; Van Rensburg & Flett, 2010). Important species that reduce crop yield in West and Central Africa are African stemborer *B. fusca*, the pink stemborer, *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae), and the African sugarcane stemborer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae; Chabi-Olaye et al., 2005). *Sesamia calamistis* is generally not considered a major pest in eastern and Southern Africa, while in West Africa, this species is a major pest of maize, sorghum and rice production. *Eldana saccharina* is primarily a pest of sugar cane in Southern Africa, but it is a major pest of maize in West Africa. *Busseola fusca* represents the majority accounting for 95% abundance of all the species in Cameroon (Cardwell et al., 1997). Its damage to maize can lead to about 40% yield loss in monocropped maize fields in the humid forest of southern Cameroon (Chabi-Olaye et al., 2005).

The fall armyworm (FAW) *Spodoptera frugiperda* (J.E. Smith) is the most recent maize pest invader in the African continent where it was first detected in 2016 (Goergen et al., 2016). The presence of FAW has been confirmed from over 44 African countries (Prasanna et al., 2018). Infestations by FAW during the maize stage may result in yield losses of 15%–73% when 55%–100% of the plants are infested (Hruska & Gould, 1997), with recent studies from the African continent reporting a loss of 8.3–20.5 mil MT and value of 2.5–6.2 billion US\$ (Day et al., 2017). FAW is a polyphagous pest with a host range of about 353 recorded plant species in 76 families (Montezano et al., 2018). It feeds primarily on maize, sorghum (Fotso Kuate et al., 2019), and certain grasses and pasture crops (Dumas et al., 2015). It also attacks millet, rice, wheat and sugar cane (Prasanna et al., 2018), which are also attacked by several species of stemborers.

FAW and *B. fusca* are known to attack all maize stages (Adamczyk et al., 1997; Atkinson, 1980; Buntin, 1986; Kaufmann, 1983; Moyal & Tran, 1989). Since the invasion by FAW from 2016, damage and yield losses traditionally from stemborers that represented the major threat to maize production in Africa suddenly lost interest and usual threat, suggesting possible displacement or at least interaction between the indigenous stemborers and the invasive FAW (Hailu et al., 2018). Cannibalism is common in FAW, and there are reports of FAW preying on larvae of different stemborer species (FAO

& CABI, 2019), but the interaction between FAW and stemborers on the same plants has not been studied, including indirect interaction through shared parasitoids, a known phenomenon among some stemborer species (Matama-Kauma et al., 2001). Previous report indicated that different oviposition behaviours and preferences of stemborer species play a role in their spatial and temporal distribution on maize (Kaufmann, 1983). *Busseola fusca* and *S. calamistis* for instance laid their eggs in the inner side of leaf sheaths. Thereafter, the first larval instars for *S. calamistis* bore directly into the stem, while *B. fusca* ascends to the whorl and may then disperse into the stem from the top after feeding on the whorl leaves producing 'windows' (Kaufmann, 1983). According to Atkinson (1980), *E. saccharina* oviposits on the ground debris so that the young larvae migrate to the plant. There are also reports from Linduska and Harrison (1986) of spatial and temporal preference by FAW on maize. The authors reported higher susceptibility of maize plants to *S. frugiperda* between 0 and 40 days after sowing. FAW moths are believed to prefer developing rather than well-developed maize plants to oviposit (De Melo et al., 2006; Hernandez-Mendoza, 1989).

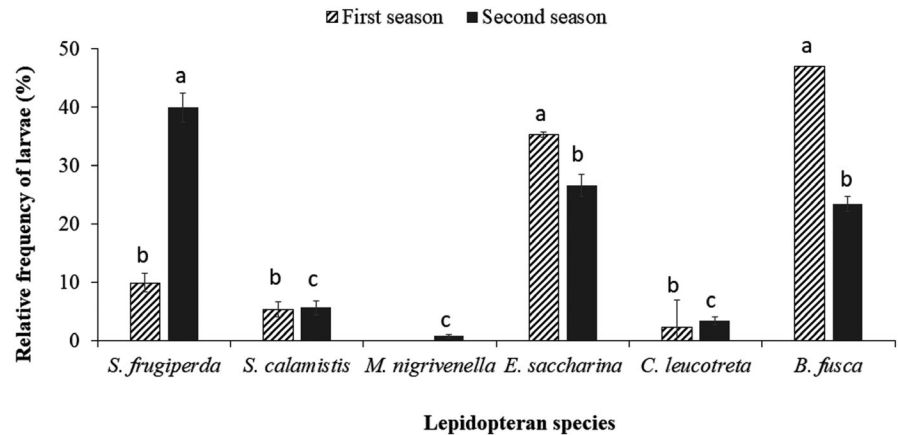
This study was conceived to (a) to determine the temporal and spatial within-plant colonization and population development patterns of the invasive FAW and indigenous stemborers on maize plants in Central Cameroon and (b) to identify the parasitoid species attacking the target maize pests and the level of parasitism of their various life stages in Central Cameroon.

2 | MATERIALS AND METHODS

2.1 | Experimental site and design

Two on-station trials were conducted in 2017 near Yaoundé, Cameroon (03°51.791'N; 011°27.706'E, 747 m.a.s.l.)—during the first (April–August) and second (September–December) cropping seasons. The site is in the humid forest with bimodal rainfall agro-ecological zone with 125–175 days of rainfall distributed over 7–9 months in 2 rainfall seasons, from March through mid-July and from September through November. Average temperature and relative humidity ranged from 22.4 to 24.6°C and from 84.5% to 89.9%, and total rainfall of 1,024.6 mm during the first cropping season, and from 23.0 to 24.6°C and 82.7%–88.2%, and a lower total rainfall (805 mm) during the second cropping season. The size of the experimental plot was 5 × 3 m, replicated four times along soil fertility and relative humidity gradient. Plots were planted with the maize variety PVA Syn6, sown in 5 rows at 25 cm within rows, and 50 cm between rows. PVA Syn6 is a yellow and early variety developed by IITA with high yield, tolerance to low soil nitrogen and resistance to Striga. Similar spacing was used for buffer plots, consisting of 3 rows each, established at a 1-m spacing from each of the four experimental plots. Locally sourced poultry manure (0.01%N, 1.82%K, 1.16%P) was applied to the fields at ploughing two weeks before sowing. Synthetic fertilizer from ADER was applied twice: (a) eleven grams per plant of NPK (20-10-10) at 2 weeks after planting (soon after

FIGURE 1 Relative frequency of Lepidoptera species found infesting maize plants during the first and second cropping seasons. Bars with the same letter for each season are not significantly different (Tukey's test, $\alpha = 0.05$)



thinning and replacement of missing plant stands) and 11 g/plant of urea (46-0-0) 4 weeks after planting (after weeding and mounding).

2.2 | Sampling procedure and data collection

Data collection was initiated at the first appearance of FAW damage in any of the plots and continued at 2-week intervals until the end of the experiments. The following maize growth stages were considered during the sampling—after Belfield and Brown (2008): (1) germination, (2) emergence, (3) vegetative growth stage 1 (V1: week 2–4 after sowing), (4) vegetative growth stage 2 (V2: weeks 5–7 after sowing), (5) tasselling/silking (40–50 days after emergence), (6) cob formation, (7) milk stage (47–57 days after emergence), (8) hard dough (60–70 days after emergence) and (9) senescence (approximately 70–80 days after emergence). On each sampling date, 10 plants were randomly selected along the two diagonals of each plot. All plant parts including upper and lower surfaces of all leaves, leaf sheaths, ears, silk and tassels when available were inspected for lepidopteran eggs. The inspected plants were then cut at the base and brought to the laboratory in individually labelled paper bags, where each insect's developmental stage (dead or alive) was collected and counted. Live specimens were then reared on fresh maize leaf pieces in transparent plastic boxes (20 cm long, 14 cm wide and 5 cm high), while dead ones were monitored in vials (7 cm height and 2.5 cm diameter) aerated with plastic lids in the insectary for possible parasitoid emergence. The incidence of each pest species was calculated after each sampling date as the percentage of plants infested with eggs, larvae or pupae of each pest species or all stages of each pest species together. Parasitized egg masses of each species (recognized by the characteristic blackening spot on the eggs) were placed individually in 9-dr snap-cap vials closed with a muslin cloth and monitored for emergence in the insectary at room temperature ($25 \pm 1^\circ\text{C}$). After emergence, adult parasitoids were chilled in a freezer for 1 min at -4°C to facilitate counting under the microscope. Larvae and pupae were placed in appropriately labelled containers and monitored until adult emergence. Adult parasitoids from eggs, larvae or pupae were identified by the Natural History Museum in London, United Kingdom. Parasitism rates were calculated for each

species of parasitoids on each lepidopteran species by dividing the number of emerged and unemerged (including dissected unhatched cocoons) parasitoids over the number of incubated eggs, larvae or pupae of each lepidopteran species.

2.3 | Data analysis

Individual counts on plants were log-transformed to reduce the variability inherent in insect counts. Average values were compared between species for each crop stage and between crop stages for each species using analysis of variance (ANOVA) with the generalized linear model procedure with Poisson distribution in R software version 3.5.2. Tukey's test was used for post hoc separation of means at $p < .05$ significance threshold. We used a 2-way contingency table to test the independence between maize infestation by FAW, stem borers or both and the maize growth stages. Correspondence analysis between maize growing stage and lepidopteran species was subsequently used to explore the association between the two parameters.

3 | RESULTS

3.1 | Species composition and population dynamics of maize lepidopteran pests

Five Lepidoptera species were recorded during the first season (Figure 1). *Busseola fusca* larva abundance was almost half of all the species pooled together, followed in the descending order by *E. saccharina* and *S. frugiperda* ($F_{(4,15)} = 33.96, p < .001$). Six Lepidoptera species were found infesting the maize plants during the second cropping season. FAW was the most abundant, while *B. fusca* and *E. saccharina* larvae occurred at almost the same abundance, followed by *M. nigrivenella* with the lowest abundance ($F_{(5,18)} = 61.62, p < .001$; Figure 1).

Average percentage of plants infested with each lepidopteran species across sampling dates were statistically similar in both cropping seasons [FAW: $8.6 \pm 2.8\%$ and $15.0 \pm 4.3\%$; $F_{(1,12)} = 0.51, p = .49$; *B. fusca*: $22.5 \pm 4.7\%$ and $14.3 \pm 3.0\%$; $F_{(1,12)} = 0.70, p = .42$; *E. saccharina*: $16.1 \pm 4.4\%$ and $12.9 \pm 3.0\%$; $F_{(1,12)} = 0.10, p = .75$;

S. calamistis: $2.9 \pm 1.3\%$ and $3.6 \pm 1.3\%$; $F_{(1,12)} = 0.07$, $p = .79$; and *C. leucotreta*: $2.1 \pm 1.1\%$ and $2.5 \pm 1.0\%$; $F_{(1,12)} = 0.04$, $p = .85$]. *Mussidia nigrivenella* was found only at maize plant senescence during the second season. Temporal incidence of the different maize species followed a similar trends over the course of the two cropping seasons, with FAW being the only species found during the vegetative stages but overtaken by stemborers at tasselling and silking and subsequent stages (Figure 2).

During both seasons, FAW infestations were numerically higher during the vegetative plant growth than during other growth stages but statistically higher only during the second season ($F_{(6,21)} = 11.2$; $p < .001$). For stemborers, larvae were absent during all vegetative stages; they appeared at tasselling/silking, and their densities increased in subsequent stages. The infestations of two species, *B. fusca* and *E. saccharina*, were statistically greater during the reproductive crop stages in both seasons ($F_{(6,21)} = 8.5$; $p < .001$ for *B. fusca* and $F_{(6,21)} = 20.4$; $p < .001$ for *E. saccharina* in season 1; $F_{(6,21)} = 9.7$; $p < .001$ for *B. fusca* and $F_{(6,21)} = 4.5$; $p = .004$ for *E. saccharina* in season 2) compared with the other lepidopteran species.

3.2 | Co-occurrence of fall armyworm and stemborers

Stemborers and FAW co-occurred at a very low frequency on the same plants at cob formation (2.5%) and hard dough (2.5%) during

season 1, while in season 2, they co-occurred on the same plants at tasselling (2.5%), cob formation (8.3%), milk stage (5%) and hard dough (2.5%; Table 1). FAW was the only lepidopteran infesting maize plants at vegetative stages I and II in season 1 and season 2 (Table 1). At senescence, only stemborer larvae were found during both seasons (Table 1). There was a clear indication that maize infestation by each lepidopteran pest was determined by the maize growth stage with FAW prevalent at vegetative stages I and II while stemborers dominating at cob formation, hard dough and senescence stages (season 1: $\chi^2 = 1,778$, $df = 18$, $p < .001$; season 2: $\chi^2 = 1,664.8$, $df = 18$, $p < .001$; Figure 3).

3.3 | Within-plant distribution of stemborers and FAW on maize

Eggs of FAW and *B. fusca* were the only lepidopteran pest eggs found on maize plants. FAW eggs were present only on the abaxial and adaxial surface of maize leaves, while *B. fusca* eggs were found only in the leaf sheath. No eggs were found in the maize whorls, in the closed tassels or in the corn ears for any of the two species, and FAW and *B. fusca* eggs were never found sharing the same space on maize plants during the two seasons of experimentation.

FAW larvae were found in the whorl leaf during all vegetative growth stages (62.5% and 82.9% in season 1 and 2, respectively), in the closed tassels (halfway anthesis; 20.8% and 9.76% in season 1

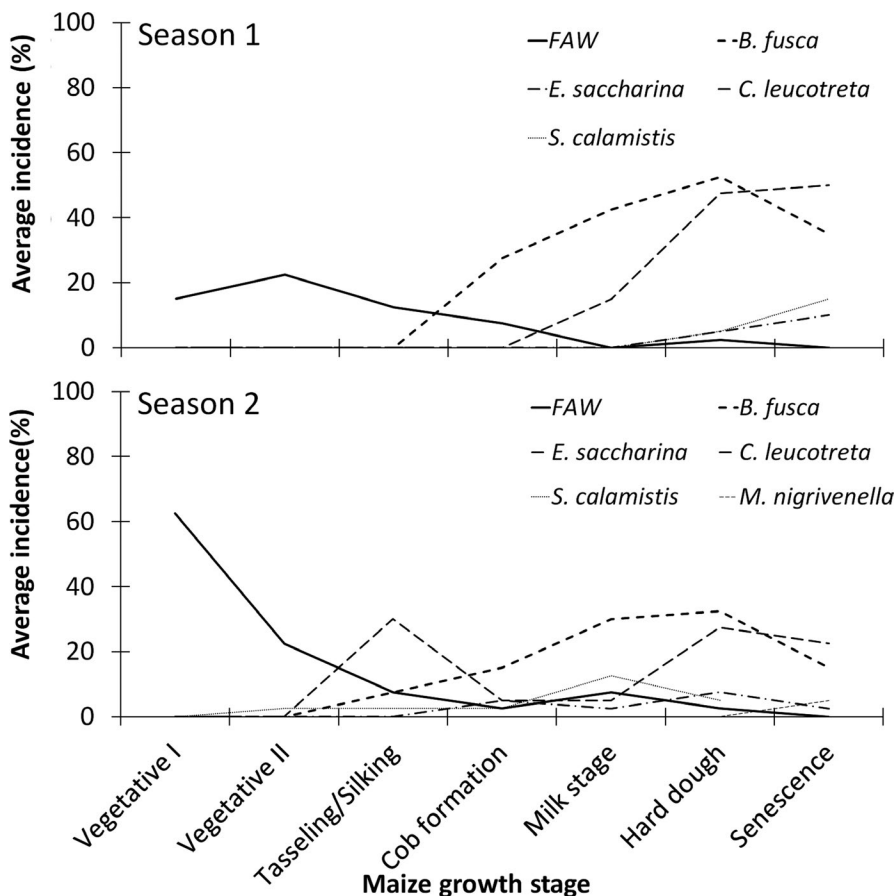


FIGURE 2 Average incidence (%) infested plants) of FAW and stemborers on maize plants during two cropping seasons

TABLE 1 Percentage of plants (mean ± SE%) infested either by FAW larvae, stemborer larvae or both during the two seasons in Central Cameroon

Growth stage	None	Only FAW	Only stemborers	Both
Season 1				
Vegetative I	85.0 ± 9.6 ^a	15.0 ± 9.6 ^{ab}	0 ^d	0 ^a
Vegetative II	77.5 ± 13.1 ^a	22.5 ± 13.1 ^a	0 ^d	0 ^a
Tasselling/silking	87.5 ± 7.5 ^a	12.5 ± 7.5 ^{ab}	0 ^d	0 ^a
Cob formation	72.5 ± 2.5 ^a	0 ^b	25.0 ± 2.9 ^c	2.5 ± 2.5 ^a
Milk stage	52.5 ± 7.5 ^{ab}	0 ^b	47.5 ± 7.5 ^b	0 ^a
Hard dough	22.5 ± 16.5 ^b	0 ^b	75.0 ± 15.5 ^a	2.5 ± 2.5 ^a
Senescence	25.0 ± 6.5 ^b	0 ^b	75.0 ± 6.5 ^a	0 ^a
Season 2				
Vegetative I	37.5 ± 10.3 ^{ab}	62.5 ± 10.3 ^a	0 ^b	0 ^a
Vegetative II	75.7 ± 9.4 ^{ab}	24.3 ± 10.4 ^b	0 ^b	0 ^a
Tasselling/silking	58.1 ± 9.0 ^{ab}	4.7 ± 2.5 ^c	34.9 ± 8.5 ^{ab}	2.5 ± 2.5 ^a
Cob formation	40.0 ± 8.3 ^{ab}	0 ^c	53.3 ± 9.6 ^a	8.3 ± 8.3 ^a
Milk stage	42.9 ± 8.6 ^{ab}	7.1 ± 4.1 ^c	46.4 ± 12.7 ^a	5.0 ± 5.0 ^a
Hard dough	32.4 ± 9.8 ^b	0 ^c	64.9 ± 9.8 ^a	2.5 ± 2.5 ^a
Senescence	62.5 ± 2.5 ^a	0 ^c	37.5 ± 2.5 ^a	0 ^a

Note: Means followed by the same letter in a column during each season are not significantly different (Tukey's test, α = 0.05).

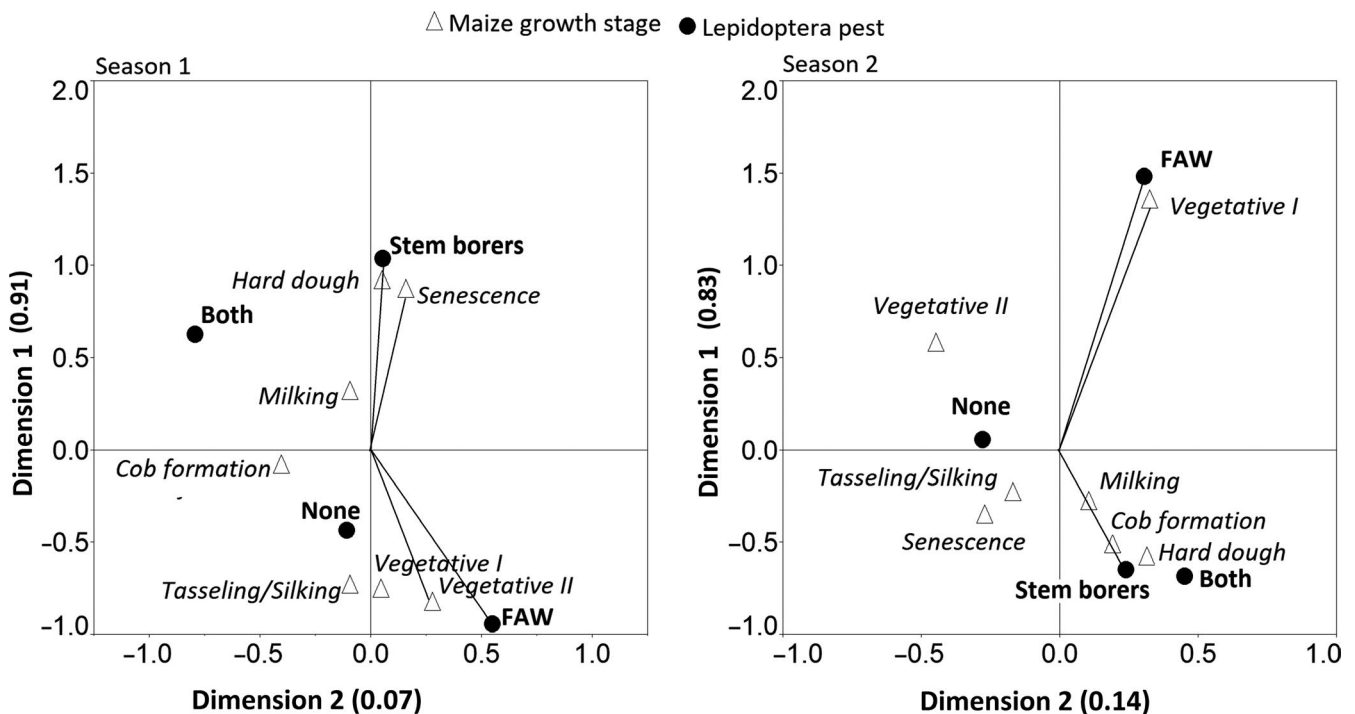


FIGURE 3 Correspondence analysis between maize growth stage and infestation by FAW, stemborers or both during the two seasons

and 2, respectively) and in the corn ear (16.7% and 7.32% in season 1 and 2, respectively; Table 2). FAW larvae were never found on or in the maize stem. In contrast, more than 75% of stemborer larvae (86.8% in season 1 and 79.9% in season 2) were collected from the maize stem, while 13.2% and 16.5% were found in the maize ear in season 1 and 2, respectively. No larvae of stemborers were found between tasselling and halfway to anthesis, and only 3.8% of larvae

were found in whorls in season 2 (Table 2). The co-occurrence of the different species on the same plant was very low (0.71% in season 1 and 1.67% in season 2). However, during both cropping seasons, a higher percentage of plants were infested by stem borers (31.8% and 31.3%) than FAW (7.1% and 15.8%) in season 1 and 2, respectively. Where the pests were found on the same plant, they were located consistently on different plant parts. (Table 2).

TABLE 2 Spatial distribution of FAW and *B. fusca* on maize plants

Plant part	FAW eggs		<i>B. fusca</i> eggs		FAW larvae		<i>B. fusca</i> larvae	
	S1	S2	S1	S2	S1	S2	S1	S2
Adaxial leaf surfaces	+	+	-	-	-	-	-	-
Abaxial leaf surfaces	+	+	-	-	-	-	-	-
Leaf sheath	-	-	+	+	-	-	-	-
Whorl leaves	-	-	-	-	+	+	-	+
Maize stems	-	-	-	-	-	-	+	+
Closed tassel	-	-	-	-	+	+	-	-
Corn ear	-	-	-	-	+	+	+	+

Note: +, recorded; -, not recorded; S1, season 1; S2, season 2.

TABLE 3 Parasitism rates (mean % ± SE) of lepidopteran species: eggs by *Telenomus remus*, larvae by *Cotesia icipe* and pupae by *Procerochasmias nigromaculatus*

Lepidoptera species	Parasitoid species		
	<i>Telenomus remus</i>	<i>Cotesia icipe</i>	<i>Procerochasmias nigromaculatus</i>
<i>S. frugiperda</i>	34.4 ± 9.5 ^a	0.4 ± 0.3 ^b	0.2 ± 0.1 ^b
<i>B. fusca</i>	8.1 ± 2.2 ^a	0.6 ± 0.2 ^b	0.6 ± 0.1 ^b
<i>E. saccharina</i>	0	0	0
<i>S. calamistis</i>	0	0	0
<i>C. leucotreta</i>	0	0	0
<i>M. nigripenalla</i>	0	0	0

Note: Mean value followed by the same letter within the same row is not statistically different following the *t* test at 0.05.

3.4 | Parasitoid species of FAW and stemborers

Three parasitoid species emerged from FAW and *B. fusca* eggs, larvae, and pupae. None of the parasitoids emerged from any life stage of other stemborer species. The egg parasitoid *Telenomus remus* Nixon (Hymenoptera: Platygasteridae) emerged from 34.4 ± 9.5% and 8.1 ± 2.2% of FAW and *B. fusca* egg masses, respectively, amounting to fourfold difference in *T. remus* parasitism of the two pests (Table 3). The larval parasitoid *Cotesia icipe* Fernandez-Triana & Fiaboe (Hymenoptera: Braconidae) and the pupal parasitoid *Procerochasmias nigromaculatus* (Cameron; Hymenoptera: Ichneumonidae) parasitized FAW and *B. fusca* at <1%. There was a significant difference in the rate of parasitism by the three parasitoids for each lepidopteran species ($p < .001$; Table 3).

4 | DISCUSSION

Maize stemborer species' diversity and abundance observed during the present study are in line with those reported by Cardwell

et al. (1997) and Ndemah et al. (2001) with *B. fusca* continuing to be the predominant maize stemborer pest in Central Cameroon. FAW, however, has now taken over as the main maize lepidopteran pest in Cameroon (Fotso Kuate et al., 2019) and the rest of Africa (Baudron et al., 2019; Day et al., 2017) as it has been the case in the Americas for centuries (De Melo et al., 2006; De Polanía et al., 2009). Our study also presents three key findings that can have substantial consequences for the management of lepidopteran pests of maize in Cameroon and possibly in numerous other countries in Africa with similar maize pest composition.

First, our study found a near-complete negative association between FAW and the indigenous stemborers on the plants; that is, plants with FAW were nearly always free of stemborers and vice versa. FAW was substantially more abundant at early plant growth, with 100% of its larvae found during the maize vegetative stages of both cropping seasons, as shown by Linduska and Harrison (1986). All FAW eggs were collected at the vegetative stage. FAW moths are thought to prefer not well-developed maize plants to oviposit (De Melo et al., 2006; Hernandez-Mendoza, 1989), which helps to explain the presence of eggs only at early plant growth recorded in the present study. FAW infestations though at low levels at the reproductive stage of maize plants are consistent with other findings (FAO & CABI, 2019). Hernández-Mendoza et al. (2008) indicated, however, that in Mexico, the youngest maize stages were less frequently attacked by FAW than the late vegetative stages (V8 and V9). They however indicated that these relatively low infestation levels of younger maize plants in their study could have been the result of the resistance of the two maize varieties (Blanco and Aperlado), coupled with unfavourable weather conditions for FAW. It is therefore imperative to determine whether, apart from variety and climate, crop morphology influences FAW temporal dynamics.

FAW also exhibits both intraspecific and interspecific (predation) cannibalism (Chapman et al., 1999; FAO & CABI, 2019), which could be responsible for the temporal exclusion of stemborers that remain in the whorl at the vegetative stage. Additional investigations are however needed to determine the mode of competition and other biological factors leading in temporal exclusion of stemborers by FAW. This competition between FAW and stemborers may be direct through predation or indirect (or apparent) through shared parasitism.

Unlike FAW, stemborers were first detected on maize plants in this study at tasselling/silking, beginning with *B. fusca*, and their abundance increased with crop development. Late infestations by stemborers were reported by Van Rensburg et al. (1987) on 12- to 16-week-old plants, but only when these were planted very late in the season. Before the FAW invasion, stemborers were reported to have an oviposition preference for 3- to 6-week-old maize plants (Calatayud et al., 2014) or less than 40 days after sowing (Linduska & Harrison, 1986). Moreover, oviposition rarely occurs after tasselling, except in the case of late planting (Calatayud et al., 2014). No eggs were collected at the reproductive stage (tasselling, silking and cob stages) corroborating findings by Ndemah et al. (2001) who had indicated a strong oviposition preference of *B. fusca* for young plant parts

(vegetative growth). The absence of stemborers at vegetative maize in both seasons in our study provides evidence (in part) for a competitive (temporal) displacement of stemborers by FAW. Such temporal displacement, while reducing the economic importance of stemborers, when taken in isolation, is expected to exacerbate total lepidopteran damage to maize now occupying each, a section of the development of the crop (Ntiri et al., 2019). During this study, FAW and stemborers–FAW population dynamic curve displayed opposite trend, with that of FAW being above that of stemborers at the early stage of maize growth and start decreasing while that stemborers increased, clearly suggesting a process of mutual exclusion. The crop will therefore remain under pest pressure throughout its growth, leading to higher combined damage. According to Van Rensburg et al. (1987), the first generation of *B. fusca* moth flight results in the infestation of maize in the whorl stage corresponding to stage VE (emergence when coleoptile leaf or first leaf is visible) to V6 (collar of sixth leaf visible approximately 3 weeks after emergence) of plant development, while the second and third generation infests older maize plants. Limited only to the third generation, *B. fusca*, which in this case occurred at later maize growing stage, significantly reduced the importance of stemborer in terms of specific damage and yield loss potential in maize. The third-generation moth flight is not considered to be economically important, whereas it was during this generation that stemborer infestation was important during the current study, with FAW displacing stemborers to a later stage of maize cropping. There is a need to investigate the effects of planting date to understand its potential effect on the temporal occurrence of both FAW and stemborers, as well as the relationship between phenological asynchrony between maize and the two pest species and their co-occurrence. Further studies are also warranted under different agro-ecological conditions to assess the extent of the potential temporal displacement by the invader of stemborers sharing the same niche on maize plant.

Second, the invasion of FAW appears to have shifted the temporal (start of infestation) and spatial (within-plant) distribution of particularly *B. fusca*. FAW were collected mainly in the funnel or whorl in both seasons. All eggs were collected on the under or upper side of leaves, although eggs can be found on any part of the plant. Few larvae were found in closed tassels, on young cobs in the silk above the ear. Although the abundance of FAW larvae decreased when tassels, silk and cobs were present, their presence on all plant parts provides evidence of the ability of FAW to infest and damage all maize plant parts as indicated by FAO & CABI (2019). Few FAW larvae were found in the tassel and tip of the ear in the silk, and none were found in the cob, probably because these organs are not as hard as the cob, suggesting that these are entry points of young larvae that may eventually get to the cob and grains through the ear silk to either compete or exclude stemborers that infest the cobs. In line with this argument, when both pest types were found on the same plant (which was rare), they occurred on separate plant organs, further strengthening the hypothesis of spatial avoidance between stemborers and FAW.

The differences in spatial distribution among the various maize lepidopteran species, where most stemborers infest the stem,

could be attributed to differences in their feeding preferences (Kaufmann, 1983). The first larval instars for *S. calamistis* bore directly into the stem, while *B. fusca* ascends to the whorl and may then disperse into the stem from the top after feeding on the whorl leaves producing 'windows' (Kaufmann, 1983). Since both FAW and *B. fusca* can occur at the same time, we can expect a direct competition for space in the whorl, but this study has shown a delay in *B. fusca* infestation, which starts colonizing the maize at tasselling/silking stage. Furthermore, younger larvae of the *B. fusca* and *C. partellus* feed in the whorl, but the older larvae bore into the stems (FAO & CABI, 2019). The absence of stemborers, especially *B. fusca* in the whorl, is therefore unusual, and we hypothesize that this could be an avoidance adaptation of *B. fusca* to FAW, by ensuring spatial partitioning from the invader particularly that the invader is also known to be a predator of other lepidopterans (Chapman et al., 1999; FAO & CABI, 2019). Stemborers may then find refuge in the stem as most of the stemborer larvae were found in the stems, or induce a decrease in stemborer infestation due to increase in FAW infestation as recently reported by Hailu et al. (2018). In our study, *Mussidia nigripenella* was collected from both maize stem and ear, while *C. leucotreta* was only infesting the maize ear. Typically, larvae of the two species enter the cob through the silk tube (Moyal and Tran (1989). These species can be in direct competition with FAW in the ear during the maize productive stage since they are cob borers, but the later will thrive due to their comparative advantage.

Among the borers, only *B. fusca* eggs were found during this study, and all of them were from the inner side of the leaf sheath of plants at pre-tasselling. Similarly, Kaufmann (1983) reported that *B. fusca* lay their eggs on the inner side of leaf sheaths. The leaf sheath of older or reproductive plants is avoided probably because it fits loosely around the stem (Van Rensburg et al., 1987). Kaufmann (1983) also indicated that the differences in spatial distribution among the various maize lepidopteran species could be attributed to the difference in oviposition behaviours. Hence, oviposition behaviour can influence spatial partitioning during oviposition. No eggs were collected from the maize ears, in line with the suggestion of Mally (1920) that *B. fusca* rarely oviposits underneath the outer husk of leaves of ears and this behaviour was not affected by the presence of FAW.

Third, our study presents evidence of shared parasitism, particularly by the egg parasitoid *T. remus* on both FAW and *B. fusca*. Biological control with parasitoids is a natural way of reducing crop damage and yield losses (Tomasetto et al., 2018), and it is an environmentally viable alternative to insecticide use (van Lenteren, 2000). FAW and *B. fusca* in this study shared the same parasitoids at different developmental stages, with much greater parasitism by the egg parasitism *T. remus* than parasitism of the other life stages. Parasitism of FAW by *T. remus* shows the presence of this natural enemy locally prior to invasion by FAW. This parasitoid originates from Asia and is reported on FAW in the Americas, and we hypothesize that its future population increase will contribute significantly to the control of the invasive pest (Kenis et al., 2019). That two pest species shared the same parasitoids could lead to indirect interactions between them

through this shared parasitism. The earlier availability of FAW eggs, compared with the absence of FAW, provides an opportunity for the parasitoid to increase on FAW eggs, particularly early in the crop's growth cycle, which could later exert a greater level of parasitism on *B. fusca* and lead to a reduction in infestations of this species. This shared parasitism could lead to apparent competition between FAW and *B. fusca* with a greater negative impact on the latter. Similar inter-species host sharing by various parasitoids that can lead to apparent competition (Murdoch, 1969), particularly when the parasitoid or predator switches to the more abundant host (Holt and Lawton, 1994). For instance, *Venturia canescens* (Gravenhorst; Hymenoptera: Ichneumonidae), which parasitizes a range of pyralid pests such as *Plodia interpunctella* (Hübner; Lepidoptera, Pyralidae) in Leeds, developed a new association with the new invader *Ephesthia kuehniella* (Zeller; Lepidoptera, Pyralidae; Jones et al., 2015). The novel host initially reduced the parasitoid's adult survival rate, but this rate was dramatically increased over three successive generations in the new host compared with its initial host (Jones et al., 2015). Therefore, we hypothesize that the currently low parasitism rates recorded could increase with the FAW invasion, provided maize management includes options that contribute to the conservation of natural enemies of maize insect pests (Blibech et al., 2015).

Our study provides indications that *B. fusca* has developed a FAW avoidance strategy through shifts in the temporal and spatial distribution of their infestations. Stemborers shifted their colonization of maize plants to later maize growth stages. They did not however alter their spatial oviposition patterns, but those whose larvae feed on the whorl were now absent from the whorl in the presence of FAW. This spatial and temporal segregation in maize plant colonization by the native and invasive maize pests, while suggestive of potential displacement of stemborers and possible reduction in their impact on maize production, may limit direct competition between FAW and stemborers resulting in otherwise greater damage to maize considering the continuous infestation of the crop. Moreover, our study showed that the FAW and *B. fusca* eggs, larvae, and pupae share the same parasitoids, which could potentially lead to indirect (apparent) competition through shared parasitism and further alter the dynamics of the maize pest complex. We hypothesize that the sharing of the same parasitoids coupled with the diversity of parasitoids also provides an opportunity for combined conservation and augmentation biocontrol of FAW and stemborers.

Our article presented results from one experiment using on maize variety and repeated during two maize cropping seasons within the same calendar year. Conceivably, the observed spatial and temporal patterns of FAW and stemborer infestations could be different under weather and soil conditions, maize varieties and maize intercropping patterns. Examination of long-term temperature and relative humidity data from the same experimental site (IITA-Cameroon climate data repository) indicated that monthly low and high temperatures and relative humidity during the first and second maize cropping seasons are quite similar. There are however yearly variations in rainfall patterns but not enough to cause considerable changes in maize growth patterns. It is possible, however, the

patterns of FAW and stemborer infestations may be different on other maize varieties and under different cropping systems using intercrops (Hailu et al., 2018; Midega et al., 2018). The results of our study are suggestive and certainly warrant further investigations under different biophysical environments.

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CONFLICT OF INTEREST

No conflict of interest was declared.








AUTHOR CONTRIBUTION

AFK, AFA and RH conceived the research. AFA, AFK, RMOE and SNN conducted experiments. ANN, AFA and AFK analysed data and conducted statistical analyses. AFA, AFK, KKMf and RH wrote the manuscript. KKMf, CM and RN reviewed the manuscript. RH and KKMf secured funding. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available on the CKAN online data repository of IITA at <https://doi.org/10.25502/4WDN-E812/D> (Fotso Kuate et al., 2020).

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