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# Spatio-Temporal Interactions Between Maize Lepidopteran Stemborer Communities and Possible Implications From the Recent Invasion of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Sub-Saharan Africa

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## Abstract

Spatio-temporal dynamics of multi-species pest communities and the interactions between them influence the structure of pest complex that attack crops. In East and Southern Africa, cereal crops, especially maize, is attacked by a complex of lepidopteran stemborer species made up of *Busseola fusca* (Fuller) and *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae), and *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae). There is inadequate information on the extent of single- and multi-species infestations by this pest complex, their current spatio-temporal variations, and the primary abiotic factors that influence these. Furthermore, the recent invasion of the fall armyworm, *Spodoptera frugiperda* J.E. Smith, in sub-Saharan Africa will likely influence this stemborer community structure. Sampling was conducted in maize fields to record stemborer species and larval numbers from infested plants, in 28 localities found in six agro-ecological zones (AEZs) of Kenya and parts of Tanzania, as well as in one locality in the mid-altitudes where the three stemborer species occurred together. Both single- and multi-species stemborer communities characterized infestation of maize at field and plant levels, but varied in proportions between the AEZs. Infestation patterns and larval densities varied between seasons at mid-locality stemborer communities followed a clustered distribution pattern. Temperature was the most significant abiotic factor influencing the composition of stemborer communities at all spatial scales. Rainfall was significant only at the local scale. Results are discussed in relation to current stemborer community structures in maize fields and what the likely potential implications are, in the light of climate change and the recent establishment of the fall armyworm in Africa.

**Key words:** *Busseola fusca*, *Chilo partellus*, community ecology, pest invasion, *Sesamia calamistis*

Plants host a diversity of arthropods, forming communities that utilize the resource both spatially and temporally (Strong et al. 1984, Liss et al. 1986, Lewinsohn et al. 2005). Based on functional groupings irrespective of their taxonomic group (Hawkins and MacMahon 1989, Simberloff and Dayan 1991), arthropod communities could consist of leaf chewers, sap suckers, leaf miners, borers, gall-makers, and root feeders (Stiling et al. 1999, Imura 2003, Cornelissen et al. 2008, Stam et al. 2014, Truter et al. 2014). Issues concerning the co-occurrence of such multi-species form part of the major challenging questions in ecological studies (Sutherland et al. 2013)

Direct or indirect interactions within and between populations of insects on a given plant can have positive or negative influences on

the structure and functions of that community (Hudson and Stiling 1997, Kaplan and Eubanks 2005, Wootton and Emmerson 2005, Soler et al. 2012, Sánchez-Galván et al. 2014). The role of these species interactions, especially competition, in the organization of insect communities has however been questioned (Connell 1983, Karban 1986, Gurevitch et al. 1992, Denno et al. 1995). Two critical reviews on the subject showed strong evidence for the dominance of competition and the role it plays in structuring phytophagous insect communities (Denno et al. 1995, Kaplan and Denno 2007). Competition is regarded to be higher among species that share the same niche including stem and wood borer guilds and those that are closely related. It is also higher within insect populations that are invasive

and those that are sessile and aggregative (Denno et al. 1995, Kaplan and Denno 2007).

In addition to species interactions, insect community structure is also influenced by abiotic factors such as temperature, humidity, rainfall, salinity, soil chemistry, and carbon dioxide concentrations (Dunson and Travis 1991, Denno et al. 1995, Jiang and Morin 2004, Ovadia and Schmitz 2004, Sanders et al. 2004). Temperature, however, is the most determining abiotic factor, since it directly drives the rate of growth, development, fecundity, and mortality of insects. It also influences resource utilization and intra- and interspecific interactions, and limits the geographic distribution of insect species (Howe 1967, Bale et al. 2002, Sporleder et al. 2004, Hodkinson 2005, Speight et al. 2008, Damos and Savopoulou-Soultani 2012, Ntiri et al. 2016, Yonow et al. 2017). In addition, it indirectly influences the biology and distribution of insect species through the impacts it has on host plants, competitors, and natural enemies (Bale et al. 2002, Estay et al. 2009). The importance of temperature in structuring biological communities has been highlighted by the possible effect that climate change, particularly temperature increase, could have on these communities (Woiwod 1997, Bale et al. 2002, Tylianakis et al. 2008, Cornelissen 2011).

In sub-Saharan Africa, several lepidopteran stemborer species have become major pests of cereal crops (Kfir et al. 2002). Two indigenous noctuids, *Busseola fusca* (Fuller) and *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae), and one exotic crambid, *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae), attack maize and sorghum in East and Southern Africa (Polaszek and Khan 1998, Reddy 1998, Kfir et al. 2002). These three species occur as communities of single or mixed species infesting not only cereal crops (Van den Berg et al. 1991; Kalule et al. 1997; Tefera 2004; Ong'amo et al. 2006a,b; Krüger et al. 2008), but also wild graminaceous plants (Le Ru et al. 2006, Moolman et al. 2014). The composition of these stemborer communities varies with locality, altitude, and season. For example, in Kenya, *B. fusca* is the dominant species in the highlands, while *C. partellus* dominates in the lowlands. *Sesamia calamistis* is present at all altitudes in low numbers. In the mid-altitudinal regions, the stemborers occur as a mixed community of the three species, but with variation in species dominance with respect to locality, season and year (Guofa et al. 2001; Ong'amo et al. 2006a,b). In parts of southern Africa *C. partellus* occurs in mixed populations with *B. fusca* in both the highland (Bate et al. 1991, Van Rensburg and Van den Berg 1992, Ebenebe et al. 1999) and lowland regions (Cugala and Omwega 2001, Krüger et al. 2008), but the dominance of a species might vary with environment.

Despite frequent reports on these spatial and temporal variations in maize stemborer communities (e.g., Matama-Kauma et al. 2001, Kfir et al. 2002), there is inadequate information on the extent of single- and multi-species infestations (at field and plant level) of these stemborer species, in the different maize agro-ecological zones (AEZs). In addition, knowledge on the function of spatio-temporal interactions among lepidopteran stemborer communities in maize-based agro-ecosystems in sub-Saharan Africa is not fully understood. The current spatial and temporal variations in maize stemborer communities may, however, soon change due to the invasion of a dominant and aggressive other lepidopteran pest of maize, the invasive fall armyworm, *Spodoptera frugiperda* J.E. Smith (Goergen et al. 2016). This species is currently starting to interact/compete strongly with lepidopteran stemborer communities, particularly during the early instars when stemborers are also leaf feeders and then occupy the same niche as *S. frugiperda* (P.-A. Calatayud, personal observation). This exotic pest is a new invasive species in sub-Saharan Africa where outbreaks in maize fields were recorded for the first time during early 2016 (Goergen et al. 2016, Prasanna et al. 2018). This

pest will therefore be in competition with the currently well-known lepidopteran stemborers such as the exotic crambid *C. partellus*. The latter species, which was introduced from Asia, has competitively displaced *B. fusca* in the highlands of South Africa (Kfir 1997) and *Chilo orichalcociliellus* Strand (Lepidoptera: Crambidae) in the coastal region of Kenya (Ofomata et al. 1999). This invasion by *C. partellus* not only changed the stem borer community structure in maize and sorghum in parts of southern Africa (Bate et al. 1991, Van Rensburg and Van den Berg 1992), but also added to crop losses (Soul-kifouly et al. 2016) and complicated chemical (Bate and Van Rensburg 1992, Van den Berg and Van Rensburg 1996, Van den Berg et al. 1997) and cultural control methods (Van den Berg et al. 1998, Ebenebe et al. 2001, Van den Berg and Ebenebe 2001).

There is therefore a need to describe the current spatio-temporal interactions within multi-species communities of the aforementioned three maize stemborer species which infest maize fields. Knowledge of the spatio-temporal dynamics of stemborer communities contributes to answering some of the important questions in ecology (Sutherland et al. 2013). In addition, the structures of stemborer communities will most likely be modified by both climate change (Mutamiswa et al. 2017) and the recent invasion of *S. frugiperda*.

The aims of this study were to (1) describe the magnitude of single- and multi-species composition of stemborer communities at maize plant and field level in different AEZs prior to the introduction of *S. frugiperda*; (2) describe the spatio-temporal dynamics of multi-species stemborer communities that infest maize in the mid-altitudinal regions; and (3) examine the main abiotic factor(s) that influence these dynamics.

## Materials and Methods

This study involved surveys conducted in maize fields in different localities in the maize AEZs of Kenya and parts of Tanzania, and then another season-long monitoring survey in one locality in the mid-altitudes in Kenya.

### Study Areas

#### Community Structure of Stemborers at Plant and Field Levels in Different AEZs

Sampling was done in 28 localities situated in the six maize AEZs described by Hassan et al. (1998) in Kenya and extrapolated for localities in Tanzania (Supp Fig. S1 [online only]). Eleven localities were distributed from the lowlands in the Coast region (sea level) to the highlands in the Western region (2,343 m a.s.l.) in Kenya. The others were situated along three mountainous gradients in Kenya (six localities on Taita hills at 800–1,800 m a.s.l. and five on the Machakos hills at 1,100–2,000 m a.s.l.). In Tanzania, six localities were established on the Kilimanjaro mountain at 700–1,700 m a.s.l. (Supp Table S1 [online only]). Sampling was done between 2011 and 2014.

#### Spatio-Temporal Dynamics of Multi-Species Stemborer Communities at Mid-Altitudes

The monitoring survey on the spatio-temporal dynamics of stemborer community was conducted in Makuyu (S 0°55.387, E 37°09.004) in Murang'a County in the central province of Kenya. This locality is situated within the mid-altitudinal range (1,490–1,500 m) where *B. fusca*, *S. calamistis*, and *C. partellus* are known to occur together (Guofa et al. 2001; Ong'amo et al. 2006a,b). The area has two rainy seasons, the long-rain season from April to June and the short-rain season from October to December.

## Field Sampling Protocol

### Community Structure of Stemborers at Plant and Field Levels in Different AEZs

At each locality, 10 maize farms were sampled during the growing season and the incidence of infested maize plants recorded. Sampling followed the protocols described by Overholt et al. (1994). Ten infested maize plants were randomly selected from each maize field and dissected to record the numbers of stemborer larvae according to species.

### Spatio-Temporal Dynamics of Multi-Species Stemborer Communities at Mid-Altitudes

Ten maize fields (each between 0.5 and 1.5 ha) at a distance of at least 100 m from each other were selected in Makuyu. Each field was divided into four quadrats to facilitate random sampling of infested maize plants. The sampling followed the protocols described by Overholt et al. (1994). In each quadrat, one person randomly sampled 15 maize plants, following a zig-zag pattern. For each plant, the geographic positions of infested plants among the 15 sampled plants were recorded with a GPS unit (Garmin Etrex 20 [USA]). Infested plants were then dissected to record the number of larvae (and pupae) per stem according to species. Samplings were done over three seasons in this locality: the (1) short-rain season (XI, 2012-I, 2013)-SR1, (2) long-rain season (IV, 2013-VI, 2013)-LR, and (3) short-rain season (XI, 2013-I, 2014)-SR2.

Weekly sampling was conducted from the third week after seedling emergence in all 10 fields selected in SR1 and LR. Sampling was done at weekly intervals for 11 wk. However, in SR2, sampling was carried out weekly, for only 7 wk due to the short duration of the rainfall period and subsequent plant stress. Daily temperatures were recorded with a Hobo data logger (which recorded every hour) and rainfall with a rain gauge.

## Data Analysis

The number of single- and multi-species infestations in each AEZ were determined and expressed as a percentage of total infestation within each AEZ. A canonical correspondence analysis (CCA) method of multivariate analysis (Zuur et al. 2007) was used to determine which climatic factors could have the strongest influence on the composition of stemborer communities in each AEZ. Temperature and rainfall were the two climatic factors chosen for the analysis, since these influence biological communities the most. The average annual rainfall and temperatures for all the sampling localities were extracted from the WorldClim dataset (<http://www.worldclim.org>) and used in the multivariate analysis.

The incidence of infestation as recorded from the locality at the mid-altitude was analyzed using the generalized linear model (GLM) with binomial errors structure. Odds ratios with a 95% confidence interval (OR [95% CI]) were calculated for each season from the GLM results obtained. Larval densities of the stemborer species were analyzed using the generalized linear mixed model (GLMM), with field set as a random effect. The GLMM was also used to analyze the effect of temperature and rainfall on larval densities, with temperature and rainfall as fixed effects and field as a random effect (Zuur et al. 2007). The spatial distribution of the stemborer community in Makuyu was analyzed using the Ripley's K function on the GPS positions of species infestations, assuming homogeneity (Baddeley 2008, Bivand et al. 2008). All analyses were carried out in R v. 3.4.2 (R Development Core Team 2017).

## Ethical Approval

This article does not contain any studies with human participants or animals performed by any of the authors.

## Results

### Stemborer Community Structure (Single- and Multi-Species) in Different AEZs

#### Field Level

Both single- and multi-species stemborer infestations of maize plants were recorded at field level, but at varying proportions between the different studied AEZs although the maize plants sampled were exhibiting similar height and plant stem diameter among AEZs (data not shown). Single-species infestations were more common in fields sampled in the lowland (76%) and highland tropical (67%) zones than in other AEZs. Fields sampled in the moist transitional (63%), dry mid-altitude (77%), and moist mid-altitude (90%) zones were dominated by multi-species infestations. The dry transitional zone was the only AEZ in which all sampled fields were characterized by multi-species infestations (Fig. 1A).

#### Plant Level

The composition of stemborer communities infesting maize plants varied between the different AEZs (Fig. 1B). *Chilo partellus* dominated maize plant infestations (90%) in the lowland tropical zone, while *B. fusca* dominated infestations (79%) in the highland tropical zone. *Sesamia calamistis* was present in lower proportions in these two respective zones. All three species did, however, occur together in the other four AEZs, but with variations in species dominance between zones. *Chilo partellus* was the dominant species in the dry transitional (60%) and dry mid-altitude (57%) AEZs, while *B. fusca* was the dominant species in the moist mid-altitude (71%) and moist transitional (69%) AEZs. *Sesamia calamistis* was present in all AEZs, but in lower and varying proportions. Multi-species infestations were recorded in all AEZs. However, only the moist mid-altitude had all possible species combinations and it had the highest proportions of multi-species infestations.

### Effect of Temperature and Rainfall on the Composition and Distribution of Stemborer Communities

The multivariate analysis (Fig. 2) showed that average annual temperature and rainfall together explained 56% of the variation in the stemborer composition in the different AEZs. This is represented by the constrained component of the model output (Zuur et al. 2007; Table 1, A). The eigenvalues of each axis of the bi-plot and the proportions of variation explained by these are provided in Table 1 (B).

The analysis showed that communities in the lower altitudes, where *C. partellus* dominated, were associated with higher temperatures and lower rainfall, while lower temperatures and higher rainfall characterized higher altitudes, which were dominated by *B. fusca*. *Sesamia calamistis* did not show a strong association with either rainfall or temperature. In addition, multi-species communities of *C. partellus* + *S. calamistis* were associated with higher temperatures, while *B. fusca* + *C. partellus* communities were associated with higher rainfall. *B. fusca* + *S. calamistis* did not show a strong association with either temperature or rainfall (Fig. 2).

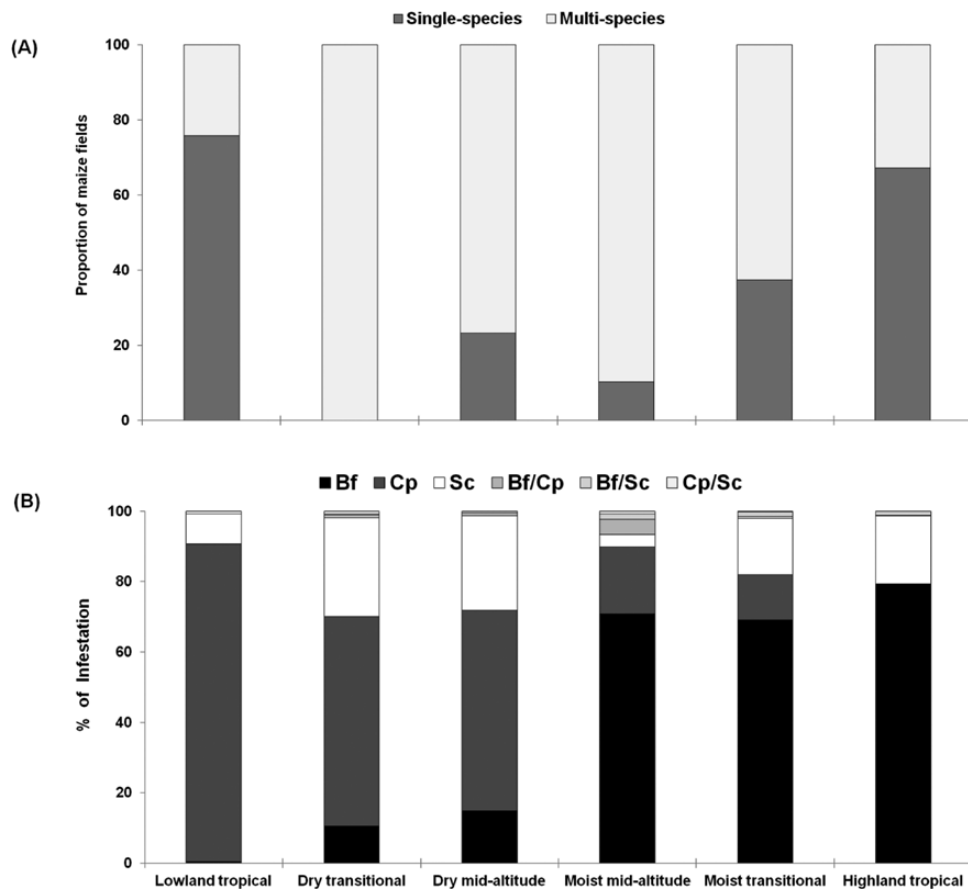


Fig. 1. Proportion of single- and multi-species infestations at the field level (A) and of each species (B) in different AEZs.

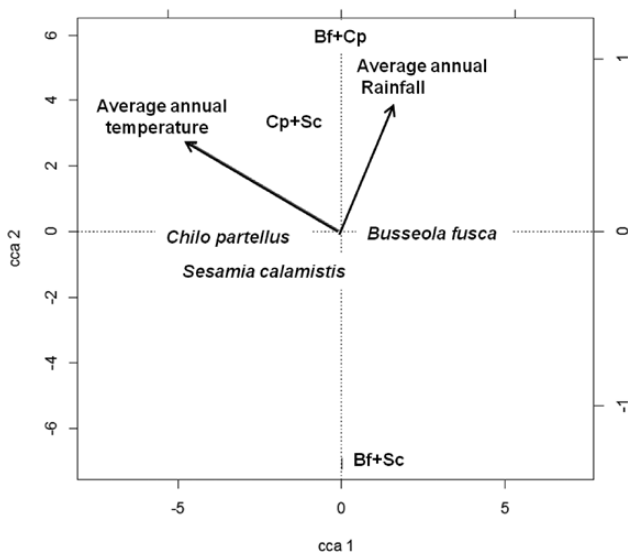


Fig. 2. Bi-plot showing the relationship between average annual temperature and rainfall and the occurrence of single- and multi-species communities consisting of *Busseola fusca* (Bf), *Chilo partellus* (Cp), and *Sesamia calamistis* (Sc).

Temperature was the most significant ( $P < 0.05$ ) environmental factor influencing the composition of stemborer communities in all AEZs. Rainfall did not have a significant effect on the composition of stemborer communities at this higher spatial level (Table 1, C).

### Spatio-Temporal Dynamics of Infestation of Stemborer Species at Mid-Altitudes

#### Incidence of Infestation

The incidence of infested plants in fields increased over time in all three sampling periods (Fig. 3A). There was no significant difference in the incidence of infestation between seasons (Table 2).

#### Proportion of Single- and Multi-Species Infestation

Single-species infestations were more frequent than multi-species infestations during the three seasons. *Busseola fusca* was the dominant species during all three seasons. However, during the long rainy season, the proportion of infestation by *S. calamistis* was higher than those of the two other species early in the season. Thereafter, *B. fusca* dominated from mid-season onwards until the end of the season. The occurrence of single-species infestation of *C. partellus* and multi-species communities was higher during the long-rain season than during the short-rain seasons (Fig. 3B).

#### Spatial Distribution of Each Species Among Plants

Almost all fields harbored the presence of two stemborer species infesting maize plants, with *B. fusca* as the dominant species associated either with *C. partellus* and/or *S. calamistis*. Only one field had single-species infestation of *B. fusca*. Irrespective of the species present, spatial distribution followed a clustered pattern (Fig. 4). *Busseola fusca* as the dominant species showed a clustered intraspecific and interspecific distribution with *C. partellus* and *S. calamistis* in almost all fields during both the short- and long-rain seasons (Fig. 4).

**Table 1.** Results of multivariate analysis (CCA) of the influence of temperature and rainfall on stemborer communities at the AEZ level

		Inertia	Proportion
A)	Total	0.877	1
	Constrained	0.492	0.561
	Unconstrained	0.385	0.439
B)	Importance of components	CCA1	CCA2
	Eigenvalue	0.49	0.002
	Proportion explained	0.558	0.003
	Cumulative proportion	0.558	0.561
C)		F	P-value
	Average annual temperature	18.5	0.001
	Average annual rainfall	2.4	0.29

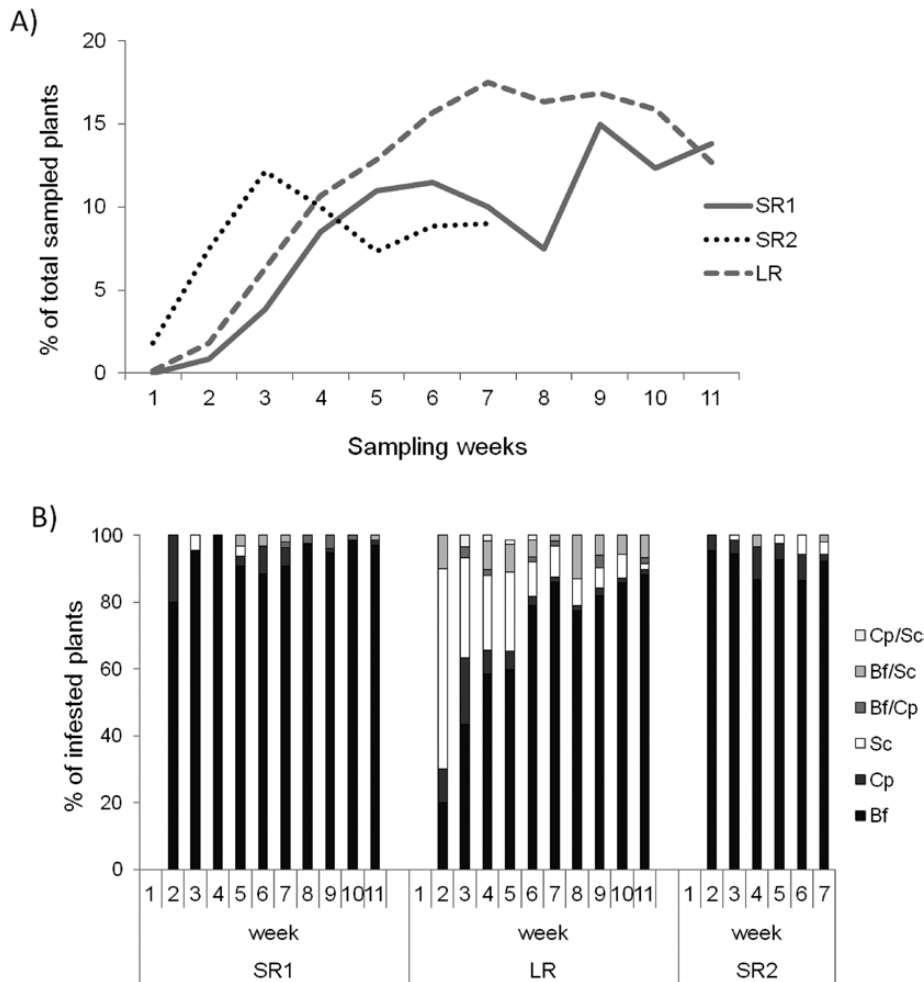
(A) The proportion of variation in stemborer community composition explained by the axes of the bi-plot (constrained) and the unexplained or residuals of regression (unconstrained); (B) eigenvalues of each axes of the bi-plot, showing their contributions to the explained variations in the compositional stemborer data; and (C) results from the forward selection method to test the significance of the influence of average annual temperature and average annual rainfall on the composition and distribution of the different stemborer communities. Number of permutations = 9,999.

**Effect of Sampling Season, Temperature, and Rainfall on Larval Density**

*Busseola fusca* had the highest larval density compared with *C. partellus* and *S. calamistis*, for all seasons (Fig. 5). However, the larval density of *B. fusca* was not significantly different between the SR and LR seasons. Larval densities of *C. partellus* and *S. calamistis* were significantly different between the LR season and the SR seasons. These variations in larval densities of all the three species were significantly affected by temperature and rainfall (Table 3).

**Discussion**

This study showed the extent of single- and multi-species infestations of maize stemborers, as they occur, at both plant and field level in different AEZs prior to the establishment of *S. frugiperda*. Furthermore, the study indicates the level of potential intraspecific (single-species infestations) and interspecific (multi-species) interactions that occur in stemborer multi-species interactions in maize. Such interactions among lepidopteran stemborers sharing the same maize resource could be competitive, as previously shown by Ntiri et al. (2016, 2017) in laboratory and greenhouse experiments. These field and plant levels present finer spatial scales to understand the processes responsible for the formation of different compositions of stemborer communities in each AEZ (Wiens 1989, Levin 1992).



**Fig. 3.** (A) Incidence of stemborer-infested plants over time during the different cropping seasons in Makuyu. (B) The incidence of plants infested with single-species and combinations of *Busseola fusca* (Bf), *Chilo partellus* (Cp), and *Sesamia calamistis* (Sc) over time during the different cropping seasons at Makuyu. LR, long-rain season; SR, short-rain season.

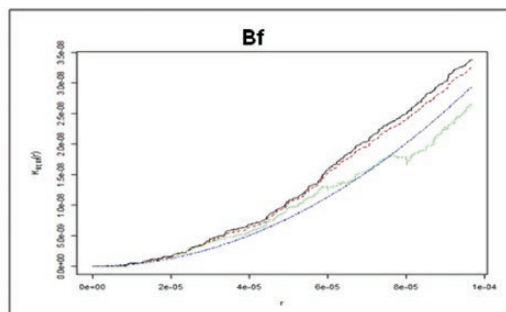
The proportion of single- or multi-species infestations varied with spatial scale. Single-species infestations were pronounced at the plant level, while multi-species infestations were pronounced at field and AEZ scales. Spatial scaling influences the degree of community concordance (or similarity in patterns; Paavola et al. 2006). The variability of stemborer infestations among spatial scales could be due to the habitat specializations of the different stemborer species at the broader agro-ecological scale and also the variable influence of environmental factors at different spatial scales (Kneitel and Chase 2004). This study indeed established that temperature is the primary factor influencing the formation and spatio-temporal dynamics of multi-species stemborer communities at all spatial levels, while the impact of rainfall was limited to the local (finer) levels only. Furthermore, these factors also affect the varied composition of stemborer communities as found in this region. Intra- and interspecific infestations by communities of only *C. partellus* and *S. calamistis* characterize AEZs found in warmer temperatures. The two species, although congenerically different, are physiologically adapted to higher temperatures than *B. fusca* (Khadioli et al. 2014a,b). In addition, higher temperatures also enhance the competitive edge of *C. partellus* over the noctuids in their common use or co-infestations of maize crops (Ntiri et al. 2016). On the other hand, AEZs with high rainfall, but lower temperatures, are favorable for the domination of *B. fusca* in multi-infestations. It was

reported from South Africa that seasons of high rainfall, through its accompanying humidity, was likely to result in higher infestation levels of *B. fusca* (Van Rensburg et al. 1987). This further indicates that the areas of co-existence and stemborer community structure may be predicted on the basis of rainfall and temperature conditions that are favorable for their survival. So multi-species infestations by *C. partellus* and *S. calamistis* are therefore likely to be high in regions with higher temperatures, while *B. fusca* is likely to dominate in areas with relatively high rainfall and lower temperatures (Guofa et al. 2001, Ong'amo et al. 2006a).

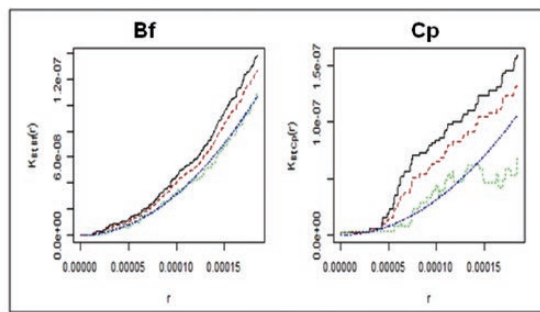
Irrespective of the different compositions, most maize fields are infested by at least a two-species complex of stemborers. It appears that the complexity of stemborer communities increases away from the two extreme AEZs, which favors high single-species infestations of either *B. fusca* or *C. partellus*. The Moist mid-altitude can be described as a 'transitional zone' where all three species are found infesting the same maize fields. Further, these infestations could be characterized by intra- and interspecific interactions (potentially competition) between the multi-species communities utilizing the same maize stems (Ntiri et al. 2016, 2017). The infestation levels also vary spatially and over time (in-season and between seasons). For instance, infestations by *S. calamistis* and *C. partellus* and multi-species infestations of the three species were higher during the long than the short rainy season, albeit with *B. fusca* predominating. Yet, sampling done in the same area between 2001 and 2006 showed that the density of *B. fusca* and *C. partellus* varied in dominance over years (B. P. Le Ru, unpublished data). Such rotation in dominance of species with seasons seems a characteristic of multi-species stemborer communities, as similar observations have also been reported for a community of stemborers in Eastern Uganda (Matama-Kauma et al. 2001), Cameroon (Ndemah et al. 2001b), and South Africa (Van Rensburg et al. 1987; Van Rensburg and Van den Berg 1992). Given that all three species occur together in the Moist mid-altitudes,

**Table 2.** Results from GLM (binomial) analysis of the incidence of stemborer infestation between seasons in Makuyu

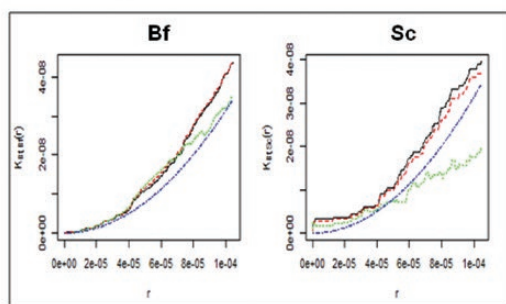
Seasons	OR (95% CI)	P-value
Short rain 1	1	
Long rain	1.25 (0.87–1.78)	0.24
Short rain 2	0.85 (0.58–1.25)	0.42



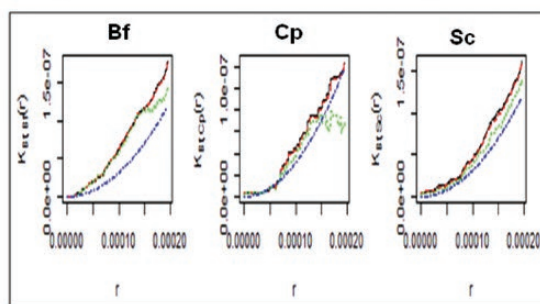
**Intraspecific distribution - *B. fusca***



**Interspecific distribution - *B. fusca* & *C. partellus***



**Interspecific distribution - *B. fusca* & *S. calamistis***



**Interspecific distribution - *B. fusca*, *C. partellus* & *S. calamistis***

**Fig. 4.** Clustered distribution pattern of *Busseola fusca* (Bf) intra-specifically and inter-specifically with *Chilo partellus* (Cp) and *Sesamia calamistis* (Sc) in maize fields.

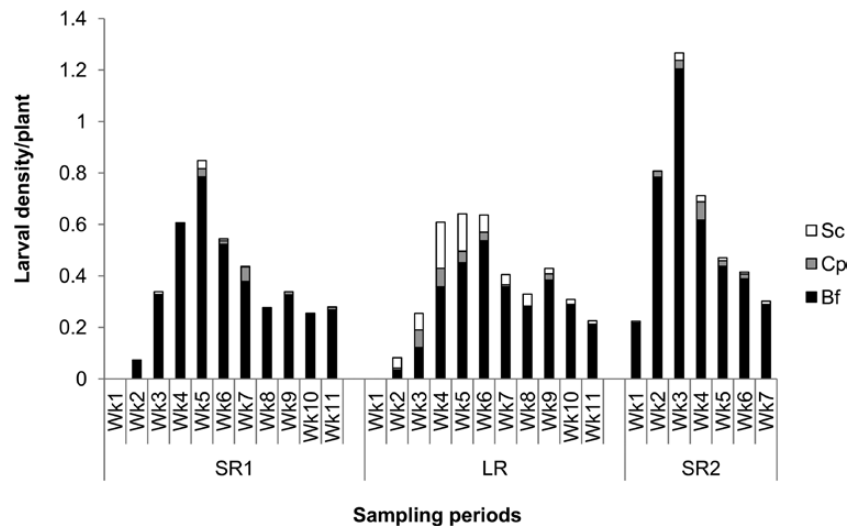


Fig. 5. Larvae density of *Busseola fusca*, *Chilo partellus*, and *Sesamia calamistis* in each sampling period.

Table 3. GLMM results on the variation of larval densities of the three species between seasons and the effects of temperature and rainfall

	Estimate	SE	z-value	P(> z )
<i>Busseola fusca</i>				
Long-rain vs short-rain season	0.015	0.047	0.311	>0.05
Temperature	0.093	0.013	7.353	<0.001
Rainfall	-0.088	0.005	-17.2	<0.001
<i>Chilo partellus</i>				
Long-rain vs short-rain season	1.518	0.251	6.037	<0.001
Temperature	0.394	0.067	5.919	<0.001
Rainfall	-0.252	0.033	-7.539	<0.001
<i>Sesamia calamistis</i>				
Long-rain vs short-rain season	4.661	0.347	13.421	<0.001
Temperature	0.575	0.078	7.374	<0.001
Rainfall	-0.191	0.025	-7.616	<0.001

the implication will be that maize fields in this AEZ will most likely have higher damage levels than in other areas, as the damage level here should be a combination of the individual damage that each stemborer species can cause (Van den Berg et al. 1991, Dangles et al. 2009). In fact, their combined contributions to potential maize harvest loss (26%) was the highest in this zone versus all other zones (see also Ong'amo et al. 2006a).

The intra- and interspecies clustered larval distribution patterns among the communities indicate that these could be intrinsic characteristics of these species. Ndjomatchoua et al. (2016) showed that the spatio-temporal pattern of damage by *B. fusca* in maize fields spreads from an initial patch of damaged plants to nearby undamaged maize plants. This clustering pattern by *B. fusca* has also been reported from South Africa (Van Rensburg and Pringle 1989), the forest zones of Cameroon (Ndemah et al. 2001a), and West Africa (Gounou and Schulthess 2004) and also by *C. partellus* on the Kenya coast (Overholt et al. 1994). Thus, the incidence of multi-species infestations of a single maize stem could therefore be by means of the movement of larvae of different species from one plant, to co-infest adjacent, or nearby infested maize plants (Van den Berg et al. 1991, Ndemah et al. 2001a, Erasmus et al. 2016) or from oviposition by stemborer females, mediated by the conspecific or heterospecific infested plant (Ntiri et al. 2018). With future changes in climatic conditions, especially where ambient temperature increases, one

possible impact could be the change in the community structure of multi-species stemborers, especially in the mid-altitude and highland areas, where *C. partellus* might displace *B. fusca* as the dominant species. Recent reports show that *C. partellus*, with its superior basal and higher thermal tolerance plasticity (Mutamiswa et al. 2018), and highly competitive ability in interspecific interactions at higher temperatures (Ntiri et al. 2016, 2017), compared to the indigenous noctuids, is expanding its range into highlands regions (Khadioli et al. 2014b). It is also likely that if climatic change induces more frequent rainfall, especially in low-rainfall areas, *B. fusca* has the potential to become established and possibly dominate stemborer infestations in these regions.

Moreover, there is additional uncertainty regarding how intra- and interspecific interactions in stemborer communities will change in the presence of *S. frugiperda* which now infests maize throughout sub-Saharan Africa (Prasanna et al. 2018). Several studies in the Americas report that *S. frugiperda* is a tropical species that does not go into diapause (Johnson 1987, Goergen et al. 2016, Prasanna et al. 2018). The optimum temperature for its larval development and growth is between 25 and 30°C (Isenhour et al. 1985, Barfield and Ashley 1987, Ali et al. 1990), similar to that of the established invasive *C. partellus* (25–32°C; Khadioli et al. 2014b) and of *B. fusca* and *S. calamistis* (20–30°C; Khadioli et al. 2014a, Glatz et al. 2017). However, *S. frugiperda* has a shorter developmental



**Table 4.** Developmental time for the fall armyworm (*Spodoptera frugiperda*) and African stemborer species (*Chilo partellus*, *Busseola fusca*, and *Sesamia calamistis*) under different constant temperatures within their optimum temperature range

Temperature	Mean development time (days from egg hatch to adult eclosion)			
	<i>Spodoptera frugiperda</i> <sup>a</sup>	<i>Chilo partellus</i> <sup>b</sup>	<i>Busseola fusca</i> <sup>c</sup>	<i>Sesamia calamistis</i> <sup>c</sup>
25°C	28.4	42.1	65.4	57.7
30°C	19.3	28.9	74.7	45.2

<sup>a</sup>Barfield and Ashley (1987).<sup>b</sup>Khadioli et al. (2014b).<sup>c</sup>Khadioli et al. (2014a).

time than all three stemborer species under these temperatures (Table 4). In addition, *S. frugiperda* larvae are known for its voracity on gramineous crops, and superior competitive abilities to other noctuids that inhabit the same guild (Goergen et al. 2016, Bentivenha et al. 2017). The species is also cannibalistic (Chapman et al. 1999, 2000).

Three possible scenarios are likely to emerge with the future co-existence of *S. frugiperda* and other lepidopteran stemborers in Africa. First, *S. frugiperda* may be additive to the already established lepidopteran complex that attacks maize, depending on the intensity of competition with these stemborers. The intensity of competition may be influenced by the trade-offs between FAW cannibalism and/or predation on other lepidopteran species in their multi-species infestations. This will likely change the structure and dynamics of multi-species communities of stemborers that attack maize. Such changes in community structure, through possible elimination or significant suppression, may also influence secondary pest formation (Truter et al. 2014). Secondly, increased damage to cereal crops, particularly maize, may result due to the combined infestations of *S. frugiperda* and the already established stemborer complex (Goergen et al. 2016). It is unclear how variation in temperature and rainfall are likely to enhance or otherwise alter the establishment of *S. frugiperda* in other regions of Africa, or how climate change will influence the impacts of the lepidopteran pest complex on the continent. Third, another possible scenario is that stemborer damage levels to maize may decrease due to *S. frugiperda* outcompeting and suppressing or possibly eliminating other established species in areas where multi-species communities occur. *Spodoptera frugiperda* control will likely change pest management in maize since it feeds and destroys whorl leaves as well as increasing ear damage, and also has a quicker generation than any of the other species.

Given the implications of this analysis, new research is needed to improve our understanding of interspecific competition among the existing stemborer species, within the context of the invasion of *S. frugiperda*, and to provide information that will contribute to the development of effective management tools to control the increasingly important lepidopteran pest complex which threatens food security in Africa. Thus, current research surveys should re-examine these infestation dynamics following *S. frugiperda* establishment in these different AEZs. These results also suggest that a comprehensive study which develops a model that incorporates climate change scenarios for temperature and rainfall (e.g., in the year 2025 and 2050), with intra- and interspecific stemborer interactions, should be undertaken, to more thoroughly examine potential outcomes.

## Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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## References Cited

- Ali, A., R. G. Luttrell, and J. C. Schneider. 1990. Effects of temperature and larval diet on development of the fall armyworm (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* 83: 725–733.
- Baddeley, A. 2008. Analysing spatial point patterns in R. Technical report, CSIRO, 2010. Version 4. ([www.csiro.au/resources/pf16h.html](http://www.csiro.au/resources/pf16h.html)) (accessed 27 July 2014).
- Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown, J. Butterfield, A. Buse, J. C. Coulson, and J. Farrar. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biol.* 8: 1–16.
- Barfield, C., and T. Ashley. 1987. Effects of corn phenology and temperature on the life cycle of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Fla. Entomol.* 70: 110–116.
- Bate, R., and J. Van Rensburg. 1992. Predictive estimation of maize yield loss caused by *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) in maize. *S. Afr. J. Plant Soil* 9: 150–154.
- Bate, R., G. D. J. Van Rensburg, and J. B. J. Van Rensburg. 1991. Distribution and occurrence of stem-borer *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) on maize in South Africa. *J. Afr. Zool.* 105: 11–15.
- Bentivenha, J. P., D. G. Montezano, T. E. Hunt, E. L. Baldin, J. A. Peterson, V. S. Victor, L. E. Pannuti, A. M. Vélaz, and S. V. Paula-Moraes. 2017. Intraguild interactions and behavior of *Spodoptera frugiperda* and *Helicoverpa* spp. on maize. *Pest Manag. Sci.* 73: 2244–2251.
- Bivand, R. S., E. J. Pebesma, V. Gómez-Rubio, and E. J. Pebesma. 2008. *Applied spatial data analysis with R*. Springer, New York.
- Chapman, J. W., T. Williams, A. Escibano, P. Caballero, R. D. Cave, and D. Goulson. 1999. Fitness consequences of cannibalism in the fall armyworm, *Spodoptera frugiperda*. *Behav. Ecol.* 10: 298–303.
- Chapman, J. W., T. Williams, A. M. Martínez, J. Cisneros, P. Caballero, R. D. Cave, and D. Goulson. 2000. Does cannibalism in *Spodoptera frugiperda* (Lepidoptera: Noctuidae) reduce the risk of predation? *Behav. Ecol. Sociobiol.* 48: 321–327.
- Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* 122: 661–696.
- Cornelissen, T. 2011. Climate change and its effects on terrestrial insects and herbivory patterns. *Neotrop. Entomol.* 40: 155–163.

- Cornelissen, T., G. Wilson Fernandes, and J. Vasconcellos-Neto. 2008. Size does matter: variation in herbivory between and within plants and the plant vigor hypothesis. *Oikos* 117: 1121–1130.
- Cugala, D., and C. Omwega. 2001. Cereal stemborer distribution and abundance, and introduction and establishment of *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) in Mozambique. *Int. J. Trop. Insect Sci.* 21: 281–287.
- Damos, P., and M. Savopoulou-Soultani. 2012. Temperature-driven models for insect development and vital thermal requirements. *Psyche* 2012: 13.
- Dangles, O., V. Mesías, V. Crespo-Perez, and J.-F. Silvain. 2009. Crop damage increases with pest species diversity: evidence from potato tuber moths in the tropical Andes. *J. Appl. Ecol.* 46: 1115–1121.
- Denno, R. F., M. S. McClure, and J. R. Ott. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. *Annu. Rev. Entomol.* 40: 297–331.
- Dunson, W. A., and J. Travis. 1991. The role of abiotic factors in community organization. *Am. Nat.* 138: 1067–1091.
- Ebenebe, A., J. Van den Berg, and T. D. K. Van der Linde. 1999. Distribution and relative abundance of stalk borers of maize and grain sorghum in Lesotho. *Afr. Plant Protect.* 5: 77–82.
- Ebenebe, A., J. Van den Berg, and T. Van der Linde. 2001. Farm management practices and farmers' perceptions of stalk-borers of maize and sorghum in Lesotho. *Int. J. Pest Manage.* 47: 41–48.
- Erasmus, A., J. Marais, and J. Van den Berg. 2016. Movement and survival of *Busseola fusca* (Lepidoptera: Noctuidae) larvae within maize plantings with different ratios of non-Bt and Bt seed. *Pest Manag. Sci.* 72: 2287–2294.
- Estay, S., M. Lima, and F. Labra. 2009. Predicting insect pest status under climate change scenarios: combining experimental data and population dynamics modelling. *J. Appl. Entomol.* 133: 491–499.
- Glatz, J., H. du Plessis, and J. Van den Berg. 2017. The effect of temperature on the development and reproduction of *Busseola fusca* (Lepidoptera: Noctuidae). *Bull. Entomol. Res.* 107: 39–48.
- Goergen, G., P. L. Kumar, S. B. Sankung, A. Togola, and M. Tamò. 2016. First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera, Noctuidae), a new alien invasive pest in West and Central Africa. *PLoS ONE* 11: e0165632.
- Gounou, S., and F. Schulthess. 2004. Spatial distribution of lepidopterous stem borers on indigenous host plants in West Africa and its implications for sampling schemes. *Afr. Entomol.* 12: 171–178.
- Guofa, Z., W. A. Overholt, and M. B. Mochiah. 2001. Changes in the distribution of lepidopteran maize stemborers in Kenya from the 1950s to 1990s. *Int. J. Trop. Insect Sci.* 21: 395–402.
- Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. *Am. Nat.* 140: 539–572.
- Hassan, R. M., J. D. Corbett, and K. Njoroge. 1998. Combining geo-referenced survey data with agroclimatic attributes to characterize maize production systems in Kenya, pp. 43–68. *In* R. M. Hassan (ed.), *Maize technology development and transfer: a GIS application for research planning in Kenya*. CAB International, Wallington, Oxon, United Kingdom.
- Hawkins, C. P., and J. A. MacMahon. 1989. Guilds: the multiple meanings of a concept. *Annu. Rev. Entomol.* 34: 423–451.
- Hodkinson, I. D. 2005. Terrestrial insects along elevation gradients: species and community responses to altitude. *Biol. Rev. Camb. Philos. Soc.* 80: 489–513.
- Howe, R. W. 1967. Temperature effects on embryonic development in insects. *Annu. Rev. Entomol.* 12: 15–42.
- Hudson, E. E., and P. Stiling. 1997. Exploitative competition strongly affects the herbivorous insect community on *Baccharis halimifolia*. *Oikos* 79: 521–528.
- Imura, O. 2003. Herbivorous arthropod community of an alien weed *Solanum carolinense* L. *Appl. Entomol. Zool.* 38: 293–300.
- Isenhour, D. J., B. R. Wiseman, and N. W. Widstrom. 1985. Fall armyworm (Lepidoptera: Noctuidae) feeding responses on corn foliage and foliage/artificial diet medium mixtures at different temperatures. *J. Econ. Entomol.* 78: 328–332.
- Jiang, L., and P. J. Morin. 2004. Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. *J. Anim. Ecol.* 73: 569–576.
- Johnson, S. J. 1987. Migration and the life history strategy of the fall armyworm, *Spodoptera frugiperda* in the Western Hemisphere. *Insect Sci. Appl.* 8: 543–549.
- Kalule, T., M. Ogenga-Latigo, and V. Okoth. 1997. Seasonal fluctuations and damage of lepidopteran stemborers of maize in a major agroecozone of Uganda. *Afr. Crop Sci. J.* 5: 385–393.
- Kaplan, I., and R. F. Denno. 2007. Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecol. Lett.* 10: 977–994.
- Kaplan, I., and M. D. Eubanks. 2005. Aphids alter the community-wide impact of fire ants. *Ecology* 86: 1640–1649.
- Karban, R. 1986. Interspecific competition between folivorous insects on *Erigeron glaucus*. *Ecology* 67: 1063–1072.
- Kfir, R. 1997. Competitive displacement of *Busseola fusca* (Lepidoptera: Noctuidae) by *Chilo partellus* (Lepidoptera: Pyralidae). *Ann. Entomol. Soc. Am.* 90: 619–624.
- Kfir, R., W. A. Overholt, Z. R. Khan, and A. Polaszek. 2002. Biology and management of economically important lepidopteran cereal stem borers in Africa. *Annu. Rev. Entomol.* 47: 701–731.
- Khadioli, N., Z. E. H. Tonnang, G. O. Ong'amo, T. Achia, I. Kipchirchir, J. Kroschel, and B. P. Le Ru. 2014a. Effect of temperature on the life history parameters of noctuid lepidopteran stem borers, *Busseola fusca* and *Sesamia calamistis*. *Ann. Appl. Biol.* 165: 373–386.
- Khadioli, N., Z. E. H. Tonnang, E. Muchugu, G. Ong'amo, T. Achia, I. Kipchirchir, J. Kroschel, and B. P. Le Ru. 2014b. Effect of temperature on the phenology of *Chilo partellus* (Swinhoe) (Lepidoptera, Crambidae); simulation and visualization of the potential future distribution of *C. partellus* in Africa under warmer temperatures through the development of life-table parameters. *Bull. Entomol. Res.* 104: 809–822.
- Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecol. Lett.* 7: 69–80.
- Krüger, W., J. Van den Berg, and H. Van Hamburg. 2008. The relative abundance of maize stem borers and their parasitoids at the Tshiombo irrigation scheme in Venda, South Africa. *S. Afr. J. Plant Soil* 25: 144–151.
- Le Ru, B. P., G. O. Ong'amo, P. Moyal, L. Ngala, B. Musyoka, Z. Abdullah, D. Cugala, B. Defabachew, T. Haile, and T. K. Matama. 2006. Diversity of lepidopteran stem borers on monocotyledonous plants in eastern Africa and the islands of Madagascar and Zanzibar revisited. *Bull. Entomol. Res.* 96: 555–563.
- Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award Lecture. *Ecology* 73: 1943–1967.
- Lewinsohn, T. M., V. Novotny, and Y. Basset. 2005. Insects on plants: diversity of herbivore assemblages revisited. *Ann. Rev. Ecol. Evol. Syst.* 36: 597–620.
- Liss, W., L. Gut, and P. Westgard. 1986. Perspectives on arthropod community structure, organization, and development in agricultural crops. *Annu. Rev. Entomol.* 31: 455–478.
- Matama-Kauma, T., S. Kyamanywa, J. Ogwang, C. Omwega, and H. Willson. 2001. Cereal stemborer species complex and establishment of *Cotesia flavipes* Cameron in eastern Uganda. *Int. J. Trop. Insect Sci.* 21: 317–325.
- Moolman, J., J. Van den Berg, D. Conlong, D. Cugala, S. Siebert, and B. Le Ru. 2014. Species diversity and distribution of lepidopteran stem borers in South Africa and Mozambique. *J. Appl. Entomol.* 138: 52–66.
- Mutamiswa, R., F. Chidawanyika, and C. Nyamukondiwa. 2017. Dominance of spotted stemborer *Chilo partellus* Swinhoe (Lepidoptera: Crambidae) over indigenous stemborer species in Africa's changing climates: ecological and thermal biology perspectives. *Agric. Forest Entomol.* 19: 344–356.
- Mutamiswa, R., F. Chidawanyika, and C. Nyamukondiwa. 2018. Superior basal and plastic thermal responses to environmental heterogeneity in invasive exotic stemborer *Chilo partellus* Swinhoe over indigenous *Busseola fusca* (Fuller) and *Sesamia calamistis* Hampson. *Physiol. Entomol.* 43: 108–119.
- Ndemah, R., F. Schulthess, M. Pochling, and C. Borgemeister. 2001a. Spatial dynamics of lepidopterous pests on *Zea mays* (L.) and *Pennisetum purpureum* (Moench) in the forest zone of Cameroon and their implications for sampling schemes. *J. Appl. Entomol.* 125: 507–514.
- Ndemah, R., F. Schulthess, S. Korie, C. Borgemeister, and K. F. Cardwell. 2001b. Distribution, relative importance and effect of lepidopterous

- borers on maize yields in the forest zone and mid-altitude of Cameroon. *J. Econ. Entomol.* 94: 1434–1444.
- Ndjomatchoua, F. T., H. E. Tonnang, C. Plantamp, P. Campagne, C. Tchawoua, and B. P. Le Ru. 2016. Spatial and temporal spread of maize stem borer *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) damage in smallholder farms. *Agric. Ecosys. Environ.* 235: 105–118.
- Ntiri, E. S., P. A. Calatayud, J. Van Den Berg, F. Schulthess, and B. P. Le Ru. 2016. Influence of temperature on intra- and interspecific resource utilization within a community of lepidopteran maize stemborers. *PLoS ONE* 11: e0148735.
- Ntiri, E. S., P. A. Calatayud, J. Van den Berg, and B. P. Le Ru. 2017. Density dependence and temporal plasticity of competitive interactions during utilisation of resources by a community of lepidopteran stemborer species. *Entomol. Exp. Appl.* 162: 272–283.
- Ntiri, E. S., P.-A. Calatayud, B. Musyoka, J. Van den Berg, and B. P. Le Ru. 2018. Influence of feeding-damaged plants on the oviposition responses within a community of female moths. *Phytoparasitica* 46: 607–615.
- Ofomata, V., W. Overholt, A. V. Huis, R. Egwuatu, and A. Ngi-Song. 1999. Niche overlap and interspecific association between *Chilo partellus* and *Chilo orichalcociliellus* on the Kenya coast. *Entomol. Exp. Appl.* 93: 141–148.
- Ong'amo, G. O., B. P. Le Ru, S. Dupas, P. Moyal, P.-A. Calatayud, and J.-F. Silvain. 2006a. Distribution, pest status and agro-climatic preferences of lepidopteran stem borers of maize in Kenya. *Ann. Soc. Entomol. Fr.* 42: 171–177.
- Ong'amo, G. O., B. P. Le Ru, S. Dupas, P. Moyal, E. Muchugu, P.-A. Calatayud, and J.-F. Silvain. 2006b. The role of wild host plants in the abundance of lepidopteran stem borers along altitudinal gradient in Kenya. *Ann. Soc. Entomol. Fr.* 42: 363–370.
- Ovadia, O., and O. J. Schmitz. 2004. Weather variation and trophic interaction strength: sorting the signal from the noise. *Oecologia* 140: 398–406.
- Overholt, W., K. Ogedah, and P. Lammers. 1994. Distribution and sampling of *Chilo partellus* (Lepidoptera: Pyralidae) in maize and sorghum on the Kenya coast. *Bull. Entomol. Res.* 84: 367–378.
- Paavola, R., T. Muotka, R. Virtanen, J. Heino, D. Jackson, and A. Maki-Petäys. 2006. Spatial scale affects community concordance among fishes, benthic macroinvertebrates, and bryophytes in streams. *Ecol. Appl.* 16: 368–379.
- Polaszek, A., and Z. R. Khan. 1998. Host plants, pp. 3–10. *In* A. Polaszek (ed.), *African cereal stem borers; economic importance, taxonomy, natural enemies and control*. CAB International, Wallingford, United Kingdom.
- Prasanna, B., J. Huesing, R. Eddy, and V. Peschke. 2018. *Fall armyworm in Africa: a guide for integrated pest management*. CIMMYT, CDMX, Mexico.
- R Development Core Team. 2017. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reddy, K. 1998. Maize and sorghum: East Africa, pp. 25–27. *In* A. Polaszek (ed.), *African cereal stem borers: economic importance, taxonomy, natural enemies and control*. CABI, Wallingford, United Kingdom.
- Sánchez-Galván, I. R., J. Quinto, E. Micó, E. Galante, and M. A. Marcos-García. 2014. Facilitation among saproxylic insects inhabiting tree hollows in a Mediterranean forest: the case of cetonids (Coleoptera: Cetoniidae) and syrphids (Diptera: Syrphidae). *Environ. Entomol.* 43: 336–343.
- Sanders, N. J., R. T. Belote, and J. F. Weltzin. 2004. Multitrophic effects of elevated atmospheric CO<sub>2</sub> on understory plant and arthropod communities. *Environ. Entomol.* 33: 1609–1616.
- Simberloff, D., and T. Dayan. 1991. The guild concept and the structure of ecological communities. *Ann. Rev. Ecol. Syst.* 22: 115–143.
- Soler, R., F. R. Badenes-Pérez, C. Broekgaarden, S. J. Zheng, A. David, W. Boland, and M. Dicke. 2012. Plant-mediated facilitation between a leaf-feeding and a phloem-feeding insect in a brassicaceous plant: from insect performance to gene transcription. *Funct. Ecol.* 26: 156–166.
- Soul-kifouly, G. M., H. D. Affognon, I. Macharia, G. Ong'amo, E. Abonyo, G. Ogola, H. De Groot, and B. LeRu. 2016. Assessing the long-term welfare effects of the biological control of cereal stemborer pests in East and Southern Africa: evidence from Kenya, Mozambique and Zambia. *Agric. Ecosys. Environ.* 230: 10–23.
- Speight, M. R., M. D. Hunter, and A. D. Watt. 2008. *Ecology of insects: concepts and applications*, 2nd ed. John Wiley & Sons Ltd, Chichester, United Kingdom.
- Sporleder, M., J. Kroschel, M. R. G. Quispe, and A. Lagnaoui. 2004. A temperature-based simulation model for the potato tuberworm, *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae). *Environ. Entomol.* 33: 477–486.
- Stam, J. M., A. Kroes, Y. Li, R. Gols, J. J. van Loon, E. H. Poelman, and M. Dicke. 2014. Plant interactions with multiple insect herbivores: from community to genes. *Annu. Rev. Plant Biol.* 65: 689–713.
- Stiling, P., A. M. Rossi, M. Cattell, and T. I. Bowdish. 1999. Weak competition between coastal insect herbivores. *Fla Entomol.* 82: 599–608.
- Strong, D. R., J. H. Lawton, and S. R. Southwood. 1984. *Insects on plants. Community patterns and mechanisms*. Blackwell Scientific Publications, Oxford, United Kingdom.
- Sutherland, W. J., R. P. Freckleton, H. C. J. Godfray, S. R. Beissinger, T. Benton, D. D. Cameron, Y. Carmel, D. A. Coomes, T. Coulson, and M. C. Emmerson. 2013. Identification of 100 fundamental ecological questions. *J. Ecol.* 101: 58–67.
- Tefera, T. 2004. Lepidopterous stem borers of sorghum and their natural enemies in eastern Ethiopia. *Trop. Sci.* 44: 128–130.
- Truter, J., H. Van Hamburg, and J. Van Den Berg. 2014. Comparative diversity of arthropods on Bt maize and non-Bt maize in two different cropping systems in South Africa. *Environ. Entomol.* 43: 197–208.
- Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11: 1351–1363.
- Van den Berg, J., and A. Ebenebe. 2001. Integrated management of stemborers in Lesotho. *Int. J. Trop. Insect Sci.* 21: 389–394.
- Van den Berg, J., and J. Van Rensburg. 1996. Comparison of various directional insecticide sprays against *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Pyralidae) in sorghum and maize. *S. Afr. J. Plant Soil* 13: 51–54.
- Van den Berg, J., J. Van Rensburg, and M. Van der Westhuizen. 1991. The effect of single and mixed populations of *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Pyralidae) on damage to grain sorghum. *J. Entomol. Soc. S. Afr.* 54: 231–242.
- Van den Berg, J., G. Van Rensburg, and M. Van Der Westhuizen. 1997. Economic threshold levels for *Chilo partellus* (Lepidoptera: Pyralidae) control on resistant and susceptible sorghum plants. *Bull. Entomol. Res.* 87: 89–93.
- Van den Berg, J., A. F. Nur, and A. Polaszek. 1998. Cultural control, pp. 333–347. *In* A. Polaszek (ed.), *African cereal stem borers; economic importance, taxonomy, natural enemies and control*. CAB International, Wallingford, United Kingdom.
- Van Rensburg, J. B. J., and K. L. Pringle. 1989. A sequential sampling technique for surveys of eggs laid by the maize stalk borer, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). *J. Entomol. Soc. S. Afr.* 52: 223–228.
- Van Rensburg, J. B. J., and J. Van den Berg. 1992. Infestation patterns of the stalk borers *Busseola fusca* Fuller (Lep.: Noctuidae) and *Chilo partellus* Swinhoe (Lep.: Pyralidae) in grain sorghum. *J. Entomol. Soc. S. Afr.* 55: 197–212.
- Van Rensburg, J., G. Van Rensburg, J. Giliomee, and M. Walters. 1987. The influence of rainfall on the seasonal abundance and flight activity of the maize stalk borer, *Busseola fusca* in South Africa. *S. Afr. J. Plant Soil* 4: 183–187.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Funct. Ecol.* 3: 385–397.
- Woiwod, I. P. 1997. Detecting the effects of climate change on Lepidoptera. *J. Insect Conserv.* 1: 149–158.
- Wootton, J. T., and M. Emmerson. 2005. Measurement of interaction strength in nature. *Ann. Rev. Ecol. Evol. Syst.* 36: 419–444.
- Yonow, T., D. J. Kriticos, N. Ota, J. Van Den Berg, and W. D. Hutchison. 2017. The potential global distribution of *Chilo partellus*, including consideration of irrigation and cropping patterns. *J. Pest Sci.* (2004). 90: 459–477.
- Zuur, A., E. N. Ieno, and G. M. Smith. 2007. *Analysing ecological data*. Springer Science & Business Media, Springer-Verlag, New York.