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Author(s): S. Mwalusepo, E.S. Massawe, T. Johansson, E. Abdel-Rahman, M. Gathara, E. Njuguna, P.A. Calatayud, O.J. James, T. Landmann & B.P. Le Ru

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Modelling the distributions of maize stem borers at local scale in East African mountain gradients using climatic and edaphic variables

S. Mwalusepo^{1,2*}, E.S. Massawe³, T. Johansson^{1,4}, E. Abdel-Rahman^{1,5},
M. Gathara⁶, E. Njuguna¹, P.A. Calatayud^{1,7}, O.J. James⁸, T. Landmann¹ &
B.P. Le Ru^{1,7}

¹ICIPe – International Centre of Insect Physiology and Ecology, P.O. Box 30772-00100, Nairobi, Kenya

²Department of General Studies, Dar es Salaam Institutes of Technology, P.O. Box 2958, Dar es Salaam, Tanzania

³Department of Mathematics, University of Dar es Salaam, P.O. Box 35062, Dar es Salaam, Tanzania

⁴Department of Geosciences and Geography, University of Helsinki, P.O. Box 68, FI-00014, Finland

⁵Department of Agronomy, Faculty of Agriculture, University of Khartoum, Khartoum North 13314, Sudan

⁶Kenya Forestry Research Institute (KEFRI), P.O. Box 20412-00200, Nairobi, Kenya

⁷UMR IRD 247, Laboratoire Evolution, Comportement et Ecologie, Diversité, Ecologie et Evolution des Insectes Tropicaux, CNRS, 91198 Gif/Yvette, France and Université Paris-Sud 11, 91405, Orsay, France

⁸Invertebrate Zoology Section, National Museums of Kenya, P.O. Box 40658, 00100, Nairobi, Kenya

Lepidopteran stem borers are among the most important pests of maize in East Africa. Understanding the factors that influence maize stem borers' distribution is crucial in predicting their response to future climate change. The hypothesis of this study was that the potential distribution of the maize stem borers *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) and *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) at small scale along altitudinal gradients at Mount Kilimanjaro and Taita Hills in Tanzania and Kenya, respectively, depends on other climatic and edaphic factors besides temperature. The species distribution was studied using the maximum entropy (Maxent) application with three climatic (temperature, rainfall and relative humidity) and five soil variables [soil silicon (Si), potassium (K), phosphorus (P), nitrogen (N) concentrations and water-holding capacity (WHc)]. The model accuracy was evaluated using area under the curve (AUC) values based on 25 % independent test data set. The results revealed that in addition to temperature, rainfall, and relative humidity, soil characteristics were affecting the geographical distribution of *C. partellus* and *B. fusca* at both the Mount Kilimanjaro and Taita Hills study sites. The relative importance of all studied variables varied between the two study sites. At Mount Kilimanjaro, WHc exhibited the greatest influence on *C. partellus* distribution while at Taita Hills it was relative humidity. For *B. fusca* distribution, the temperature was found more crucial at both Mount Kilimanjaro and Taita Hills.

Key words: *Chilo partellus*, *Busseola fusca*, Taita Hills, Mount Kilimanjaro, climatic and soil variables, potential distribution.

INTRODUCTION

Maize is one of the most important staple crops in East Africa (Smale *et al.* 2001; De Groote *et al.* 2004; AATF 2009) but production is constrained by various biotic and abiotic factors. In East Africa, the most important insect pests associated with maize are lepidopteran stem borers; among them are *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) and *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae) (Kfir *et al.* 2002; Ong'amo *et al.* 2006). The distribution of the lepidopteran stem borers

and relative abundance vary among different regions and altitudes depending on climatic and ecological conditions (Mwalusepo *et al.* 2015), maize variety, cropping pattern and soil fertility (Kfir *et al.* 2002).

Understanding the factors that influence the geographic distribution and abundance of insect species is crucial, because arthropods have species-specific responses to changes in the ecological attributes of their habitats, which vary in space



*Author for correspondence. E-mail: mwalusepo@yahoo.com

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and time (Blach-Overgaard *et al.* 2010; Wisz *et al.* 2013; Stewart *et al.* 2015). Comprehensive analyses of the factors determining the range limits of species are scarce despite decades of study (Gaston 2009; Wisz *et al.* 2013; Stewart *et al.* 2015). Temperature is often considered the most predominant factor determining insect species distribution and abundance on a large scale (Bale *et al.* 2002; Hodkinson 2005; Khadioli *et al.* 2014a, b). However, relative humidity and rainfall are also important factors determining the geographical distribution of insects. Insects are washed off crop plants by heavy rains (Lowe 1970; Moran *et al.* 1987; Sithole *et al.* 1989; Lawton 1990; Hill *et al.* 1993; Norris *et al.* 2002), and the intensity of precipitation is often associated with declines in insect populations (Weisser *et al.* 1997; Norris *et al.* 2002). Relative humidity, on the other hand, may influence insect growth and behaviour by affecting their ability to regulate water loss. Thus, low relative humidity is often detrimental to insect development and survival (Jay *et al.* 1971; Subramanyam & Hagstrum 1993; Dickerson 2007; Jaworski & Hilszczanski 2013; Norhisham *et al.* 2013).

Edaphic variables also affect plants directly or indirectly *via* changes in soil characteristics, which, in turn, influence development and survival of insects (Rasmann *et al.* 2014; Calatayud *et al.* 2016). The physiological state of the plant may also determine the expression of defence mechanisms such as secondary metabolites in dicotyledons and silicon in monocotyledons (Rasmann *et al.* 2014; Calatayud *et al.* 2016).

Soil component characteristics have been found to play an important role in determining the abundance of insect pests (Allsop *et al.* 1993; Ndemah *et al.* 1999; Calatayud *et al.* 2016). For instance, silicon (Si) helps the plants to overcome various adverse biotic and abiotic conditions (Epstein 1999; Ma 2004; Ma & Yamaji 2006; Calatayud *et al.* 2016) by mediating plant resistance against insect herbivores as a mechanical barrier to insects feeding (Vicari & Bazely 1993). This has been shown to significantly disturb the performance of larvae of lepidopteran stem borers such as *Sesamia calamistis* (Hampson) (Lepidoptera, Noctuidae) and *Eldana saccharina* Walker (Lepidoptera, Pyralidae) (Sétamou *et al.* 1993; Keeping & Meyer 2006; Kvedaras & Keeping 2007; Keeping *et al.* 2009; Kvedaras *et al.* 2009).

Other soil components such as nitrogen, on the

other hand, enhance not only plant growth but also the development of herbivores feeding on such plants (Mattson 1980). A survey in farmers' fields in West Africa showed a positive relationship between soil nitrogen and stem borer densities (Sétamou & Schulthess 1995). Also, nitrogen application increased survival and growth rates as well as the fecundity of *C. partellus* and *S. calamistis* (Sétamou *et al.* 1993; Jiang & Schulthess 2005; Mgoo *et al.* 2006). However, some plant nutrients such as potassium can have negative effects on herbivorous insects, for example on *B. fusca* and *S. calamistis* (Ndemah *et al.* 1999; Denké *et al.* 2000).

Phenology models that include a set of functions describing temperature-dependency have been developed to describe the life history of maize stem borers (Khadioli *et al.* 2014a, b). They were used to predict *C. partellus*, and *B. fusca* distribution and abundance at local scale in East Africa (Mwalusepo *et al.* 2015). These models and risk mapping tools have been shown to be useful for predictions on global, regional and local scales (Overholt *et al.* 2000; Khadioli *et al.* 2014a, b; Mwalusepo *et al.* 2015; Yonow *et al.* 2016). However, such models have limitations because they do not take into consideration other climatic factors such as precipitation and relative humidity and soil characteristics. Soil factors have rarely been used as input in ecological niche modelling (Gaisan & Zimmermann 2000) because of the high cost and long duration of field work required for relevant soil data (Piedallu *et al.* 2011). The objective of this study was to estimate the influence of climatic variables, *i.e.* rainfall, relative humidity and temperature, as well as soil characteristics on the distribution of the maize stem borers *C. partellus* and *B. fusca* at local scale along two East African mountain gradients on Mount Kilimanjaro, Tanzania, and in the Taita Hills, Kenya, respectively.

MATERIAL AND METHODS

Study sites

In Kenya, the study area was situated in Taita Hills in southeastern Kenya (Taita Taveta County), between latitude 3°25'S and longitude 38°20'E. In Tanzania, the study area was located in the Pangani River Basin in northeastern Tanzania with a focus on the small catchment areas on the southeastern slope of Mount Kilimanjaro, approximately between latitude 3°4'S and longitude

37°4'. A detailed description of the study sites was done by Mwalusepo *et al.* (2015).

Climatic data

The climatic data (temperature, relative humidity and rainfall) required for spatial simulations were obtained from locally installed weather stations. Automatic onset HOBO™ U10-003 data loggers (hourly records) and GENERAL® wireless rain gauges were installed at each station across the study sites within a minimum distance of 600 m from each other to keep track of daily maximum, minimum, monthly minimum, mean and maximum air temperatures (°C), relative humidity, and rainfall over a 3-year period (2012–2015). The six localities were selected for installing the data loggers and rain gauges (Mwalusepo *et al.* 2015). At each locality, the geographical coordinates (longitude and latitude) and altitudes in metres were recorded using a Global Positioning System receiver (German eTrex Vista®) with less than 3 m position accuracy.

Soil data

Soil sampling was conducted in 10 randomly selected cultivated maize plots in each locality using the protocol described by Calatayud *et al.* (2016). Each plot represented one replicate per altitudinal zone. First, 1–2 cm upper surface soil layers were removed to avoid contamination of the samples by foreign materials such as crop residues. A soil auger was used to collect three to four soil sub-samples at two depths (0–25 cm and 25–50 cm). Sampling was done during October 2012 when maize was in the mid-vegetative growth stages. For each plot, soil sub-samples were bulked and homogenised according to depth in order to obtain two samples per maize plot.

Concentrations (ppm) of silicon (Si), phosphorus (P), potassium (K) and nitrogen (N) in soils were determined by a private laboratory (Crop Nutrition Laboratory Service, Nairobi, Kenya). Si, P and K was extracted using Mehlich 3 extraction method (Mehlich 1984) with diluted ammonium fluoride (NH₄F) and ammonium nitrate (NH₄NO₃) was used. Si, P and K levels of each soil sample were determined by atomic emission spectrometry (Calatayud *et al.* 2016). The water-holding capacity (WHc) for each soil sample was determined using the 'European' maximum water-holding capacity (WHc) method of Gardner (1986). Briefly, each soil sample was saturated with

water in a cylinder and WHc was calculated based on the weight of the water held in the sample relative to the sample dry mass (dried at 105 °C for 24 h).

Stem borer data

Data on *C. partellus* and *B. fusca* were collected in maize fields along the two altitudinal gradients. Permissions to conduct research were obtained from the small-scale farmers of the plots sampled. The same protocol of Mwalusepo *et al.* (2015) was used. Briefly, a total of six localities per study site were selected on the basis of the annual mean temperature, whereby each locality differed from the closest one by 1 °C. Ten maize plots were randomly selected at each locality. All stem borers recovered were sorted according to their developmental stage and species, counted and placed individually in glass vials containing artificial diet developed by Onyango & Ochieng-Odero (1994). Each vial was labelled according to the larval stage, species name, location, plot number and date. The larvae were taken to the laboratory and kept until parasitoid emergence or pupae formation. Pupae were kept until adult emergence to confirm species identity. Stem borer occurrence data were used as response (dependent) variable to model their distribution at the test sites (Mwalusepo *et al.* 2015).

Data pre-processing and preparation

Three variables were selected as climatic factors, namely annual average temperature, annual average rainfall and relative humidity, while the soil factors considered were soil Si, K, P, N concentrations and WHc. The climatic and soil variables were interpolated to a 0.25 × 0.25 km resolution (grid size) using a thin plate spline algorithm. Data processing and analysis were carried out with a computer program written in R software (R Core Team 2014) and linked with a Geographic Information System (GIS). In R software all variables were generated as tiff raster layers in Arc 1960/UTM 37S WGS-84 (World Geodetic System 1984). A raster layer was converted to ASCII raster format as required for modelling purpose with same geographic reference system and grid size (Mwalusepo *et al.* 2016).

Modelling approach

The maximum entropy (Maxent) software, version 3.3.3k (Phillips *et al.* 2006) was used for

modelling the potential distribution of *C. partellus* and *B. fusca* using presence-only occurrence records. The Maxent was selected due to its computational efficiency (Elith *et al.* 2011; Fard *et al.* 2013; Brown *et al.* 2014; Chlond *et al.* 2015; Urbani *et al.* 2015; Georgopoulou *et al.* 2016). Models were calibrated using 75 % of the records of species occurrence data as training data, and the remaining 25 % were used test data. Twenty replicates and 5000 maximum iterations were set in the Maxent. Logistic output format was used to describe the probability of species presence (Phillips & Dudík 2008). A Jack-knife technique was used to examine the contribution of each environmental variable. A receiver operation characteristic (ROC) analysis was used to assess the accuracy and performance of the model (Chlond *et al.* 2015). A measure of the area under the ROC curve (AUC) was also calculated. The model with an AUC value of 1 indicates perfect discrimination, a value of 0.5 indicating that the model is not better, whereas AUC values higher than 0.75 are considered in the best model (Pearce & Ferrier 2000; Elith *et al.* 2006, 2011). The maximising sums of sensitivity and specificity (maxSSS) (Liu *et al.* 2005, 2013) were used to select threshold of occurrence for both *C. partellus* and *B. fusca*.

In addition, to address our hypothesis, we ran Maxent with 10 models based on different combinations of the variables for each stem borer species. These were single groups of variables in isolation: (1) temperature, (2) rainfall, (3) relative humidity, (4) soil Si, (5) soil K, (6) N, (7) soil P, and (8) soil WHc. The remaining models included a combination of all climate variables (9) (temperature + rainfall + relative humidity), and (10) a combination of all environmental variables (temperature + rainfall + relative humidity + silicon + potassium + nitrogen + phosphorus + water-holding capacity). Mathematically these models are defined as follows:

$$P(sp|T) = \frac{P(T|sp)P(sp)}{P(T)} \quad (1)$$

$$P(sp|R) = \frac{P(R|sp)P(sp)}{P(R)} \quad (2)$$

$$P(sp|Rh) = \frac{P(Rh|sp)P(sp)}{P(Rh)} \quad (3)$$

$$P(sp|Si) = \frac{P(Si|sp)P(sp)}{P(Si)} \quad (4)$$

$$P(sp|N) = \frac{P(N|sp)P(sp)}{P(N)} \quad (5)$$

$$P(sp|K) = \frac{P(K|sp)P(sp)}{P(K)} \quad (6)$$

$$P(sp|Ps) = \frac{P(Ps|sp)P(sp)}{P(Ps)} \quad (7)$$

$$P(sp|WHc) = \frac{P(WHc|sp)P(sp)}{P(WHc)} \quad (8)$$

$$P(sp|T, R, Rh) = \frac{P(T, R, Rh|sp)P(sp)}{P(T, R, Rh)} \quad (9)$$

$$P(sp|T, R, Th, Si, N, Ps, K, WHc) = \frac{P(T, R, Rh, Si, N, Ps, K, WHc|sp)P(sp)}{P(T, R, Rh, Si, N, Ps, K, WHc)} \quad (10)$$

where *T* stands for temperature, *R* for rainfall, *Rh* for relative humidity, *Si* for soil silicon, *N* for nitrogen, *Ps* for phosphorus, *K* for potassium, *sp* for species presence, and *WHc* for water-holding capacity. In addition, Equation 10 represents the full matrix of conditional probability distribution of adaptation, given all the variables.

RESULTS

Chilo partellus

WHc was the most important variable linked to the distribution of *C. partellus* followed by soil N, rainfall, temperature, soil Si, relative humidity and soil K, whereas soil P did not contribute at all at Mount Kilimanjaro. In contrast, at Taita Hills, relative humidity had the highest contribution followed by soil P, soil Si, soil N, rainfall, WHc, temperature and soil K (Table 1).

AUC measures provided highly consistent estimates of model performance (Table 2). The AUC values for independent test data varied markedly among Mount Kilimanjaro and Taita Hills study sites. In general, the AUC values were relatively high when all variables (climatic and soil factors) were included in the model at Mount Kilimanjaro and Taita Hills, respectively, followed by temperature, rainfall and relative humidity as considered the only factors at Mount Kilimanjaro. Relative humidity, water-holding capacity and phosphorus were similar at Mount Kilimanjaro, while soil N and relative humidity were similar at Taita Hills. However, rainfall in isolation was equal at both Mount Kilimanjaro and Taita Hills. At both study

Table 1. Environmental variables and their percentage contribution to *Chilo partellus* and *Busseola fusca* species distribution in Mount Kilimanjaro and Taita Hills.

Variable	<i>Chilo partellus</i>		<i>Busseola fusca</i>	
	Mount Kilimanjaro	Taita Hills	Mount Kilimanjaro	Taita Hills
Temperature	6.5	0.6	57.1	48.9
Rainfall	10.0	2.3	5.4	17.7
Relative humidity	4.9	50.2	4.1	8.8
Nitrogen	13.5	2.7	31.4	3.4
Soil silicon	5.5	7.3	0.0	0.0
Potassium	0.2	0.1	1.9	4.5
Phosphorus	0.0	35.0	0.0	27.0
Water-holding capacity	59.4	1.9	0.0	3.7

Table 2. Comparisons of the predictive ability among species distributions models based on different sets of predictors at both study sites. The Area under the receiver operating curve (AUC) was used to estimate of models (M) performance.

Model	<i>Chilo partellus</i>		<i>Busseola fusca</i>	
	Mount Kilimanjaro	Taita Hills	Mount Kilimanjaro	Taita hills
	AUC	AUC	AUC	AUC
M1 (<i>T</i>)	0.55	0.60	0.78	0.75
M2 (<i>R</i>)	0.57	0.57	0.73	0.74
M3 (<i>Rh</i>)	0.69	0.66	0.68	0.68
M4 (<i>Si</i>)	0.66	0.65	0.60	0.73
M5 (<i>N</i>)	0.67	0.66	0.79	0.69
M6 (<i>WHc</i>)	0.69	0.61	0.50	0.71
M7 (<i>K</i>)	0.54	0.51	0.75	0.76
M8 (<i>P</i>)	0.69	0.61	0.54	0.76
M9 (<i>T+R+Rh</i>)	0.71	0.65	0.79	0.79
M10 (<i>All</i>)	0.75	0.65	0.86	0.86

sites, the poorest model performance was obtained with soil K (Table 2).

At both the Mount Kilimanjaro (Fig. 1a, d, g, h) and the Taita Hills (Fig. 2a, d, g, h) study sites, the probability of the presence of *C. partellus* increased linearly with increasing temperature, Si, K and P, and decreased with an increase in rainfall, relative humidity, soil N and WHc (Figs 1 and 2b, c, e and f). Predicted climatic suitability indicated that low altitudes were more suitable for *C. partellus*, both at Mount Kilimanjaro and Taita Hills (Fig. 3a, b).

Busseola fusca

For *B. fusca* distribution the most important contributor at the Mount Kilimanjaro site was temperature followed by soil N, rainfall, relative humidity

and soil K whereas soil Si, P, whereas WHc did not contribute at all. Similarly, at Taita Hills, temperature was the most important factor followed by soil P, rainfall, relative humidity, soil K and soil N while Si did not contribute at all (Table 1).

The AUC was high at both Mount Kilimanjaro and Taita Hills when all variables were included in the model, followed by temperature, rainfall and relative humidity as considered only driving variables. Soil K and P in isolation performed equally in Taita Hills with an AUC value of 0.76. At the Mount Kilimanjaro site, the poorest model performance was for WHc, while at Taita Hills the poorest results were obtained with relative humidity (Table 2).

The probability of *B. fusca* presence increased

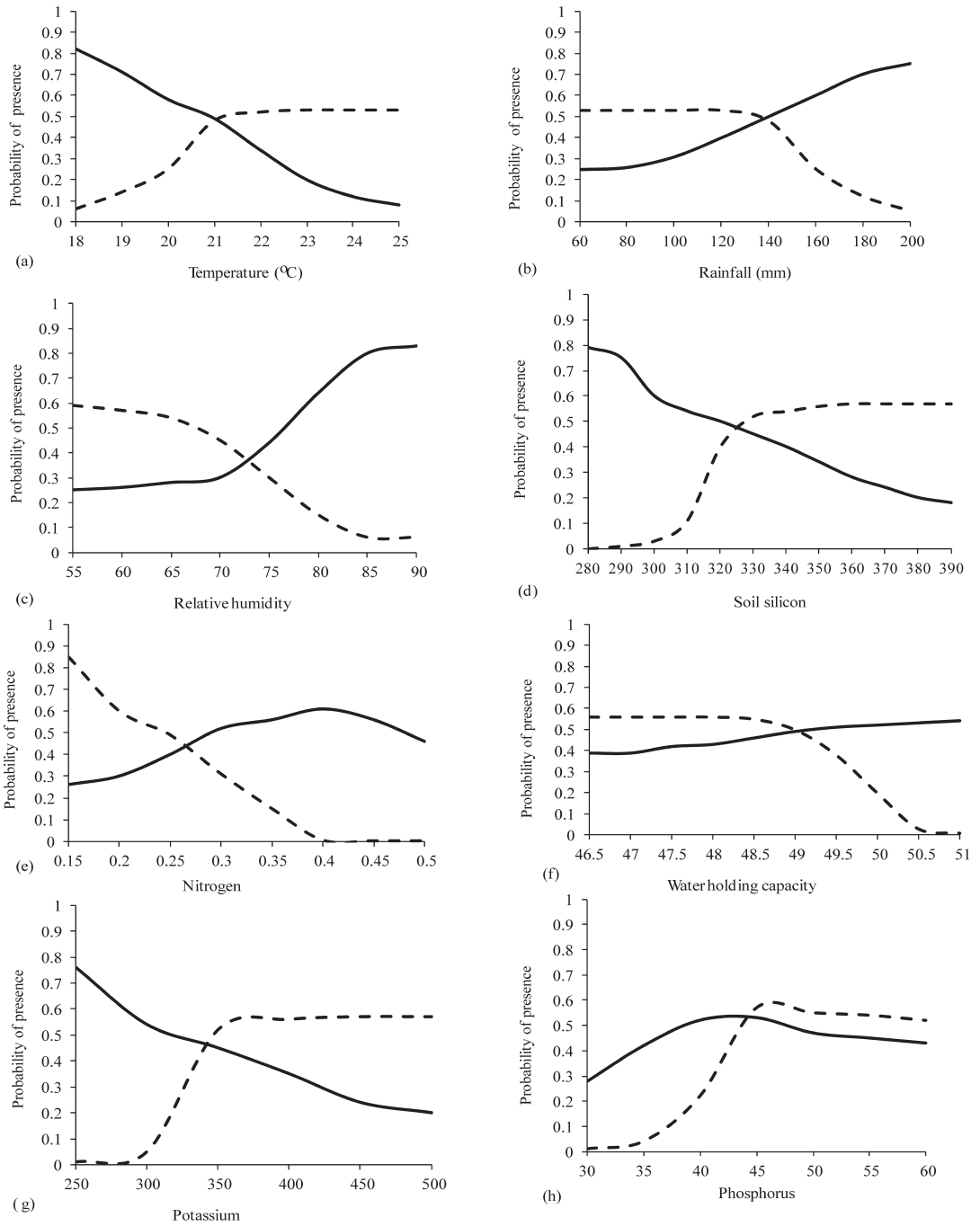


Fig. 1. Response curves illustrating the relationship of probability of presence to environmental variables at the Mount Kilimanjaro study site. The dashed lines represent *Chilo partellus* and solid lines represent *Busseola fusca*.

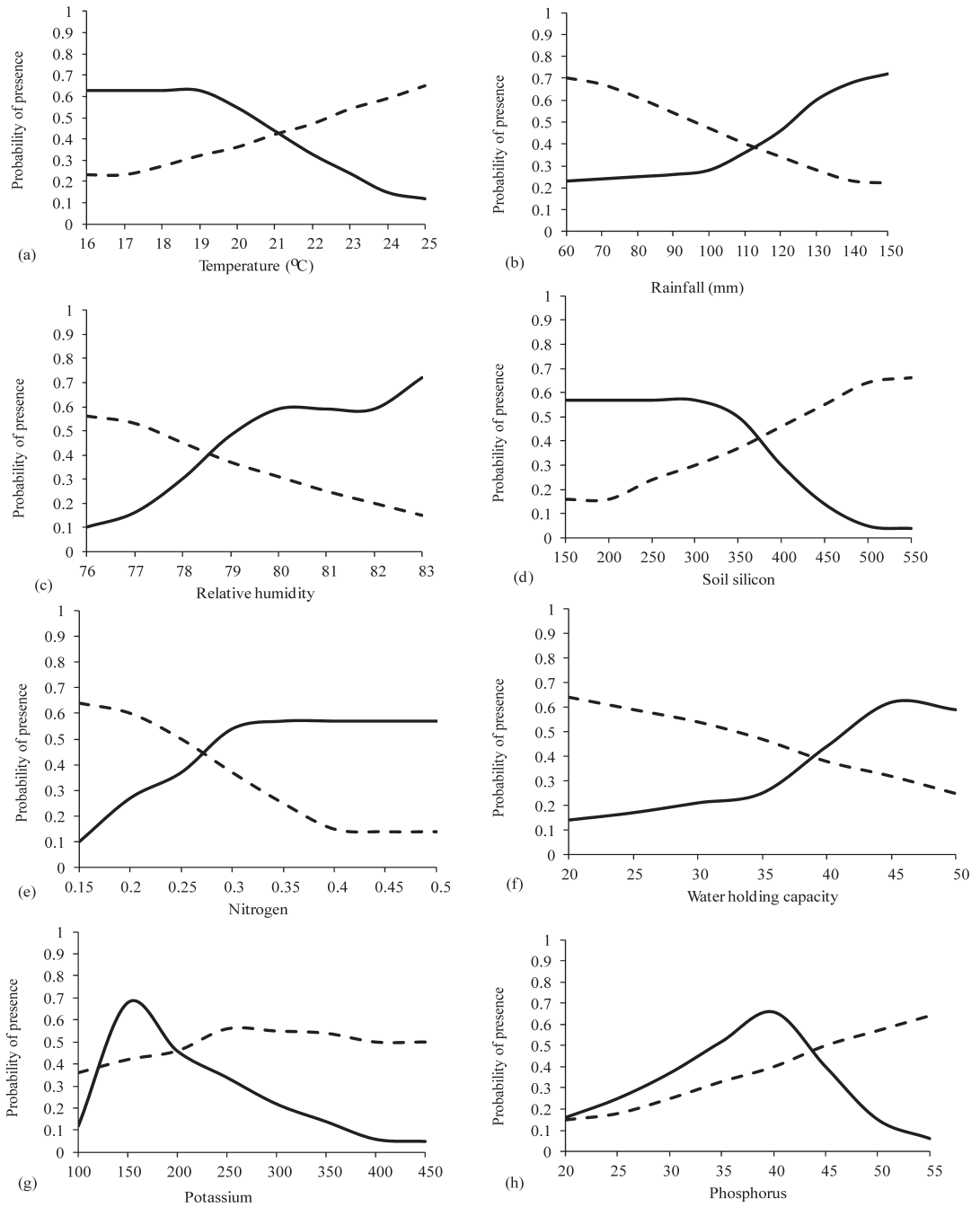


Fig. 2. Response curves illustrating the relationship of probability of presence of the species to environmental variable at the Taita Hills study site. The dashed lines represent *Chilo partellus* and solid lines represent *Busseola fusca*.

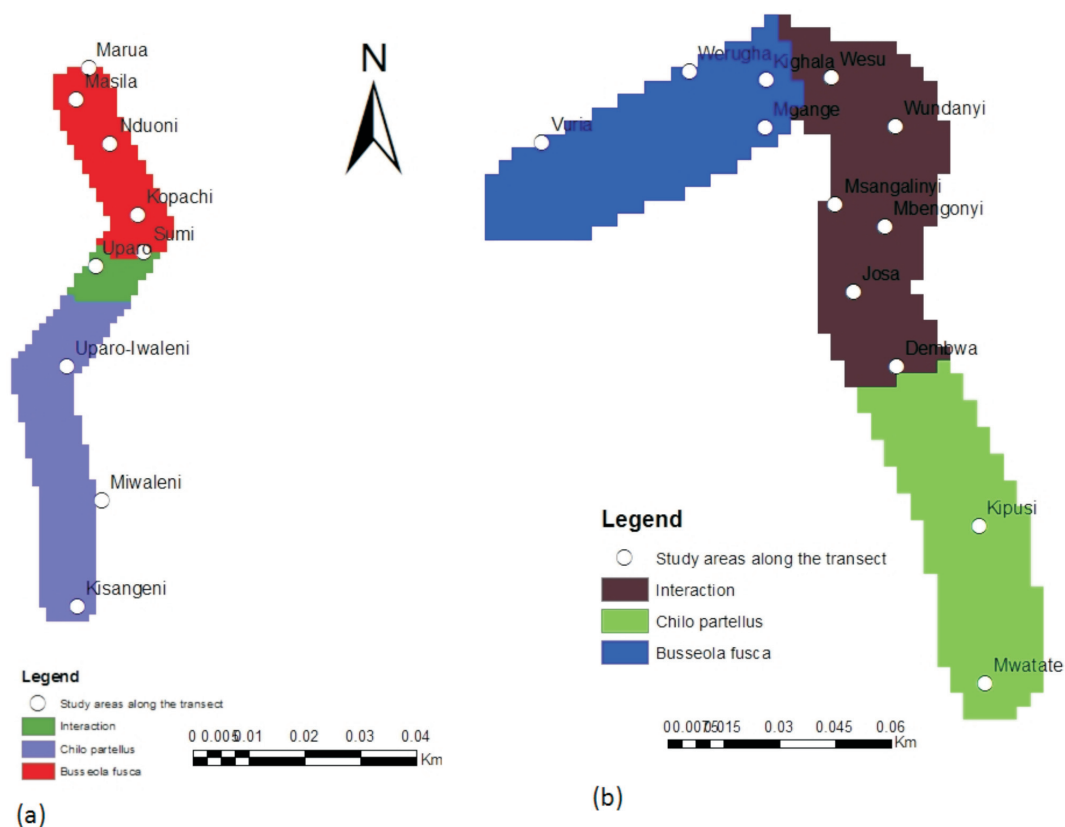


Fig. 3. Predicted potential geographical distribution for *Busseola fusca* and *Chilo partellus* using all occurrences records and environmental variables. The results are given (a) for Mount Kilimanjaro and (b) for Taita Hills. Three colours indicate suitability for one species only and where suitable, for both species.

as rainfall, relative humidity, soil N and WHc increased at both Mount Kilimanjaro (Fig. 1b, c, e, f) and Taita Hills (Fig. 2b, c, e, f) study sites. By contrast, probability of *B. fusca* presence decreases with increasing temperature, soil Si and K at both the Mount Kilimanjaro (Fig. 2a, d, g) and Taita Hills (Fig. 2a, d, g) study sites. High altitudes appeared to be more suitable for *B. fusca* at both sites (Fig. 3a, b). However, the probability of coexistence of *C. partellus* and *B. fusca* was high in the mid-altitudes at both study sites (Fig. 3a, b).

DISCUSSION

In this study we attempted, for the first time to our knowledge, to incorporate different climatic and edaphic variables into a single model to evaluate their respective contributions to maize pest distribution at the local scale on East African

mountain gradients. At both study sites, temperature appeared not to be the main driving variable linked with the geographic distribution of *C. partellus*, in contrast to *B. fusca*. This does not mean that *C. partellus* occurrence is unrelated to temperature but that temperature probably is indirectly confounded by other variables used in the model. Our results are in agreement with related studies that underscored the significance of other types of variables (besides temperature) such as rainfall, relative humidity (Getu 2007; Tamiru *et al.* 2012; Yadav & Chaudhary 1986) and soil characteristics on insect distribution. For example, a study by Parassiti *et al.* (2013) indicated that the amount of fine soil and average annual rainfall was associated with the incidence of *Hyalesthes obsoletus* Signoret (Hemiptera: Cixiidae).

The importance of rainfall in determining insect species distribution has been reported by various studies. Rainfall has been shown to amplify popu-

lation fluctuations and leading to extinction of species (McLaughlin *et al.* 2002). In another study in Zimbabwe, rainfall has been found to be the most important environmental variable in determining the distribution of the white coffee stem borer, *Monochamus leuconotus* (Pascoe) (Coleoptera: Cerambycidae) (Kutywayo *et al.* 2013). Gupta (1959) reported rainfall to be the main factor affecting *Chilo tumidicostalis* (Hampson) (Lepidoptera: Crambidae) abundance in India. Relative humidity, on the other hand, can affect insect development in different ways (Rahim *et al.* 1991). For instance, a study by Duyck *et al.* (2006) showed that survival of different species of Tephritidae, *Ceratitis catovirii* Guérin-Méneville, *Ceratitis rosa* Karsch, *Ceratitis capitata* (Wiedemann) and *Bactrocera zonata* (Saunders) decreased significantly under dry conditions. However, the species differed in their tolerance to desiccation with *C. capitata* and *B. zonata* being more tolerant than the other species. Sithole (1987) and Abraham *et al.* (1972) noted that apart from temperature, other environmental variables such as rainfall and relative humidity also influence the distribution of sorghum and rice stem borers.

This study also shows that soil characteristics, in addition to climatic factors, were significantly linked to *C. partellus* and *B. fusca* distribution since these variables are indirectly related to the influence of soil nutrients on the host plant physiology. Soil nutrients influence not only plant growth but indirectly, through its influence on host plant status, also lepidopteran stem borer development (Sétamou & Schulthess 1995; Sétamou *et al.* 1993; Ndemah *et al.* 1999; Denké *et al.* 2000; Jiang & Schulthess 2005; Mgoo *et al.* 2006). In addition, among the soil components, Si is particularly important for grasses such as maize. These monocotyledons usually contain much lower concentrations of secondary metabolites than dicotyledons (Elger *et al.* 2009) and they may depend on other mechanisms such as silicon (Si)-based defences through their accumulation mechanisms in aerial plant organs (Massey & Hartley 2006; Reynolds *et al.* 2009). Si has been shown to influence negatively the performance of *B. fusca* larvae (Juma *et al.* 2015). In addition, Calatayud *et al.* (2016) showed that *B. fusca* was more susceptible to Si than *C. partellus* and observed that *B. fusca* was more abundant when Si in soils and maize plants decreased compared to *C. partellus* that was more abundant when Si in soils and maize plants

increased. However, in this study the climatic and edaphic variables did not have any relationship with pest distribution according to the species and the studied site. For example Si was significantly linked with the distribution of *C. partellus* at both sites whereas not for *B. fusca* at any of the sites. The differences in species distribution between sites were probably due to differing farming practices, planting pattern and land cover characteristics between the study sites. The differences between pest species response were probably due to biotic factors such as natural enemies controlling the two species as well as the competition/facilitation interactions between *B. fusca* and *C. partellus* sharing the same resources (maize) which have not been considered in this study. *Chilo partellus* and *B. fusca* coexist and then interact in the mid-altitudes at both Mount Kilimanjaro and Taita Hills, where the prevailing temperatures are suitable to both species (Mwalusepo *et al.* 2015). However, Ntiri *et al.* (2016) showed significant competition between *C. partellus* and *B. fusca* at certain temperatures with *C. partellus* being the most effective competitor in such interspecific interactions. This aspect has not been considered in the model.

In conclusion, the limitation of our study was that all possible dimensions in modelling species distribution have not been explored. In this context, we recommend further studies by including both abiotic and biotic factors and by considering their interaction in future predictive models of the potential distribution of both *C. partellus* and *B. fusca* maize stem borers.

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