

**MODELLING THE IMPACT OF CLIMATE CHANGE ON THE
MAIZE STEM BORER COMMUNITIES AND THEIR MAIN
NATURAL ENEMIES ALONG ALTITUDINAL GRADIENTS IN
EAST AFRICA**

Sizah Mwalusepo

**Ph.D (Mathematics) Thesis
University of Dar es Salaam**

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EAST AFRICA**

By

Sizah Mwalusepo

**A Thesis Submitted in Fulfilment of the Requirements for the Degree of Doctor of
Philosophy (Mathematics) of the University of
Dar es Salaam**

University of Dar es Salaam

CERTIFICATION

The undersigned certify that they have read and hereby recommend for acceptance by the University of Dar es Salaam the thesis titled: "***Modelling the Impacts of Climate Change on the Maize Stem Borer Communities and their Main Natural Enemies along Altitudinal Gradients in East Africa***" in fulfilment of the requirements for the degree of Doctor of Philosophy (Mathematics) of the University of Dar es Salaam.

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DEDICATION

This work is dedicated

To my late mother, Evelyne Lyene Mwangonji, who taught me the value of hard work and gave me an excellent foundation.

To my father, Issa Mwangonji for always loving and believing in me.

To Baraka and Brian, my beloved sons: who have made my fatherhood a pleasure, and who have taught me the art of being a father by demanding from me the things a father need to give his sons.

ABSTRACT

Maize is one of the most important staple foods in East Africa. In spite of its importance, maize production in the region faces increased risk of being attacked by maize stem borers due to climate changes. This thesis aims at modelling the impact of climate change on the distribution and abundance of two maize stem borers crambid *Chilo partellus* (Swinhoe), noctuid *Busseola fusca* (Fuller), and two of their main natural enemies, *Cotesia flavipes* and *Cotesia sesamiae* Cameron at local scale along Mount Kilimanjaro and the Taita Hills transects in Tanzania and Kenya, respectively. Mathematical models for the impact of the climate changes on the distribution and abundance of the maize stem borers and their natural enemies are adapted and/or developed, simulated and the data obtained both from model simulation and from field and laboratory experiments are analysed. Analysis of the data reveals three main changes occurring simultaneously: (1) Spread of the maize stem borers and their natural enemies to higher altitude areas of the gradients due to climate change; (2) Increase in abundance (number of generations) of both maize stem borers at all altitudes, most importantly by year 2055 predictions, suggest that *Chilo partellus* and *Busseola fusca* will cause more damage in the most productive maize zones of both Mount Kilimanjaro and Taita Hills; (3) Disruption of the geographical distribution between the maize stem borers and their main natural enemies suggesting improvement of biological control of maize stem borers by both *Cotesia flavipes* and *Cotesia sesamiae*. The findings also indicate that both climatic factors and soil characteristics are important in determining the potential distribution of maize stem borers.

ABBREVIATIONS

IRD	Institut de Recherche pour le Developpment
icipe	International Centre of Insect Physiology and Ecology
IPCC	Intergovernmental Panel on Climate Change
CEPF	Critical Ecosystem Partnerships Fund
MSE	Mean Square Error
ERI	Establishment Risk Index
GI	Generation Index
DEM	Digital Elevation Model
SRTM	Shuttle Radar Topography Mission
ASCII	America Standard Code for Information Interchange
QGIS	Quantum Geographical Information System
AI	Activity Index
FAO	Food and Agriculture Organization
CIP	International Potato Center
NAPA	National Adaptation Programme of Action

GPS	Global Positioning System
DD	Decimal Degree
EABH	Eastern Afromontane Biodiversity Hostspot
UN	United Nation
TPS	Thin Plate Spline
GCV	Generalized Cross Validation
GIS	Geographical Information Systems
RMSE	Root Mean Square Error
AUC	Area Under the Curve
RCPs	Representative Concentration Pathways scenarios
AR5	Fifth Assessment Report
RCM	Regional Climate Models
AIC	Akaike Information Criterion
ILCYM	Insect Life Cycle Modelling
ROC	Receiver Operating Characteristics
Maxent	Maximum Entropy

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CHAPTER ONE

INTRODUCTION

1.1 Impact of climate change on insects

The average global Earth surface temperature has increased by about 0.6°C during the past century (Menendez 2007, Aemro *et al.* 2012, IPCC 2013, Milano *et al.* 2013, Ravi *et al.* 2013, Schellnhuber *et al.* 2013), mainly due to human activities, caused in particular by emission of greenhouse gases from fuel combustion, deforestation, urbanization and industrialization (Malla 2008, Aemro *et al.* 2012, Vose *et al.* 2012, IPCC 2013, 2014, Bustamante *et al.* 2014). However, continental and sea temperatures are expected to continue to rise regardless of human interventions for at least the next two decades (IPCC 2013, 2014). It is anticipated that the impact of climate change will be greater in the tropical regions of the world, and developing countries are predicted to be more at risk because of their lower capacity to adapt resulting from various socio-economic, demographic and policy trends (IPCC 2007, 2013, 2014). This may exacerbate food security, livelihoods and economic prosperity (Boko *et al.* 2007, Collie *et al.* 2008, Schlenker and Lobell 2010, Waithaka *et al.* 2013).

Climatic predictions show that Eastern Afromontane Biodiversity Hotspot (EABH) regions will be particularly affected by extreme climatic changes (Lovett *et al.* 2005, Mumbi *et al.* 2008, Platts *et al.* 2008, 2012, CEPF 2012), while the goods and services these ecosystems provide are under significant threat (Boko *et al.* 2007, Maeda *et al.* 2010, 2011), mainly due to land use changes exacerbated through high population. The EABH has important ecosystem service values arising from the water towers it provides for low lying areas, food production from crops like maize, cabbages and plantation crops

like coffee and avocado, recreation and eco-tourism and nutrient recycling (CEPF 2012). Also, it is known for rich biodiversity with 7598 plant and 3258 animal species of which 30% are endemic (Mittermeir *et al.* 2004, CEPF 2012).

In EABH, agricultural productivity of crops grown for human consumption is at risk due to the incidence of crop pests. In spite of several crop protection measures, arthropod pests are reducing crop production significantly, with estimated East African yield losses of 18% (Thornton *et al.* 2011, Niang *et al.* 2014). This challenge is further complicated by climate changes which influence the distribution of crop pests. Since insects are poikilotherms, they cannot internally regulate their own temperatures, and hence, temperature is among the major abiotic factors affecting insect development, reproduction and survival (Bale *et al.* 2002). It affects life histories (growth rates, generation times, number of generations per year), species distributions (expansion of geographic ranges at the higher latitudes and altitudes), interactions with their host-plant (extension of the development season, crop–pest synchrony), and interaction with their natural enemies (disruption of the temporal or geographical distribution, host abundance, parasitism) (Porter *et al.* 1991, Yamamura and Kiritani 1998, Bale *et al.* 2002, Wilson *et al.* 2005, Kiritani 2006, Hance *et al.* 2007, Menendez, 2007, Ward and Masters 2007, Bale and Hayward 2010, Ladanyi and Horvath 2010, Bebber *et al.* 2013, Khadioli *et al.* 2014, Bassler *et al.* 2014, Rasmann *et al.* 2014).

The responses of insects to temperature have had considerably more attention in temperate regions (Battisti *et al.* 2006, Stoeckli *et al.* 2012, Kroschel *et al.* 2013). Milder winter and decreasing frequencies of temperature extremes, enhanced reproduction capacity and changes in distribution are to be expected for a variety of pest species (Bale

et al. 2002). Whereas, distribution and abundance of some insect species vulnerable to high temperature in the temperate regions may decrease as a result of climate change (Coulson *et al.* 2002, Khai *et al.* 2007, Tran *et al.* 2007, Jepsen *et al.* 2008), because of the continual favourable climatic conditions for pest reproduction and host availability, tropical countries are more prone to insect pest problems and outbreaks (Kroschel *et al.* 2013). In light of this, prediction of impact of climate change on insect pest distribution, abundance and dynamic has become more relevant for developing effective pest management strategies and food security in future.

Maize is one of the most important staple food in most East Africa countries (Smale *et al.* 2001, Odendo *et al.* 2003, Mgoo *et al.* 2006, AATF 2009, Mboya *et al.* 2011), mainly cultivated by subsistence farmers for human consumption, while the surplus is used as animal fodder (Minja 1990, Kfir *et al.* 2002). In spite of its importance, maize production is constrained by biotic (stem borer, gray leaf sport, maize streak virus) and abiotic (drought, soil fertility due to population pressure and land constraints) factors. In East Africa, the insect pests associated with maize are lepidopteran stem borers. Among the most important lepidopteran stem borer attacking maize are *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) and *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). Yield losses in maize due to stem borer infestation is currently estimated between 12 % to 50% of the total production, as a result of leaf feeding, dead heart, stem tunneling, direct damage to grain, and increased susceptibility of attacked plants to stalk rots and lodging; it depends on the pest species, agro-climatic zone, maize variety, cropping pattern and soil fertility level (Bosque-Perez and Mareck 1991, Polaszek 1998, Kfir *et al.* 2002, De Groote *et al.* 2002, 2003, 2004).

Distribution of *C. partellus* and *B. fusca* varies among different regions and altitude depending on climatic and ecological requirements. *C. partellus* invaded Africa from Asia sometime before 1930 when it was first found in Malawi (Tams 1932). Currently, it has spread to nearly all countries in Eastern and Southern Africa. It has become the most serious pest of cereals in the hot lowlands of the region and is now expanding its distribution to higher elevations (Kfir 1997, Overholt *et al.* 2000, Getu *et al.* 2001, Zhou *et al.* 2001, Ong'amo *et al.* 2006). The *B. fusca* is indigenous to Africa and it is generally a more serious pest in cold highlands. However, its distribution and pest status varies with the region; while in Eastern and Southern Africa it is a pest at cold highland (above 600 meters (m)) only, in Central Africa it occurs from sea level to over 2000 m, and in West Africa it is primarily a pest of sorghum in the dry savannah zone (Harris 1992, Ong'amo *et al.* 2006).

In order to reduce the damage and control the population growth, stem borer species have been the subject of extensive research in East Africa; and biological control, particularly using parasitoids, has been found to be effective against the stem borers species (Calatayud *et al.* 2006). The most important natural enemies of stem borer are parasitic Hymenoptera of which the majority belong to the Braconidae Family. *Cotesia sesamiae* Cameron is one of the most important native larval parasitoids of stemborers, attacking mid to late larval instars of both exotic and indigenous borer species (Mohyuddin and Greathead 1970, Schulthess *et al.* 1997). In East Africa, *C. sesamiae* has been found particularly effective against *B. fusca* (Overholt *et al.* 1994b, Bonhof *et al.* 1997). However, *C. sesamiae* is unable to effectively suppress *C. partellus* populations in Kenya (Overholt *et al.* 1994b). Another natural enemy is *Cotesia flavipes* Cameron. *C. flavipes* is native to the Indo-Australian region. It was introduced into Kenya from Pakistan and

India in 1993 and has played a role in controlling *C. partellus* (Overholt *et al.* 1994b). In brief, the adult wasp is small about 3-4 mm in length and lives for only a few days. Females lay about 15-65 eggs into the host larva and eggs hatch after about 3 days. The parasitoid larvae develop through three instars within the stemborer larva feeding on body fluids. The egg-larval period takes about 10-15 days. The final larval instars of this parasitoid emerge from the host body by chewing through the stemborer larval integument and immediately spin a cocoon and pupate. Adult parasitoids emerge at 6 days, usually, in the morning hours, and start mating soon afterwards (Smith *et al.* 1993). The natural enemies reportedly cause 32-55% decrease in stem borer densities in various cereal crops (Kfir *et al.* 2002).

Over the past 40 years until end of year 90's the exotic *C. partellus* started to spread into the cooler mid and higher altitude of East Africa, partly because of competitive advantages against *B. fusca* (Ong'amo *et al.* 2006). Thus, the abundance and distribution of stem borers pest and their main natural enemies is expected to vary considerably with climatic variability and altitude.

1.2 Mathematical models of climate

One of the best approaches to understand the consequences of climate change on insect distribution and abundance in pest management is mathematical modelling (Regniere *et al.* 2012). Mathematical models are also useful in risk assessment, which helps in making more informed policy and management decision (Sporleider *et al.* 2008). With respect to climatic variables, several approaches are available for modelling the potential distribution of species (Guisan and Zimmermann 2000, Kriticos and Randall 2001, Baker 2002, Elith *et al.* 2006, Pearson 2007, Venette *et al.* 2010). The approaches used in these

studies can be divided into two categories; inductive and deductive approaches. Inductive approaches use statistical analyses of the known distribution of a species and climatic data to estimate its climatic preference (Guisan and Zimmerman 2000). The occurrence of the species and environmental variable for this approach can be performed using climate match functions that look for the potential exploitation of a non-indigenous invasive species to new areas (Philips *et al.* 2006). This function uses a meteorological database consisting of monthly long-term average climatic variables for any number of locations where the species are not present with the location where the species exists (Guisan and Zimmerman 2000, Peterson 2006). However, this method was useful as a first attempt to understand the potential distribution of a species provided the current distribution data are well documented and geo-referenced, and when there is not enough knowledge of the lifecycle and the biology of the species. Deductive approaches use detailed knowledge of climatic preferences determined from laboratory assessments (that is phenology model) to understand the condition a species prefer. Deductive approaches are commonly adopted because the information used to develop the forecasts is completely independent of the observed occurrences. However, this approach may predict a much broader geographical range than will actually be observed if other limiting factors are ignored or unknown (Venette *et al.* 2010).

The difference between the two modelling approaches is the level of abstraction. Whereas the inductive approach has higher abstraction level with the mathematical methods used leading to a greater generality; deductive approaches (phenology models) have lower abstraction but with detailed mathematical models, which describe the physiological needs of insect species' growth, such as development, survival and reproduction (Sutherst *et al.* 2000). Nevertheless, inductive modelling of georeferenced

species occurrences is a powerful approach for identifying suitable environments on continuous and ordinal variables such as elevation and climatic gradients, whereas deductive modelling framework is best with categorical variables. More elaborate phenology models use non-linear equations of higher biological significance and include stochastic functions for variability during the development times within a population and among individuals (Logan *et al.* 1976, Sharpe and DeMichele 1977). Since temperature is the most critical factor affecting insect development, different models have been used to describe the relationship between temperature and insects development processes (Stinner *et al.* 1974, Wagner *et al.* 1991, Worner *et al.* 1992, Wang and Ferro 1998, Briere *et al.* 1999, Hartley and Lester 2003, Damos and Savopoulous-Soultani 2010, Kroschel *et al.* 2013). However, these models differ with respect to parameter number and basic assumptions about the temperature effects.

The following are some examples of functions used to predict the activity and seasonal population dynamics of pest and natural enemies in the field situation: polynomial equations have been used to describe the development time and rates. Although they are nonlinear with respect to independent variable, cubic and quadratic equations are used most frequently. For example, the Tanigoshi and Browne model (1978) is defined by: $r(T) = a_0 + a_1T + a_2T^2 + a_3T^3$ where a_0, a_1, a_2 and a_3 are constant parameters; T is the temperature and $r(T)$ is the rate of development at temperature T . The Taylor model

(1981) is simple normal function of the form: $r(T) = R_m \exp\left(\frac{-1}{2}\left(\frac{T - T_m}{T_e}\right)^2\right)$ where R_m is

the maximum development rate at temperature T , T_m is the temperature where the development is highest, and T_e is the shape parameter giving the spread of the curve. The

Sharpe and DeMichele (1977) biophysical model, reparameterized by Shoolfied *et al.* (1981) is based on enzyme reaction rate theory and all six parameters are assumed to have a thermodynamics biochemical interpretation (Wagner *et al.* 1984). This model has been used to predict development of arthropod preys and predators (Staubli *et al.* 1997).

The Sharpe and DeMichele model is defined by the equation:

$$r(T) = \left(\rho T / T_0 e^{(H_A / R(1/T_0 - 1/T))} \right) / \left(1 + \left(e^{(H_L / R(1/T_L - 1/T))} \right) + \left(e^{(H_H / R(1/T_H - 1/T))} \right) \right)$$

where R is a universal gas constant (1.987 cal⁰/mol); ρ is the development rate at 25⁰C; H_A is the enthalpy of activation of reaction; H_L is the change in enthalpy at lower temperatures; T_L is temperatures at which the rate controlling enzyme is half active and half low-temperatures inactive. H_H is the change in enthalpy at high temperature; T_H is the temperature at which the rate-controlling temperature is half active at high-temperature inactive; and T_0 is costant parameter (298.15K), because assuming no enzyme inactivation. This model was recently used to predict the development of an aphid with biological potential against a weed (Ma and Bechinski 2008).

In addition, competition is a central component of many of the fundamental ecological theories (Tilman 1982) and is commonly cited as one of the processes determining the response of species communities to environmental change drivers such as climate change (Brooker 2006). The dynamic relationship between two or more competing species is one of the dominant subjects in mathematical ecology due to its universal existence and importance. There are many classical theories of ecological competitive interaction between species (Kaplan and Denno 2007). For example, Lotka (1925)-Voltera (1931) competition model, this describes the phonomenology of competition (Tilman 1994, The

Lotka-Volterra model, mathematically is given by: $\frac{dN_i}{dt} = r_i N_i \left((k_i - N_i - \sum_{j=1}^n \alpha_{ij} N_j) / k_i \right)$

where N_i is the population density; r_i is the intrinsic rate; k_i is the carrying capacity; α_{ij} is the competition coefficient; n is the number of species, and $i = 1, \dots, n$.

In this context the importance of interspecific competition is a highly controversial and unresolved issue for community ecology in general, and for phytophagous insects in particular (Kaplan and Denno 2007). Numerous field studies have shown that interspecific competition is a major force determining species abundances in different ecosystems (Miller *et al.* 2005). In spite of the many studies that have been done to model interspecific competition among species, there is little information on how to incorporate environmental factors such as temperature in the theoretical studies between resource and competition insect.

The main goal of this study was to model the impact of climate change on the maize stem borer communities' distribution and abundance, and their natural enemies along altitudinal gradients. The result of the study will help to develop strategies of adapting to climate change by developing and supporting farmers with practical pest management strategies.

1.3 Statement of the research problem

Stem borer pests limit both the yield and stability of maize production in East Africa. The problem is particularly acute in the small-scale resource-poor farming system under which maize is typically grown. This exacerbates existing vulnerabilities of the poor peasant farmers who depend on agriculture. Thus, if adequate pest management strategies are not developed and made available to farmers it could ultimately lead to greater crop

and quality losses. As maize is the main staple food in East Africa countries, more and in-depth research is needed on its predominant insect pests and their natural enemies to guide the formulation of appropriate adaptation strategies. However, little has been done on the use of mathematical models to assess the impact of climate change on insect pests, stem borers in particular at local scale along East Africa Mountain, gradients. This study used mathematical models to determine geographical distributions and abundance of maize stem borers and their natural enemies with response to climate change.

1.4 Research objectives

The general objective of this study was to model and analyse the impact of climate changes on the maize stem borer communities and their main natural enemies along altitudinal gradients in East Africa.

Therefore, the study was conducted along three specific objectives as follows:

- i. To investigate the impact of temperature changes to the maize stem borers and their natural enemies along altitudinal gradients in two mountains of East Africa, using temperature based phenology models.
- ii. To establish a resource based mathematical model which can determine the impact of temperature changes on insect communities and determine stability of the equilibrium points of the model
- iii. To model the contribution of different factors (temperature, rainfall, relative humidity and soil characteristics) in predicting the distribution and abundance of maize stem borers.

1.5 Significance of the study

The outcome of this study will be useful in the prediction of changes in dynamics and geographical distribution of maize stem borers. It will be helpful in adapting the pest management strategies and to provide important information in predicting the stem borer population growth potential in maize growing areas. It will be valuable in visualizing the potential pest distribution and the economic damage it may inflict on crops. It will provide knowledge to policy makers and managers in the related field in formulating strategic pest management decisions, such as restrictions on importation of certain crops through international trade, implementation of quarantine measures and the design of pest surveys. The findings will be important to farming communities, agricultural extension agents, government institutions, international and local NGO's engaged in agricultural interventions. In addition, the methodologies and tools developed by this research and the lessons learned will be of interest, for both the scientific and public communities at large, to better understand the future effects of climate changes on insects.

1.6 Outlines of the content of this thesis

This thesis is organized as a set of research papers addressing each of the objectives listed in section 1.4. The papers are either published in or submitted to peer-reviewed journals or under preparation for submission to referred international journals. The thesis consists of seven chapters. Chapter 1 highlighted the significance of theoretical investigation of the combined impact of climate change and maize borer species distribution on the maize crop production. Relevant literatures were reviewed to buttress the significance of the investigation in chapter 2. Chapter 3 describes a general overview material and methodology including the field survey data collection approach. The problems were

presented and tackled in chapter 4 to 6 and the results were graphically presented and discussed. In Chapter 4 present the impact of temperature changes on the maize stem borers and their natural enemies along altitudinal gradients in two mountains of East Africa, using phenology models. Modelling the role of temperature in competing insects for a single resource is presented in Chapter 5. Modelling the potential distribution of maize stem borer with environmental variables is presented in chapter 6. The findings are summarized and conclusions derived from the preceding chapters are presented in chapter 7. Some relevant recommendations for future researches are outlined. A single reference list and an appendeces are provided at the end of the thesis.

CHAPTER TWO

REVIEW OF RELATED LITERATURE

Climate and weather patterns are of primary importance for the distribution, development, and population dynamics of insects (Lastuvka 2009). Parmesan (2007) reported that change in climate may result in geographical distribution, increased overwintering, changes in population growth rates, increase in the number of generations, extension of the development season, changes in crop-pest synchrony of phenology, changes in interspecific interactions, and increased risk of invasion by migrant pests. Furthermore, some insect herbivores have already changed dynamics and range expansion associated with climate change has been observed in many places (Williams and Lifebold 1995, Wang *et al.* 1998, Parmesan *et al.* 1999, Lovett *et al.* 2005, Parmesan 2006, Hillstrom and Lindroth 2008, Netherer and Schopf 2010).

Climate change may bear serious consequences on diversity and abundance of arthropods, the extent of losses due to insect pests, which will impact both crop protection and food security (Kannan and James 2009). The relationships between insect pests and the natural enemies will change as a result of climate change resulting in both increases or decreases in the status of individual pest species (Hill and Dymock 1989). Some authors have observed that quantifying the effect of climate change on the activity and effectiveness of natural enemies for pest management will be a major concern in future pest management programs (Hill and Dymock 1989).

Most studies demonstrated that climate change is expected to force species distributions towards higher elevations and latitudes, leading to extinctions of species whose future

habitable climate space become too small or too isolated from their current geographical ranges (Thomas *et al.* 2004, Robinson *et al.* 2005).

Altitude strongly segregates organism distribution, the main factor being temperature preference, which means decreased temperature at high altitude affects insect performance because physiological reaction rates are strongly determined by variation of temperatures (Huey and Kingsolver 2011). Insects vary in their population response to altitude with insects showing increasing, declining or no altitudinal trends in abundance. According to Whittaker (1952) population densities of herbivorous insects at any given altitude are ultimately determined by the tritrophic interaction among the host plant, the insect and its parasitoids and predators. Many insect species are broadly distributed along elevation gradient, such that populations living at the upper and lower altitudinal extremes develop in quite different environmental conditions (Bale *et al.* 2002).

Predation and parasitism have generally been reported to decline with altitude (Hodkinson 2005). Recently, a quantitative review of the scientific literature reported similar patterns of insect parasitoid richness and parasitism rate decrease along 140m elevation gradients in a wide range of natural habitats (Pere *et al.* 2013). On average, the relative decrease in the parasitism rate was approximately 15% per 100 m for individual parasitoid species.

Recent reviews have suggested that climate change will increase the incidence of insect pests, particularly via increased population growth and reduced plant resistance (Klapwijk *et al.* 2011). The same studies pointed out that increasing temperature might also benefit natural enemies and thus negatively affect herbivores but have failed to estimate the strength of this topdown effect due to lack of data. Furthermore, life-history

traits are known to affect host and parasitoid species and community response to climate (Pere *et al.* 2013, Hance *et al.* 2007). Crop plants used as food by human beings are damaged by over 10,000 species of insects, and cause an estimate annual loss of 13.6% globally (Benedict 2003). These values might significantly rise under changing climatic conditions whereby new and more aggressive pest levels destabilize crop yield, thus threatening food security. Yet another similar study reported that the major insect pests such as cereal stem borer, the pod borer, aphids and whiteflies may move to colder temperature regions, leading to greater damage in cereals grain legume, vegetables, and fruit crops (Dhaliwal *et al.* 2004).

According to FAO since the 1980s, many countries in sub-Saharan Africa have remained net importers of maize (FAO 1999). This is attributed to a rapidly expanding population and stagnating yields over the years. In spite of this, it is projected that by the year 2020, the global demand for maize will grow by 45%; of which 72% will be in developing countries; while only 18% in the industrialized nations (James 2003). Over-dependence on rainfed agriculture poses a major obstacle to sustainable maize production because the rains are often low and unreliable (FAO 2004). This is exacerbated by other factors such as: outbreak of diseases, the lack of farm inputs like seed and fertilizers, inability to control weeds and crop losses due to damage by insect pests (Bonhof 2000).

Crop losses estimates vary greatly in different regions and agro-ecological zones (De Groote *et al.* 2002). In Kenya alone, losses due to stemborer damage fluctuates around 14% on average (De Groote *et al.* 2002).

Songa *et al.* (2002) showed that stem borer damages including, plant height and stem diameter are key factors affecting maize grain yield. For instances, one centimeter of

stem borer tunnel reduces yield by 3.0 gram per plant due to the damage of a single stem borer.

Biological control agents such as ants, spiders and earwigs, have been observed to affect stemborer population densities, by directly causing a high mortality of stemborer eggs and young larvae (Mohyuddin and Greathead 1970, Girling 1978, Oloo 1989). This agreed with several previous attempts over the past fifty years to establish exotic parasitoids for control of stemborers in Africa particularly for suppression of the invasive exotic stemborers such as *C. partellus* (Overholt 1998). In addition, the growth rate of the parasitoid is significantly influenced by temperature and host age (Jiang *et al.* 2004, Hailemichael *et al.* 2008). *C. flavipes* and *C. sesamiae* were attracted to stemborer-infested plants irrespective of the species used (Potting *et al.* 1993, Ngi-Song *et al.* 1995, 1996, 1997, Cugala *et al.* 2001, Matama-Kauma *et al.* 2001, Ellers and Van Alphen 2002, Asgari *et al.* 2003).

A study on the interaction of *C. flavipes* with native, non-target lepidopteran stemborer species in Africa showed that this exotic parasitoid has a high specificity for its aboriginal host *C. partellus* and with minimal non-target harm (Obonyo *et al.* 2005, 2008). Furthermore, *C. flavipes* has a higher searching efficiency attacking more larvae than *C. sesamiae* when *C. partellus* is the host. This shows that it is a more efficient parasitoid against *C. partellus* than the indigenous *C. sesamiae* (Sallam *et al.* 1999).

Insect phenology models are important tools in pest management strategies (Tauber *et al.* 1986). They provide the means to predict seasonal occurrence of pest populations, which can be used to schedule field-sampling programs and to time control measures. In addition, phenological models are the core of any realistic system model of population

dynamics. The idea of using ambient temperature and time to describe development of cold-blooded animals is greater than 270 years old (Young and Young 1998), consequently a variety of rate functions or models have been proposed to describe the relationship between temperatures and arthropod development (Janisch 1932, Davidson 1944, Pradhan 1945, Stinner *et al.* 1974, Tanigoshi *et al.* 1975, 1976, Logan *et al.* 1976, Sharpe and DeMichele 1977, Tanigoshi and Browne 1978, Analytis 1980, 1981, Taylor 1981, Lamb and Laschiavo 1981, Wang *et al.* 1982, Ratkowsky *et al.* 1983, Hilbert and Logan 1983, Lamb *et al.* 1984, Wagner *et al.* 1984, Worner 1992, Lactin *et al.* 1995, Briere *et al.* 1999, Roy *et al.* 2002, Kontodimas *et al.* 2004). Furthermore, temperature driven models have been frequently used to predict the occurrence and seasonal population dynamics of pest and natural enemies in field situation (Tobin *et al.* 2001), The models help in determining suitable conditions for mass rearing of natural enemies (Rodriguez-Saona and Miller 1999), and predict trophic interactions in various ecosystems associated with possible consequence of climate change (Logan *et al.* 2006).

Arguably, the models that aim to predict the effects of temperature must account for the nonlinear nature of the thermal response, as well as the intraspecific and intrapopulation variability in these responses (Regniere and Logan 2003). In addition, the improvement of models is an active area of research, with new models attempting to take into account factors such as life-history traits of species or processes such as migration when predicting distribution changes (Regniere and Logan 2003).

There are several approaches that have been used to predict how temperature and precipitation change could modify the abundance, distributions or status of insect pests (Estay *et al.* 2008). For instance, Estay *et al.* (2008), evaluate how temperature and

humidity influence the density of two stored grain insect pests, *Tribolium confusum* (Jacquelín Du Val) (Tenebrionidae) and *Callosobruchus chinensis* (Latreille) (Bruchidae) and they found that both imply a severe change in the pest status of the species. International Potato Center (CIP) has developed a temperature-driven phenology model for the potato tuber moths that provides good predictions of the potential for population growth for wide ranges of climate conditions where the pests prevails today (Sporleider *et al.* 2008). The authors further noted that this approach can be utilized for other insect species and also used for predicting growth potentials for natural enemies of pests (that is parasitoids) to determine their potential efficacy in classical biological control programs.

Competition was suggested as likely phenomena to modify the biological impacts of climate change on the distribution and abundance of plant species (Brooker 2006). Accordingly a new paradigm that account for indirect interaction and facilitation is required to describe how interspecific competition contributes to the organization of phytophagous insect communities and perhaps to other plant and animals communities as well (Kaplan and Denno 2007).

To simulate models, statistical procedure and validation is an essential stage in model development incorporating at least two parameters, which have to be considered in the validation process (Welch *et al.* 1981). But consideration of potential risk to user or cost-benefit criteria for evaluating management models and rigorous statistical procedure are required to validate such models. Further, selection of inappropriate criteria could lead to unnecessary delays in the implementation or use of poorly validated models. However, in light of the above mentioned perspectives, this study brings a new aspect into the knowledge of ecology, which has not yet been analyzed qualitatively and quantitatively

in any of the recent studies in mathematical modelling. The new dimension is the prediction of how climate change will influence maize stem borer communities and their main natural enemies at local scale along East Africa mountain gradients.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study site description

The study sites are localized in the Eastern Afromontane Biodiversity Hostspot (EABH) in East Africa. In Kenya, the target area is situated in Taita hills in South-Eastern Kenya (Coast Province) (Figure 3.1). The elevation of the Taita hills ranges from 700 to 2000 m above sea level (m.a.s.l.), between latitude $3^{\circ}25'$ and longitude $38^{\circ}20'$. The mean annual rainfall ranges from 500 mm in the low altitude to over 1500 mm in the upper mountain zone and with an average rainfall of 1200 mm and the annual mean temperature ranging from 16.5 to 23.5°C . The area is characterized of a bimodal rainfall distribution, where the long rains occur from March to May/June and short rains from September/October to December.

In Tanzania the target area is situated in the Pangani river basin in North East (NE)-Tanzania with a focus on the small catchment areas on the South Eastern slope of Mount Kilimanjaro (700-1800 m) above sea level in NE-Tanzania, approximately located between latitude $3^{\circ}4'$ and longitude $37^{\circ}4'$ (Figure 3.2). The mean annual temperature ranges from 18 to 23.6°C and mean annual rainfall range between 1000mm to 1300mm. It experiences two distinct rainy seasons: the long rains from March to May and the short rains between October and December. The Pangani river basin is chosen as it is predicted to be hit hard by negative climate change impacts. The area experience a 2-4°C increase in temperature, as well as decreasing rainfall and increasing evaporation in the basin (NAPA 2007).

Taita hills and Mount Kilimanjaro were chosen as model development areas for the following reason: (i) they form a relatively small areas, which act as natural experiments by providing variation in abiotic factors under which biotic interaction can be evaluated; (ii) the areas are small and can be well covered by a limited number of weather stations to measure air temperature, relative humidity and precipitation; (iii) a reasonable good road infrastructure to have access to the weather stations and for household and field surveys; (iv) existence of historical climate data; (v) ecological, population pressure and maize grown, and (vi) politically safe region. Furthermore, in comparison to larger-scale, altitudinal gradients minimize the confounding effects of historical and bio geographical difference.

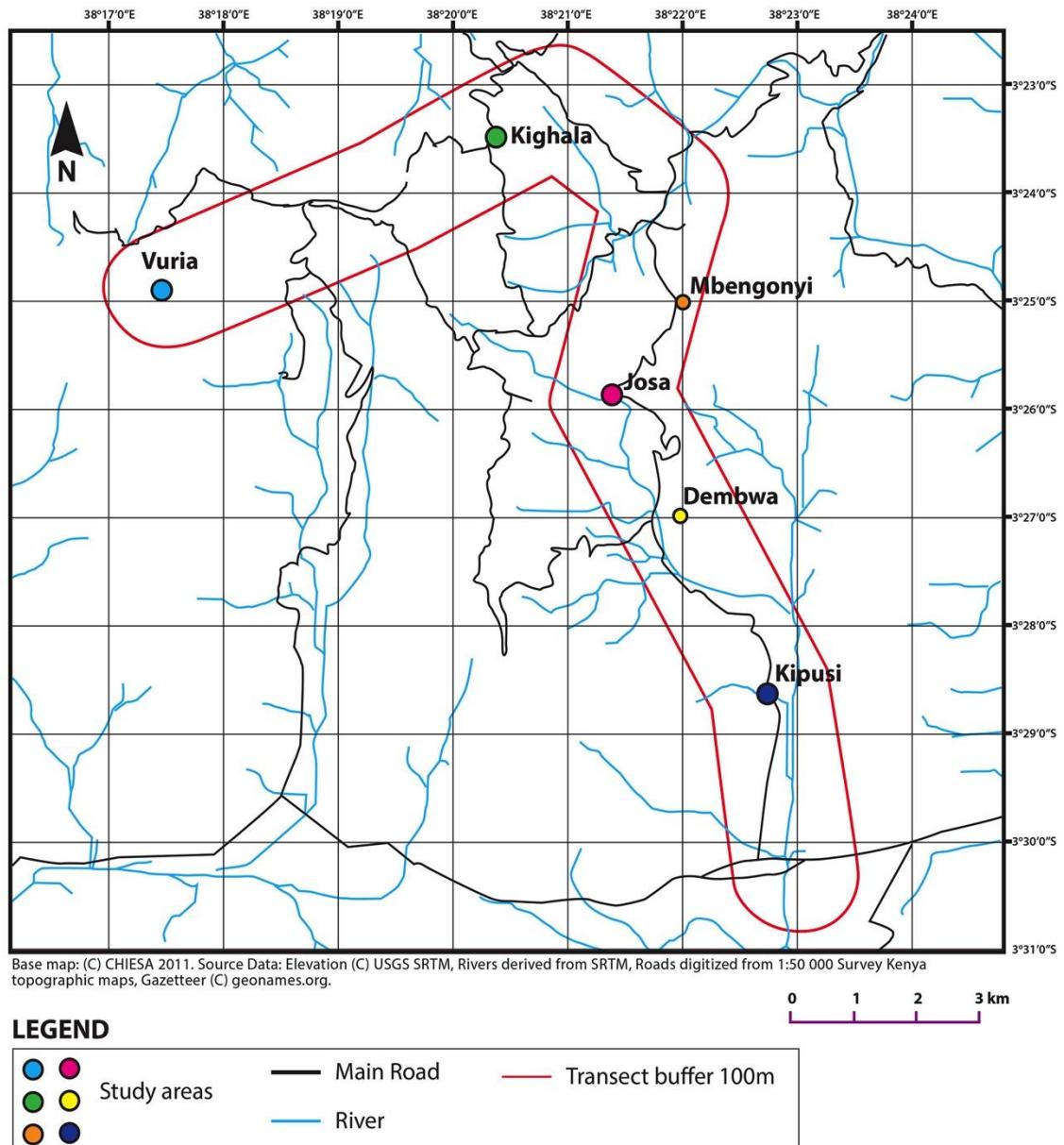


Figure 3.1: The study areas in Taita hills transect; the circles indicate the location where the data loggers and rain gauges for the stemborer sampling and climate data collection have been installed along the altitudinal gradients.

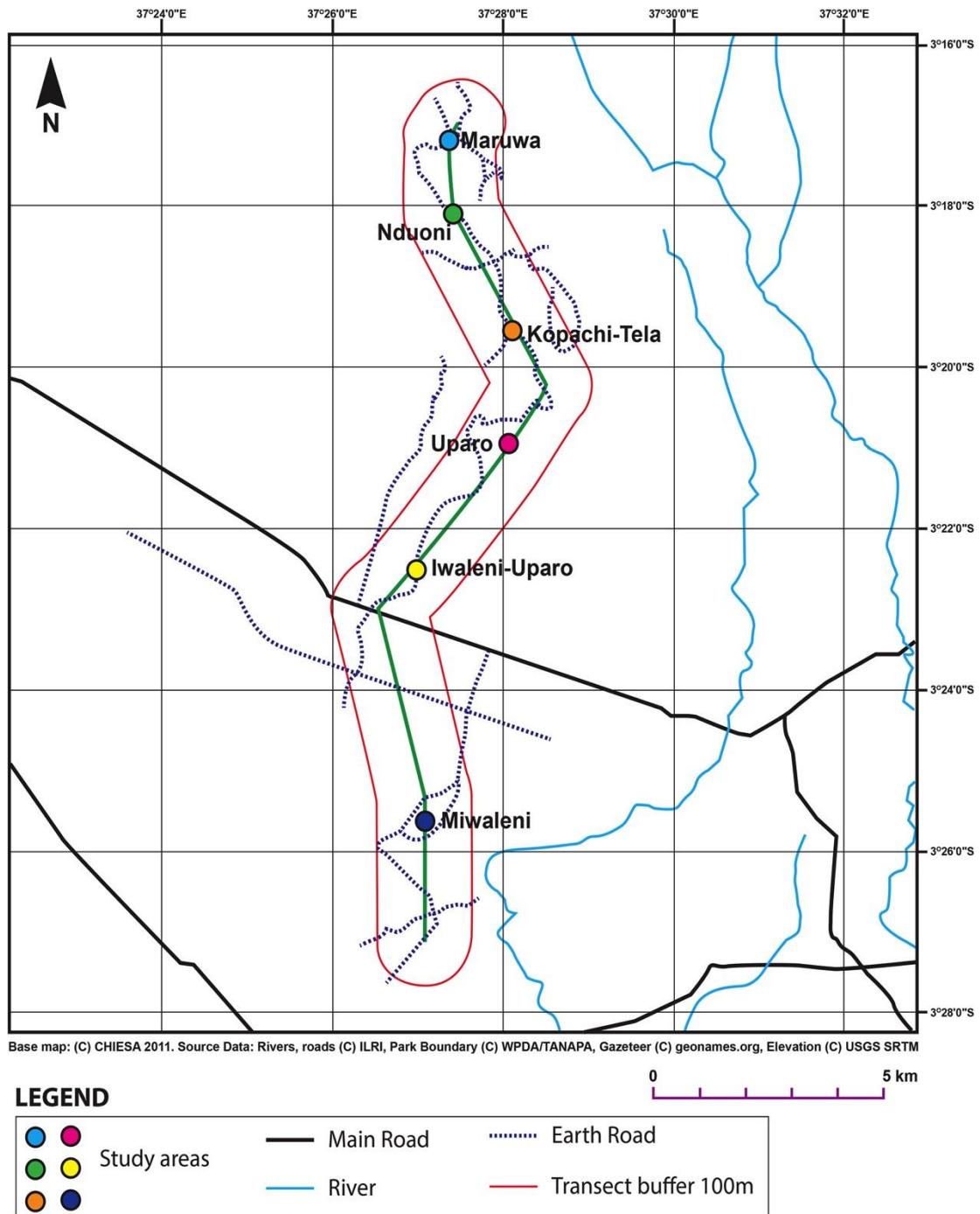


Figure 3.2: The study areas in Mount Kilimanjaro transect; the circles indicate the location where the data loggers and rain gauges for the stemborer sampling and climate data collection have been installed along the altitudinal gradients.

3.2 Climate data

The climate data (temperature, relative humidity and rainfall) required for carrying out the spatial simulations at the current climatic conditions were obtained from local weather stations by an elevation gradient from 700 to 1900 meters above sea level (m.a.s.l). A total of 24 automatic onsetTM HOBO U10-003 data loggers (hourly records) with an accuracy of $\pm 0.53^{\circ}\text{C}$, and 12 GENERAL Wireless rain gauges were installed at each station across the transects (Figures 3.1 and 3.2), within a minimum distance of 600 m from each others, to keep track of daily maximum, minimum, monthly minimum, mean and maximum air temperatures ($^{\circ}\text{C}$), relative humidity, and rainfall (Tables 3.1 and 3.2) over the period 2012-2014. The following localities were considered: Kipusi, Dembwa, Josa, Mbengonyi, Kighala and Vuria in Taita hills (Figure 3.1) and Miwaleni, Uparo Iwaleni, Uparo, Kopachi, Nduoni and Marua in the Mount Kilimanjaro transect (Figure 3.2). At each locality, the geographical coordinates (longitude and latitude) and altitudes were recorded using a Global Positioning System (GPS) (German eTrex Vista^(R)). The geographical coordinates were in format of “degree, minute, second”, then were convert into decimal degree (DD) by using the mathematical equation (3.1). The decimal degree (DD) is defined as:

$$DD = D + \frac{M}{60} + \frac{S}{3600} \quad (3.1)$$

where D is the degree; M is the minutes; and S is the second.

Additional localities for the historical data, over the last thirty years (1981-2010) were provided by the Kenya Meteorological Department and Tanzania Meteorological Agency (Tables 3.1 and 3.2).

For simulation under future climatic conditions, downscaled data of the Representative Concentration Pathways scenarios, Fifth Assessment Report (RCPs-AR5) (IPCC 2013, 2014) and future climate change scenario were used in this study. The RCPs provide spatially resolved data set of land use change and sector-based emissions of air pollutants, and it specifies annual greenhouse gas concentrations and anthropogenic emissions up to 2100 (IPCC 2013). However, because the study areas were very small and human population are concentrated in mountain, AFRICLIM data were used, since in these areas, climatic gradients are steep and feedback between land, water and atmosphere are much more localized than the pixel resolution of general circulation model. The AFRICLIM dataset provides high resolution, regionally downscaled AR5 climate projections for Africa. These data are well documented by Platts *et al.* (2015). The downscaling of the data were obtained from regional climate models (RCMs), RCMs better capture local climate feedbacks, especially in biologically rich and highly populous mountains and coastal regions (Platts *et al.* 2015). For studying the effect of future climate conditions on stem borers and their natural enemies, the year 2055 time periods were used. This year was chosen because of the time horizon (30 years) for the mid-century, which are more realistic compared to year 2080 and beyond. Furthermore, by 2050, the world's population is likely to reach 9.6 billion (UN 2013). Most of these people are expected to live in developing countries and have higher incomes than currently is the case, with consequent increase in food demand (UN 2013). In the best of circumstances, the challenge of meeting this demand in a sustainable manner will be enormous. When one takes into account the effects of climate change (higher temperatures, shifting seasons, more frequent and extreme weather events, flooding and drought) on food production, that grows even more daunting.

Table 3.1: Localities in Taita hills

Locality Names	Longitude (°)	Latitude (°)	Altitude (m)
Voi	38.5667	-3.4000	597
Kipusi	38.3803	-3.4777	831
Mwatate	38.3815	-3.5081	832
Sisal Estate	38.4000	-3.5500	869
Dembwa	38.3645	-3.4469	1093
Maktau	38.1333	-3.4000	1099
Bura Catholic	38.3167	-3.4500	1145
MurryGirls School	38.3500	-3.4500	1244
Josa	38.3561	-3.4323	1358
Wundanyi	38.3642	-3.4005	1407
Kighala	38.3621	-3.4199	1480
Msangalinyi	38.3526	-3.4155	1501
Wesu	38.3518	-3.3911	1505
Training Centre	38.3500	-3.4333	1676
Wesu Hospital	38.3500	-3.4000	1676
Mbengonyi	38.3392	-3.3914	1688
Werugha	38.3243	-3.3898	1701
Mwanda	38.2807	-3.4011	1714
Catholic Mission	38.3167	-3.4000	1748
Chief's Office	38.3167	-3.4000	1768
Vuria	38.2958	-3.4037	1797
Mgange	38.3391	-3.4006	1805

Table 3. 2: Localities in Mount Kilimanjaro

Locality Names	Longitude (°)	Latitude (°)	Altitude (m)
Kisangeni	37.4534	-3.4533	729
Miwaleni	37.4611	-3.4204	763
Moshi	37.3256	-3.3628	813
Uparo-Iwaleni	37.4502	-3.3785	891
Uparo	37.4594	-3.3476	1159
Sumi	37.4742	-3.3431	1221
Kibong'oto	37.1167	-3.2000	1249
Kopachi	37.4724	-3.3317	1365
Lyamung'o,	37.2500	-3.2333	1371
Kilema,	37.5000	-3.3000	1458
Nduoni	37.4637	-3.3097	1559
Rombo	37.6000	-3.2000	1560
Iwa	37.4540	-3.2966	1634
Masila	37.4532	-3.2957	1651
Marua	37.4569	-3.2862	1683
Marua A	37.4542	-3.2851	1684

3.3 Stem borers data

Field surveys were carried out in farmer's cultivated maize plots and more precisely on maize plants along an altitudinal gradient for two years in 2012 and 2013. No specific permissions were required for these maize fields; however permissions to conduct research were asked to the small-scale farmers (owners of the maize plots). The field studies did not involve endangered or protected species. A total of 6 localities along each altitudinal transect were selected as follows; Kipusi, Dembwa, Josa, Mbengonyi, Kighala, and Vuria of Taita hills transect (Figure 3.1) and Miwaleni, Uparo-Iwaleni, Uparo, Kopachi, Nduoni, and Marua for Mount Kilimanjaro transect (Figure 3.2). These localities were selected on the basis of the annual mean temperature, whereby each locality differed from the closest one by 1°C. In addition, these localities belong to some

of the maize agro-ecological zones as defined by Hassan *et al.* (1998). The lowland tropical and dry mid altitude zones situated mainly below 1300 m.a.s.l belong to low potential zones, whereas the moist transitional and highland tropics located above 1300 m.a.s.l belong to high potential zones for maize. Ten maize plots corresponding to the cardinal points (north, south, east and west), with minimum distance of 200meters between the plots were selected in each locality. The plots were inspected by walking every 5 meters and stop to inspect a plant to the left or right along a straight line. Each selected plant was inspected for external signs of stem borer attack (dead heart, leaf damage, damaged stems and exit holes). In case of infestation, a maximum of twelve infested plants were sampled every 5–6 weeks in each plot and dissected.

All stem borers recovered were sorted according to their developmental stage and possible species name. All stem borer larvae recovered were counted and placed individually in a glass vial containing food (artificial diet) as described by Onyango and Ochieng'-Odero (1994) to allow them to develop up to an adult (the necessary stage for definitive species identification). Each vial was labelled according to the larval stage, potential species name, location, plot number and date. The larvae were taken to the laboratory and kept until parasitism emergence or pupa formation. All pupae were kept until adult emergence for confirmation of species identity. All parasitoids cocoons recovered were recorded and the parasitoids identified. Adult stem borers and *Cotesia* species were identified at *icipe*-African Insect Science for Food and Health, Nairobi, Kenya.

In addition, life table experiments were conducted under laboratory conditions under constant and variable temperatures (Khadioli *et al.* 2014a, b) to determine the effect of temperature on the developmental time, survival, longevity and reproduction of the

targeted stem borer pests and their natural enemies, in order to predict different demographic parameters (number of generations, finite rate of increase, reproduction, and doubling time), and to generate distribution maps of the stem borer pests and their main parasitoids under different climatic scenario after validation with the field data.

3.4 Soil sampling and analysis

For each transect and altitudinal zone, soil samplings were collected from 10 cultivated plots. Each cultivated plot was representing by one replicate per altitudinal zone. For each plot, 3-4 sub-samples were selected in such a manner as to represent the entire farmer's plot were sampled and grouped. Before any soil sampling, 1-2 centimeters (cm) upper surface soil layers were first removed from the each sampling site to avoid contamination of the samples with foreign material such as crop residues. Two types of soil sample were collected at a depth of between 0-25 cm and 25-50 cm by the use of soil augur. The time when the soil samplings were done, corresponded in most altitudinal zones to an off-season for maize cultivation or a beginning of maize cultivation. For each plot, soil sub-samples were bulked and homogenized according to different depth in order to obtain two samples per cultivated plot.

Determinations of the levels of silicon (Si), phosphorus (P), potassium (K) (all expressed in parts per million (ppm) in soils was done by a Private Crop Nutrition-Laboratory Services. For Si, P and K, the Mehlich 3 extraction method (Mehlich 1984) with diluted ammonium fluoride (NH_4F) and ammonium nitrate (NH_4NO_3) was used. Then, Si, P and K levels of each soil sample were determined by atomic emission spectrometry.

Since one of the main functions of soil is to store moisture and supply it to plants between rainfalls or irrigations, the water holding capacity is a parameter allowing us to

characterize each soil in terms of their capacity to retain water after rainfalls or irrigations. This parameter depends on the textural makeup of the soil, the compaction of the soil, and the amount of organic matter in the soil. The “European” maximum water holding capacity method (Gardner 1986) was used to measure the water holding capacity of each soil sample. In this method, each soil sample is saturated with water in a cylinder and the water holding capacity is calculated based on the weight of the water held in the sample against the sample dry mass (dried at 105°C for 24 hours). The mathematical expression used to estimate water hold capacity is defined as follows:

$$WHc = \frac{w-a}{a} \times 100\% \text{ where } WHc \text{ is the water holding capacity; } w \text{ is wet soil and } a \text{ is}$$

the air dry soil.

3.5 Environmental variable interpolation

The thin plate spline (TPS) algorithm was used to interpolate environmental variables. The variables used were categorized into two groups: climatic and soil factors. Three climatic variables were used to represent the climatic control, hereof representing annual temperature, annual rainfall and relative humidity. The soil factors were represented by soil silicon, nitrogen, and water holding capacity, potassium, and phosphorus. TPS is the mathematical method for surface estimations progressively developed over the last decade (Wahba and Wendeberger 1980) and derives its names from the physical situation of bending of a thin surface. It is a deterministic interpolation technique with a local stochastic component (Hartkamp *et al.* 1999). This method was chosen because it has been used in other global studies, and performed well in comparative tests of multiple interpolation techniques (Hartkamp *et al.* 1999, Price *et al.* 2000, Jarvis and Stuart 2001a, Yan *et al.* 2005). In addition, it is computationally efficient and easy to handle large data

sets (Hutchinson 1995, Jarvis and Stuart 2001b). Further, it is able to provide a direct estimation of interpolation error and efficient diagnosis of data errors (Hutchinson and Gesseler 1994). The mathematical expression of thin plate spline is defined as

$$S_\lambda(f) = \frac{1}{n} \sum_{i=1}^n \left[\frac{f(x_i, y_i) - z_i}{w_i} \right]^2 + \lambda J_m(f) \quad (3.2)$$

with $i \in \{1, \dots, n\}$ where n is the total number of data; x_i is the longitudes; y_i is the latitudes; z_i is the environmental variable observation; w_i is the known local relative standard deviation as weight by default equal to one; and λ (lambda) is positive number called smoothing parameter, which is for controlling the amount of smoothing, and varies from zero to infinity, and $J_m(f)$ is a measure of the complexity of f , and m is called the degree for the thin-plate smoothing spline.

The TPS is calibrated by optimizing the smoothing parameter. This is usually done automatically by minimizing the generalized cross validation (GCV) (Craven and Wahba 1979). The GCV is a direct measure of the predictive error of the fitted surface, calculated by removing each data point in turns, and forming a weighted sum of the square of the discrepancy of each omitted data point from a surface fitted to all other data points. Data processing and analysis were carried out using computer program written in R software (R core Team, 2012) (Appendix A) and linked with Geographic Information System (GIS). In R software all environmental variables were generated as Tiff raster layer in Arc 1960/UTM 37S WGS 84 at 0.25 x 0.25 km spatial resolution and convert to ASCII raster format as required for modelling purpose by using ArcGIS software (version 10.1) with same geographic bounds and cell size.

3.6 Validation of thin plate spline algorithm

The accuracy of the environmental variables surface was assessed by comparing surface values with data withheld from the interpolation procedure. Three statistics were used to evaluate accuracy namely; (i) R-square (R^2), which measure how successful the fit is in explaining the variation of the data. R-square explained variability in the model, it is expected that the model tested shows the maximum variability which means that this indicator tends 1. R-squared is defined as:

$$R^2 = 1 - \left(\sum_{i=1}^n \omega_i \left(y_i - \hat{y}_i \right)^2 / \sum_{i=1}^n \omega_i \left(y_i - \bar{y}_i \right)^2 \right) \quad (3.3)$$

where n is the number of observations; y_i is the observed data value; \hat{y}_i is the predicted value from the fit or modelled value; \bar{y}_i is the mean of the observed data; and ω_i is the weighting applied to each data or residual of acquisition i ; (ii) The root Mean Square Error (RMSE), is a frequently used measure of the differences between values predicted by a model and the values actually observed from the environment that is being modelled. In other words RMSE it is one of the commonly used error index statistics (Chu and Shirmohammadi 2004). It is normally accepted that the lower the RMSE the better the model performance. The RMSE of a model prediction with respect to the estimated variable X_{model} is defined as the square root of the mean square error:

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (X_{obs,i} - X_{model,i})^2}{n}} \quad (3.4)$$

where X_{obs} is observed values and X_{model} is the modelled values; and (iii) the relative Root Mean Square Error (RMSEr), to know the variation of standard deviation of error around the mean expressed in %. The RMSEr is defined as:

$$RMSEr = \frac{\sqrt{\frac{1}{n} \sum_{i=1}^n (X_{obs,i} - X_{model,i})^2}}{\bar{y}_i} \times 100 \quad (3.5)$$

3.7 Basic mathematical formulation

The relationship between species occurrences data and environmental variables were used to build conditional probability. Bayesian modelling technique was used for building predictive relationships between species and the environment variables. This method was used because of its ability to deal with uncertainty (Pearl 1990). However, to formulate the mathematical expressions on the unknown probability distribution, the following assumptions were taken into account. Let Z be a set of finite discrete grid cells assumed to be finite and, represent some geographic regions of interest. Also given a set of points z_1, \dots, z_m in Z , each representing a locality where the insect species has been observed and recorded. Assume Φ to be the true distribution of insect species, and is represented as a probability distribution over the set Z of locality of study area. Sets of environmental variables defined on Z , are temperature, rainfall, relative humidity, soil silicon, nitrogen, potassium, phosphorus, and water holding capacity were used.

To understand how Φ represent the distribution of the insect species; the response variable (presence or absence) assumed and denoted as y . An observer first picks a random locality z from the set Z in the study area, and then records 1 if the insect species is present (that is $y = 1$) at the locality z , and 0 if the insect species is absent (that

is $y = 0$). Then $\Phi(z)$ is the conditional probability distribution $p(z | y = 1)$, which is the probability of the observer being at z , given that the insect species is present. According to Bayes theorem (Heckerman 1995, O'brien 2004), Φ is proportional to the species probability of occurrence (Phillips and Dudik 2008), thus $p(y = 1 | z)$ gives:

$$P(y = 1 | z) = \frac{p(x | y = 1)p(y = 1)}{p(z)} = \Phi(z)p(y = 1)|Z| \quad (3.6)$$

where $p(z) = 1/|Z|$; $p(y = 1)$ is the overall occurrence of the species in the study area. The quantity $P(y = 1 | z)$ is the probability that the species is present at the locality z , which ranges between 0 and 1. Solving (3.6) for $\Phi(z)$ gives

$$\Phi(z) = \frac{p(y = 1 | z)}{p(y = 1)|Z|} \quad (3.7)$$

By replacing z , with the set of environmental characteristic of Z , the transfer from the Maxent distribution Φ in abstract geographical space, to environmental variables space, in expression (3.6) gives:

$$P(y = 1 | Z) = \frac{p(Z | y = 1)p(y = 1)}{p(Z)} \quad (3.8)$$

Expression (3.8) shows that the probability distribution of Φ estimate is proportional to $p(y = 1 | z)$, the real probability that the insect species is present, with $\frac{1}{p(y = 1)|Z|}$ as proportionality factor. The probabilities on the right-hand side of (3.8) are interpreted as follows: $p(y = 1 | Z)$ is the probability that the insect species is present in the study area, given that environmental characteristics are suitable; $p(Z | y = 1)$ is the conditional probability of the environmental characteristics at Z , given that the insect species is present; and $p(Z)$ is the unconditional probability that a study area has environmental

characteristics Z. Moreover, to address the hypothesis, ten models based on combinations of the environmental variables and single groups of variables in isolation of the species based on Bayes theorem technique were formulated. These include; single groups of predictor in isolation; (i) temperature ($^{\circ}\text{C}$), (ii) rainfall (mm), (iii) relative humidity (%), (iv) soil silicon, (v) nitrogen, (vi) potassium (mmol/L), (vii) water holding capacity (%), (viii) phosphorus (mmol/L). The remaining models included (ix) a combination of all climate factors (temperature + rainfall + relative humidity), and (x) a combination of all environmental variables (temperature + rainfall + relative humidity + soil silicon + potassium + water holding capacity + nitrogen + phosphorus). According to, Bayes Theorem, mathematical expressions are defined in the form:

$$P(sp | T) = \frac{P(T | sp)P(sp)}{P(T)} \quad (3.9)$$

$$P(sp | R) = \frac{P(R | sp)P(sp)}{P(R)} \quad (3.10)$$

$$P(sp | Rh) = \frac{P(Rh | sp)P(sp)}{P(Rh)} \quad (3.11)$$

$$P(sp | Si) = \frac{P(Si | sp)P(sp)}{P(Si)} \quad (3.12)$$

$$P(sp | N) = \frac{P(N | sp)P(sp)}{P(N)} \quad (3.13)$$

$$P(sp | K) = \frac{P(K | sp)P(sp)}{P(K)} \quad (3.14)$$

$$P(sp | WHc) = \frac{P(WHc | sp)P(sp)}{P(WHc)} \quad (3.15)$$

$$P(sp | Ps) = \frac{P(Ps | sp)P(sp)}{P(Ps)} \quad (3.16)$$

$$P(sp | T, R, Rh) = \frac{P(T, R, Rh | sp)P(sp)}{P(T, R, Rh)} \quad (3.17)$$

$$P(sp | T, R, Rh, Si, N, Ps, K, WHc) = \frac{P(T, R, Rh, Si, N, Ps, K, WHc | sp)P(sp)}{P(T, R, Rh, Si, N, Ps, K, WHc)} \quad (3.18)$$

where T is the temperature; R is the rainfall; Rh is the relative humidity; Si is the soil silicon; N is the nitrogen; Ps is the phosphorus; K is the potassium; WHc is the water holding capacity; and sp is the species presences. In addition, the equation (3.18) represents the full matrix of conditional probability distribution of adaptation, given all the variables.

3.8 Modelling approach

The impact of environmental variables on potential species distribution was implemented by using maximum entropy (Maxent) software (version 3.3.3k) (Phillips *et al.* 2006) due to its high performance compared to other predictive algorithms in a recent comparative methodology study (Elith *et al.* 2006, Pearson 2007, Austin 2007, Blach-Overgaard *et al.* 2010). Maxent is a machine learning method that estimates the distribution of a species by finding the probability distribution of maximum entropy subject to constraints representing incomplete information about the distribution (Dudik *et al.* 2004, Halvorsen 2012). The constraints are that the expected value of each environmental variable should match its average over sampling locations derived from environmental layers (Phillips *et al.* 2006, 2009). Maxent has many advantages, including (i) it requires only presence data, together with environmental information for the whole study area; (ii) it can use both continuous and categorical data and can incorporate interactions between different variable; (iii) the Maxent probability distribution has a simple and precise mathematical formulation (Della-Pietra *et al.* 1997, Dudik *et al.* 2004,

Phillips *et al.* 2006, Dudik and Philips, 2009). Over-fitting in maxent can be avoided by using inbuilt regularization (Zhang 2005) that is reliable and known to perform well (Hastie *et al.* 2009), and the output is continuous, allowing fine distinctions to be made between the modelled suitability of different areas (Philips *et al.* 2006). Furthermore, in recent comparisons among several techniques of prediction of species distribution, Maxent resulted to be the most effective method using presence-only data, and showed sometimes a performance comparable to several traditional tools using presence/absence data, such as general linear models and general additive models (Rushton *et al.* 2004, Elith *et al.* 2006, Hernandez *et al.* 2006). Additionally, maxent is also designed to integrate with geographical information system (GIS) software such as ArcGIS or GRASS GIS by using ESRI ASCII grid format files. Further, it takes as input comma separated values file that includes species occurrences and environmental data, thus making data input and predicted output easier to handle. By default the Maxent software includes a five mathematical feature types to treat each environmental variable (Elith *et al.* 2011). However, in this study auto feature option which automates the task of choosing feature types based on sample size was used.

Model performances were assessed by dividing the species occurrence data into random training (80%) and test (20%) datasets. A given model was calibrated on the training data and evaluated on the test data using the Area Under the Curve (AUC) of the receiver operating characteristics (ROC) criterion. AUC evaluate how well model prediction discriminate between locations where the species are present and absent, and is one of the most widely used threshold-independent evaluators of the model discriminatory power (Fielding and Bell 1997, Philips and Dudik 2008, Baldwin 2009, Lobo *et al.* 2010, Blach-Overgaard *et al.* 2010). Further, AUC is a convenient index because it provides a single

measure of overall prediction accuracy that is not dependent upon a particular threshold. ROC curves are constructed by using all possible thresholds to arrange the scores from confusion matrix (Table 3.3). The confusion matrix is rather more straightforward than its names suggests, and is alternatively termed as a contingency table or an error matrix. The confusion matrix records the frequencies of each possible types of prediction from analysis of test data: the entries in the confusion matrix have the following meaning in the context of this study: (a) true positive (the model predicts that the species is present and test data confirm this to be true); (b) false positive (the model predicts presence but test data show absence); (c) false negative (the model predicts absence but test data show presence); (d) true negative (the model predicts and test data absence). The frequencies are commonly recorded in a confusion matrix as described in Table 3.3 and obtaining sensitivity and specificity for each matrix and then plotting sensitivity against the corresponding proportion of false positive (equal to 1-specificity) (Allouche *et al.* 2006). Sensitivity represents how well the data correctly predict presence, whereas specificity provide a measure of correctly predicted absences (Baldwin 2009). In this case presence only data is used so the model is tested against a random model. A good model is defined by the curves that maximize sensitivity for low values of the false-positive fraction (Hernandez *et al.* 2006). The significance of the curve is quantified by the area under the curves (AUC) and has a value that ranges from 0 to 1, where a score of 1 indicates perfect discrimination, a value of 0.5 indicating that the model is not better than random guess and values <0.5 indicate performance worse than random. The worse than random model can occur because a model may fit the modelling data but predict badly, while AUC values ≥ 0.75 are considered in the best model category (Elith *et al.* 2009). An AUC value can be interpreted as indicating the probability that, when a presence locality and

absence locality are drawn at random from the population (Elith *et al.* 2006, Phillips *et al.* 2006).

Moreover, during the model training process, the algorithm tracks which environmental variables make the most significant contribution to final prediction and produces a table which ranks the importance for each environmental variable (Philips and Dudik 2008). In this study to assess the relative influence of each environmental variable for a given species, the built in jack-knife were used to examine the contribution of each variable to the final regularised training gain when all the variables of the particular model were included in the Maxent run. The principal steps used to build and validate a species distribution are outlined in figure 3.3.

In addition, a preliminary agreement between the model predicted and observed species presence was conducted using Nash-Sutcliffe Coefficient index (E), which is a measure of statistical association, which indicates the percentage of the observed variance that is explained by the predicted data (Nash and Sutcliffe 1970). This efficiency criterion is commonly used to assess the predictive power of hydrological models, because it involves standardization of the residual variance, and its expected value does not change with the length of the record. Mathematically the index is defined as:

$$E = 1 - \frac{\sum_{i=1}^n (X_{obs,i} - X_{pred})^2}{\sum_{i=1}^n (X_{obs,i} - \bar{X}_{obs})^2} \quad (3.19)$$

where n is the sample size; X_{obs} is the observed values; X_{pred} is the predicted or simulated values; and \bar{X}_{obs} is the average measured observed values. The second terms

in equation (3.19) represent the ratio between the mean square error (MSE) and the variance of the observed data. The value of E usually ranges from $-\infty$ to 1. An efficiency of 1 ($E = 1$) corresponds to a perfect match between model and observations. An efficiency of 0 indicates that the model predictions are as accurate as the mean of the observed data, whereas an efficiency less than zero ($-\infty < E < 0$) occurs when the observed mean is a better predictor than the model, the closer the model efficiency is to 1, the more accurate the model. Also, the goodness of fit revealed by graphical comparison of results such as the plots of observed values (X_{obs}) against predicted (X_{pred}).

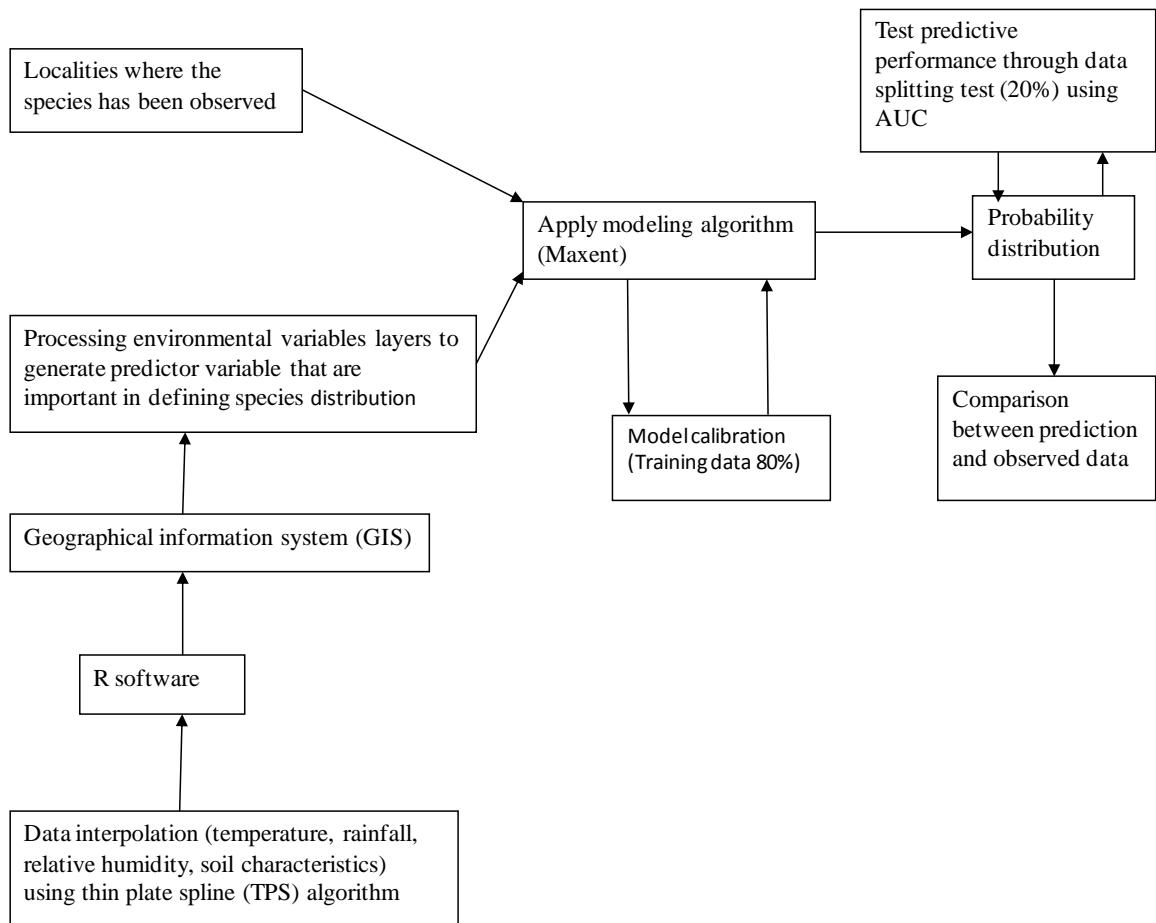


Figure 3.3: Flow diagram summarizing of the modelling potential distributions of *Chilo partellus* and *Busseola fusca* with environmental variables.

Table 3.3: Schematic of a confusion matrix which predicted presences and absences are related to their known status as observed presences or absence.

Predicted	Observed	
	Presence (+)	Absence (-)
Presence (+)	True positive(TP)	False positive(FP)
Absence (-)	False negative(FN)	True negative(TN)

3.9 Transforming probability suitabilities to presence or absence of the species

In this study, optimal occurrence threshold for each species model by maximizing the sum of sensitivity and specificity (MaxSSS) was used. This approach was chosen due to its high performance compared to other selection threshold methods (Liu *et al.* 2005, 2013), especially when models are constructed using presence-only data (here, background data are generated by Maxent). Furthermore, maxSSS is an objective method and it optimizes the discrimination between presence and absence rather than between presence and random point (Cantor *et al.* 1999, Liu *et al.* 2005). The mathematical descriptions of MaxSSS are derived as follows; assume that ψ is the species prevalence within the test data; m represents the estimates of a metric calculated with presence/absence data and m_1 represents the presences data only. From the true presence of the test data, the sensitivity (Se) of the model can be estimated, which is appropriate for both presence/absence data and presence-only data because no absence data are required for its estimation, then $Se = Se_1$. But, this is not the case for specificity (Sp),

which can only properly be estimated with presence/ absence data (Liu *et al.* 2005); that is $Sp \neq Sp_1$. Therefore, the pseudo- specificity (Sp_1) can be formulated as:

$$Sp_1 = \left(\frac{\lambda(1-Se) + (1-\psi)Sp}{1-\psi+\lambda} \right) \quad (3.20)$$

$$\text{Thus, } Se_1 + Sp_1 = Se + Sp_1 \quad (3.21)$$

By substituting equation (3.20) into (3.21), gives

$$Se_1 + Sp_1 = \frac{\lambda}{1-\psi+\lambda} + \frac{(1-\psi)(Se + Sp)}{1-\psi+\lambda} \quad (3.22)$$

Assume λ is the constant for a set data and $\frac{1-\psi}{1-\psi+\lambda} > 0$, then $SSS_1 \equiv Se_1 + Sp_1$ is a monotonically increasing function of $SSS \equiv Se + Sp$. Hence, if a threshold maximizes SSS_1 , it will also maxSSS, and vice versa. That is, the same threshold value is selected by maxSSS using either presence/absence or presence-only data.

Using the dichotomised presence-absence predictions, it becomes possible to generate combined maps of co-occurrence across more than one species. In the confusion matrix below (Table 3.4), predictions are combined for two species: *C. partellus* and *B. fusca*. The entries in the confusion matrix have the following meaning in the context of this section: value (1, 1) corresponds to grid cell predicted to be suitable for both species, value (1, 0) indicate predictions suitable for *B. fusca*, (0, 1) is the prediction suitable for *C. partellus* and value of (0, 0) indicate unsuitable predictions for both species. However, for confusion classification matrix construction, the following assumptions were made: suppose χ is the maxSSS threshold value, $0 \leq \chi \leq 1$, with which to predict the value of the dichotomous response χ , and π is the estimated probabilities. The decision rule based on the threshold is defined as follows:

$$U = \begin{cases} 1, & \text{if } \pi > \chi \\ 0, & \text{if } \pi < \chi \end{cases} \quad (3.23)$$

Using this decision rule the generic confusion (classification) matrix is obtained (Table 3.4).

Table 3.4: A confusion (classification) matrix for *Chilo partellus* and *Busseola fusca*

		<i>C. partellus</i>	
		1	0
<i>B. fusca</i>	1	(1,1)	(1,0)
	0	(0,1)	(0,0)

CHAPTER FOUR

PREDICTING THE IMPACTS OF TEMPERATURE CHANGES TO THE MAIZE STEM BORERS AND THEIR NATURAL ENEMIES ALONG ALTITUDINAL GRADIENTS IN TWO MOUNTAINS OF EAST AFRICA

4.1 Introduction

The agricultural sector, due to its size and sensitivity, is at risk from global climate change with a projected average global yield loss of up to 50% by 2050 (IPCC 2007, Mendelson 2009). Developing countries, which already have low productivity due to other development challenges, are vulnerable to the risks of climate change (Waithaka *et al.* 2013). In East Africa, agriculture plays a major role in economic development, poverty alleviation, job creation, and food security. The sector is highly vulnerable to climate changes because of over dependence on natural resources such as water and rainfed traditional agricultural systems (Arendse 2010). Climate changes are also predicted to extremely influence the dynamics and the status of insect pests (Porter *et al.* 1991, Cammell and Knight 1997, Bale *et al.* 2002). For the last 30 years, a change in climate particularly global warming has caused numerous shifts in the distribution and abundance of insect species (Lastuvka 2009).

Maize stem borers are the most damaging field pests of maize production in East Africa, with majority of species belonging to the Noctuidae, Pyralidae and Crambidae families. These pests often occur as a complex of species with overlapping spatial and temporal distributions, though they are individually adapted to survive in regions that provide for their specific ecological requirements. Unfortunately, temperature which is one of the most important climatic variables that directly affect herbivorous insects is predicted to

increase by about 1.4°C to 5.8°C towards the year 2100 (IPCC 2007, Karuppaiah and Sujayanad 2012). This change could profoundly affect population dynamics and status of cereal stem borers because their population growth potentials are mainly temperature driven. The predicted rise in temperature may increase or decrease stem borer development rates and results in variation in crop damages depending on species optimum temperature range (Hassan *et al.* 1998). These changes could thus have major impacts on food security. Despite the many studies that have been conducted on maize stem borer distribution, no information exists for predicted future distributions of maize stem borers and their main natural enemies under climate change scenarios for any maize production areas at local scale in East Africa. The fundamental hypothesis of the present chapter is that the distribution and abundance of maize stem borers and their natural enemies will shift and increase towards higher elevations as consequence of climate change and most likely lead to higher yield losses. Therefore, the objective of the this chapter was to predict the impact of temperature changes on distribution and abundance of *C. partellus*, *B. fusca*, *C. flavipes* and *C. sesamiae* at local scale along two East Africa Mountains gradients through phenology modelling.

4.2 Material and Methods

4.2.1 Climate data

In this chapter, current temperature data (2013) and future temperature (2055) were used, and the sources of these data are described in chapter three, sections 3.2.

4.2.2 The *C. partellus*, *B. fusca*, *C. flavipes* and *C. sesamiae* phenology models

The temperature-driven phenology models for *C. partellus*, *B. fusca*, *C. flavipes* and *C. sesamiae* were developed based on laboratory experimental data at constant temperatures,

which was validated through life table data collected at fluctuating temperatures in field conditions (Khadioli *et al.* 2014a, b). Daily minimum and maximum temperatures obtained during these experiments were used in stochastic simulation.

A good agreement was observed between simulated and experimental results, for example for *B. fusca*, the simulated development time were 8.86, 67.39 and 9.91 days when the observed development times were 8.92, 68.74 and 19.33 days for eggs, larvae and pupae respectively.

Similarly for *C. partellus*, the simulated development times were 8.30, 46.23 and 13.81 days when the observed development times were 8.22, 48.36 and 14.86 days for eggs, larvae and pupae, respectively (Khadioli *et al.* 2014a, b). These results show that the phenology models developed, can be applied to predict the insect population abundance and demographic parameters in other agro-ecological zones, which justified their application in the current study in both transects. The term life table in the present chapter allow for characterization of species in terms of age-specific mortality (or survivorship) and fecundity. Fecundity is defined as the number of eggs deposited by an individual female during her entire life period. In addition, life tables are powerfull tools for analyzing and understanding the impact of external factors such as temperature on the growth, survival, reproduction and rate of increase of insect populations (Khadioli *et al.* 2014a, b). The Phenology models consist of a set of functions that describe temperature-dependent development in the immature life stages. The Logit model was used to describe the variation of development time in eggs, larvae and pupae, whereas complementary ClogLog model was used for female and male pupae (Taylor 1981, Khadioli *et al.* 2014, Fand *et al.* 2014a). The mathematical expression of Logit and Cloglog are given as:

$$\text{Logit model: } h(x) = \frac{1}{1 + \exp(-(δ_i + σ \ln x))} \quad (4.1)$$

$$\text{Clog-log model: } h(x) = 1 - \exp(-\exp(δ_i + σ \ln x)) \quad (4.2)$$

where $h(x)$ is the probability to complete development (an insect success or failure to develop to next life stage) at time x ; $\ln x$ is the natural logarithm of the days observed, $δ_i$ and $σ$ are the parameters to be estimated; $σ$ is the slope of the regression model representing the dispersion of development time in the life stage, and $δ_i$ is the intercept corresponding with temperature (i).

In addition, before fitting data to these models, the cumulative emergence distribution through time was calculated in terms of percentile for each temperature and then normalized by dividing the emergence time by the mean emergence time for each cumulative distribution (Wagner *et al.* 1984). The cumulative frequency distribution at different temperatures approximately coincided and thus a single temperature-independent distribution was obtained at a normalized age scale using equations (4.1) and (4.2). The development time (d) was used to calculate development rates. Development rate was expressed by the reciprocal of the mean development times of eggs, larvae and pupae. The linear model was fitted to establish the relationship between development rates and temperature (Khadioli *et al.* 2014a, b). This model is commonly used to determine thermal constant and lower development threshold from development rate of arthropod stage (Lopez-Arroyo *et al.* 1999). Theoretical lower development threshold temperatures and thermal constant were estimated from the slope and intercept of the model. The equation used for estimating the linear relationship is:

$$r(T) = η + η_1 T \quad (4.3)$$

where $r(T)$ is the rate of development ($1/d$) at temperature T ($^{\circ}\text{C}$); and, η and η_1 represent the y-intercept and slope of the equation, respectively.

The function used to describe development rate for all three species and their natural enemies is the non-linear Logan model (Logan *et al.* 1976, Shi *et al.* 2011). The mathematical expression of this version of the Logan model was used:

$$r(T) = \Delta \left(\exp(\rho T) - \exp\left(\rho T_{\max} - \frac{(T_{\max} - T)}{v}\right) \right) \quad (4.4)$$

where T is the temperature in Celsius; $r(T)$ is the development rate at T ; Δ is the constant defining maximum development rate; ρ is the constant defining the increase rate at optimal temperature; T_{\max} is the maximum temperature threshold; and v is the temperature range over which physiological breakdown becomes the overriding influence. The effect of temperature on the mortality of *B. fusca*, *C. partellus*, *C. flavipes* and *C. sesamiae* of the immature life stages (egg, larva and pupae) was described by second order exponential polynomial function (Zahiri *et al.* 2010, Khadioli *et al.* 2014a, b). The following expression of polynomial model was used:

$$m(T) = \exp(b_1 + b_2 T + b_3 T^2) \quad (4.5)$$

where $m(T)$ is the rate of mortality at temperature T ; b_1 is the intercept of T ; b_2 and b_3 are the coefficient of T . A three parameter Stinner model (4.6) (Stinner *et al.* 1974, Shi *et al.* 2011) was used to determine the relationship between longevity of female adults and temperature for *B. fusca*, *C. partellus*, and *C. sesamiae*. Hilbert and Logan model (4.7) (Hilbert and Logan 1983, Zahiri *et al.* 2010) was used to describe the effect of temperature on longevity for *C. flavipes*. The mathematical expressions of Stinner, Hilbert and Logan models are given below, respectively:

$$s(T) = \frac{c}{1 + \exp(k_1 + k_2 T)} \quad (4.6)$$

$$s(T) = \psi \left(\frac{(T - T_{\min})^2}{(T - T_{\min})^2 + \zeta} - \exp \left(-\frac{(T_{\max} - (T - T_{\min}))}{\Delta T} \right) \right) + \theta \quad (4.7)$$

where $s(T)$ is the senescence at temperature T ; ψ , ζ , θ and c are empirical constants; k_1 and k_2 are constants representing the intercept and slope, respectively; ΔT is the width of the high-temperature boundary area; T_{\max} is the maximum (upper) temperature threshold and T_{\min} is the minimum (lower) temperature threshold.

The reproduction model consists of a function that describes temperature-dependent oviposition per female and functions that describe daily proportions of fecundity for females by using female normalized age as the predictor variables. The following function (4.8) (Tonnang *et al.* 2013, Khadioli *et al.* 2014a, b) below was used to determine the effects of temperature on the total number of eggs laid per female for *C. partellus*, *C. flavipes* and *C. sesamiae*.

$$t(T) = b_1 + b_2 T + b_3 T^d \quad (4.8)$$

where $t(T)$ is the total number of egg per female at temperature T ; and d is the constant. However, the expression used to determine the effects of temperature on the total number of eggs laid per female for *B. fusca* is defined as

$$t(T) = \exp(b_1 + b_2 T + b_3 \sqrt{T}) \quad (4.9)$$

Gamma distribution (Press *et al.* 2007) was used to assess the relative oviposition for *B. fusca*, *C. partellus*, *C. flavipes* and *C. sesamiae*. The probability density function can be defined based on the gamma function as follows:

$$l(T) = \int_0^T \frac{1}{b^a \Gamma(a)} T^{a-1} e^{-\left(\frac{T}{b}\right)} dT \quad (4.10)$$

$l(T)$ is the relative oviposition frequency at temperature T ; a is the shape parameter and b is the scale parameter; Γ is the gamma function. These functions are then combined to yield the overall phenology model of the species.

4.2.3 Statistical criteria for models selection

Five statistical criteria were used to determine the best model described in section 4.2.2, these include: (i) Akaike information criterion (AIC) (Burnham and Anderson 2004) developed and proposed by (Akaike 1974), that demonstrates the deviation between observed and predicted data and which depends on the number of parameters of statistical model, and the maximum value of the likelihood function for the estimated model. In selecting a model, one with the smallest value of AIC compared with other models is

considered the best. AIC is defined as $AIC = n \ln \left(\sum_{i=1}^n w_i \left(y_i - \hat{y}_i \right)^2 / n \right) + 2k$ where k is

the number of fitted parameters in the model;

(ii) Model Selection Criterion (MSC), which is a modification of AIC, and the model

equation is $MSC = \ln \left(\sum_{i=1}^n w_i \left(y_i - \bar{y}_i \right)^2 / \sum_{i=1}^n w_i \left(y_i - \hat{y}_i \right)^2 \right) - 2k/n$;

(iii) R-square (R^2) the mathematical expression is defined in chapter three, section 3.6;

(iv) Adjusted R-square (R^2_{adj}) is a modification of R-square that adjusts for the number of terms in a model. R -square always increases when a new term is added to a model, but adjusted R-square increases only if the new term improves the model more than would be expected by chance. The adjusted R-square statistic can take on any value less than or

equal to 1, with a value closer to 1 indicating a better fit. (R^2_{adj}) is defined as

$$R^2_{adj} = 1 - \frac{(n-1)}{n-k} (1 - R^2) \text{ where } n \text{ is the number of response values (sample size); and}$$

(v) Deviance, is the statistic that measures the total deviation of the response values from the fit to the response values. It is also called the summed square of residuals (sum of error square), and this value is expected to be small otherwise the variability is not being fully explained by temperature and observed days. A value closer to 0 indicates that the model has a smaller random error component, and that the fit will be more useful for prediction. A female ratio of 0.5 was established for all the temperatures that were studied.

4.2.4 Spatial analysis

The phenology models of the species are temperature dependent, in selected geographical coordinates, minimum and maximum temperatures were inferred in the phenology model through a cosine function (Sporleider *et al.* 2008). The cosine function T_i is defined as:

$$T_i = \frac{(T_{\max} - T_{\min})}{2} \cos\left(\frac{\pi \times (i-0.5)}{48}\right) + \frac{(T_{\max} - T_{\min})}{2} \quad (4.11)$$

where T_i is the temperature (in Celsius) of time step i ($i = 1, 2, 3, \dots, 48$), and T_{\min} and T_{\max} are daily minimum and maximum temperatures, which was then applied for direct estimate of the following life table parameters:

4.2.4.1 Generation length in days

One of the important aspects of insect development is their number of generations per year, which varies both between species and geographically within one species. The

following equation was employed to calculate this life table parameter (Kroschel *et al.* 2013).

$$G = \left(1/d_{Egg} \right) + \left(1/d_{Larva} \right) + \left(1/d_{Pupa} \right) + \left[\left(1/S_{Female} \right) \times TR_{50\%} \right] \quad (4.12)$$

where G is generation time; d_{Egg} , d_{Larva} , d_{Pupa} are the stage-specific development rates of immature life-stages; S is the mean senescence rate of female, $TR_{50\%}$ is the normalized age of the female until 50% oviposition.

4.2.4.2 The net reproduction rate

This is the rate of multiplication in one generation (Lotka 1945) and is best expressed as the ratio of total female birth in two successive generations. In other word, the net reproduction rate is the lifetime reproductive potential of the average female, adjusted for survival. This is denoted by R_0 , and is determined by multiplying age-specific fecundity and by its survival rates, and summing these products. The mathematical expression used is defined as:

$$R_0 = \sum L_x M_x \quad (4.13)$$

where x equals the female age in days; L_x is the age-specific survival of the females at age x ; and M_x is the age-specific fecundity per female at age x . Assuming survival and fertility schedules remain constant over time, if $R_0 > 1$, then the population will grow exponentially. If $R_0 < 1$, the population size will shrink exponentially, and if $R_0 = 1$, the population will not change over time.

4.2.4.3 The intrinsic rate of increase

This is a measure of the rate of growth of a population. The intrinsic rate of increase (r), was calculated through iteration of the Euler-Lotka equation (4.14) below as elaborated by Howe (1953).

$$\sum e^{-rx} L_x M_x = 1 \quad (4.14)$$

where e is the base of the natural logarithms and x subscripts age. Provided that the net reproductive rate (R_0) is near to 1, by rearranging equation (4.14) and taking natural logarithm of both sides, the intrinsic rate of increase (r) was estimated using the approximate formula;

$$r = \ln(R_0) / G \quad (4.15)$$

Alternatively, the equation (4.15) can be derived through geometric and exponential models, where the size of an exponentially growing population at some arbitrary time t is $N_t = N_0 e^{rt}$. Consider the growth of such a population from time zero through one

generation time, G ; it is $N_G = N_0 e^{rG}$, dividing both sides by N_0 gives $\frac{N_G}{N_0} = R_0 = e^{rG}$.

Since N_G / N_0 and R_0 both are estimates of the same rate of population growth over the period of one generation, then by taking the natural logarithm of both sides and dividing by G gives an estimate of intrinsic rate of increase (r) as expressed in equation (4.15).

4.2.4.4 Finite rate of increases

This is the rate of population increases from one time period to the next time period. In the assumption that generations do not overlap and constant rate of birth and death imply population will change by a constant number each year. Therefore, for the calculation in this life table parameter, the following equation was used;

$$\lambda = e^r \quad (4.16)$$

4.2.4.5 Doubling time

Doubling time refers to the time it takes for the growth of the specific insects to double.

The expression for geometric increase gives the projection to time t ;

$$N_t = N_0 e^{rt} \quad (4.17)$$

where t is the length of time; N_0 represents the initial number in the population at time zero; and N_t is the total population size at time t . If a population doubles in size (that is increase by a factor of 2), the ratio N_t / N_0 would be exactly 2, r is the intrinsic rate of increase. By taking natural logarithm of 2, thus, the expression used for the population to double (doubling time, DT) is given by

$$DT = 0.693 / r \quad (4.18)$$

The variations of pest population increase within the year due to seasonal weather fluctuations which were analysed through plotting the simulated life table parameters against Julian days of the year.

Furthermore, to understand the effect of altitude to the number of generation in specific locality, three locations per transect were selected to represent the local weather conditions as follows: Miwaleni (low altitude), Kopachi (mid-altitude) and Marua (high altitude) in the Mount Kilimanjaro and Kipusi (low altitude), Mbengonyi (mid- altitude) and Vuria (high altitude) in Taita hills. In order to estimate the potential number of generations a species could complete within a year and its potential population increases according to altitudinal gradient of these particular locations. The choice of these locations was based on the fact that *C. partellus* is dominant species at the low altitude

and *B. fusca* is dominant at high altitude (Ong'amo *et al.* 2006) and cause significant damage to the maize in these areas during main crop growing season (Hassan *et al.* 1998). The number of generations per year of borer and the natural enemies were estimated by using daily minimum and maximum temperature data from these locations and the future temperature data for the year 2055. Additionally, the variations of finite rate of increase under current and future climatic conditions were determined.

From the values of life table parameters calculated, to assess the potential distribution and abundance of the species at local scale, three risk indices as defined below were computed.

4.2.4.6 Establishment risk index (ERI)

This index identifies the geographical areas in which the pest insects may establish and survive. In addition, this index illustrates the severity and spread potential. The geographical areas with index value 1 indicate that all immature life stages of the pest survive throughout the year at certain proportions. If not, the number of days in which a single stage would not survive are counted and divided by 365 (Sporleider *et al.* 2008, Kroschel *et al.* 2013, Fand *et al.* 2014b). The values of x for egg, larval and pupa stage of an insect pest were subtracted from 1. In order to calculate of this survival index, the following formula was employed:

$$ERI = (1 - x_{Egg}) \times (1 - x_{Larval}) \times (1 - x_{Pupa}) \quad (4.19)$$

where $x = \frac{\sum N_i}{365}$; N_i is the number of days within the year; a specific life stages (Egg,

Larva, and Pupa) does not survive (mortality in stage); and *ERI* is the establishment risk index.

4.2.4.7 Generation index (GI)

This index is an estimate of the mean number of generations that a given insect pest may produce within a given year. The generation index is calculated by averaging the sum of estimated generation lengths for each Julian day, as demonstrated in the following equation (Kroschel *et al.* 2013, Fand *et al.* 2014b).

$$GI = \left(\sum_{i=1}^{365} 365 / G_i \right) / 365 \quad (4.20)$$

where 365 is the number of Julian days per year; G_i is the predicted generation length in days on Julian day i ($i = 1, \dots, 365$). The generation length decreases at high temperatures which means more generations per year leading the population size to increase. Consequently, the generation index alone does not give conclusive information about the insect pest population growth potentials and therefore, needs to be concurrent with the activity index described in the following section, which is true representative of insect pest damage potential.

4.2.4.8 Activity index (AI)

The Activity index indicates the decimal power of the estimated population growth potential within a given year. It considers the development time, immature mortality and fecundity and is based on the finite rate of population increase modelled for each day of the year. Every increase of index by value of one indicates a 10-fold increase of the insect pest population. For instance, without considering the effects of the other population limiting factors such as parasitoids, predators, humidity, food and rainfall, an index value of four would illustrate a potential population increase by a factor of 10^4 in a year

(Sporleder *et al.* 2008). The index is calculated by taking a log of the product of the estimated finite rates of increase for each Julian day as shown in the following formula:

$$AI = \log_{10} \prod_{i=1}^{365} \lambda_i \quad (4.21)$$

where λ_i is the finite rate of increase at Julian day at i ($i = 1, \dots, 365$). While computing the activity index, the whole life history of the pest is taken into account. In addition to the insect pest population growth potential, this index illustrates the severity of incidence and spread potential of the target insect pest in different agro-ecological zones. Alternately, activity index can also be linked to the doubling time (DT), another life table parameter having same biological significance.

4.2.5 Models implementation

In this chapter, the *C. partellus*, *B. fusca*, *C. flavipes* and *C. sesamiae* phenology models were implemented through the Insect Life Cycle modelling (ILCYM) software, version 3.0 (Tonnang *et al.* 2013). ILCYM is an open source computer-aided tool built on Java and R-codes, and is also linked to uDig platform, a basic GIS which allows developing phenology model, conduct population analysis and spatial mapping of the pest risk in different geographical regions. However, in this chapter, for assessing the potential distribution and abundance of the species at local scale, the index interpolator, a sub-module of the ILCYM was used to calculate the three risk indices namely; establishment risk index (ERI), generation index (GI), and activity index (AI). Using index interpolator module, the following steps were considered: the digital elevation model (DEM) was defined as co-variable; DEM was obtained from the Shuttle Radar Topography Mission (SRTM) (Platt *et al.* 2015). Phenology models and temperature data station for a year

were also inputted into the tool. The inbuilt thin plate algorithm was used for interpolation of the indices on the surfaces of DEM at local scales. The indices were generated as American Standard Code for Information Interchange (ASCII) files format and then were transferred to ArcGIS software, version 10.1 for enhancing the visualization. By using geographical coordinates (longitude and latitude), the values for establishment, generation, activity index both current and future climatic conditions were extracted from ASCII files generated for these indices using point sampling tool in quantum geographical information system (QGIS) software, version 2.6. The indices estimated were plotted against altitude to visualize the changes along altitudinal gradients. Furthermore, to understand the effect of future climate, the difference between the current (2013) and future (2055) climatic conditions were obtained by using raster calculator through quantum geographical information system.

4.2.6 Predicting maize yield losses

A relationship has been established between estimated activity index of the two stem borer species and estimated average maize yield losses associated with stem borer infestation under current climatic conditions in Kenya, based on literature reports (Hassan *et al.* 1998, De Groote *et al.* 2002, Ong'amo *et al.* 2006). Each transect was split into four maize agro-climatic zones according to altitude as defined by Hassan *et al.* (1998). From the bottom to the top they included the lowland tropical areas below 1000 m.a.s.l., a dry mid altitude between 1000-1300 m.a.s.l., a moist transitional area between 1300-1600 m.a.s.l., and the highland tropics above 1600 m.a.s.l.. By using the geographical coordinates of all these zones, the corresponding value for activity index for the current and future climatic conditions were extracted from ASCII files generated for activity

index. Since the activity index was continuous in the study area, an average activity index for current and future climatic conditions were calculated for each maize agro-climatic zone. The relationship between the estimated yield losses and activity indices for current climate was estimated by a linear equation:

$$Y = \beta_0 + \beta_1 A \quad (4.22)$$

where Y is the estimated yield loss (%) under current climatic conditions; A is the activity index representing stem borer potential damage; and β_0 and β_1 are intercept and slope of the equation, respectively. To test the significance of the fitted linear equation the F and t statistical tests were applied. Using the parameter values for β_0 and β_1 and activity index values for current climate, the predicted yield loss values were estimated for current climatic conditions. With the assumption that the yield loss will follow the same relationship as the current scenario, the linear equation established was used to estimate the yield losses in the study area under future climatic conditions and the change in yield loss due to climate change. Thus, the values for A in above equation were replaced with activity index values for the year 2055 as defined below:

$$Y_1 = \beta_0 + \beta_1 A_1 \quad (4.23)$$

where Y_1 is the estimated yield loss (%) under future climatic conditions of the year 2055; and A_1 is the activity index representing stem borers potential damage under future climatic conditions.

4.3 Results

4.3.1 Change in species distribution

Under the current climate scenario of the year 2013, the establishment risk index (ERI) range from 0.82 to 0.92, 0.80 to 0.88, 0.65 to 0.75 and 0.76 to 0.84 for *C. partellus*, *C.*

flavipes, *B. fusca* and *C. sesamiae*, respectively in the Mount Kilimanjaro area (Figures 4.1a and 4.1d), and from 0.78 to 0.89, 0.78 to 0.90, 0.69 to 0.81 and 0.79 to 0.85 for *C. partellus*, *C. flavipes*, *B. fusca* and *C. sesamiae*, respectively in the Taita hills (Figures 4.2a and 4.2d). This reflects well the current distribution of *C. partellus* with higher values at low altitude and lower values at high altitude, and *B. fusca* with higher values at high altitudes and lower values at lower altitudes. Above 1100 m.a.s.l the likelihood of establishment of *C. partellus* is reduced but it occurs. Under the present climate scenario *C. partellus* is already distributed below 1600 m.a.s.l and presents a severe risk of establishment risk index (ERI>0.82) in the higher altitudes of the gradient. Under the year 2055 temperature scenario, the boundaries of the four species are indicated to shift to higher absolute change in establishment index of up to 0.05 at the top of the gradient on Mount Kilimanjaro (Figures 4.3a, b, c and d), and up to 0.09, 0.07, 0.07 and 0.03 at the top of the gradient in the Taita hills for *C. partellus*, *C. flavipes*, *B. fusca* and *C. sesamiae*, respectively (Figures 4.4a, b, c and d).

4.3.2 Change in species abundance

Under the current climate of the year 2013, the generation index (GI) (abundance) of *C. partellus* fluctuates between 3 in areas around 1400-1600 m.a.s.l and 7 at the bottom of both transects (Figures 4.1b and 4.2b). For *C. flavipes* GI ranges from 14-17 in low altitude areas around 700-900 m.a.s.l and 10-12, respectively at the top of both transects (Figures 4.1b and 4.2b). For *B. fusca*, GI ranges from 2-4 in both transect (Figures 4.1e and 4.2e). *C. sesamiae* GI fluctuate between 12-13 in low altitude areas around 700-900 m.a.s.l and 10-11 at the high altitude in Kilimanjaro transect (Figure 4.1e); it ranges between 13-14 and 10-12 in Taita hills transect at the bottom and the top respectively.

(Figure 4.2e). Under the year 2055 scenario, the generation index is expected to increase by 0.7-0.8, 0.1-0.5, 1.2-1.6, and 1.0-1.1.4 per year in Mount Kilimanjaro for *C. partellus*, *B. fusca*, *C. flavipes* and *C. sesamiae*, respectively (Figures 4.5a and 4.5b), and 0.6-0.7, 0.2-0.7, 1.2-1.5 and 0.7-1.4 per year in the Taita hills, respectively (Figures 4.5c and 4.5d).

The activity index (AI), which is strongly correlated with the GI, indicates population growth throughout the year, for *C. partellus* varying from 7 to 14 at the bottom and the top of Mount Kilimanjaro, respectively (Figure 4.1c) and, from 6 to 13 at the bottom and the top of Taita hills respectively (Figure 4.2c). For *B.fusca*, AI varies from 4 to 8 at the bottom and the top of both transects (Figures 4.1f and 4.2f). AI varies from 23-26 at the bottom to 14-20 at the top on both transects (Figures 4.1c and 4.2c) for *C. flavipes*; for *C. sesamiae* it varies from 16-18 at the bottom to 13-14 at the top of the Kilimanjaro transect (Figure 4.1f)), and between 18-20 and 13-15 at the bottom and the top of the Taita hills, respectively (Figure 4.2f).

4.3.3 Change in species life table parameters

Figure 4.6 shows the variation of temperature per year; the bar above the x-axis indicates the maize-cropping season. At both low and high altitudes of the two transects, the temperature is predicted to increase by 1-1.9°C throughout the year due to climate change (Figure 4.6). The results in Figures 4.7 to 4.10, show simulated life-table parameter variations against Julian days at two different locations per transect. Average increase of 1-2 generation per year has been predicted for the year 2055 (Figure 4.11). Mean generation time range from 46-69 and 72-123, 78 -114 and 100 -162, 19- 26 and 27-41 days to complete one generation for *C. partellus*, *B. fusca*, *C. flavipes* (Figures 4.7a, b

and 4.9a, b) at low altitude and high altitude, respectively in the Kilimanjaro transect. In Taita hills, the minimum generation time is about 54, 84, 22, 23 at low altitude and 76, 104, 28, 29 at high altitude for *C. partellus*, *B. fusca*, *C. flavipes*, *C. sesamiae*, respectively (Figures 4.9a, b and 4.10a, b). Female adult is expected to reproduce from 127-135, 120-134, 39-45 and 22-26 females at low altitude, and from 66 -116, 114 -127, 17-31, and 18-24 females at high altitude in Kilimanjaro transect for *C. partellus*, *B. fusca*, *C. flavipes* and *C. sesamiae*, respectively (Figures 4.7c, d). *C. partellus* population double at low altitude, within less than 10 days in the Kilimanjaro transect and 12 days in Taita hills (Figures 4.7j and 4.9j), and at high altitude maximum double time is about 20 days of both transects (Figures 4.7k and 4.9k), whereas the population density for *B. fusca* doubles within less than 16 and 17 days at low altitude (Figures 4.8j and 4.10j) and less than 25 days at high altitude of both transects (Figures 4.8k and 4.10k). For *C. flavipes*, the minimum doubling time is 4 days, at low altitude, and 5 days at high altitude of both transects (Figures 4.7j, k), and doubling time range from 5 to 7 days at low altitude and 6 to 10 days at high altitude for *C. sesamiae* (Figures 4.8 and 4.10 j, k) in both transects.

The change in temperature is predicted to increase activities of *C. partellus* and *B.fusca* by 0.01-0.02 depending on the time of the year, and by 0.05 for both *C. flavipes* and *C. sesamiae* (Figures 4.12a, b, c, d and 4.13a, b, c, d). However, the change is more constant throughout the year at lower altitude for both transects (Figures 4.12a, 4.13a) than at higher altitude where the prediction suggests very weak change during the long dry season between May-September (Figures 4.12c, 4.13c).); the prediction suggests no change of *C. partellus* activity at the tasseling stage of maize. In the Kilimanjaro transect at low altitudes, the changes are more pronounced during the colder season (May-

September) while almost no change is predicted during the warmer season (November–February) for *B. fusca* (Figure 4.12c). In Taita hills the changes are almost constant throughout the year along the entire transect, and there is a small increase during the colder season (July–September), when maize is grown during the long rainy season in lower altitude, and during the long dry season at high altitudes (Figures 4.13a and c). Except at low altitudes in the Taita hills, where *B. fusca* activity is predicted to increase at the beginning of the maize cycle, the predictions suggest very small changes in *B. fusca* activity at the beginning of the maize cycle in other localities when the maize is more vulnerable to stem borer attacks.

4.3.4 Synchrony between the host borers and their respective parasitoids

The difference of ERI between *C. partellus* and *C. flavipes* (i.e. synchrony) (Figures 4.3b and 4.4b) ranges from -0.02 to 0.03 and -0.03 to 0.08 and between *B. fusca* and *C. sesamiae* (Figure 4.3d and 4.4d) ranges from -0.04 to 0.02 and -0.23 to 0.09 in Kilimanjaro and Taita hills transects respectively. These results suggests disruption between the two pest and their respective parasitoid, which is more pronounced in Taita hills than in the kilimanjaro transect, with a general trend indicating that in the future the two pest will be under better control by the parasitoid at low than high altitude.

4.3.5 Predicting future maize losses

The proposed linear equation was found satisfactory to estimate the relationship between maize yield losses and the activity index of *C. partellus* (Table 4.1) and of *B. fusca* (Table 4.2). Under current temperature conditions, estimated average maize yield losses caused by *C. partellus* range from less than 2% in highland to 23% on lowland; the trend and range of variations are similar along both transects (Table 4.3). By 2055, the losses

will increase by 5-7% along both transects in the four maize agro-ecological zones, but with a slightly greater increase by 0.50-1.55% in Taita hills (Table 4.3). Under current temperarure conditions estimated average maize yield losses caused by *B. fusca* range from less than 1% in lowland to more than 13% in highland tropic. As for *C. partellus* the trend and range of variations are similar along both transects (Table 4.4). By 2055, the losses will increase by 13% in lower altitude maize agro-ecological zones (lowland and dry mid-altitude) and by 21-23% in higher altitude maize agro-ecological zones (moist mid-altitude and highland) (Table 4.4). The predicted increase average maize yield loss due to *B. fusca* is much more important in Taita hills, almost twice in lower altitudes and between 4.3 and 17.1 times in higher altitudes (Table 4.4). If we consider both species together, the average maize loss increase range between 7% in highland tropic and more than 13% in lowland tropic area on Kilimanjaro transect and between 20% in lowland and almost 30% in highland tropic on Taita hills transect. By 2055, the estimated increase in maize loss will be globally 2.5 times higher in Taita hills than in Kilimanjaro as a result of the predicted temperature increase.

Table 4.1: Parameters of regression equations fitted to estimate the relationship between maize yield loss and activity index for *Chilo partellus*. ** Values in parentheses are standard errors.

Transect	Intercept(β_0)	Slope (β_1)	df	F-stat	t-stat	P	R ²
Mt .Kilimanjaro	-20.89(8.1)**	3.08(0.8)**	1	16.79	4.09	0.06	0.89
Taita hills	-27.96 (11.0)**	3.84 (1.1)**	1	13.15	3.62	0.07	0.87

Table 4.2: Parameters of regression equations fitted to estimate the relationship between maize yield loss and activity index for *Busseola fusca*. ** Values in parentheses are standard errors.

Transect	Intercept(β_0)	Slope (β_1)	df	F-stat	t-stat	P	R ²
Mt .Kilimanjaro	-39.55(16.5)**	6.86(0.8)**	1	8.36	2.89	0.10	0.81
Taita hills	-71.39(27.8)**	12.27 (4.3)**	1	8.10	2.85	0.10	0.80

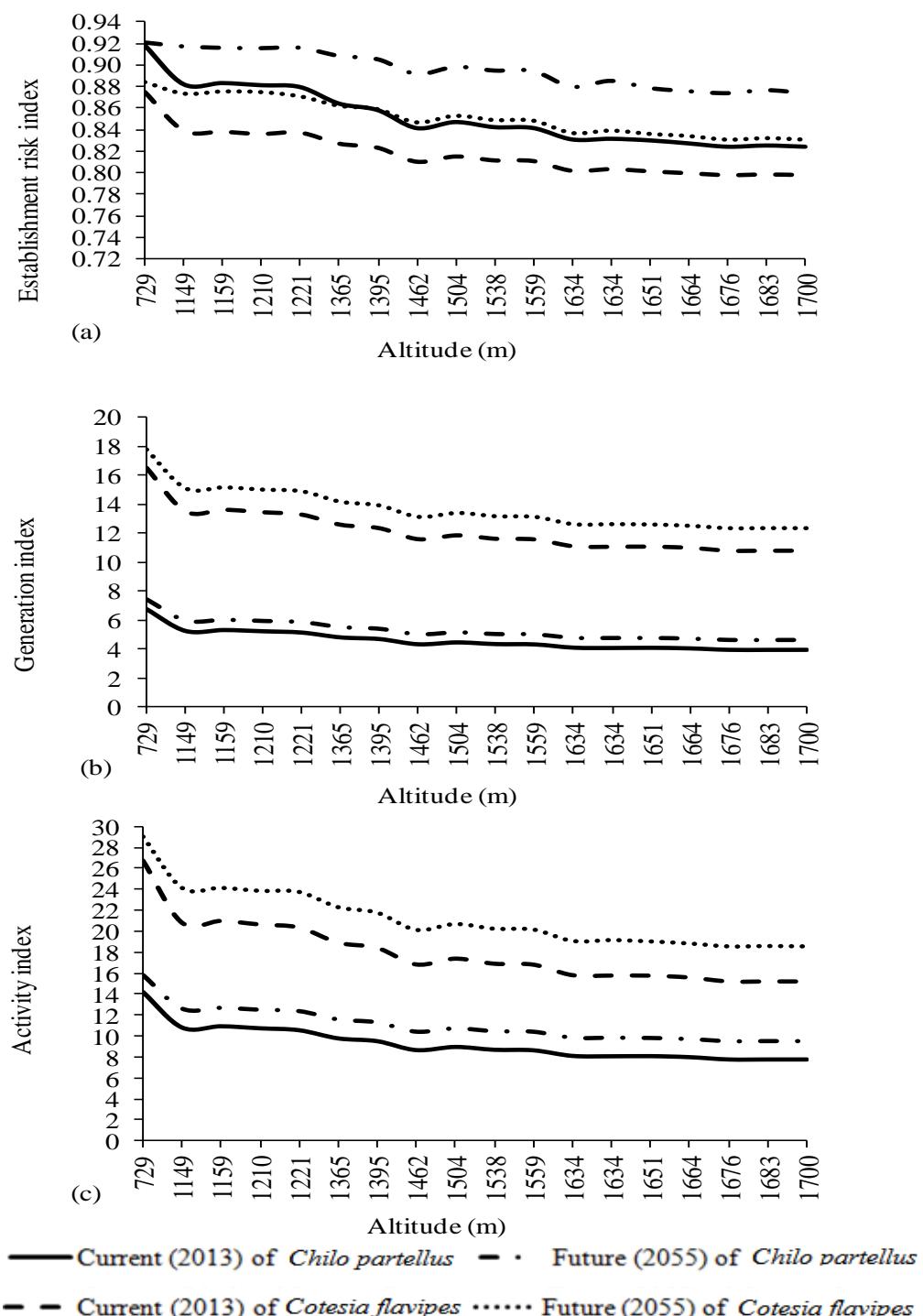
Table 4.3: Predicted losses in maize yield in Mount Kilimanjaro and Taita hills due to *Chilo partellus* infestations at current and future climatic conditions based on relationship between estimated yield loss and activity index. * estimated maize yield loss.

ACZ	m.a.s.l	OYL*	Mount Kilimanjaro			Taita hills		
			Predicted yield loss (%)			Predicted yield loss (%)		
			CMK	FMK	DiMk	CTH	FTH	DiTH
HP	>1600	0.01	2.84	8.34	5.50	1.75	7.74	6.00
	1300-							
MT	1600	11.10	6.86	12.41	5.55	7.04	13.26	6.22
	1000-							
DMA	1300	11.09	12.14	17.85	5.71	14.66	21.19	6.53
LT	<1000	22.69	23.06	28.10	5.04	21.42	28.11	6.69
Ave		11.22	11.23	16.68	5.45	11.22	17.58	6.36

Table 4.4: Predicted losses in maize yield in Mount Kilimanjaro and Taita hills due to *Busseola fusca* infestation at current and future climatic conditions based on relationship between estimated yield loss and activity index. * estimated maize yield loss.

ACZ	m.a.s.l	OYL*	Mount Kilimanjaro			Taita hills		
			Predicted yield loss (%)			Predicted yield loss (%)		
			CMK	FMK	DiMk	CTH	FTH	DiTH
HP	>1600	10.70	13.51	14.88	1.37	13.40	36.85	23.45
MT	1300-1600	14.60	10.97	15.77	4.80	10.77	31.67	20.90
DMA	1000-1300	5.54	5.69	12.27	6.58	6.91	20.65	13.74
LT	<1000	0.48	1.17	9.46	8.29	0.53	13.78	13.25
Ave		7.83	7.84	13.10	5.26	7.90	25.74	17.84

Where ACZ is agro-climatic zone, HP is the highland tropics, MT is the moist transitional, DMT is the dry mid altitude, LT is the lowland tropical, Ave is the average, OYL is the observed yield loss, CMK is the current climatic conditions in Mount Kilimanjaro, FMK is the future climatic conditions in Mount Kilimanjaro, DiMK is the difference between current climatic conditions and future climatic conditions in Mount Kilimanjaro, CTH is the current climatic conditions in Taita hills, FTH is the future climatic conditions in Taita hills, and DiTH is the difference between current climatic conditions and future climatic conditions in Taita hills.



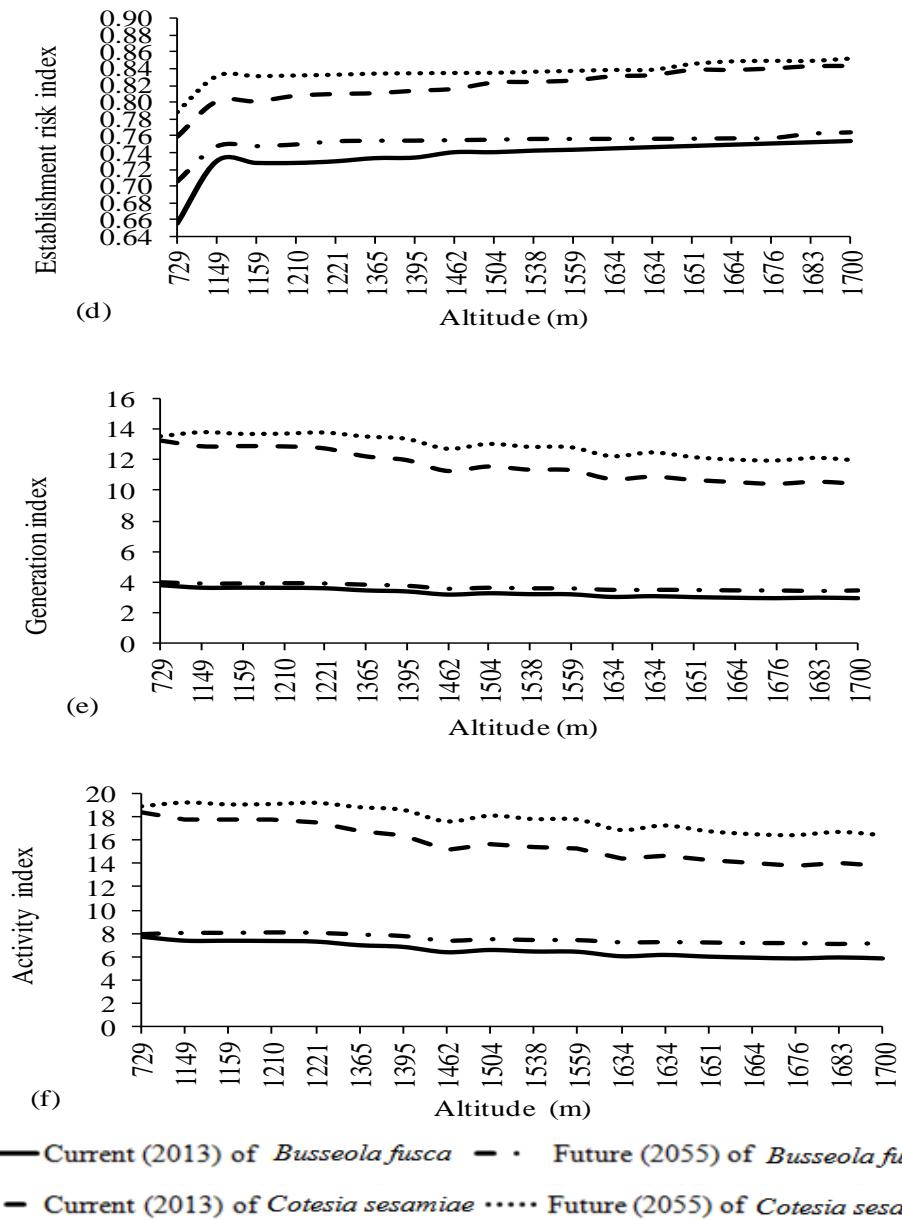
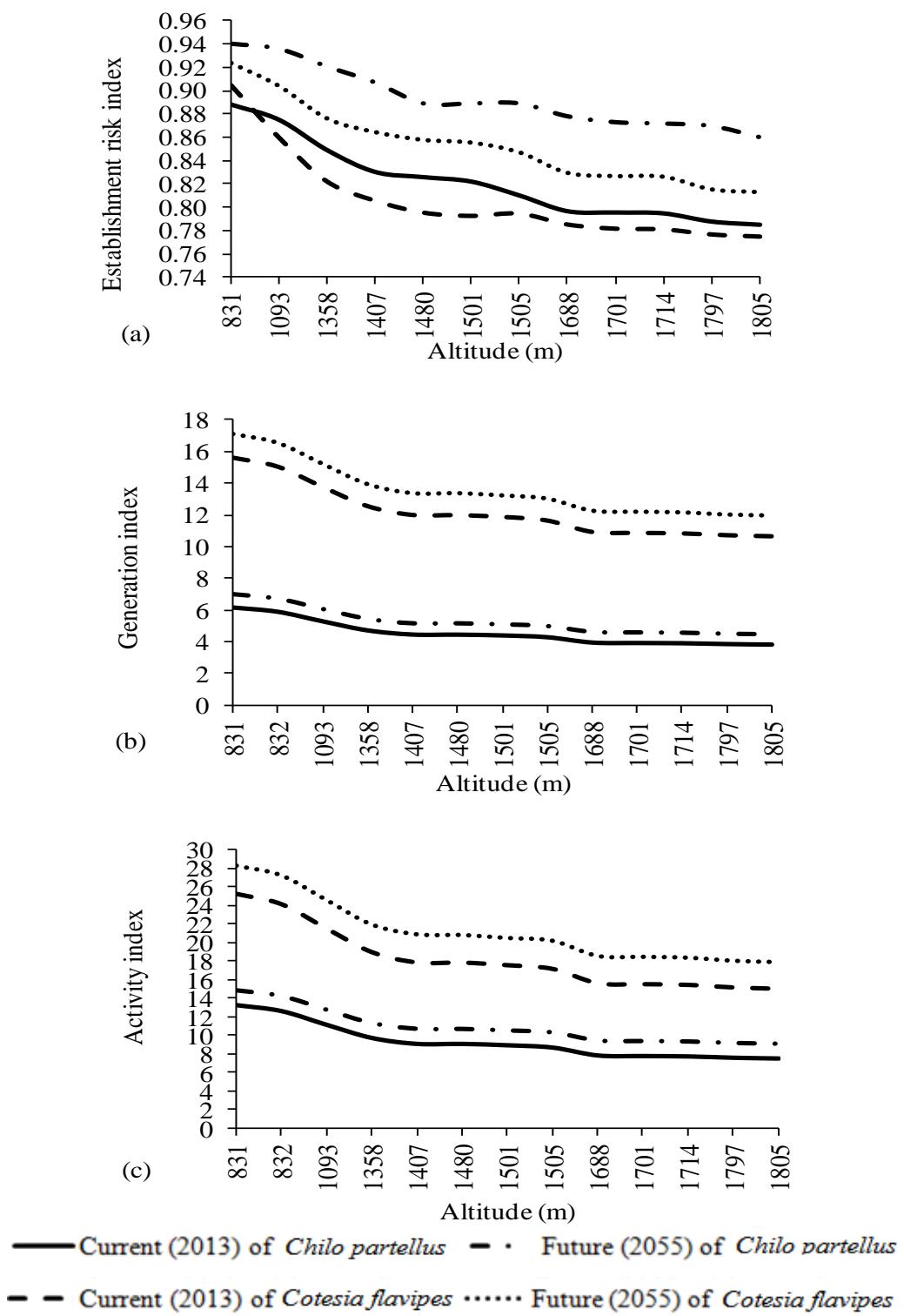


Figure 4.1: Change in the Establishment risk index (ERI), Generation index (GI) and Activity index (AI) along Mount Kilimanjaro transect for current (2013) and future (2055) climatic conditions; *Chilo partellus* and *Cotesia flavipes* distribution (a) ERI, (b) GI, (c) AI; *Busseola fusca* and *Cotesia sesamiae* distribution (d) ERI, (e) GI, (f) AI.



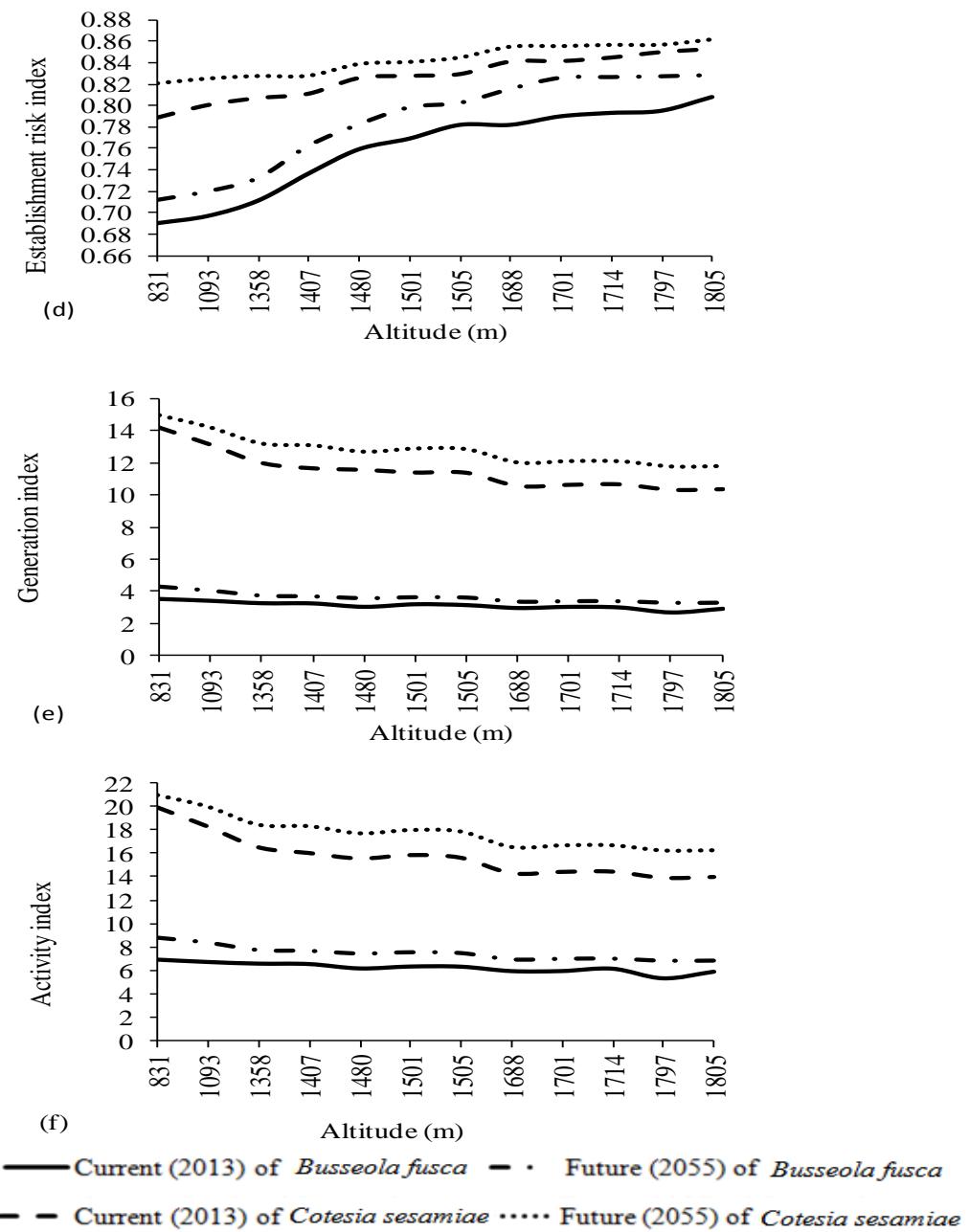


Figure 4.2: Change in the Establishment risk index (ERI), Generation index (GI) and Activity index (AI) along Taita hills transect for current (2013) and future (2055) climatic conditions; *Chilo partellus* and *Cotesia flavipes* distribution (a) ERI, (b) GI, (c) AI; *Busseola fusca* and *Cotesia sesamiae* distribution (d) ERI, (e) GI, (f) AI.

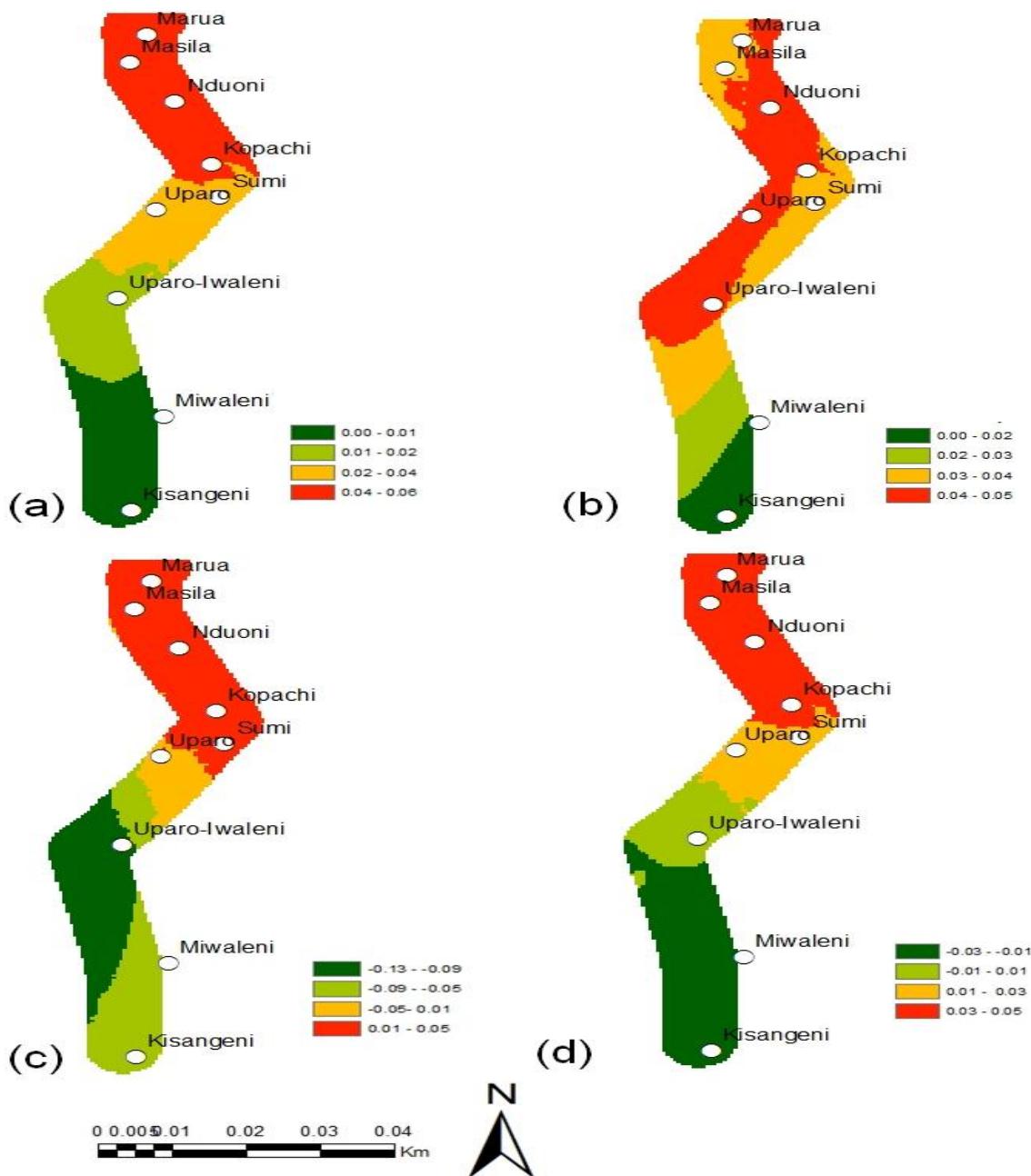


Figure 4.3: Absolute change in establishment risk index between current (2013) and future (2055); (a) *Chilo partellus*; (b) *Cotesia flavipes*; (c) *Busseola fusca* and (d) *Cotesia sesamiae* along Mount Kilimanjaro transect. Legend indicate variation change in establishment risk index along altitude.

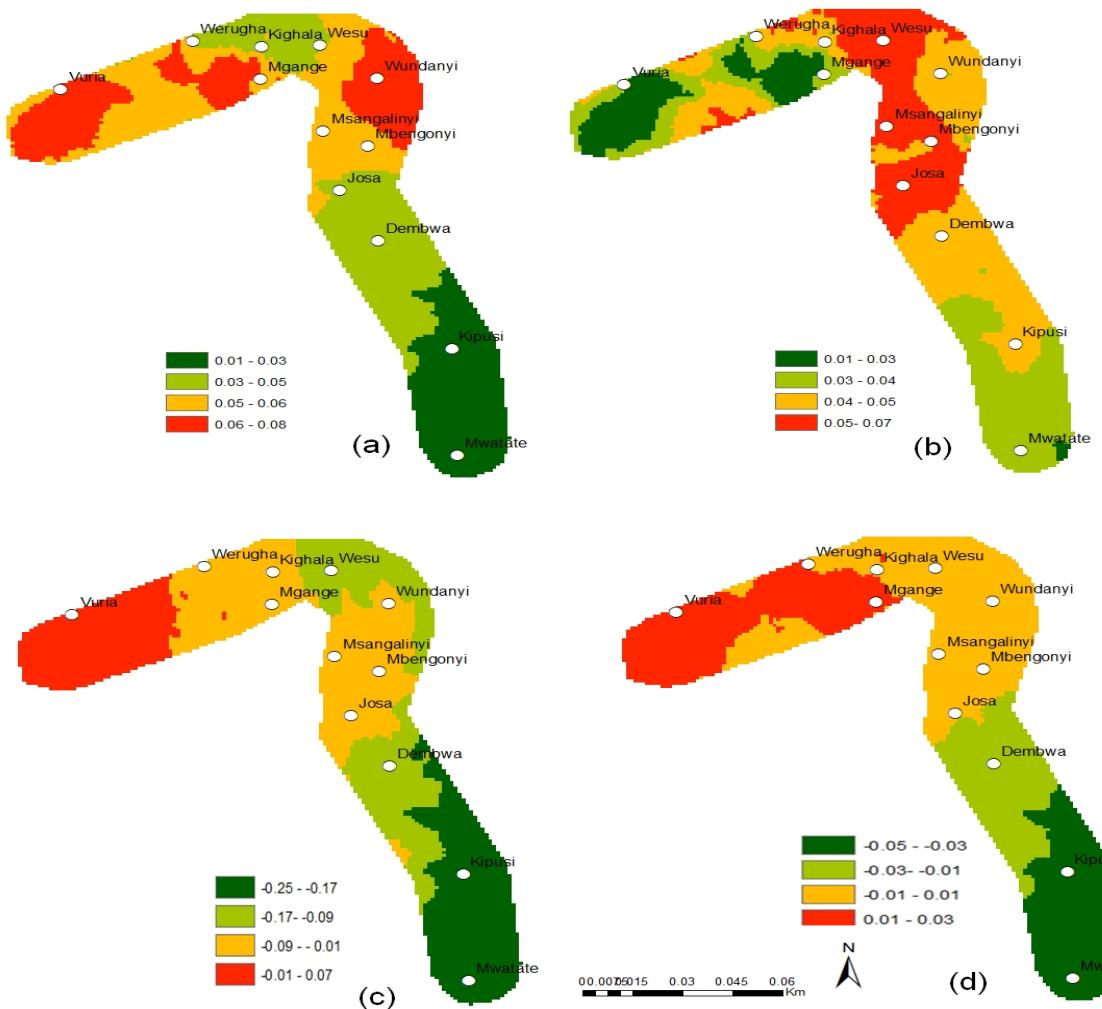


Figure 4.4: Absolute change in establishment risk index of between current (2013) and future (2055); (a) *Chilo partellus*; (b) *Cotesia flavipes*; (c) *Busseola fusca* and (d) *Cotesia sesamiae* along Taita hills transect. Legend indicate variation change in establishment risk index along altitude.

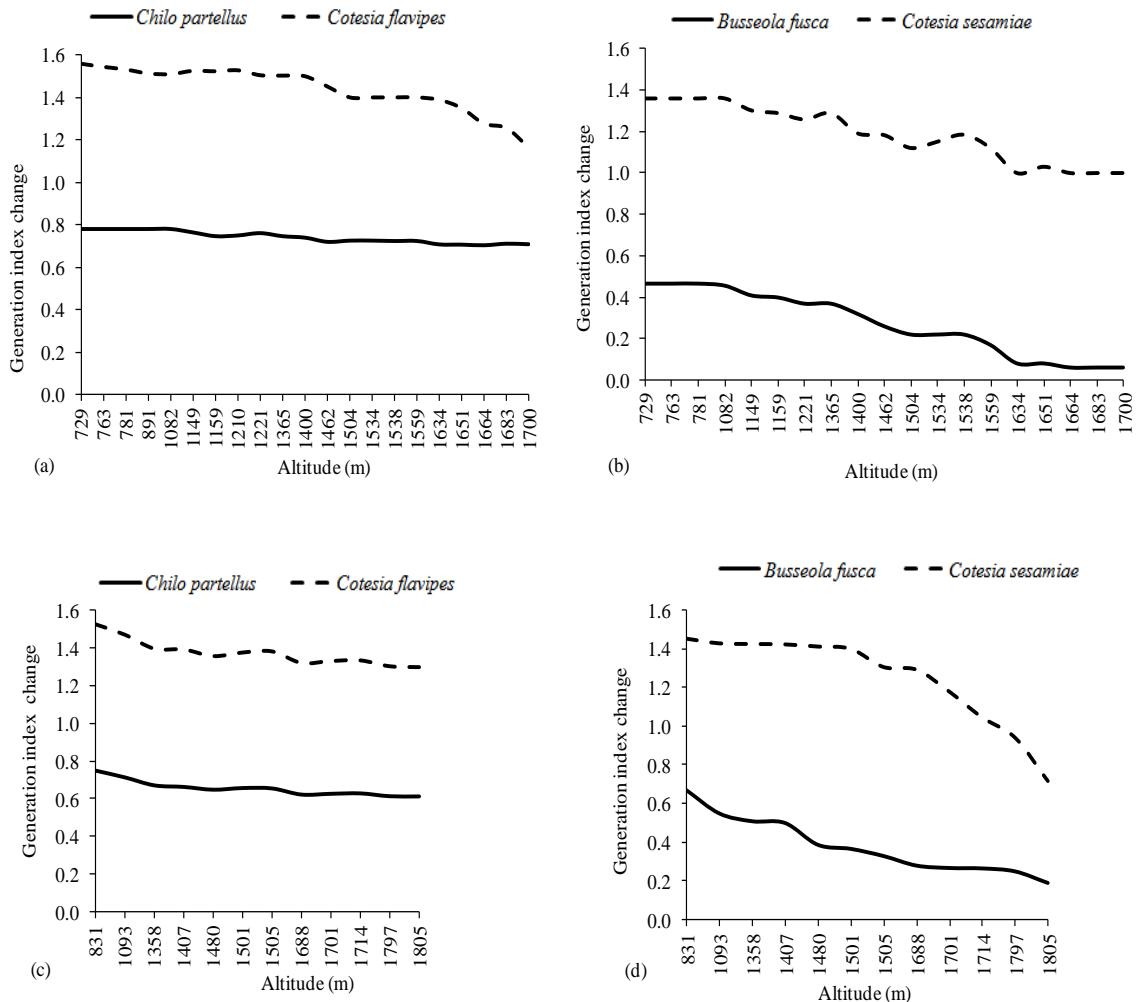


Figure 4.5: Absolute generation index change between current (2013) and future (2055); Mount Kilimanjaro transect; (a) *Chilo partellus* and *Cotesia flavipes*; (b) *Busseola fusca* and *Cotesia sesamiae*; Taita hills transect; (c) *Chilo partellus* and *Cotesia flavipes*, and (d) *Busseola fusca* and *Cotesia sesamiae*.

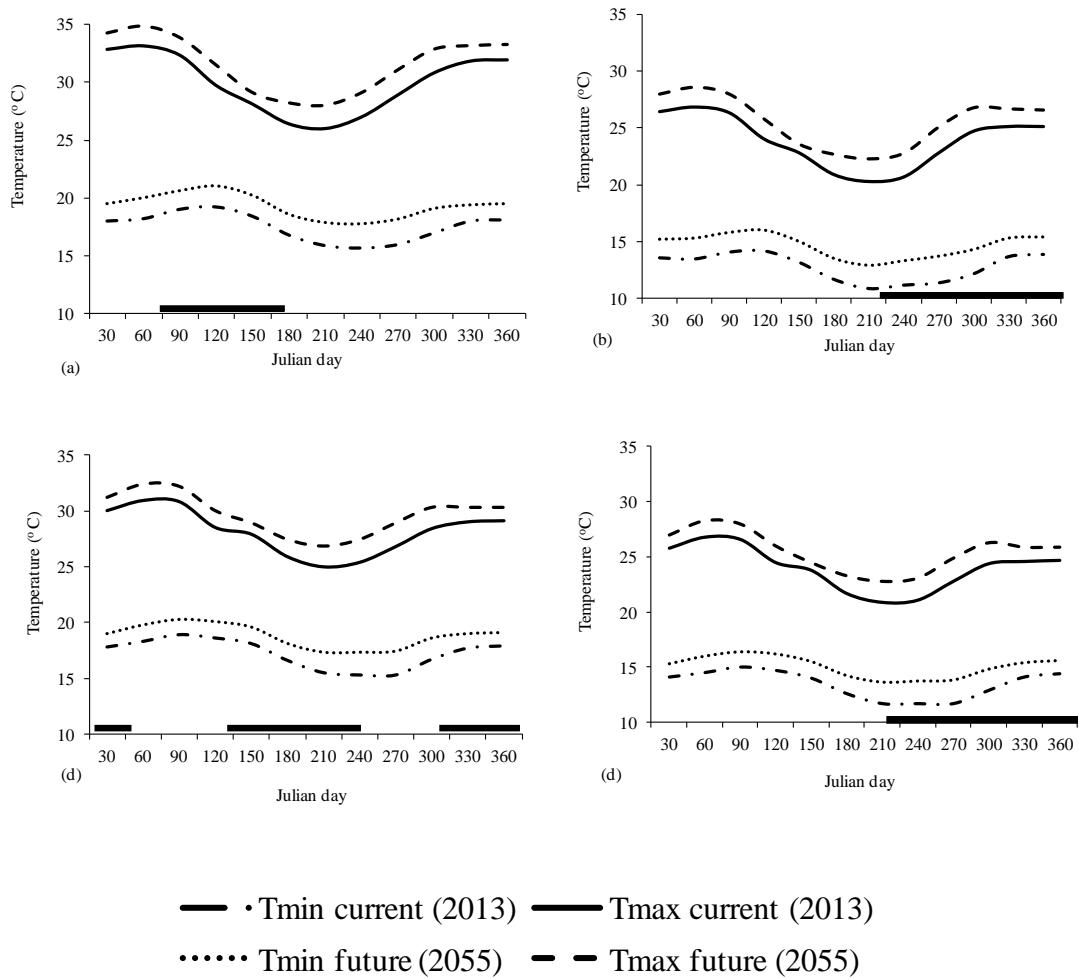


Figure 4.6: Minimum and maximum temperature curves for current (2013) and future (2055) climate change scenarios; (a) Miwaleni (764 m.a.s.l) and (b) Marua (168 m.a.s.l) along Mount Kilimanjaro transect; (c) Kipusi (832 m.a.s.l) and (d) Vuria (1800 m.a.s.l) along Taita hills transect. Bars above the x-axis indicate the maize-cropping season.

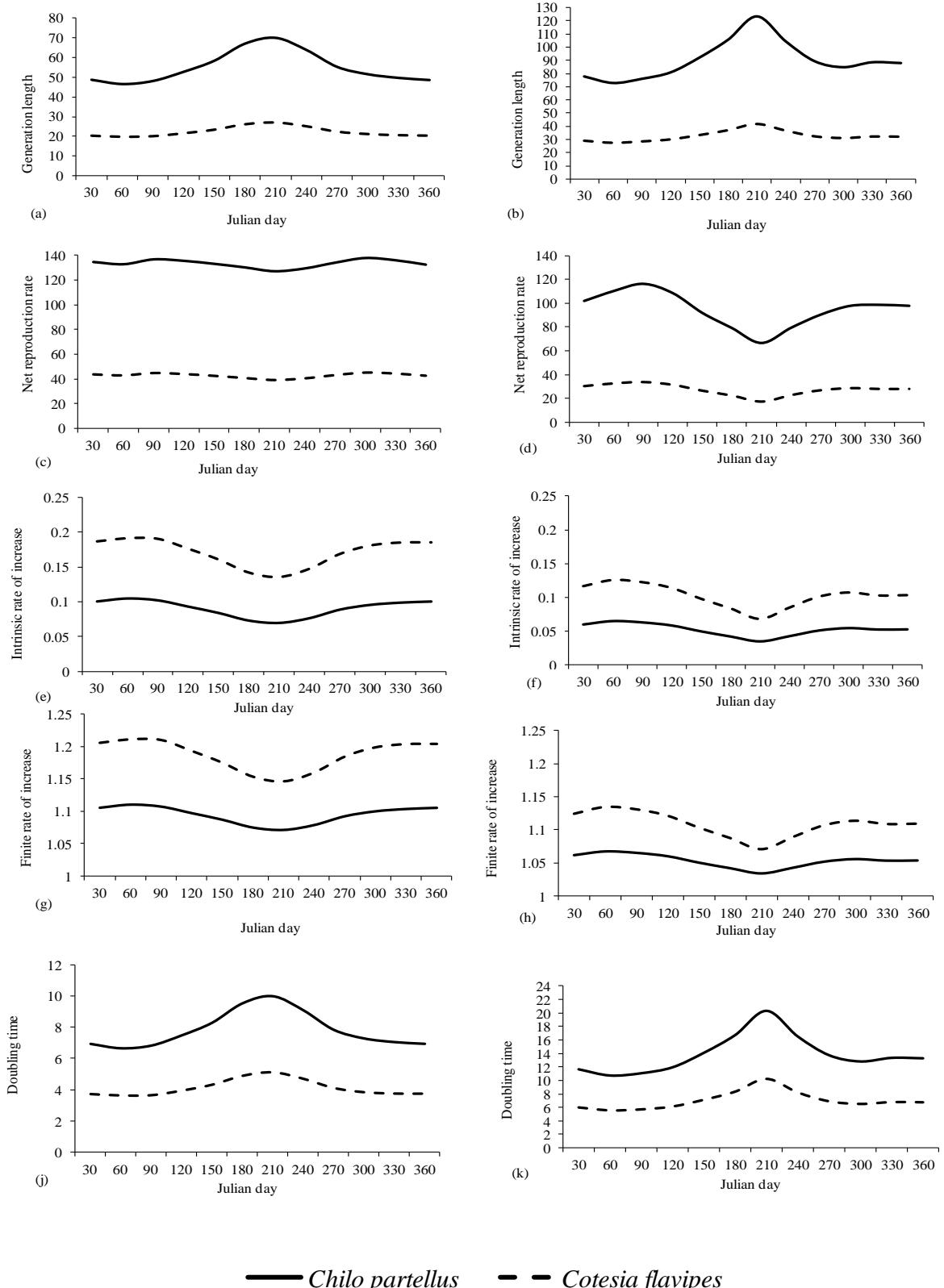
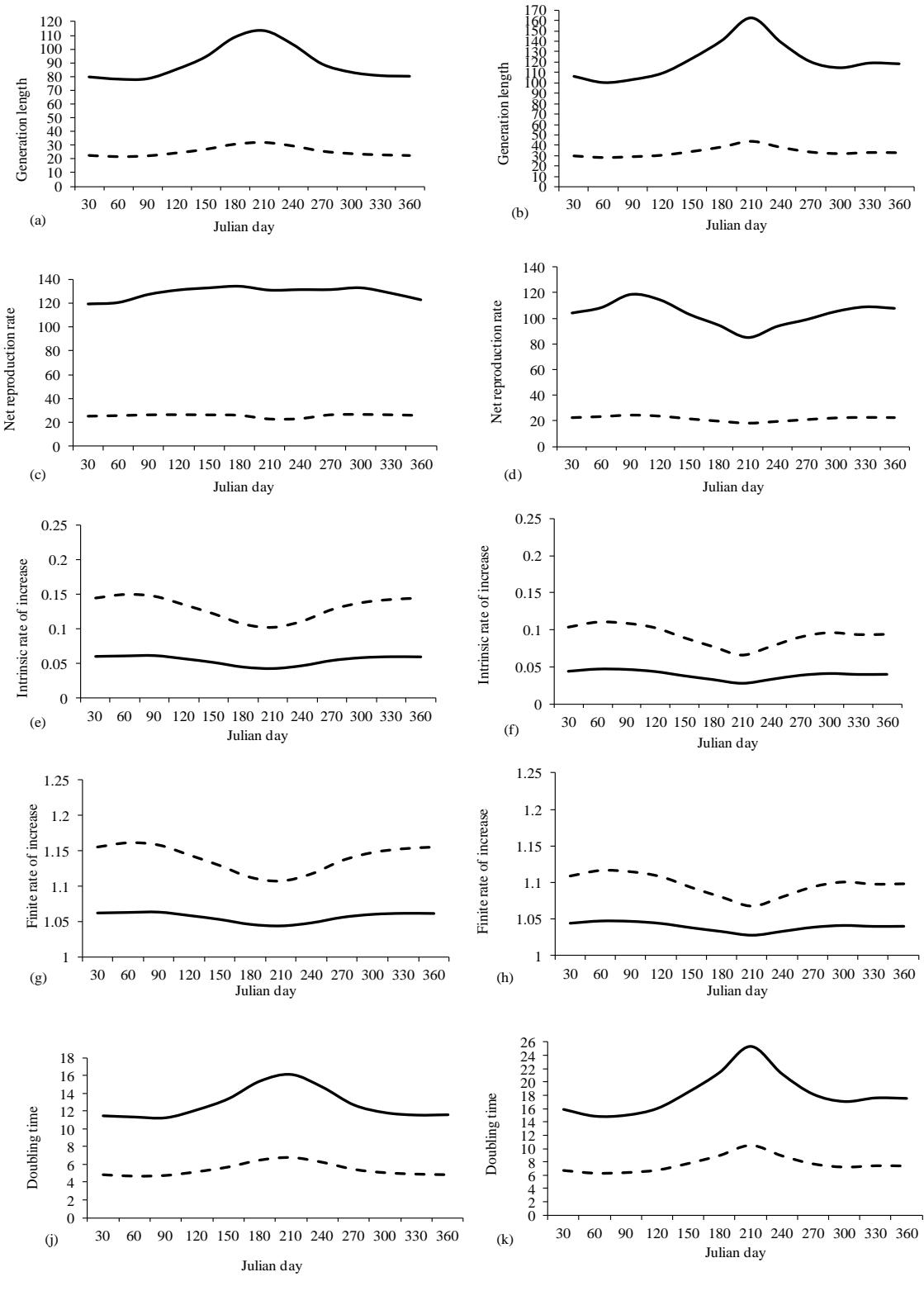


Figure 4.7: Life table parameters of *Chilo partellus* (solid lines) and *Cotesia flavipes* (dotted lines) estimated for each Julian day using daily minimum and maximum temperatures recorded at two local weather stations in Mount Kilimanjaro transect. Miwaleni (764 m.a.s.l) at the left hand graphs (low altitude) and Marua (1800 m.a.s.l) at the right hand graphs (high altitude); Generation length (a) and (b), Net reproduction rate (c) and (d), Intrinsic rate of increase (e) and (f), Finite of increase (g) and (h), Doubling time (j) and (k), respectively.



— *Busseola fusca* - - - *Cotesia sesamiae*

Figure 4.8: Life table parameters of *Busseola fusca* (solid lines) and *Cotesia sesamiae* (dotted lines) estimated for each Julian day using daily minimum and maximum temperatures recorded at two local weather stations in Mount Kilimanjaro transect. Miwaleni (764 m.a.s.l) at the left hand graphs (low altitude) and Marua (1800 m.a.s.l) at the right hand graphs (high altitude); Generation length (a) and (b), Net reproduction rate (c) and (d), Intrinsic rate of increase (e) and (f), Finite of increase (g) and (h), Doubling time (j) and (k), respectively.

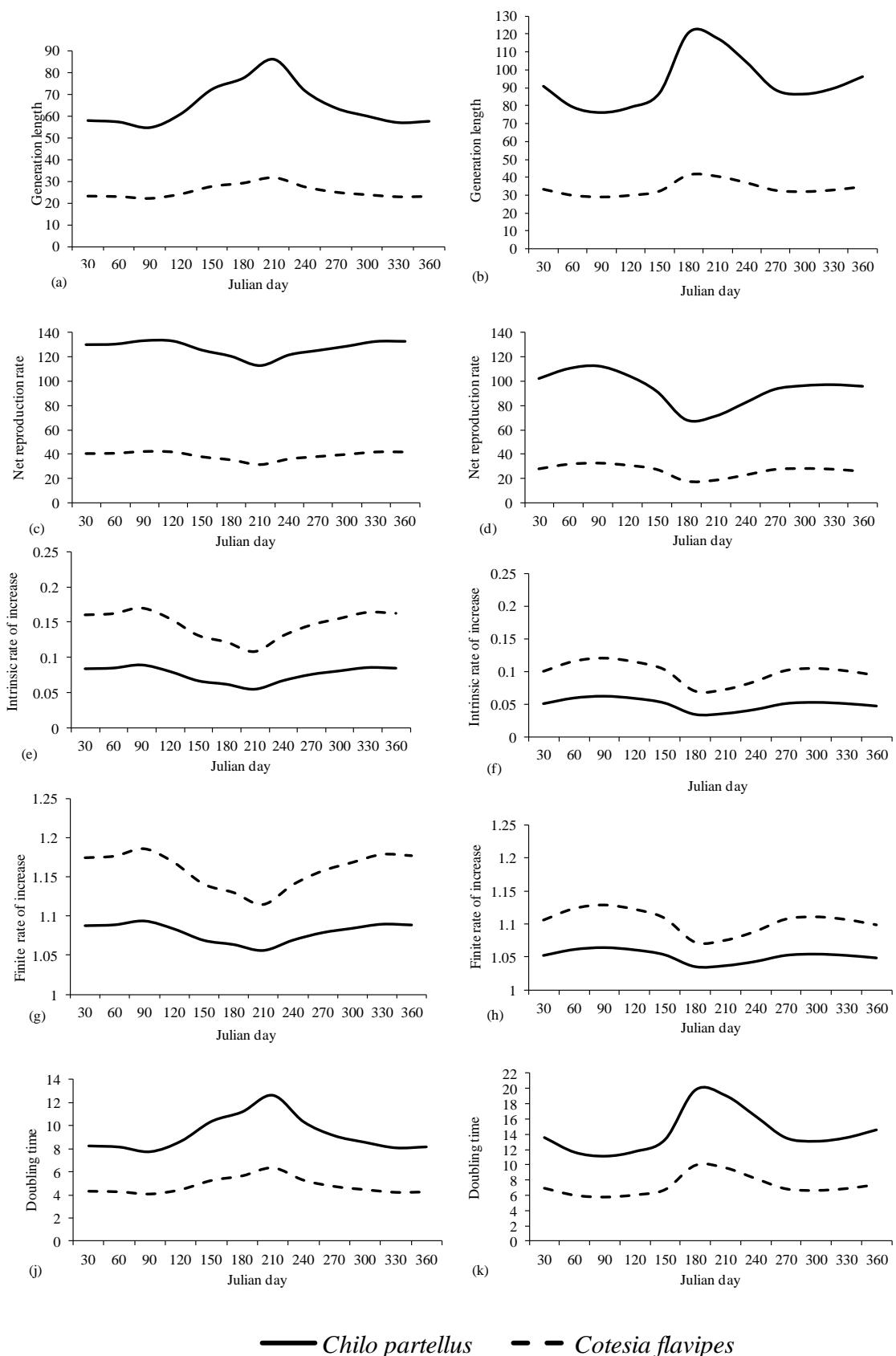
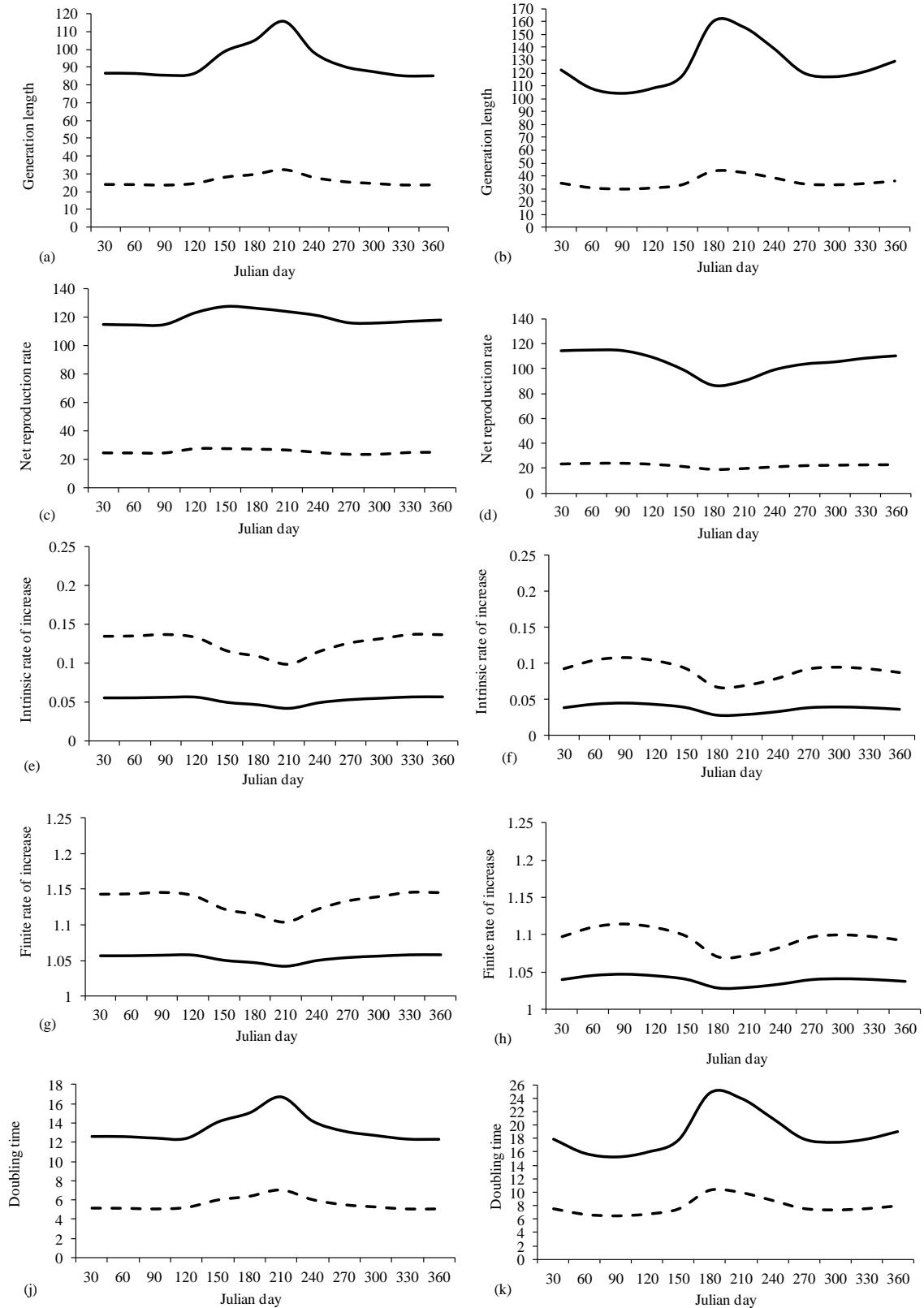


Figure 4.9: Life table parameters of *Chilo partellus* (solid lines) and *Cotesia flavipes* (dotted lines) estimated for each Julian day using daily minimum and maximum temperatures recorded at two local weather stations in Taita hills transect. Kipusi (831 m.a.s.l) at the left hand graphs (low altitude) and Vuria(1800 m.a.s.l) at the right hand graphs; (high altitude) Generation length (a) and (b), Net reproduction rate (c) and (d), Intrinsic rate of increase (e) and (f), Finite of increase (g) and (h), Doubling time (j) and (k), respectively.



— *Busseola fusca* - - - *Cotesia sesamiae*

Figure 4.10: Life table parameters of *Busseola fusca* (solid lines) and *Cotesia sesamiae* (dotted lines) estimated for each Julian day using daily minimum and maximum temperatures recorded at two local weather stations in Taita hills transect. Kipusi (831 m.a.s.l) at the left hand graphs (low altitude) and Vuria (1800 m.a.s.l) at the right hand graphs (high altitude); Generation length (a) and (b), Net reproduction rate (c) and (d), Intrinsic rate of increase (e) and (f), Finite of increase (g) and (h), Doubling time (j) and (k), respectively.

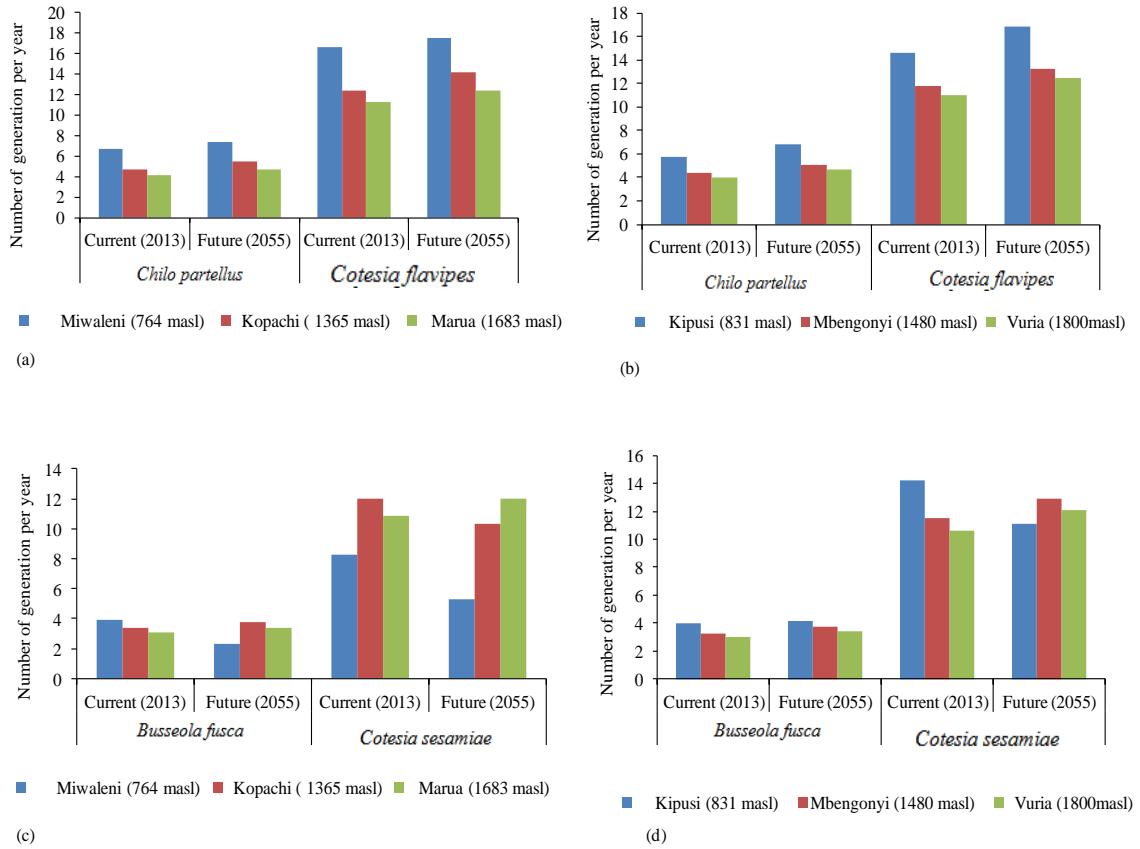


Figure 4.11: Effects of temperature on number of generations that can be completed per year by *Chilo partellus*, *Cotesia flavipes*, *Busseola fusca* and *Cotesia sesamiae* in three selected locations of Mount Kilimanjaro transect (left hand graphs) and Taita hills transect (right hand graphs) at different climate scenarios between current (2013) and future (2055); figures (a) and (b) indicate the number of generation for *Chilo partellus* and *Cotesia flavipes*; figures (c) and (d) indicate the number of generation for *Busseola fusca* and *Cotesia sesamiae*.

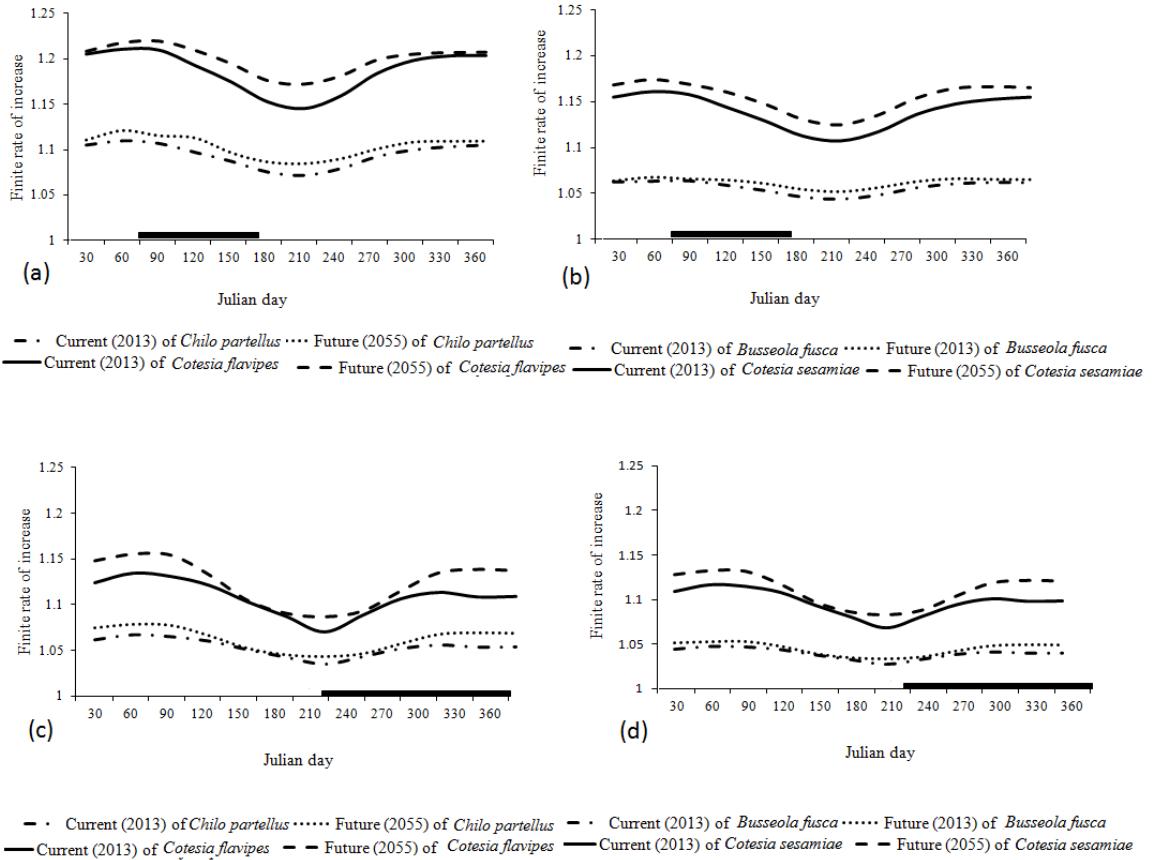


Figure 4.12: Finite rate of increase for current (2013) and future (2055) throughout the year, at two local weather stations along Mount Kilimanjaro transects; (a) *Chilo partellus* and *Cotesia flavipes*; (b) *Busseola fusca* and *Cotesia sesamiae* at Miwaleni (764 m.a.s.l); (c) *Chilo partellus* and *Cotesia flavipes*; (d) *Busseola fusca* and *Cotesia sesamiae* at Marua (1683 m.a.s.l).

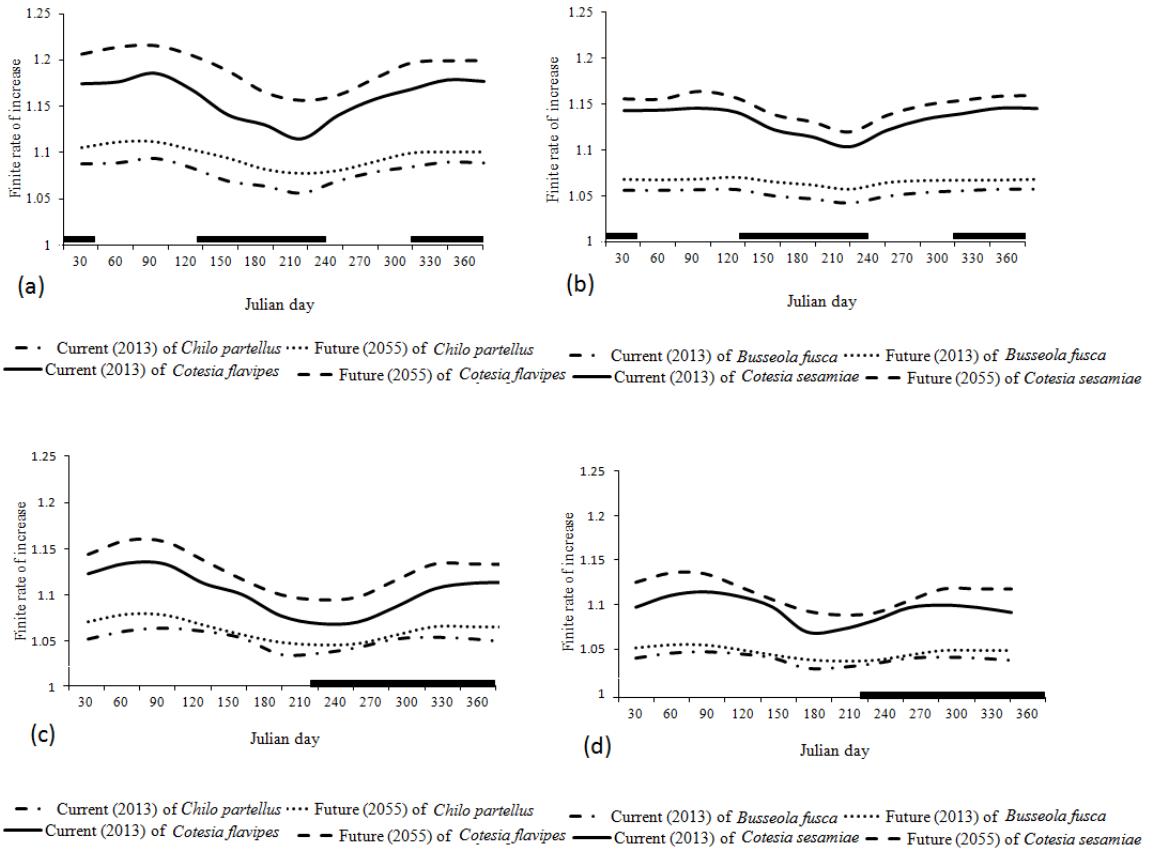


Figure 4.13: Finite rate of increase for current (2013) and future (2055) throughout the year, at two local weather stations along Taita hills transects; (a) *Chilo partellus* and *Cotesia flavipes*; (b) *Busseola fusca* and *Cotesia sesamiae* at Kipusi (832 m.a.s.l); (c) *Chilo partellus* and *Cotesia flavipes*; (d) *Busseola fusca* and *Cotesia sesamiae* at Vuria (1800 m.a.s.l.).

4. 4 Discussion

4.4.1 Change in stem borers and their natural enemies' distribution and abundance

The predictive mapping of future maize stem borer pest risks at small scale generated by point-by-point analysis, using climatic data obtained from data loggers dispatched along the two altitudinal gradients, confirm and complete results recorded at country scale generated from temperature extrapolated from available historical records by Khadioli *et al.* (2014). It confirms the precision of the temperature process based phenology model achieved with ILCYM software compared to other methods like rule-based methods (Levine *et al.* 2004) and multivariate statistical techniques (Latimer *et al.* 2006). The results indicate a worsening of their impact of the two stem borer pests on maize production along the two East Africa mountain gradients studied. The aggravation can be attributed to three main changes occurring simultaneously: range expansion to higher altitude areas; increase of the abundance (damage potential) of the pests at all altitudes; disruption of the biological control due to a mismatch of the geographical distribution between the pests and their main larval natural enemies.

In both transects, *C. partellus* is the dominant species in dry mid-altitude and dry transitional maize agro-climatic zones below 1200 m.a.s.l., reported as a zone with a low potential yield of maize (Hassan 1998, De Groote 2002, Ong'amo *et al.* 2006). The *B. fusca* is the dominant species in areas predominantly moist mid-altitude, moist-transitional and highlands tropic maize agro-climatic zones above 1200 m.a.s.l, reported as zone with high potential yield of maize (Hassan 1998, De Groote 2002, Ong'amo *et al.* 2006). The predicted increase in climatic suitability of establishment and survival will allow range expansion of both pests in higher altitude and suggests a future increase in

the proportion of *C. partellus* in moist mid-altitude and moist transitional areas in both gradients. The results are consistent with expansion of *C. partellus* to higher altitude reported since two decades in South Africa (Kfir 1997), Kenya (Overholt *et al.* 2000, Zhou *et al.* 2001, Ong'amo *et al.* 2006) and Ethiopia (Wale *et al.* 2006). Similar range expansion at higher altitude areas of tropical insect pests due to temperature increase has been reported recently in East Africa on the coffee berry borer (*Hypothenemus hampei*) (Jaramillo *et al.* 2011) and on the fruit fly *Bactrocera invadens* (Geurts *et al.* 2014). Recent meta-analysis, comparing different organisms, reported that upslope shift of insect species exceeded the expected shift (Bässler *et al.* 2013); future field surveys on stemborers should provide data to confirm if stemborer response to climate warming is consistent or not with result of this analysis. In the case of stem borers, several factors related to the competitive superiority of *C. partellus* against *B. fusca* were put forward to explain its expansion, like its shorter generation time (Kfir *et al.* 2002) and the faster termination of diapause (Kfir 1997, Kfir *et al.* 2002); but none of these studies pointed out the potential influence of the temperature change. However, over the past 40 years, Kenya's average annual temperatures increased by 1°C with an increase by 0.5 °C in western Kenya and by 1.5°C in the drier parts of Kenya (UNEP 2009). Without underestimating the factors reported in the previous studies, the present findings suggest that temperature increase should be a key factor responsible for the expansion of *C. partellus* to higher latitude areas during the past 50 years.

Accordingly, predictions on the change of abundance and activity (finite rate of increase) of both stem borer pests, which are based on life history traits generated through detailed laboratory experiments (Khadioli *et al.* 2014a, b), the number of generations and the finite rate of increase of the two stem borer pests will increase in all maize agro-climatic

zones along the two altitudinal gradients. More importantly, by 2055, maize agro-climatic zones above 1200 m.a.s.l. such as moist mid-altitude, moist transitional and highland tropics considered as unfavourable for *C. partellus* and less favourable for *B. fusca* like highland tropics will become more suitable. Predictions suggest the two pests will cause more damages in the most productive maize zones of both transect.

Predicted change in the distribution of the two insect pests largely coincided with their respective parasitoid change distribution. However, a slight disruption of the geographical distribution is predicted suggesting for both parasitoid species an improvement of the biological control of stem borers at altitudes below 1200 m.a.s.l. and deterioration above 1200 m.a.s.l. If confirmed in the future with field data observations, this prediction suggests more frequent and severe stem borer outbreaks with potential aggravation of the already predicted provocation of damages above 1200 m.a.s.l. in the most productive maize areas. The lower performance of *C. flavipes* in areas above 1200 m.a.s.l has already been reported by Zhou *et al.* (2001) and was speculated it should be largely due the stem borer composition. More recently, Mailafiya *et al.* (2010) showed that the occurrence of both parasitoid species was influenced by geographic range of their respective host suggesting their distribution may be largely driven by the distribution of their old host association. Considering the predicted future changes in stem borer composition with a higher proportion of *C. partellus* in moist mid-altitude and moist transitional areas of both gradients, could reasonably be expected a distribution shift of *C. flavipes* to higher altitude. However, the duration of the dry season has a strong influence on the availability of the two *Cotesia* species across seasons in Kenya (Mailafiya *et al.* 2010). Predicted climate change clearly indicates that large parts of Kenya will experience a 100 mm decline in long-season rainfall by 2025 (Williams and Funk 2010),

with an increase in frequency of dry years suggesting the *Cotesia* species activity should be significantly affected in the future.

The predicted distribution trends of both stem borer pests are very similar on both transects. However, *B. fusca* is recorded at all altitudes in the Taita hills while it is recorded in the Kilimanjaro transect at altitude ranging from 1100-1600 m.a.s.l. The difference between the two transects suggests that other factors likely play a role on the establishment of stem borer pests. Phenological models are purely based on temperature and do not take into consideration other climatic factors such as rainfall and relative humidity and, non climatic factors such as planting pattern and frequency, diapuses or other physiological factors that enable escape of harsh abiotic conditions (Matsuo 2006). In addition, these models assumed no immigration and no emigration influencing population dynamics; it provides only the potential population growth of stem borers in different agro-climatic zones. This way, Sithole (1989) argued that temperature, rainfall and humidity were the main factors that affect *C. partellus* distribution, with temperature being the most important. Abraham *et al.* (1972), through correlation studies, found that there was a joint influence of rainfall, relative humidity and mean minimum temperature on the stem borer infestation. In addition, biotic factors, like plant resistance strategies including direct (physical and chemical such as Silicon of the plant) and indirect (the recruitment of natural enemies) defences vary along altitudinal transect and are affected by climate change (De Lucia *et al.* 2012 ; Rasmann *et al.* 2014). For these reasons even if temperature plays a key role we should consider the effect of other abiotic factors and even biotic factors on the establishment and abundance of stem borers when predicting the future pest risk.

Due to the duration of the maize-cropping seasons ranging from 3 to 6 months depending on the altitude and the transect; and duration of the diapause ranging from 3 to 9 months depending on the pest and the altitude, the number of generations/year predicted by this study is overestimated for both the current and future scenarios. It's however, difficult to estimate the overestimation as during maize off season, in both transects, the pests can develop and survive on wild host plants commonly found in the fallow surrounding the maize plots, like wild sorghum (*Sorghum arundinaceum* L.), napier grass (*Pennisetum purpureum* Schumach.) and guinea grass (*Megathyrsus maximus* (Jacq.) B.K. Simon and S.W.L. Jacobs). In so far as the prediction was generated with the same method, the difference recorded between the current and the future scenarios should reasonably reflect the impact of the temperature increase during the two periods.

The results within-year variation analyses of population increase in two different localities on both transects provide a better understanding of the impact of the annual variations of temperature on the two stem borer pests and their respective parasitoids population growth and development; it gives useful information for a better integrated pest management in each locality. For example, this study compared two localities (Miwaleni, Kilimanjaro, 764 m.a.s.l. against Kipusi, Taita hills, 831 m.a.s.l.) belonging to the lowland tropic maize agro-ecological zones. Despite similar establishment index and finite rate of increase of *C. partellus* have been simulated in both localities, considerable differences in the field pest population dynamics due to very different cropping periods, two short maize cycles were recorded in Taita and one only in Kilimanjaro. The presence of *C. partellus* in a locality depended of the duration of the maize cycle, which in turn is affected by the duration of the rainy season. In Taita hills, the maize off-season never exceeds three months when in Kilimanjaro it reaches almost nine months. Perrenation of

C. partellus across the dry season occurs mainly through diapause in crop residues and to a lesser extent in indigenous wild grasses which stay in a vegetative stage. However, duration of the diapause would most likely affect the survival rate of the larvae (Ellers and Van Alphen 2002, Matsuo 2006). This suggestss that the prediction generated by the model should be interpreted with caution, always coupled with field observations for a better understanding of the field dynamic of the pests.

4.4.2 Predicting maize yield losses

Climate change poses serious threats to food security via change in pest distribution and their establishment in previously unsuitable regions (Bebber *et al.* 2013). In this contribution, the potential current and future distribution of two important crop pests was modelled, and found that only change in distribution might pose future threats to crops estimated. Based on the relationship between activity index of both stem borer pests and maize yield losses in Kenya from De Groote (2002) and Ong'amo *et al.* (2006), maize losses will significantly increase in all maize agro-ecological zones along both transects but much more in lower areas of Kilimanjaro and all along Taita hills transects. However, these predictions based on pests only do not consider the influence of temperature increase on the natural enemies. Current predictions reveal a small decoupling between both stem borer pests and their respective larval parasitoids suggesting higher pest numbers and more serious outbreaks than predicted with stem borers only. In addition, they do not take into account yield responses to the climate change (changing rainfall amounts and patterns, temperature increase); predictions made by Thornton *et al.* (2009a, b) suggest that by 2050, maize yield will increase in highland areas of many parts when it will decrease in lower elevation in East Africa. Similar study reported by Grisley 1997.

Finally when taking into consideration the maize pests, their parasitoids and the maize response, there are uncertainties associated with the interactions of these different factors. As a word of caution, it is worth emphasizing that the predictions rely on simplified modelling, and that additional studies running more complex model approaches are needed for a better prediction and understanding of crop response to climate change. But no doubt climate change, particularly temperature, will have a huge implication for maize production in the next decades along both transects. While the goods and services in EABH regions are already under significant treat because of land use changes (Boko *et al.* 2007, Maeda *et al.* 2010, 2011), the predicted decrease of maize yield, one of the main staple food, will exacerbate the food security and the livelihoods, consequently impacting the scope of poverty reduction (Hope 2009). Indeed, East African food production systems, mainly relying on rainfed crop production, are very vulnerable because of climate variability and unpredictability, extreme climatic events (recurrent droughts and floods) and limited capacity of adaptation due to persistent poverty (Boko *et al.* 2007).

In conclusion, altitudinal gradients are optimal spatial analogues, providing at small scale a range of different ecological conditions with variations of abiotic and biotic factors (Hodkinson and Birds 1998, Bale *et al.* 2002, Thuiller 2007); allow assessment of the response of insect pests to the climate change, particularly temperature. The predictive mapping at small scale confirms and complete results generated at country and even continental scale (Khadioli *et al.* 2014a), focusing simultaneously on the two main maize stem borer pests and their main larval parasitoids, demonstrates the important impact the predicted increase of temperature will have on the maize yield production at all altitude but particularly in the mid and high altitude most productive maize areas of the Eastern Afromontane Biodiversity Hotspot regions. It will aggravate the already significant threat

on the goods and services of these fragile ecosystems for which predictions show they will be particularly affected by extreme climatic changes (Platts *et al.* 2008, 2010, 2012, Christy *et al.* 2009, CEPF 2012). It confirms temperature is a key factor to explain the distribution of insect pest but point the likely important role played by other climatic factors and by factors related to the top-down regulation of pests by parasitoids (host-parasitoid synchrony). However, as the continuation of the present chapter to include, the effects of other abiotic factors such as rainfalls and relative humidity, and soil characteristics are presented in chapter 6.

4.5 Chapter Summary

This chapter studied the impacts of temperature change on distribution and abundance of *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) and *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae), *Cotesia flavipes* and *Cotesia sesamiae* Cameron (Hymenoptera: Braconidae) at local scale along Mount Kilimanjaro and Taita hills gradients in Tanzania and Kenya, respectively. The temperature-dependent phenology models of *C. partellus*, *B. fusca*, *C. flavipes* and *C. sesamiae* were used in geographical information system for mapping. The three risk indices namely; establishment, generation, and activity index were computed using current temperature data (2013) record from local weather station and future (2055) climatic condition based on downscaled climate change data from AFRICLIM database. All the calculations were carried out using index interpolator, a sub-module of Insect Life Cycle Modelling (ILCYM) software. The thin plate algorithm was used for interpolation of the indices. The study confirms temperature is a key factor to explain the distribution of stem borer pests and their natural enemies but point the likely important role played by other

climatic factors and by factors related to the top-down regulation of pests by parasitoids (host-parasitoid synchrony). The results based on temperature only indicate a worsening of the stem borer impact on maize production along the two East Africa mountain gradients studied. This was attributed to three main changes occurring simultaneously: (1) range expansion in higher altitude areas of the gradients due to increase of suitability of establishment and survival in areas above 1200 m.a.s.l. suggesting a future change in dominance in moist mid-altitude and moist Transitional areas of both gradients with a higher proportion of *C. partellus*; (2) increase of the abundance (number of generations and finite rate of increase) of the pests at all altitudes; more importantly, by 2055, predictions suggest the two pests will cause more damages in the most productive maize zones of both transects; (3) disruption of the geographical distribution between the pests and their main larval natural enemies suggesting for both parasitoid species an improvement of the biological control of stem borers at altitude below 1200 m.a.s.l. and a deterioration above 1200 m.a.s.l. The predicted increase pest activity will significantly increase maize yield losses in all agro-ecological zones along both transects but much more in lower areas of Kilimanjaro and all along Taita hills transects.

CHAPTER FIVE

MODELLING THE ROLE OF TEMPERATURE IN COMPETING INSECT SPECIES FOR A SINGLE RESOURCE

5.1 Introduction

During the past decades, the theory of competition has played an increasingly important role in both development of general ecological theory and the interpretation of field data (Robert 1977). Competition is one of the primary biotic factors that shape patterns of distribution, abundance and diversity in ecological communities (Kaplan and Denno 2007). The prominent status of competition in modern ecology is undoubtedly linked to views of pioneers in ecology, who strongly advocate the central role of competitive interactions between species (Lotka 1932, Gause 1934, Wolkowic and Lu 1992). Plant-feeding insects have become focal organisms for studies on population dynamics and community diversity, because competition is deeply ingrained in their activities. It became accepted as a factor organizing insect assemblages, despite the fact that empirical evidence supporting competition was mostly derived from plant, vertebrate and marine systems (Jermy 1985, Denno *et al.* 1995). Many theoretical studies of interspecific competition have dealt with the dependence of competition on the resource utilization abilities of each species (Grover 1997, Tilman 1977, 1980, Martines *et al.* 2009). The models used in these studies usually belong to two groups: the first group uses the classical theory of ecological competition between two or more species (Liu and Zhang 2009, Ebraheen *et al.* 2012) that is attributed to Lotka (1925) and Volterra (1931). These models are often “phenomenological” because the competition parameters are not independently derived values that can allow direct prediction of coexistence (Tilman

1994). The second group employs resource-based theory in ecological competition; it considers the dynamics of the resource explicitly as well as the population dynamics of the competing species (Leon and Tumpson 1975, Tilman 1994). The simplest form of resource-based competition occurs in laboratory apparatus, called a chemostat or continuous culture (Martines *et al.* 2009). In comparison with the classical models, the resource-based models may be less general and more difficult to analyse (Tilman 1977, Hsu *et al.* 1977, Hsu 1978). However, the resource-based models are often more predictive because the parameters can be measured on species alone (Hansen and Hubbell 1980). Although competition among species is often cited as a major determinant of natural distributional patterns, there have been few studies in which knowledge of the mechanism of competition is used to predict these patterns (Tilman 1994). The many biotic and abiotic factors that influence competition and possible interactions among them, makes such prediction difficult.

Climate, especially temperature, has a strong and direct influence on insect development, reproduction and survival, and is considered the dominant abiotic factor that can be used to define ecological suitability of insect species and thus dictate composition of pest communities in different agro-ecological regions (Ladanyi and Harvath 2010). However, temperature has not much been incorporated in the theoretical studies relating resource and insect competition. Therefore, the objective of the present chapter is to determine and analyse the stability of the equilibrium points of insect species competing for a single resource while accounting for temperature through qualitative analysis. The systems as a combination of three sub-models were analysed: (i) a single species with a single resource (ii) two species competing for one resource and (iii) three species competing for one resource.

5.2 Resource based mathematical model formulation

Model formulation assumes the following: (i) the growth of the insect species is limited by a single resource; (ii) all insect species require the same resource to survive and reproduce; (iii) the resource availability depends on the rate of resource supply; (iv) no biological control measure is applied, that is, no parasitoid is applied; (v) the dynamic is assumed to follow “monod’s” type function; (vi) all values of the competition coefficient are nonnegative, and (v) the growth rate of the insect is a function of both resource and temperature.

From the above assumptions, three systems of ordinary differential equations governing the growth and dependence of the species to the resource were deduced as follows:

5.2.1 Case 1: One species and one resource model

$$\begin{aligned} \frac{dN_1}{dt} &= \left(r_1 \exp\left(\frac{-1}{2}\left(\frac{T-T_1}{w}\right)^2\right) \frac{R}{k_1+R} - m_1 \right) N_1, \\ \frac{dR}{dt} &= \beta(S-R) - \alpha_1 r_1 \exp\left(\frac{-1}{2}\left(\frac{T-T_1}{w}\right)^2\right) \frac{R}{k_1+R} N_1, \end{aligned} \quad (5.1)$$

5.2.2 Case 2: Two species and one resource model

$$\begin{aligned} \frac{dN_1}{dt} &= \left(r_1 \exp\left(\frac{-1}{2}\left(\frac{T-T_1}{w}\right)^2\right) \frac{R}{k_1+R} - m_1 \right) N_1, \\ \frac{dN_2}{dt} &= \left(r_2 \exp\left(\frac{-1}{2}\left(\frac{T-T_2}{w}\right)^2\right) \frac{R}{k_2+R} - m_2 \right) N_2, \\ \frac{dR}{dt} &= \beta(S-R) - \alpha_1 r_1 \exp\left(\frac{-1}{2}\left(\frac{T-T_1}{w}\right)^2\right) \frac{R}{k_1+R} N_1 - \alpha_{12} r_2 \exp\left(\frac{-1}{2}\left(\frac{T-T_2}{w}\right)^2\right) \frac{R}{k_2+R} N_2. \end{aligned} \quad (5.2)$$

5.2.3 Case 3: Three species and one resource model

$$\begin{aligned}
 \frac{dN_1}{dt} &= \left(r_1 \exp\left(\frac{-1}{2}\left(\frac{T-T_1}{w}\right)^2\right) \frac{R}{k_1+R} - m_1 \right) N_1, \\
 \frac{dN_2}{dt} &= \left(r_2 \exp\left(\frac{-1}{2}\left(\frac{T-T_2}{w}\right)^2\right) \frac{R}{k_2+R} - m_2 \right) N_2, \\
 \frac{dN_3}{dt} &= \left(r_3 \exp\left(\frac{-1}{2}\left(\frac{T-T_3}{w}\right)^2\right) \frac{R}{k_3+R} - m_3 \right) N_3, \\
 \frac{dR}{dt} &= \beta(S-R) - \alpha_1 r_1 \exp\left(\frac{-1}{2}\left(\frac{T-T_1}{w}\right)^2\right) \frac{R}{k_1+R} N_1 - \alpha_2 r_2 \exp\left(\frac{-1}{2}\left(\frac{T-T_2}{w}\right)^2\right) \frac{R}{k_2+R} N_2 - \\
 &\quad \alpha_3 r_3 \exp\left(\frac{-1}{2}\left(\frac{T-T_3}{w}\right)^2\right) \frac{R}{k_3+R} N_3.
 \end{aligned} \tag{5.3}$$

$$\text{Let } a_i = r_i \exp\left(\frac{-1}{2}\left(\frac{T-T_i}{w}\right)^2\right),$$

$i = 1, 2, 3$ in the systems.

The Michaeli-Menten equation $\frac{R}{k_i+R}$ is employed to describe the relationship between cellular metabolism and a resource. For every large values of the resource, this equation approximates to 1. For a resource equal to k_i it gives approximately a value of $\frac{1}{2}$, which justifies why k_i is referred to as the half-saturation constant. The variables and parameters used in the models are described in Table 5.1 below:

Table 5.1: Descriptions of variables and parameters used in systems

Variables and parameters	Description/Comments
$R(t)$	Amount of resource available at time t
$N_i(t)$	Population abundance of species (i) at time t
T	The physical factor (temperature)
$T_i, i = 1, 2, 3$	The optimal temperature of species (i)

$r_i, i = 1, 2, 3$	Maximal gross productivity rate of species at T_i
a_i	Population growth rate of species (i)
α_i	Consumption rate of the resource by species (i)
m_i	Mortality rate of species (i)
k_i	The half-saturation constant of species (i)
β	The flow or supply rate of the resource
S	The total amount of all forms of the resource in the habitats
w	The width environmental tolerance

5.3 Model analysis

The mathematical model equations (5.1)-(5.3) are analysed qualitatively. An elaborative analysis of the equilibrium is performed and conditions for existence of the proposed systems are provided. The stability analysis of the equilibrium is studied by computing the variational matrices for each equilibrium point. However, the local stability is established through Jacobian matrix of the systems using the Routh–Hurwitz criteria. For linearized systems, the Jacobian matrix is given by:

$$\mathbf{J} = \begin{bmatrix} \frac{\partial f_1}{\partial N_1} & \cdot & \cdot & \cdot & \frac{\partial f_1}{\partial N_n} \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \frac{\partial f_k}{\partial N_1} & \cdot & \cdot & \cdot & \frac{\partial f_k}{\partial N_n} \end{bmatrix}$$

This is associated with the characteristic equation:

$$\det(J - \lambda I) = 0 \Rightarrow \lambda^n + b_1 \lambda^{n-1} + b_2 \lambda^{n-2} + \dots + b_n = 0 \quad (5.4)$$

In general, the characteristic equation is a polynomial expression with degree n equal to the number of species competing, λ is the eigenvalue of the linearized system and \mathbf{I} is the identity matrix.

Theorem 1. Routh-Hurwitz criteria

Given the polynomial $P(\lambda) = \lambda^n + b_1\lambda^{n-1} + b_2\lambda^{n-2} + \dots + b_n$, where the coefficients b_i are real constants, $i = 1, \dots, n$, define the n Hurwitz matrices using the coefficients b_i of the characteristic polynomial. Then all of the roots of the polynomial $P(\lambda)$ are negative or have negative real parts if and only if the determinants of all Hurwitz matrices are positive. For polynomial of degree $n = 2, 3$ and 4 , the Hurwitz criteria are summarized as follows: $\text{Re}(\lambda_i) < 0$ if: $n = 2 : b_1 > 0$, and $b_2 > 0$; $n = 3 : b_1 > 0, b_3 > 0 \quad b_1 b_2 > b_3$; $n = 4 : b_1 > 0, b_3 > 0, b_4 > 0$ and $b_1 b_2 b_3 > b_3^2 + b_1^2 b_4$.

Theorem 2. For an $n \times n$ matrix \mathbf{A} the determinant is given by the explicit formula

$$\det(A) = \sum_{\sigma \in S_n} \text{sgn}(\sigma) \prod_{i=1}^n A_{i, \sigma_i}, \text{ where } S_n \text{ is the permutation group, } \text{sgn}(\sigma) \text{ is the signum}$$

function of permutation in the permutation group, which returns +1 and -1 for even and odd permutation respectively, and σ_i represents the value in i th position after the reordering.

5.4 Models implementation and population size predictions

The calculations are carried out with computer program written in R (Appendix A). In the program, model equations are solved using the 4th order Runge-Kutta algorithm with step size of 0.01. This method is commonly used and sufficiently accurate for most application, and an important family of implicit and explicit iterative method, which are used in temporal discretization for the approximation of solution of ordinary differential

equations (Mwalusepo *et al.* 2014). Once the model equations are solved, graphs are generated displaying predictions of future species population size at fixed initial number of the resource. For a random selection of species, initial population size, the models are used to estimate the values of species at a given time interval; that may be a day, a week or a month depending on the species life cycle. However, for this analysis we assumed the time interval is in days.

5.5 Qualitative analysis of the developed models

5.5.1 One species and one resource

Solving the equations lead to two equilibrium points, namely axial equilibrium point $E_1(0, R^*)$ and interior equilibrium point $E_2(N_1^*, R_1^*)$, where

$$\begin{aligned} R^* &= S \\ R_1^* &= \frac{m_1 k_1}{a_1 - m_1} \\ N_1^* &= \frac{\beta(Sa_1 - Sm_1 - m_1 k_1)}{\alpha_1 m_1 (a_1 - m_1)} \end{aligned}$$

The asterisks on N^* and R^* indicate that this is a non-zero equilibrium value of N and R respectively, and $a_1 \neq m_1$. These equilibrium points are obtained when

$\frac{dN_i}{dt} = 0, i = 1, 2, 3$, and $\frac{dR}{dt} = 0$. The jacobian matrix of the system (5.1) is

$$J(N_1, R) = \begin{bmatrix} \frac{a_1 R}{k_1 + R} - m_1 & \frac{a_1 N_1}{k_1 + R} - \frac{a_1 R N_1}{(k_1 + R)^2} \\ -\frac{\alpha_1 a_1 R}{k_1 + R} & -\beta - \frac{\alpha_1 a_1 N_1}{k_1 + R} + \frac{\alpha_1 a_1 R N_1}{(k_1 + R)^2} \end{bmatrix}$$

The local stability of each of the equilibrium points of model system (5.1) ascertain by the following theorem.

Theorem 3. The equilibrium $E_1(0, S)$ is locally asymptotically stable if and only if

$$0 < \frac{\beta k_1 + \beta S - Sa_1 + Sm_1 + m_1 k_1}{k_1 + S}, \text{ when } \beta + m_1 > \frac{a_1 S}{k_1 + S}, \text{ and } 0 < -\frac{\beta(S(a_1 - m_1) - m_1 k_1)}{k_1 + S}.$$

Theorem 4. The interior equilibrium point $E_2\left(\frac{\beta(S(a_1 - m_1) - m_1 k_1)}{\alpha_1 m_1 (a_1 - m_1)}, \frac{m_1 k_1}{a_1 - m_1}\right)$ is locally

asymptotically stable if and only if $0 < \frac{(a_1 - m_1)(Sa_1 - Sm_1 - m_1 k_1)\beta}{a_1 k_1}$ and

$$0 < \frac{\beta a_1 k_1 m_1 + (a_1 \beta - \beta m_1)(Sa_1 - m_1 k_1 - Sm_1)}{a_1 k_1 m_1}, \text{ otherwise is unstable}$$

5.5.2 Two species one resource

Determining the equilibrium of the model (5.2) leads to three equilibrium points, which

are: $E_1(0, 0, S)$, $E_2\left(\frac{\beta(S(a_1 - m_1) - m_1 k_1)}{\alpha_1 m_1 (a_1 - m_1)}, 0, \frac{m_1 k_1}{a_1 - m_1}\right)$, and

$E_3\left(0, \frac{\beta(S(a_2 - m_2) - m_2 k_2)}{\alpha_2 m_2 (a_2 - m_2)}, \frac{m_2 k_2}{a_2 - m_2}\right)$, where $a_1 \neq m_1$ and $a_2 \neq m_2$. The Jacobian of the

system (5.2) is

$$J(N_1, N_2, R) = \begin{bmatrix} \frac{a_1 R}{k_1 + R} - m_1 & 0 & \frac{a_1 N_1}{k_1 + R} - \frac{a_1 R N_1}{(k_1 + R)^2} \\ 0 & \frac{a_2 R}{k_2 + R} - m_2 & \frac{a_2 N_2}{k_2 + R} - \frac{a_2 R N_2}{(k_2 + R)^2} \\ -\frac{\alpha_1 a_1 R}{k_1 + R} & -\frac{\alpha_2 a_2 R}{k_2 + R} & -\beta - \frac{\alpha_1 a_1 N_1}{k_1 + R} + \frac{\alpha_1 a_1 R N_1}{(k_1 + R)^2} - \frac{\alpha_2 a_2 N_2}{k_2 + R} + \frac{\alpha_2 a_2 R N_2}{(k_2 + R)^2} \end{bmatrix}$$

Theorem 5. The equilibrium points $E_1(0, 0, R^*)$, $E_2(N_1^*, 0, R_1^*)$, and $E_3(0, N_2^*, R_2^*)$ will

be locally asymptotically stable if the following conditions hold: for the polynomial degree $n=3$, the equilibrium points can be determined without explicitly solving the

characteristic polynomial $\lambda^3 + \psi_1\lambda^2 + \psi_2\lambda + \psi_3 = 0$. Then $\text{Re}(\lambda_i) < 0$ if

$\psi_1 > 0, \psi_3 > 0, \psi_1\psi_2 - \psi_3 > 0$; otherwise, the equilibrium points will be unstable. Where

$$N_2^* = \frac{\beta(S(a_2 - m_2) - m_2 k_2)}{\alpha_2 m_2 (a_2 - m_2)}, R_2^* = \frac{m_2 k_2}{a_2 - m_2}$$

5.5.3 Three species one resource

For this case, the system of ordinary differential equation has four equilibrium points.

$$E_1(0,0,0,S), E_2\left(\frac{\beta(S(a_1 - m_1) - m_1 k_1)}{\alpha_1 m_1 (a_1 - m_1)}, 0, 0, \frac{m_1 k_1}{a_1 - m_1}\right), E_3\left(0, \frac{\beta(S(a_2 - m_2) - m_2 k_2)}{\alpha_2 m_2 (a_2 - m_2)}, 0, \frac{m_2 k_2}{a_2 - m_2}\right),$$

$$\text{and } E_4\left(0, 0, \frac{\beta(S(a_3 - m_3) - m_3 k_3)}{\alpha_3 m_3 (a_3 - m_3)}, \frac{m_3 k_3}{a_3 - m_3}\right), \text{ where } a_1 \neq m_1, a_2 \neq m_2 \text{ and } a_3 \neq m_3$$

The Jacobian of the system (5.3) is

$$J(N_1, N_2, N_3, R) = \begin{bmatrix} \frac{a_1 R}{k_1 + R} - m_1 & 0 & 0 & \frac{a_1 N_1}{k_1 + R} - \frac{a_1 R N_1}{(k_1 + R)^2} \\ 0 & \frac{a_2 R}{k_2 + R} - m_2 & 0 & \frac{a_2 N_2}{k_2 + R} - \frac{a_2 R N_2}{(k_2 + R)^2} \\ 0 & 0 & \frac{a_3 R}{k_3 + R} - m_3 & \frac{a_3 N_3}{k_3 + R} - \frac{a_3 R N_3}{(k_3 + R)^2} \\ -\frac{\alpha_1 a_1 R}{k_1 + R} & -\frac{\alpha_2 a_2 R}{k_2 + R} & -\frac{\alpha_3 a_3 R}{k_3 + R} & -\beta - \frac{\alpha_1 a_1 N_1}{k_1 + R} + \frac{\alpha_1 a_1 R N_1}{(k_1 + R)^2} - \frac{\alpha_2 a_2 N_2}{k_2 + R} \\ & & & + \frac{\alpha_2 a_2 R N_2}{(k_2 + R)^2} - \frac{\alpha_3 a_3 N_3}{k_3 + R} + \frac{\alpha_3 a_3 R N_3}{(k_3 + R)^2} \end{bmatrix}$$

Theorem 6. The equilibrium point $E_1(0,0,0,S)$ is locally asymptotically stable if (i)

$A > 0$, (ii) $C > 0$, (iii) $D > 0$, (iv) $ABC > C^2 + A^2D$; otherwise, it will be unstable.

Proof. The determinant of the Jacobian matrix at $E_1(0,0,0,S)$ is given by:

$$\det \begin{bmatrix} \frac{a_1 S}{k_1 + S} - m_1 - \lambda & 0 & 0 & 0 \\ 0 & \frac{a_2 S}{k_2 + S} - m_2 - \lambda & 0 & 0 \\ 0 & 0 & \frac{a_3 S}{k_3 + S} - m_3 - \lambda & 0 \\ -\frac{\alpha_1 a_1 S}{k_1 + S} & -\frac{\alpha_2 a_2 S}{k_2 + S} & -\frac{\alpha_3 a_3 S}{k_3 + S} & -\beta - \lambda \end{bmatrix} = 0$$

Let

$$L_1 = \frac{a_1 S}{k_1 + S} - m_1, \quad L_2 = \frac{a_2 S}{k_2 + S} - m_2, \quad L_3 = \frac{a_3 S}{k_3 + S} - m_3, \quad L_4 = \frac{-a_1 \alpha_1 S}{k_1 + S}, \quad L_5 = \frac{-a_2 \alpha_2 S}{k_2 + S}, \text{ and}$$

$$L_6 = \frac{-a_3 \alpha_3 S}{k_3 + S}.$$

Then the characteristic equation of the matrix is calculated as

$$\lambda^4 + A\lambda^3 + B\lambda^2 + C\lambda + D = 0 \quad (5.5)$$

where

$$A = \beta - L_1 - L_2 - L_3,$$

$$B = L_1 L_2 + L_1 L_3 + L_2 L_3 - L_1 \beta - L_2 \beta - L_3 \beta,$$

$$C = L_1 L_2 \beta + L_1 L_3 \beta + L_2 L_3 \beta - L_1 L_2 L_3,$$

$$D = -L_1 L_2 L_3 \beta.$$

The $E_1(0,0,0,S)$ will be locally asymptotically stable if $A > 0, C > 0, D > 0$,

and $ABC > C^2 + A^2 D$ and unstable otherwise.

Theorem 7. The planar equilibrium points, $E_2(N_1^*, 0, 0, R_1^*)$, $E_3(0, N_2^*, 0, R_2^*)$,

$E_4(0, 0, N_3^*, R_3^*)$ are locally asymptotically stable if

- (i) $\Omega_1 > 0$, (ii) $\Omega_3 > 0$, (iii) $\Omega_4 > 0$, (iv) $\Omega_1 \Omega_2 \Omega_3 > \Omega_3^2 + \Omega_1^2 \Omega_4$.

Proof. The Jacobian matrix at $E_2(N_1^*, 0, 0, R_1^*)$ is given by:

$$\mathbf{J}_{E_2} = \begin{bmatrix} A_{11} & 0 & 0 & A_{41} \\ 0 & A_{22} & 0 & 0 \\ 0 & 0 & A_{33} & 0 \\ A_{14} & A_{24} & A_{34} & A_{44} \end{bmatrix},$$

where

$$\begin{aligned} A_{11} &= \frac{a_1 R_1^*}{k_1 + R_1^*} - m_1, & A_{41} &= N_1^* \left(\frac{a_1}{k_1 + R_1^*} - \frac{a_1 R_1^*}{(k_1 + R_1^*)^2} \right), & A_{22} &= \frac{a_2 R_1^*}{k_2 + R_1^*} - m_2, \\ A_{33} &= \frac{a_3 R_1^*}{k_3 + R_1^*} - m_3, & A_{14} &= \frac{-\alpha_1 a_1 R_1^*}{k_1 + R_1^*}, & A_{24} &= \frac{-\alpha_2 a_2 R_1^*}{k_2 + R_1^*}, & A_{34} &= \frac{-\alpha_3 a_3 R_1^*}{k_3 + R_1^*}, \\ A_{44} &= -\frac{\alpha_1 a_1 N_1^*}{k_1 + R_1^*} - \beta + \frac{\alpha_1 a_1 N_1^* R_1^*}{(k_1 + R_1^*)^2}. \end{aligned}$$

The determinant of \mathbf{J}_{E_2} is given by

$$\det \begin{bmatrix} A_{11} - \lambda & 0 & 0 & A_{41} \\ 0 & A_{22} - \lambda & 0 & 0 \\ 0 & 0 & A_{33} - \lambda & 0 \\ A_{14} & A_{24} & A_{34} & A_{44} - \lambda \end{bmatrix} = 0$$

The characteristic equation is

$$\lambda^4 + Z_1 \lambda^3 + Z_2 \lambda^2 + Z_3 \lambda + Z_4 = 0, \quad (5.6)$$

where

$$Z_1 = -(A_{11} + A_{22} + A_{33} + A_{44}),$$

$$Z_2 = A_{11}A_{22} + A_{22}A_{33} + A_{11}A_{33} + A_{11}A_{44} + A_{22}A_{44} + A_{33}A_{44} - A_{41}A_{14},$$

$$Z_3 = A_{41}A_{14}A_{22} + A_{41}A_{14}A_{33} - A_{11}A_{33}A_{22} - A_{11}A_{33}A_{44} - A_{22}A_{33}A_{44},$$

$$Z_4 = A_{11}A_{22}A_{33}A_{44} - A_{41}A_{14}A_{22}A_{33}.$$

The planar equilibrium point E_2 will be locally asymptotically stable if (i) $Z_1 > 0$, (ii) $Z_3 > 0$, (iii) $Z_4 > 0$, and (iv) $Z_1 Z_2 Z_3 > Z_3^2 + Z_1^2 Z_4$.

Similarly for $E_3(0, N_2^*, 0, R_2^*)$ and $E_4(0, 0, N_3^*, R_3^*)$, again through the Routh-Hurwitz criteria, we have the following: from the polynomial $\lambda^4 + n_1\lambda^3 + n_2\lambda^2 + n_3\lambda + n_4 = 0$, with $\text{Re}(\lambda_i) < 0$ if $n_1 > 0$, $n_3 > 0$, $n_4 > 0$, and $n_1 n_2 n_3 > n_3^2 + n_1^2 n_4$ the system will be conditionally stable, where $N_3^* = \frac{\beta(S(a_3 - m_3) - m_3 k_3)}{\alpha_3 m_3 (a_3 - m_3)}$, $R_3^* = \frac{a_3 k_3}{a_3 - m_3}$, where $a_3 \neq m_3$.

5.6 Resource response to temperature

It is useful to determine the quantitative behaviour of planar equilibrium in response to temperature, since the quantity of resource can vary highly within any particular region of qualitatively similar parameter space. Consider the resource as a function of temperature.

$$R_i^* = \frac{g_i}{r_i \exp\left(\frac{-1}{2}\left(\frac{T - T_i}{w}\right)^2\right) - m_i} \quad (5.7)$$

where $g_i = m_i k_i, k_i, T_i, m_i, r_i, w, T$ are constants. Then the response of R_i^* to temperature using the derivate $\frac{dR_i^*}{dT}$ was determined.

The derivative of the equilibrium of the temperature dependent resource function with respect to temperature is a damped an exponential function given by

$$\frac{dR_i^*}{dT} = \frac{g_i \left(\frac{T}{w^2} - \frac{T_i}{w^2} \right) \times r_i \exp \left(-\frac{1}{2} \left(\frac{T - T_i}{w} \right)^2 \right)}{\left[r_i \exp \left(\frac{-1}{2} \left(\frac{T - T_i}{w} \right)^2 - m_i \right) \right]^2} \quad (5.8)$$

This generates a rather simple relationship governing the directional response of equilibrium resource to temperature variation. For numerical simulation, the parameters were chosen to give the behaviour of the isoclines for species and the resource. This was done using three different sets of parameters (unequal growth rate, equal growth rate and equal consumption rates). Due to the lack of parameter values in the literature and from the field study, the following values in Table 5.2 were assumed to simulate the model.

Table 5.2: Parameters used in simulations

Parameters	Species one	Species two	Species three
r_i	0.10	0.17	0.20
m_i	0.02	0.02	0.02
β	0.01	0.01	0.01
S	70.00	70.00	70.00
k_i	0.02	0.10	0.70
α_i	3.00	0.50	0.40
w	7.00	7.00	7.00
T_i	22.00	20.00	23.00

5.7 Results

This section presents the results of the numerical simulations that were carried out to investigate the dynamical behaviour of the formulated models. In order to verify the theoretical predication of the models, the numerical simulations are carried out using fixed values of the parameters of the models. These parameter values are chosen for simulation purposes only. However, these parameters may be biologically feasible. Numerical simulations for three species are done singly at five different temperatures (10°C , 15°C , 20°C , 25°C , 30°C) and the results are represented in Figures 5.1-5.8. In these figures, dynamics of the resource are presented by solid line while those of the species are represented by dotted lines.

At 10°C (Figure 5.1a), for a single species, the results show a slow increase in the curve of the species population size and a slow decrease in the resource quantity. At 15°C , 20°C , 25°C and 30°C respectively, similar curves behaviour shape are obtained. It starts with a rapid increase of the population size of the species, followed by a slow decreases and a rapid decrease of the resource. Figure 5.1b shows the relationship between the different initial population size (10, 20, 30) with the resource at 25°C ; it was observed that at higher initial population size of the species the resource quantity decreases faster.

For two species competing for a single resource (Figures 5.2-5.4), the results show that species one is a superior competitor at all temperatures tested, when the initial population size of species one is greater than that of species two, and within $20\text{-}30^{\circ}\text{C}$ when both species started at the same initial population size. Species two is a superior competitor at all temperatures tested, when the initial population size of species two is greater than that of species one and at 10°C when both species started at the same initial population size. No

difference is observed between the two species at 15°C when the initial population size of the two species is identical.

In the case of three species competing for a single resource, the species with higher initial population size is the superior competitor at all temperatures. However, when all species have equal initial population size, species two grew faster than its two counterparts at lower temperatures (from 10°C to 15°C). Between 20°C to 25°C species one is a superior competitor. With the same growth rates, the species with the lower mortality is the superior competitor when all species have equal initial population size. It is observed that one species is the superior competitor at 10°C to 15°C and with increase in temperature ($T \geq 20^\circ\text{C}$) another species became superior when all species have equal consumption rates.

Figure 5.9 represents a combination of temperature and resource for which each species has no net population growth for a given mortality rate. Herein, the zero net growth isoclines represent equilibrium boundaries of individual species based on their requirements in resource availability. The curves show the amount of the resource that each species need at equilibrium, to have a reproductive rate that can balance its mortality rate. In general, within the unshaded region, the population size of the species will increase when it would decrease in the shaded region.

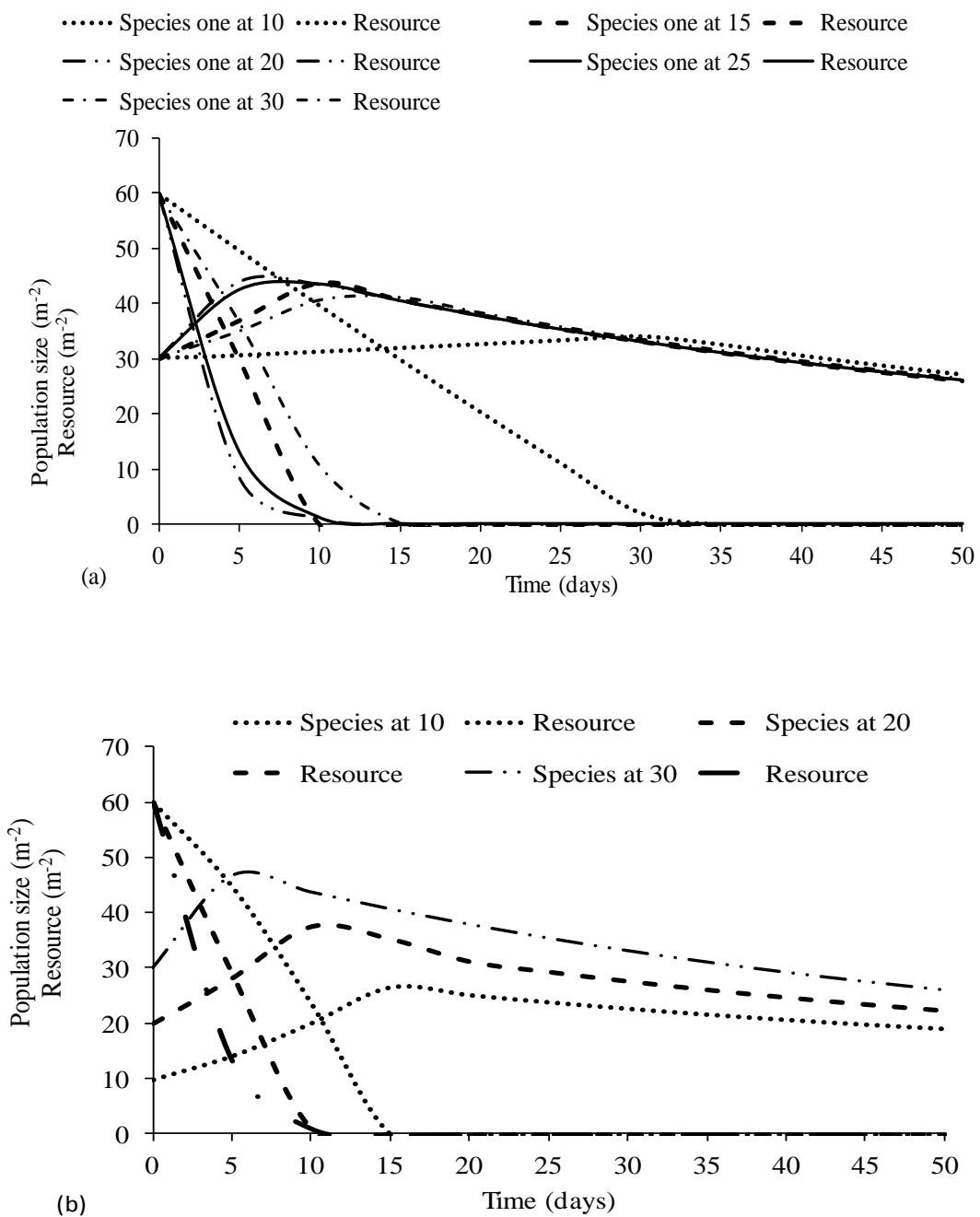
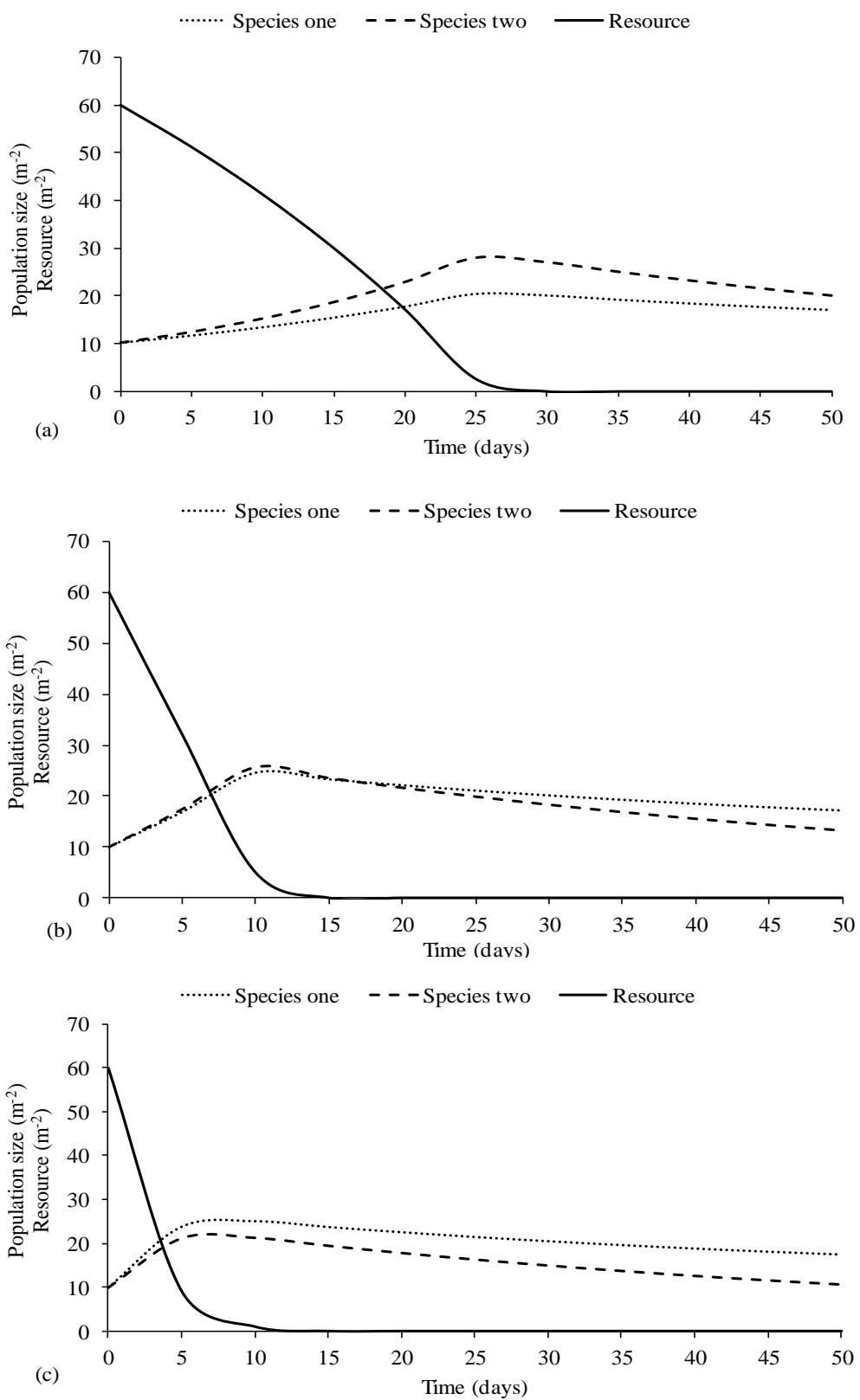


Figure 5.1: Behavior of the isoclines for one species and the resource at different temperatures; (a) show the behavior of population size and the resource at temperatures 10°C, 15°C, 20°C, 25°C and 30°C respectively; (b) show the behavior of population size and resource at different initial population size at temperature 25°C.



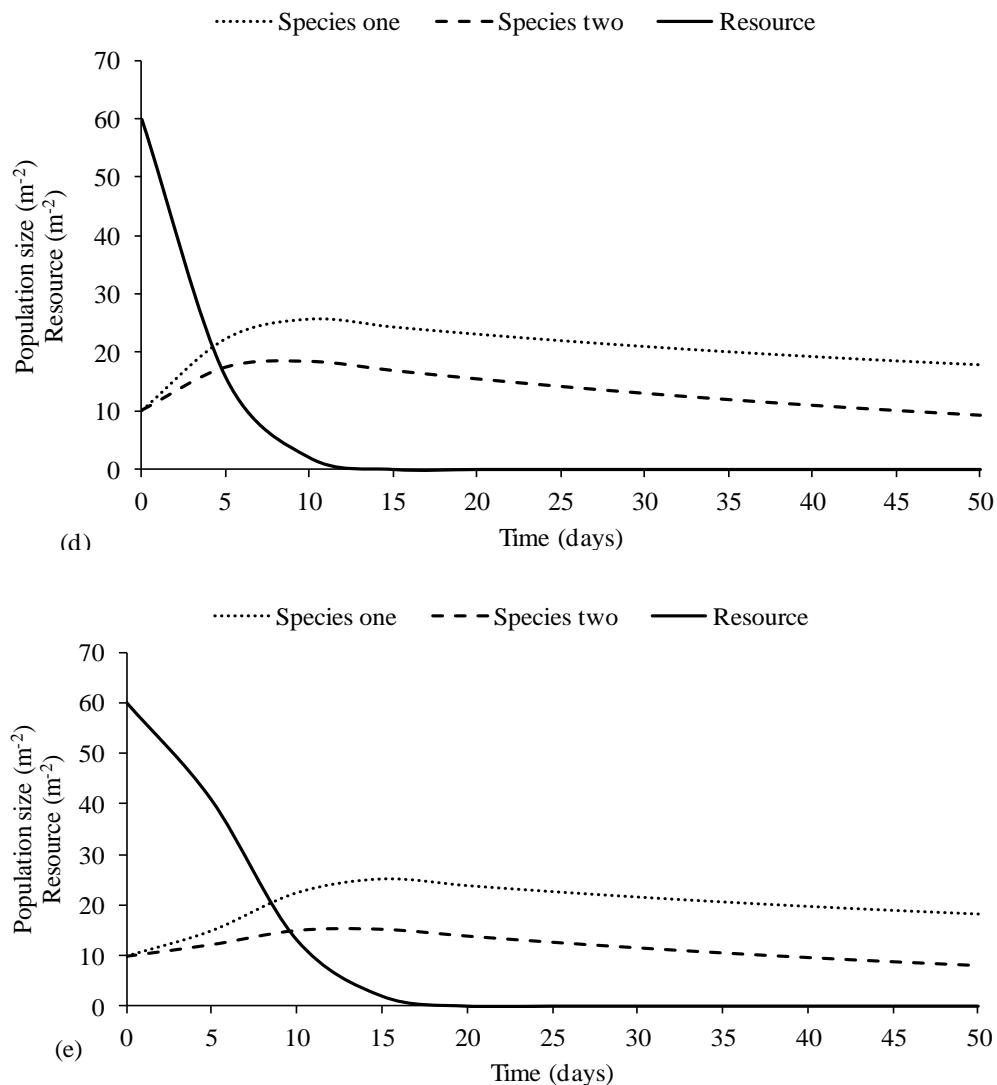
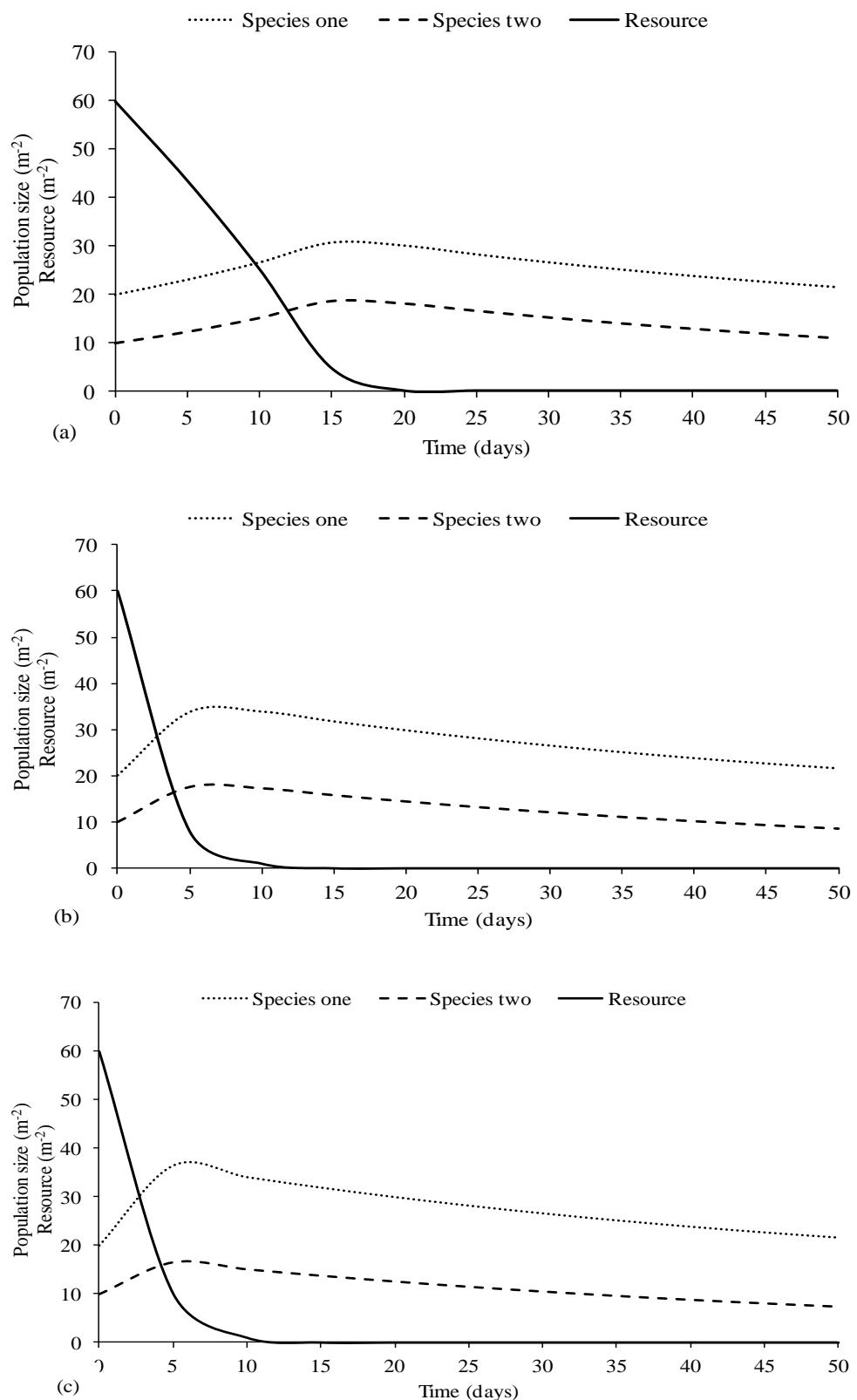


Figure 5.2: Behavior of the isoclines for two species competing for a single resource when both species initial population size are the same; curves (a)-(e) show the behavior of population size for each species and resource at temperatures 10°C , 15°C , 20°C , 25°C and 30°C , respectively. Species one is represented with round dot lines; species two is represented with dash lines and the resource with solid lines; and both species have different growth rate.



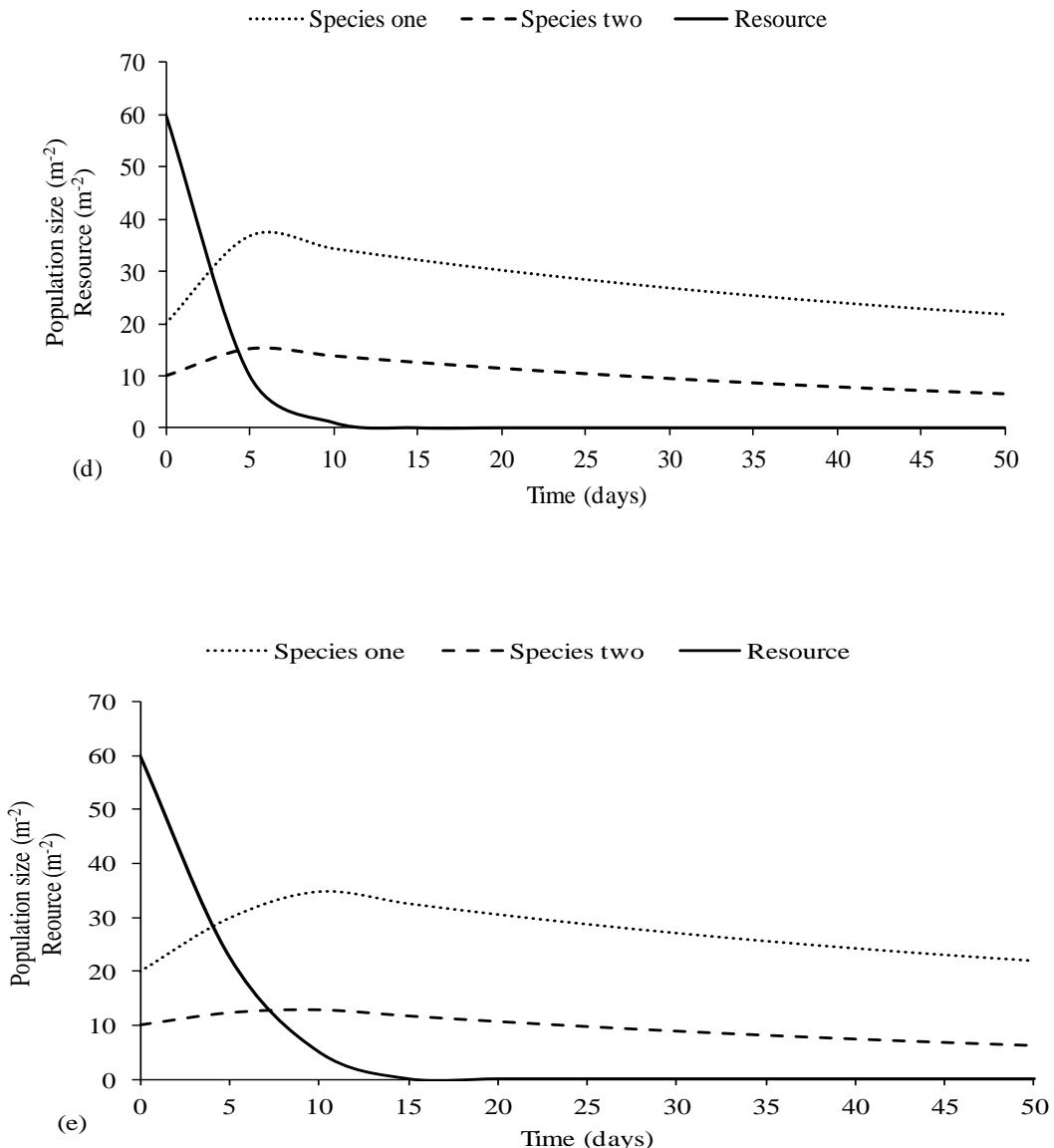
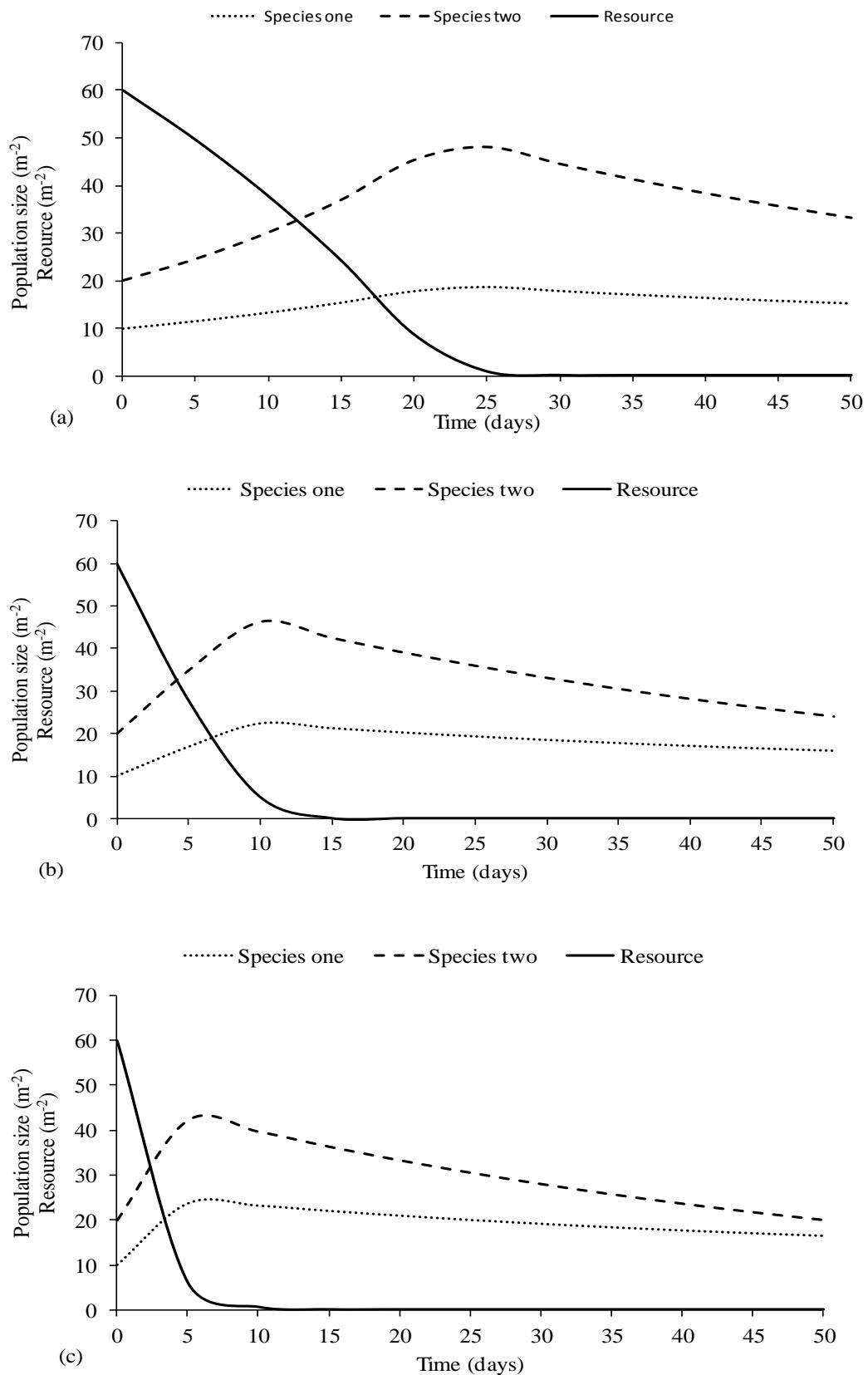


Figure 5.3: Behavior of the isoclines when the population size of species one is greater than species two; curves (a)-(e) show the behavior of population size for each species and the resource at temperatures 10°C, 15°C, 20°C, 25°C and 30°C respectively.



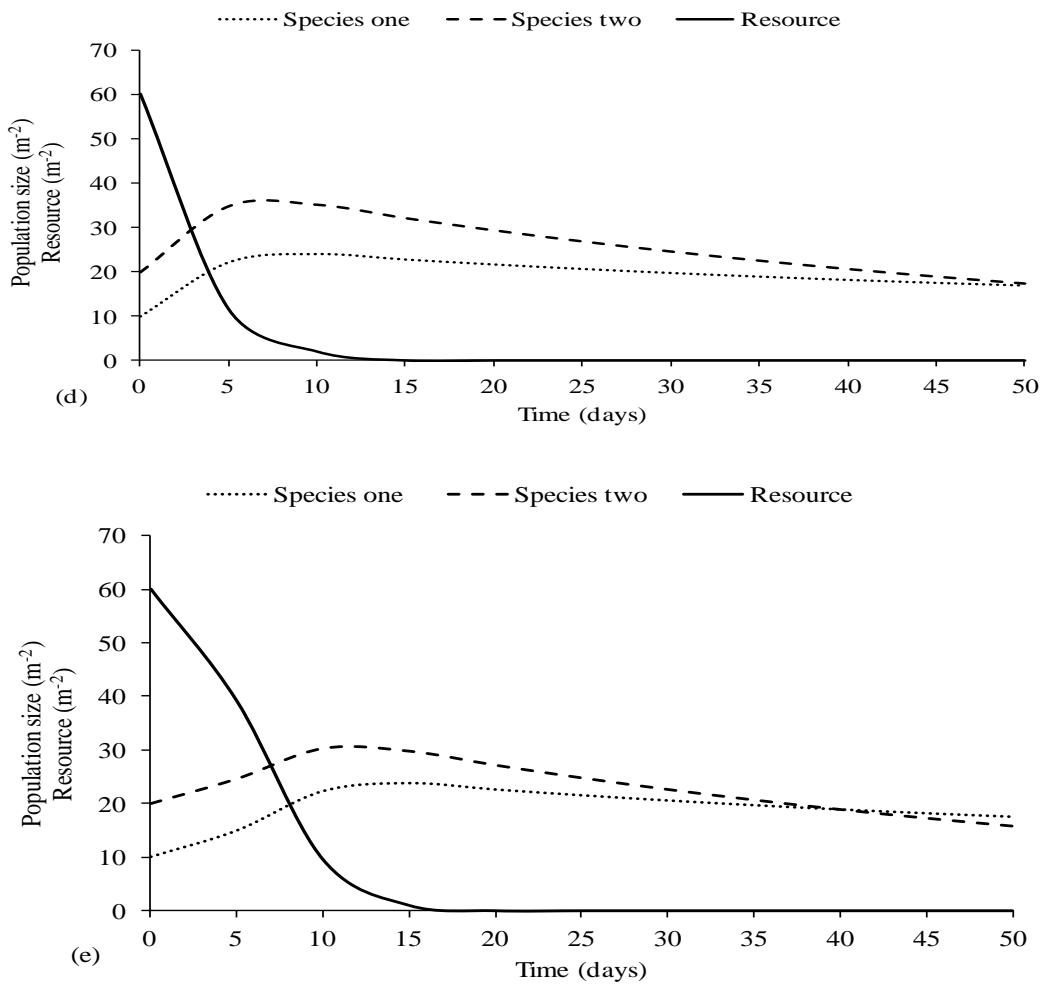
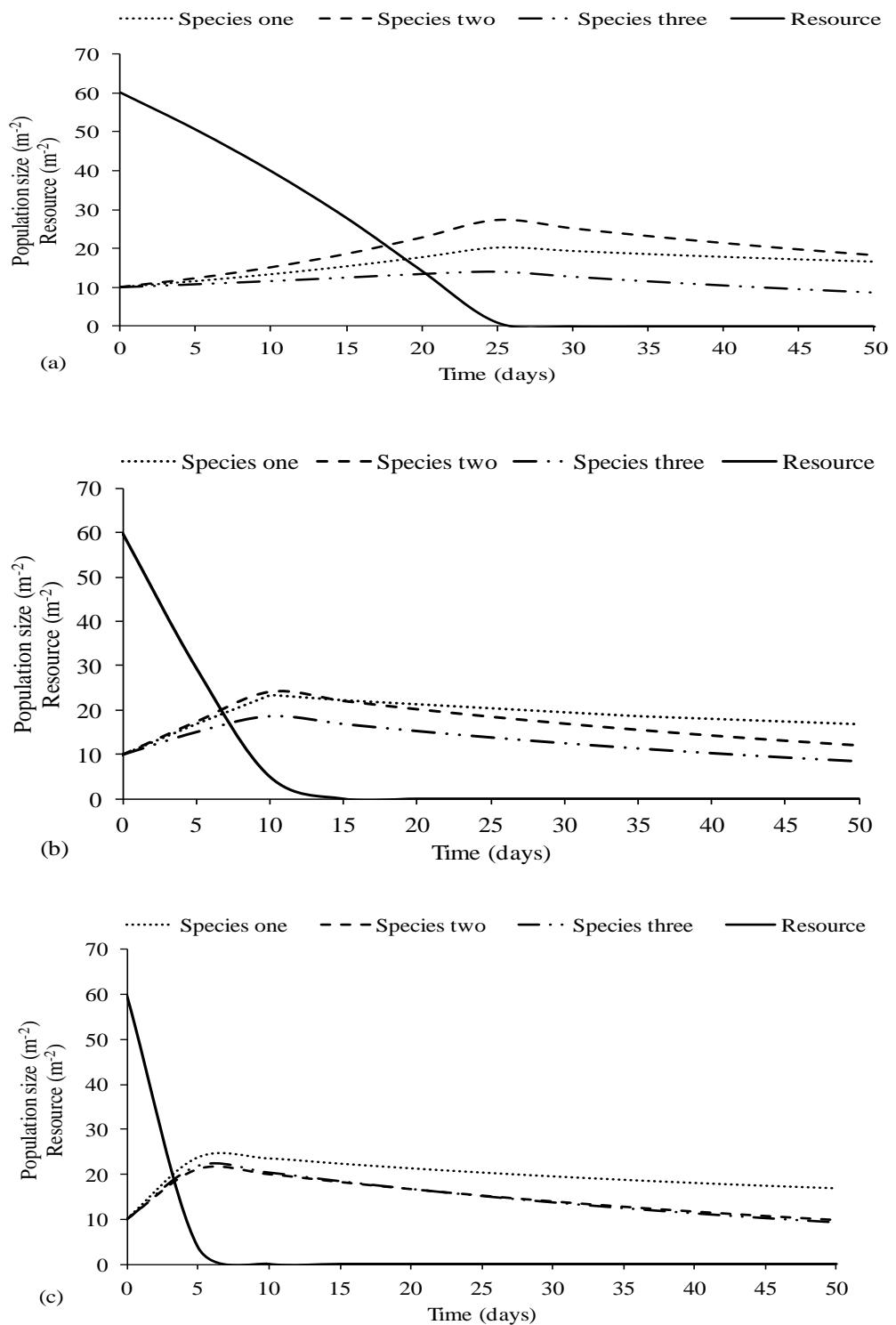


Figure 5.4: Behavior of the isoclines when the population size of species two is greater than species one; curves (a)-(e) show the behavior of population size for each species and the resource at temperatures 10°C , 15°C , 20°C , 25°C and 30°C respectively.



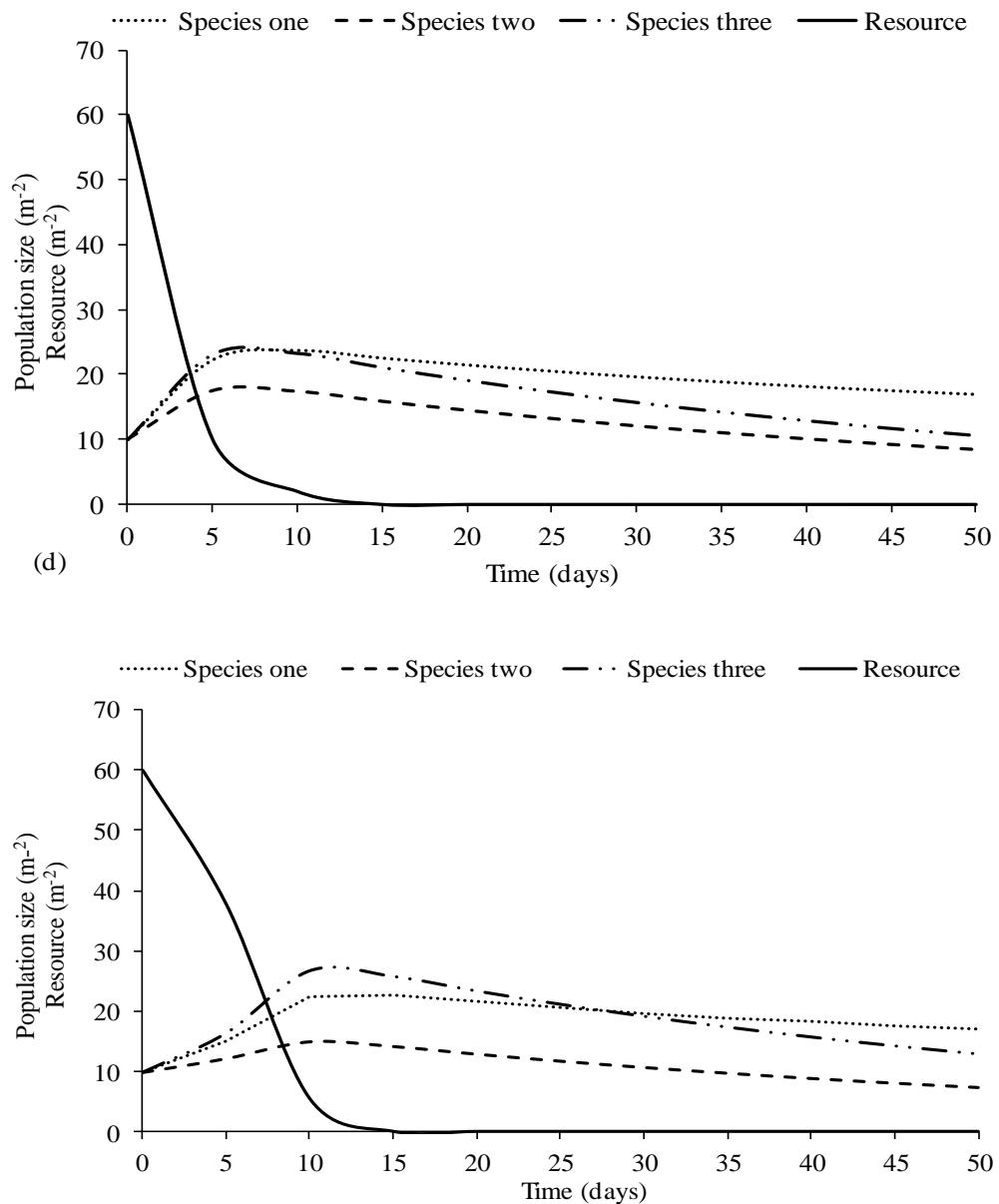
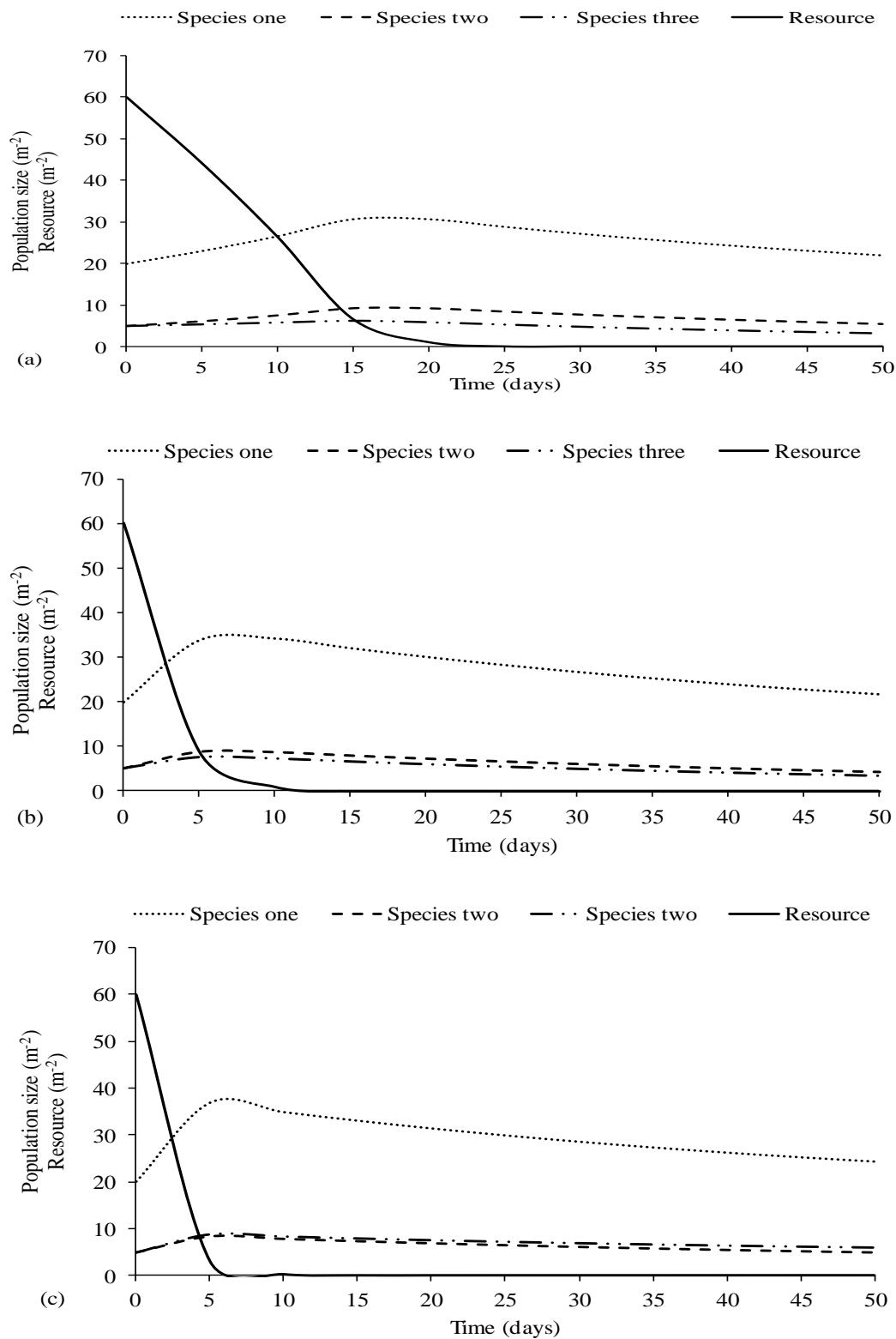


Figure 5.5: Behavior of the isolines for three species competing for a single resource when both species initial population size are the same; curves (a)-(e) show the behavior of population size for each resource at temperature 10°C , 15°C , 20°C , 25°C and 30°C respectively. Solid lines represent the resource; species one is represented with round dot lines; species two is represented with dash lines and species three is represented with long dash dot dot lines and all species have different growth rate.



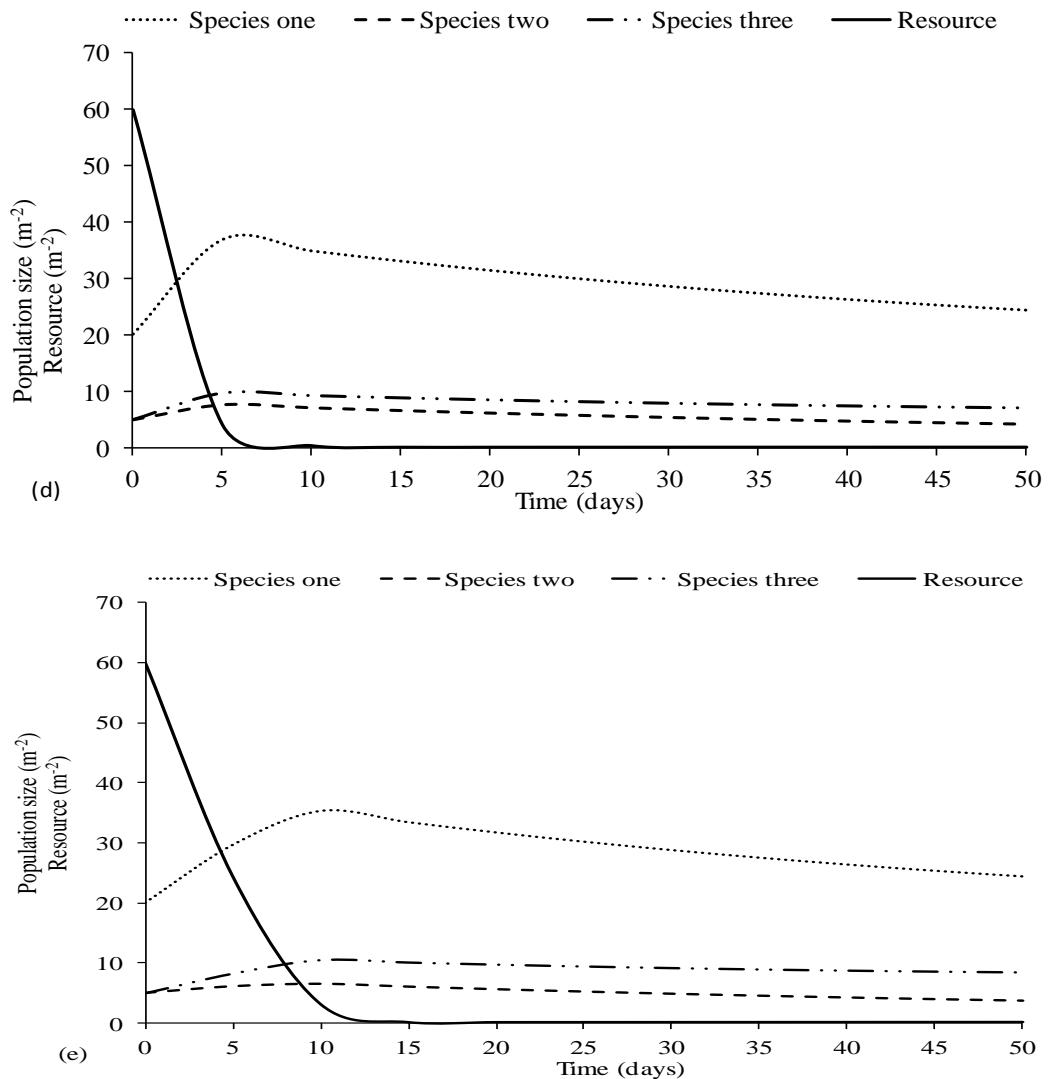
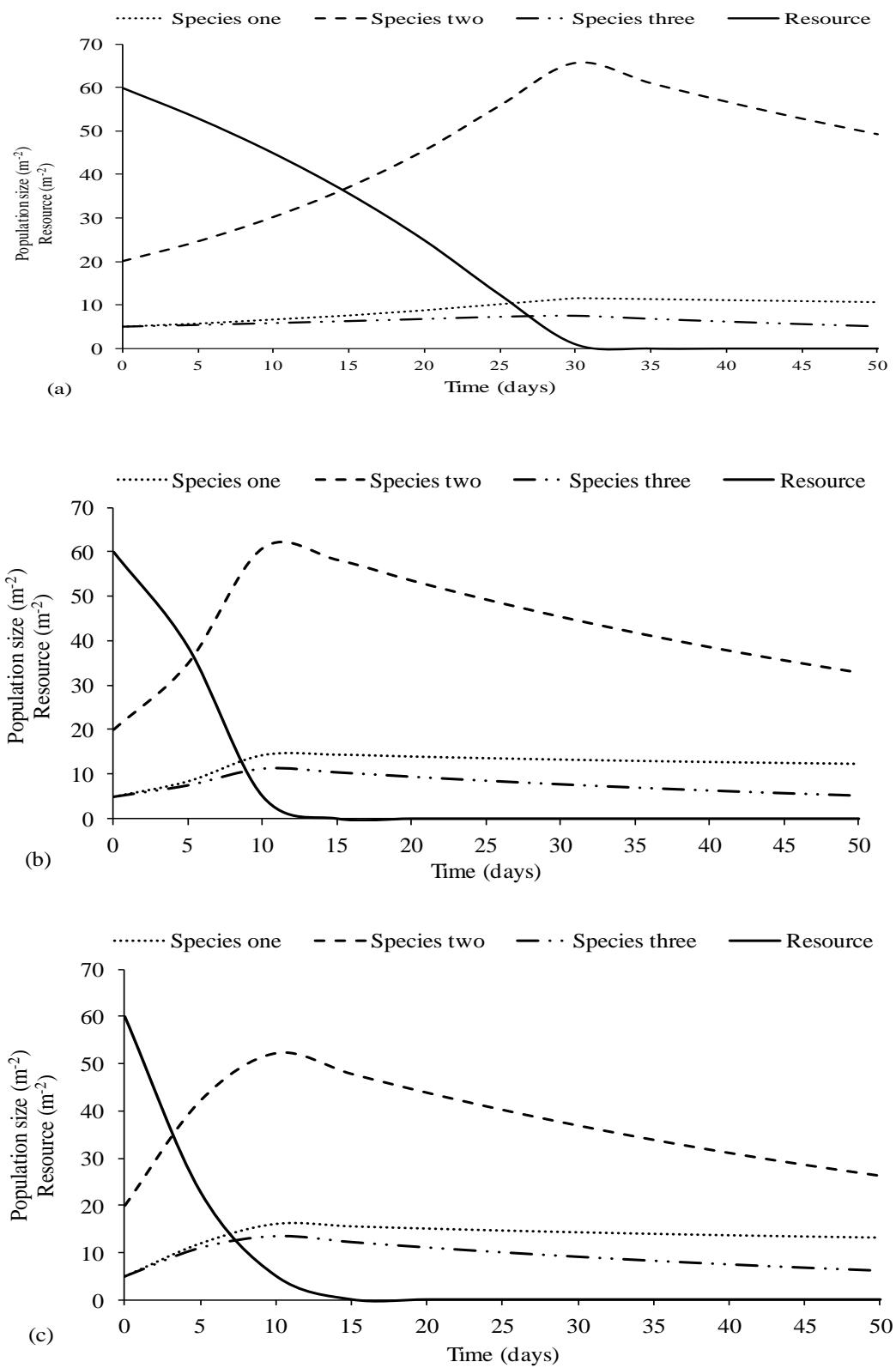


Figure 5.6: Behavior of the isoclines when initial population size of species one is greater than species two and three; curves (a)-(e) show the behavior of population size for each species and resource at temperatures 10°C , 15°C , 20°C , 25°C and 30°C respectively.



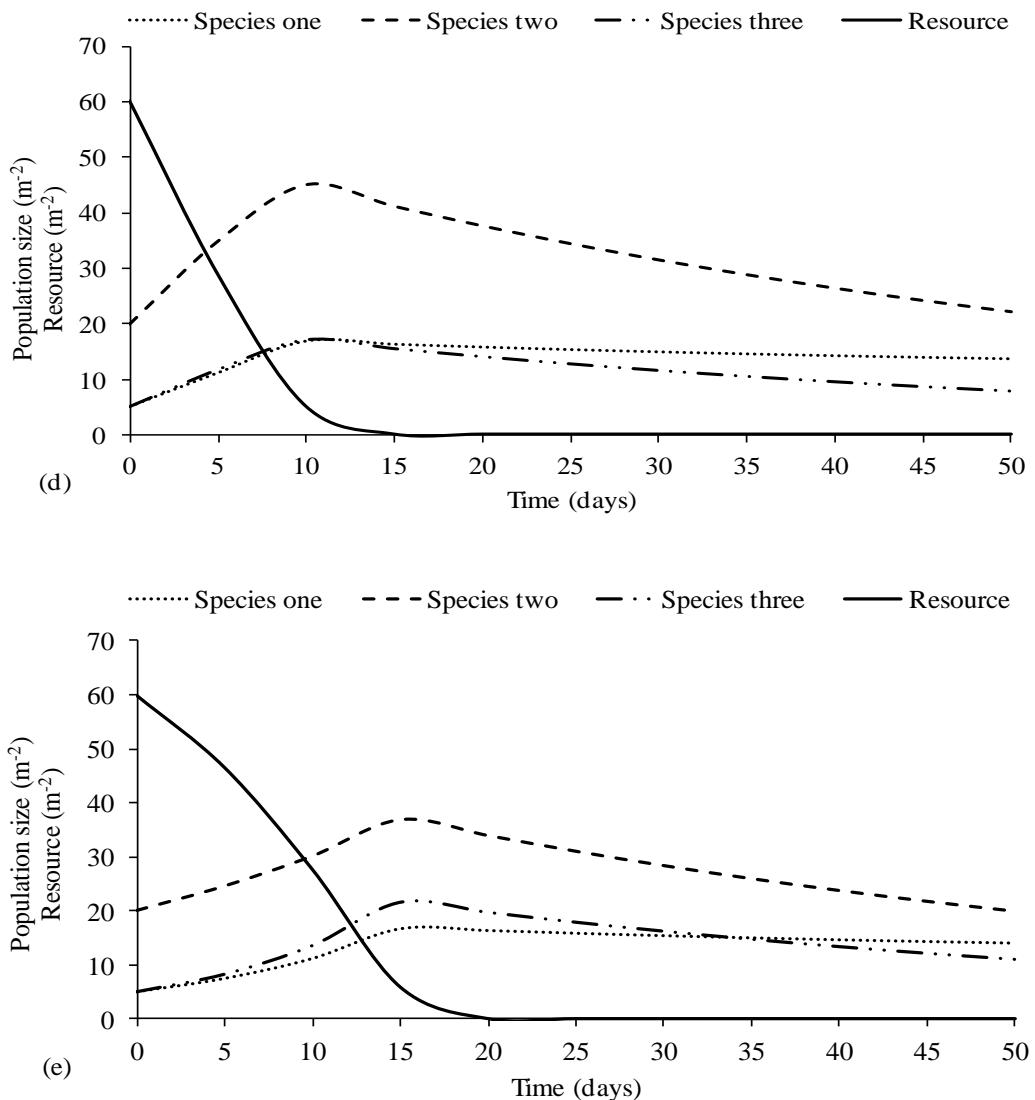
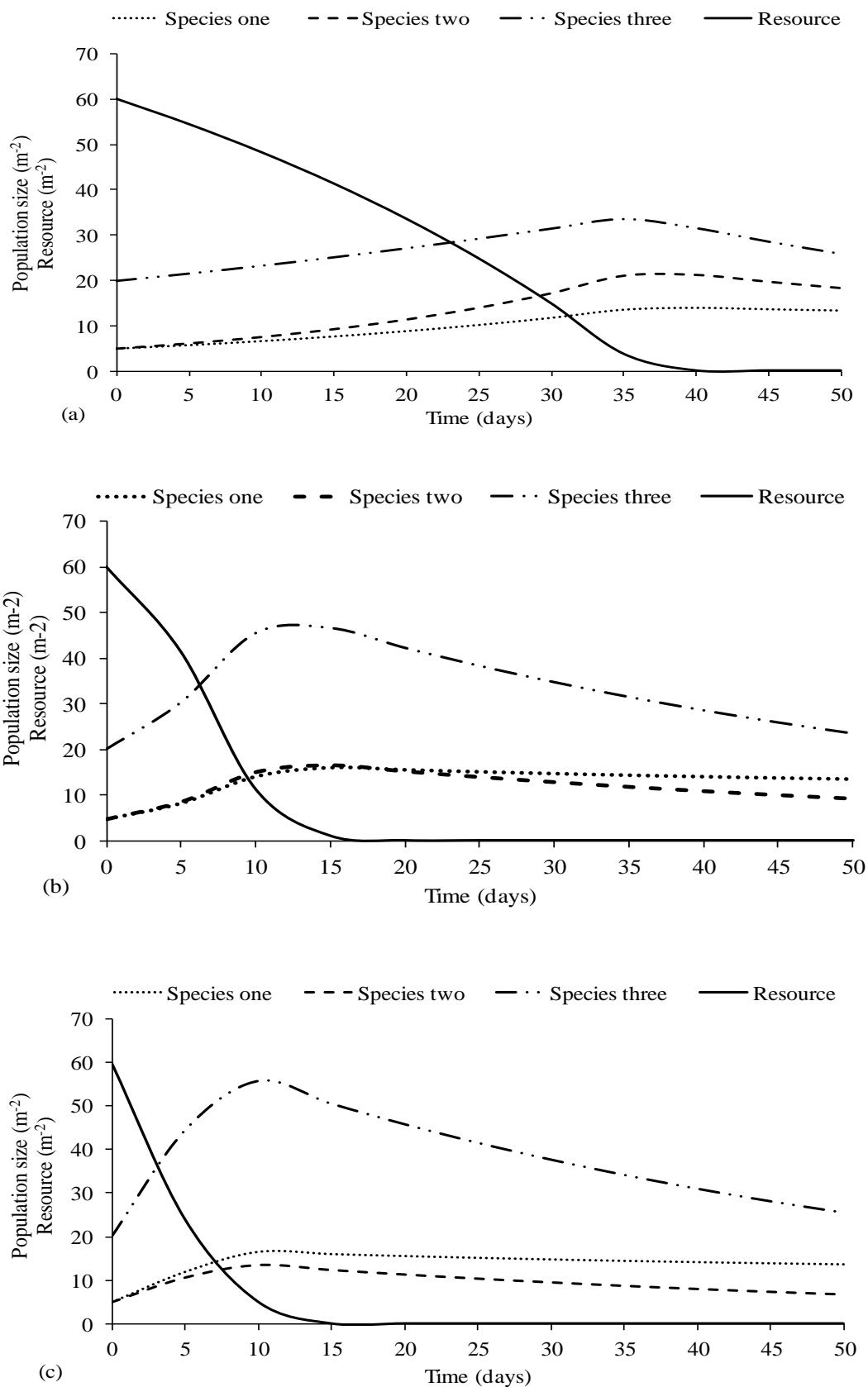


Figure 5.7: Behavior of the isolines when the population size of species two is greater than of species one and three; curves (a)-(e) show the behavior of population size for each species and resource at temperatures 10°C , 15°C , 20°C , 25°C and 30°C respectively.



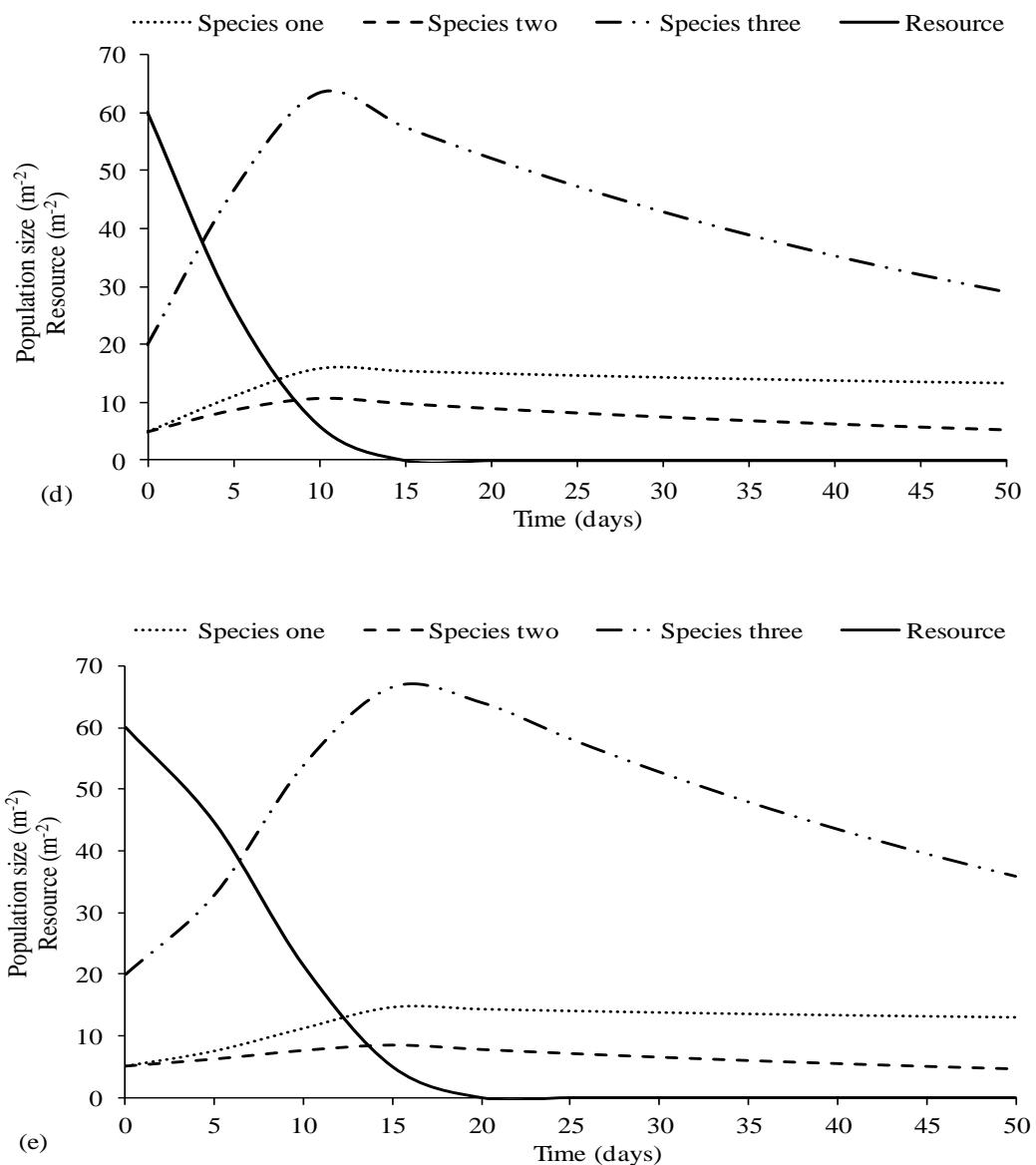
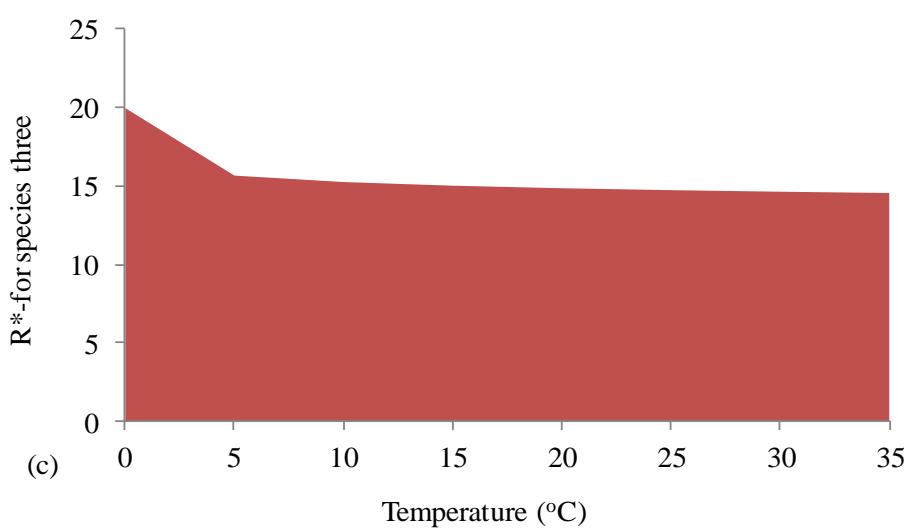
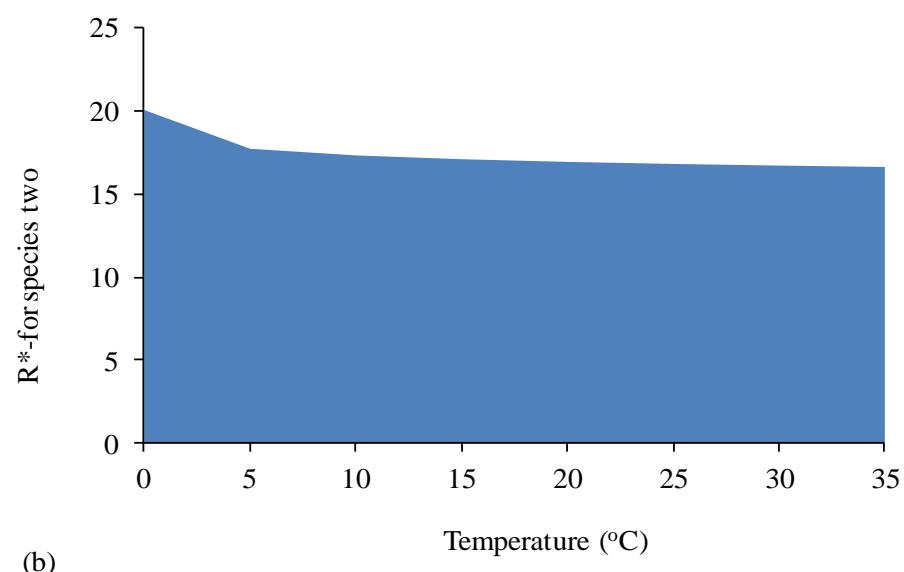
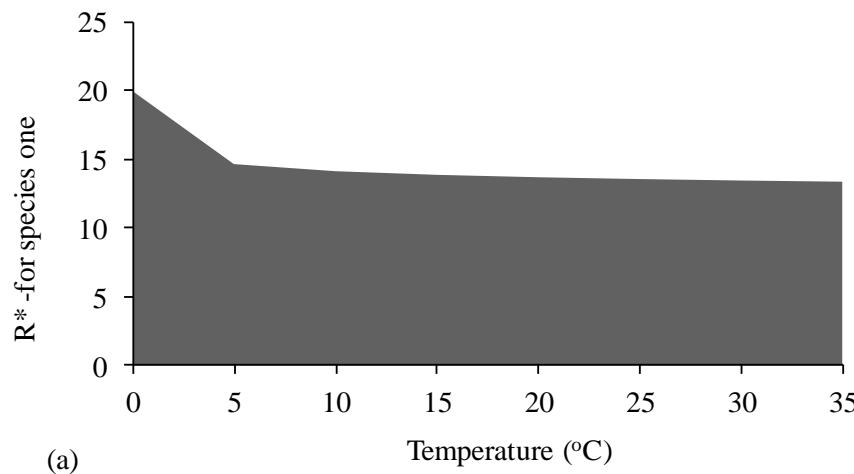


Figure 5.8: Behavior of the isolines when the population size of species three is greater than species two and one; curves (a)-(e) shows the behavior of population size for each species and the resource at temperatures 10°C , 15°C , 20°C , 25°C and 30°C respectively.



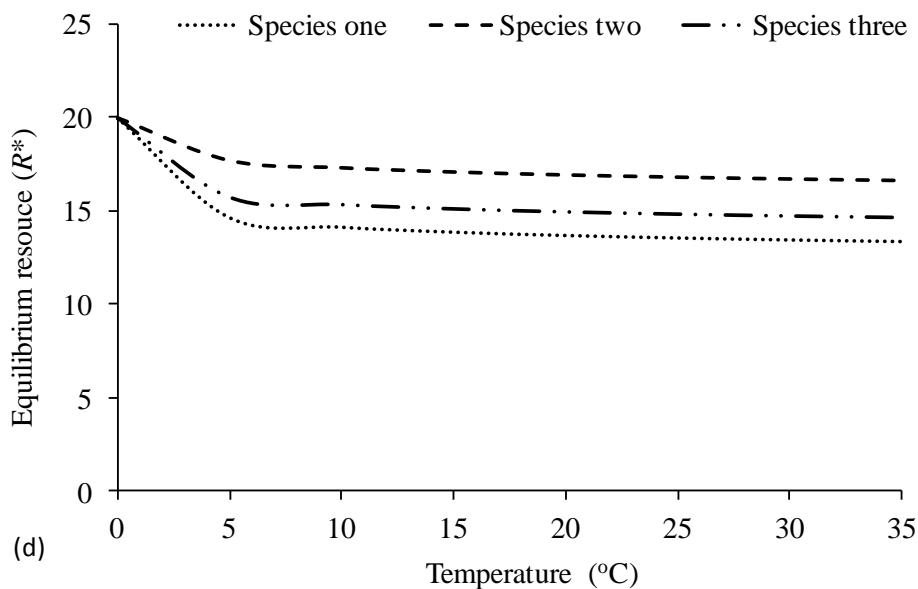


Figure 5.9: Temperature and equilibrium resource isoclines; curves (a)-(c) represent equilibrium boundaries of each species based on the requirements of equilibrium resource, in the unshaded region show population size of the species would increase and shaded region it would decreases, and in (d), illustrates three species are superimposed.

5.8 Discussion

Qualitative analysis of the effects of resource and temperature on competition between insect species was conducted. For this purpose, temperature dependent system of differential equations was formulated. Both qualitative and numerical analyses of the models were considered. In respect to each model, the axial, planar and interior equilibrium points were obtained and their stabilities were investigated. Conditions on the parameters that ensure the stability and instability of the boundary equilibrium points were presented. For a single species interacting with the resource, the local stability analyses revealed that the species could maintain a stable population when growing alone under all conditions used in the analysis. It was illustrated that as the population size of

the species grows, the resource depletes to the level of equilibrium of the resource availability where the population size of the species stop growing. Numerical simulation also revealed that the dynamical outcomes of the interactions are very sensitive to the model parameter values and to the initial population size of the species. In axial equilibrium point, it was observed that if the value of the equilibrium of the resource availability is to larger than the supply point of the resource, the population of the species cannot persist. In one hand, this is due to the fact that the resource availability directly depends on the rate of resource supply. On the other hand, if the supply of the resource is sufficiently large, the species can establish a stable population and equally control the resource to the equilibrium of the resource availability.

Generally, the obtained results highlight an essential assumption of the resource competition theory, which, suggested that when several species compete for the same resource, the species with the lowest requirement for the resource is the superior competitor at equilibrium (O'brien 1974). This species competitively displaces all its counterparts, independent of the initial size of the population for other competing species. This means that at the equilibrium points, in a habitat with a single limiting resource, the best competitor is the species that has the lowest equilibrium resource value (R_i^*). It implies that a given species i is able to continue growing as long as the resource is greater than the lowest equilibrium resource value ($R > R_i^*$). Reciprocally, species i can go to local extinction if the resource is less than the lowest equilibrium resource ($R < R_i^*$). For these values of R , the resource-dependent growth rates of the species is less than their mortality rates, and all species will experience negative exponential decline towards the

equilibrium point. These results are in agreement with findings reported by Tilman (1977).

From the formulated models, it was observed that the relationships between the available resource and resulting population size are nonlinear. This makes the analysis of the developed mathematical equations in varying temperature difficult. Therefore, this present study opted to conduct the analysis at fixed temperatures then generalize by intervals (Levins 1979, Chesson 1994, Hsu and Waltman 1998, Hsu *et al.* 2000). The study of insect physiology has demonstrated that each species has different optimum temperature that affects its competitive ability for resource exploitation (Grover 1997). To predict the outcome of competition between insect species within a range of temperatures, superimposition of the zero net growth isolines of the species, results in one species has an equilibrium resource significantly lower than its counterparts.

Furthermore, in a competing situation are observed that three parameters, half-saturation constant, growth rate and the mortality rate which determine which species wins for any given resource. The species with a high affinity for the resource can still lose if it has low growth rate and a high death rate. This relationship is simple as it demonstrates that resource-based models bring more understanding than the classical theory in ecology for species resource competition (Martines *et al.* 2009). Moreover, the use of resource-based models emphasizes the role of resource in determining competitive interactions and the abilities of each species to acquire and use the limiting resource. Classical models of competition (Zaghrouat and Kandil 1998) are useful tools for understanding insect population growth; whereas, resource-based models create direct link between the species and the resource. These types of models are more predictive.

Further still, experimental or field investigation in this direction may be helpful to verify whether or not the process prescribed by the formulated models actually function in a similar manner under practical consideration. For example should verify the accuracy of formulated models on the maize-lepidopteran stem borer pests system. In fact, maize is one of the most important staple food crops in most sub-Saharan Africa (Smale *et al.* 2001). In spite of its importance, maize production is constrained by lepidopteran stem borer pests, the most damaging being the crambid *Chilo partellus* (Swinhoe) and the noctuids *Busseola fusca* (Fuller) (Kfir *et al.* 2002), more and in-depth research is needed on its predominant insect pests at different optimal temperatures, to guide the formulation of appropriate adaptation strategies to the current climate change (James and Washington 2013). Therefore, these models can be a useful tool to test how temperature can affect the competition between these insect pests, their future distribution and incidence on maize production.

5.9 Chapter summary

In this chapter, the models explored the effects of resource and temperatures on competition between insect species were proposed and analysed qualitatively using stability theory. A local study of the models is performed around trivial, axial, planar and interior equilibrium points to successively estimate the effect of: i) one species interacting with a resource, ii) two species competing for a single resource, and iii) three species competing for a single resource. The local stability analysis of the equilibrium is discussed using Routh-Hurwitz criteria. Numerical simulation of the models is performed to investigate the sensitivity of certain key parameters. The models are used to predict population dynamics in the selected cases studied. The results show that when

a single species interact with a resource, the species will be able to establish and sustain a stable population. However, in a competing situation it is observed that the combinations of three parameters (half-saturation, growth rate and mortality rate) determine which species wins for any given resource. The results indicate that each species is the superior competitor for the resource for the range of temperature for which it has the lowest equilibrium resource.

In conclusion, the present study qualitatively analysed a series of mathematical equations to demonstrate competition of insect species feeding on one resource. Therefore, it would be interesting to conduct further quantitative and qualitative studies for all kind of insect communities with different feeding behaviours (boring insects, chewing insects, phloem-feeding insects) competing for one resource for possible improvement of integrated pest management strategies. Furthermore, many questions remain open including applying or improving the model and obtaining the results when the resource and insect species are in different stages (neonates and old instars larvae). Thus, purely observational methods may give an indication of whether competition is occurring, particularly if time-series data are used.

CHAPTER SIX

MODELLING POTENTIAL DISTRIBUTIONS OF MAIZE STEM BORERS WITH ENVIRONMENTAL VARIABLES

6.1 Introduction

Understanding the factor-driven influence on the geographic distribution of insect species is a fundamental issue in ecological systems (Blach-Overgaard *et al.* 2010). Despite decades of study, comprehensive thought of which factors control range limit for the distribution of any species is not well documented (Gaston 2009). Climate, in particular temperature, is often considered to be the predominant a range-limiting factor determining species distribution, especially at large scale (Bale *et al.* 2002, Hodkinson 2005, Deutsch *et al.* 2008, Tylianakis *et al.* 2008, Garibaldi *et al.* 2011, Khadioli *et al.* 2014). There are good examples of direct effects of temperature on insect geographic distribution (Cescatti and Battisti 1992, Battisti *et al.* 2005). The effect of temperature in altitudinal gradient, however, cannot be considered in isolation from other factors that also change with altitude (Bale *et al.* 2002). Apart from the temperature, other environmental parameters like precipitation, relative humidity and soil characteristics are useful in explaining and understanding the insect geographical distribution (Setamou *et al.* 1993, Bale *et al.* 2002, Hodkinson 2005).

Precipitation is one of the key environmental variables responsible for insect distribution and diversity, by its direct influence on host-plant (Hodkinson 2005). Orographic precipitation, like snow or rain, often rises with elevation (Egger and Hoinka 1992, Körner 2007). Although rainfall and relative humidity fluctuation are linked to the season, these fluctuations appear less predictable annually than before due to climate

change. Most tropical regions experience alternating wetter and drier seasons that vary greatly in seasonal timing and overall duration due to unreliable rainfall; this also can influence insect indirectly by changes in host plant metabolism and physiology (Netherer and Schopf 2010). Thus, the phytophagous insects exhibit mechanisms of escape in space and time that allow them to synchronize their reproduction efforts with suitable wet periods of the year. Furthermore, some insects are sensitive to rainfall and are either removed or killed from crop by heavy rains.

Soil characteristic, in particular soil element nutrients have been found to play an important role in determining the distribution of insect pests (Allsopp *et al.* 1993, Setamou *et al.* 1993, 2005, Ndemah *et al.* 2006). For instance, Silicon (Si) is the second most abundant element on the earth and it is now well admitted to be a beneficial soil element for plant growth, characterized by helping the plant to overcome various stresses including biotic and abiotic stress (Epstein 1999, Richmond and Sussman 2003, Ma 2004, Ma and Yamaji 2006). This element is very important to consider for grasses. Grasses usually contain much lower concentrations of secondary metabolites than dicotyledons (Elger *et al.* 2009), suggesting that grasses depend on other defences to fight off herbivores (Grime *et al.* 1996). Silicon based defences in containing herbivores and pathogens are well established as the main physical defences employed by grasses (Massey and Hartley 2006, Reynolds *et al.* 2009). For instance, Si mediates plant resistance against insect herbivores via Si mechanical barrier (Ma 2004, Kvedaras and Keeping 2007, Kvedaras *et al.* 2009). This has been shown to disturb significantly, the larval performance of Lepidoptera stem borers such as *Sesamia calamistis* (Lepidoptera, Noctuidae) and *Eldana sacharina* (Lepidoptera, Pyralidae), important pests of maize in West Africa and sugarcane in South Africa, respectively (Setamou *et al.* 1993, Keeping

and Meyer 2006, Kvedaras and Keeping 2007) by an increase in leaf abrasion, which subsequently increases wear on insect mandibles and may physically deter larval feeding (Keeping *et al.* 2009, Kvedaras *et al.* 2009).

In contrast, some other soil components such as plant nutrients have been found to improve not only the plant growth but also the development of their herbivores living on them (Mattso 1980). For example, surveys in farmer's fields in West Africa showed a positive relationship between soil nitrogen and stemborer densities (Sétamou and Schulthess 1995). Previous laboratory studies showed that nitrogen application increased survival, growth rates, and fecundity of *S. calamistis* (Sétamou *et al.* 1993). The studies concluded that a greater use of nitrogen fertilizer in order to increase maize yields could also increase borer populations and aggravate the pest problem especially during the second planting season. Moreover, increased plants nutritional status leads to a concomitant increase in borer attacks during early stages of plant growth, but it also improved plant vigour, resulting finally in a net benefit in the form of increased grain yield (Chabi-Olaye *et al.* 2005). However, some other plant nutrients have negative effects on the herbivorous insects. For instance, Soil potassium has a negative relationship with *B. fusca* densities, suggesting a potential detrimental effect of potassium on *B. fusca* development (Ndemah *et al.* 1999).

The temperature-driven phenology models for maize stem borers, that include a set of functions describing temperature-dependency to determine the pest life history, has been developed (Khadioli *et al.* 2014a, b) and used to predict *C. partellus*, and *B. fusca* distribution and abundance in East African mountains (Mwalusepo *et al.* 2015). In addition, risk mapping tools have been shown to be useful for predictions on regional and

local scales (Khadioli *et al.* 2014a, b, Mwalusepo *et al.* 2015). However, there is still lack of information for predictions of maize stem borers with other environmental variables. Although soil factors have been recognized for their importance, they are poorly used as input in environmental niche modeling (Guisan and Zimmermann 2000, Coudun *et al.* 2006), particularly for small areas, due to the high cost and long duration of fieldwork required to obtain relevant data.

The hypothesis in this chapter is that the potential distribution of maize stem borers depends not only on temperature but also on other environmental variables along East African mountain gradients. Therefore, this chapter aimed to estimate the impact of environmental variables on potential distribution of *Chilo partellus* and *Busseola fusca* at local scale along East Africa mountain gradients.

6.2 Material and Methods

The insect species data occurrence used are from field surveys collection (described in chapter three, section 3.3). As an example, in this chapter, two species were considered namely: *C. partellus*, which is the dominant species at the low altitudes and *B. fusca*, which is the dominant species at high and middle altitudes (Mwalusepo *et al.* 2015). These species were recorded at six localities per transect as shown in figures 3.1 and 3.2. The environmental variables and models used are described in sections 3.4 to 3.7. The dataset contains a set of geographical coordinates of recorded presence for each species, and the analysis of this chapter was done by using thin plate and maxent methods as described in sections 3.5 to 3.9.

6.3 Results

6.3.1 Validation of interpolated data

Figure 6.1 shows the results between the interpolation values and actual values. The model predicted and observed had significantly higher agreement ($R^2 = 77\%$, RMSE = 1.7 and RMSEr = 8%). According to these results, the algorithm used is good for interpolation of environmental variables.

6.3.2 Current distribution of *C. partellus* and *B. fusca* with environmental variables

The results revealed that the species distributions of *C. partellus* is more suitable at low altitude on both Mount Kilimanjaro and Taita hills (Figure 6.2), while the least suitable conditions are at higher altitude, in contrast *B. fusca* are does better at higher altitudes and less successful at lower altitudes, and the two species coexist at middle altitudes. Table 6.1 shows the environmental variables used in the model and their predictive percent contribution for each variable, which indicates their importances vary with study areas. Jackknife test of variable importance showed that water holding capacity was the most important predictors (59.4%), of distribution and the least contributor was phosphorus with 0% contribution for *C. partellus*. For *B. fusca* the most contributors are temperature (57.1%) and soil silicon, phosphorus, and the water holding capacity are less important contributor with 0% on Mount Kilimanjaro. Whilst in Taita hills, relative humidity had the highest predictive contribution of 50.2% and potassium the least with 0.1% for *C. partellus*, temperature was the best predictor of *B. fusca* (48.9%) and soil silicon was the poor predictor at 0%.

The marginal response curves show the probabilities of species presence on Mount Kilimanjaro and Taita hills, respectively (Figures 6.3 and 6.4). These curves show how

the logistic prediction changes with environmental variables. *C. partellus* showed a positive response to increase of temperature, soil silicon, potassium, and phosphorus (Figures 6.3 and 6.4), this results indicate that probability of presence of *C. partellus* increase linearly as these variables increase, and negative response to increase in rainfall, relative humidity, water holding capacity, and nitrogen on both Mount Kilimanjaro and Taita hills (Figures 6.3 and 6.4). The response curves for temperature (Figure 6.3a) shows the highest probability of *C. partellus* range between 20 and 24°C. In contrast, *B. fusca* response negatively as temperature increases (Figure 6.3a).

The area under the curve (AUC) measures provided highly consistent estimate of models performance (Table 6.2). The AUC values for independent test data varied markedly across the study areas, for examples, *C. partellus*, the AUC scores were generally high when all environmental variables are included in the model (mean values of 0.75) on Mount Kilimanjaro and mostly poor for potassium (means value of 0.54 and 0.51 on Mount Kilimanjaro and Taita hills respectively (Table 6.2). There was no significant difference between the temperature model with rainfall, soil silicon, relative humidity, water holding capacity, nitrogen, phosphorus, climatic predictors (temperature + rainfall + relative humidity), and the more complex environmental models (temperature + rainfall + relative humidity + soil silicon + potassium + water holding capacity + nitrogen + phosphorus) in Taita hills (Table 6.2). For *B. fusca* the AUC was 0.86 on both Mount Kilimanjaro and Taita hills when all the environmental variables are included (Table 6.2). The model predictions and observed species presence had significantly positive relationship ion both Mount Kilimanjaro and Taita hills ($E = 0.99$ and $E = 0.56$, respectively) for *C. partellus* (Figures 6.5a, c) and of *B. fusca* had negative relationship in Mount Kilimanjaro transects (Figure 6.5 b).

Table 6.1: Environmental variables and their percent contribution for *Chilo partellus* and *Busseola fusca* species in Taita hills and Mount Kilimanjaro

Variable	<i>Chilo partellus</i>		<i>Busseola fusca</i>	
	Mount Kilimanjaro	Taita hills	Mount Kilimanjaro	Taita hills
Temperature	6.5	0.6	57.1	38.7
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 6.2: Comparisons of the predictive ability among species distributions models based on different sets of predictors in both transects, and the Area under the receiver operating curve (AUC) was to estimate of models performance.

	<i>Chilo partellus</i>		<i>Busseola fusca</i>	
	Mount Kilimanjaro	Taita hills	Mount Kilimanjaro	Taita hills
Model (M)	AUC	AUC	AUC	AUC
M3.9 (<i>T</i>)	0.55	0.60	0.78	0.75
M3.10 (<i>R</i>)	0.57	0.57	0.73	0.74
M3.11(<i>Rh</i>)	0.69	0.66	0.68	0.68
M3.12 (<i>Si</i>)	0.66	0.65	0.60	0.73
M3.13(<i>N</i>)	0.67	0.66	0.79	0.69
M3.14(<i>WHc</i>)	0.69	0.61	0.50	0.71
M3.15(<i>K</i>)	0.54	0.51	0.75	0.76
M3.16(<i>P</i>)	0.69	0.61	0.54	0.76
M3.17(<i>T,R,Rh</i>)	0.71	0.65	0.79	0.79
M3.18 (All)	0.75	0.65	0.86	0.86

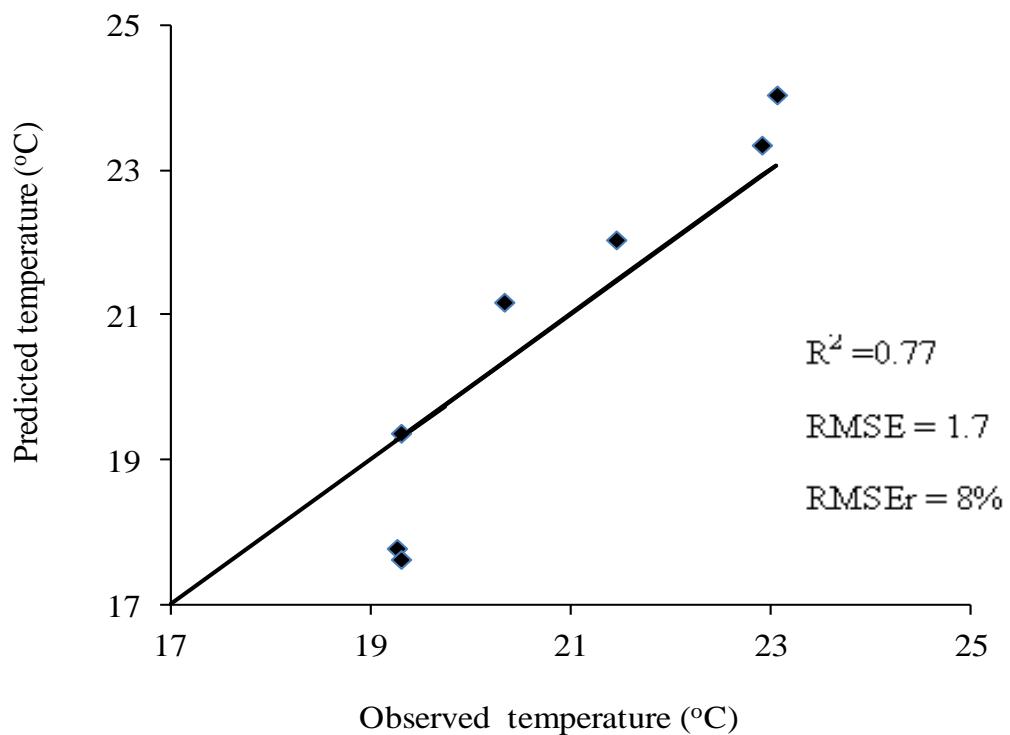


Figure 6.1: Relationship between observed and predicted temperature by thin plate spline algorithm in Taita hills.

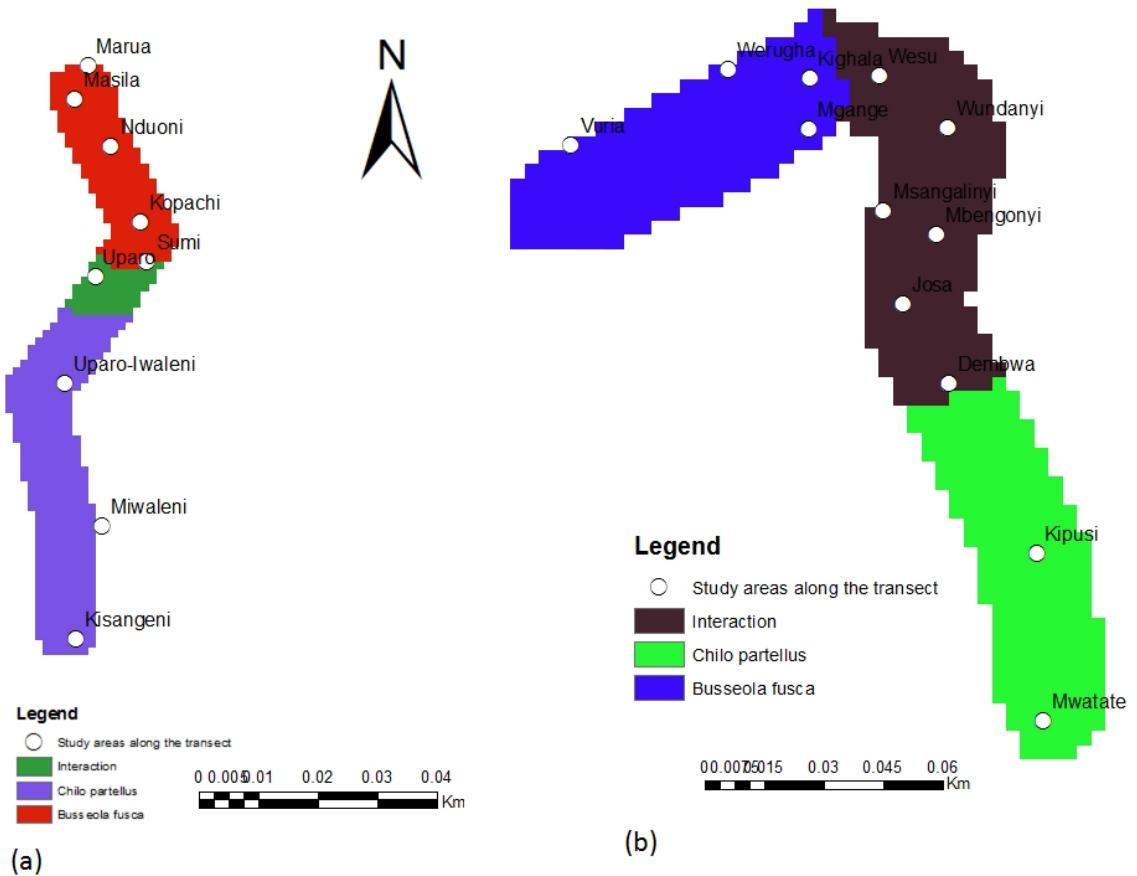


Figure 6.2: Predicted potential geographical distribution for *Busseola fusca* and *Chilo partellus* made using all occurrences record and environmental variables. The results are given (a) for Mount Kilimanjaro (left) and (b) for Taita hills (right). Three colors are used to indicate suitability for one species only and where suitable for both species.

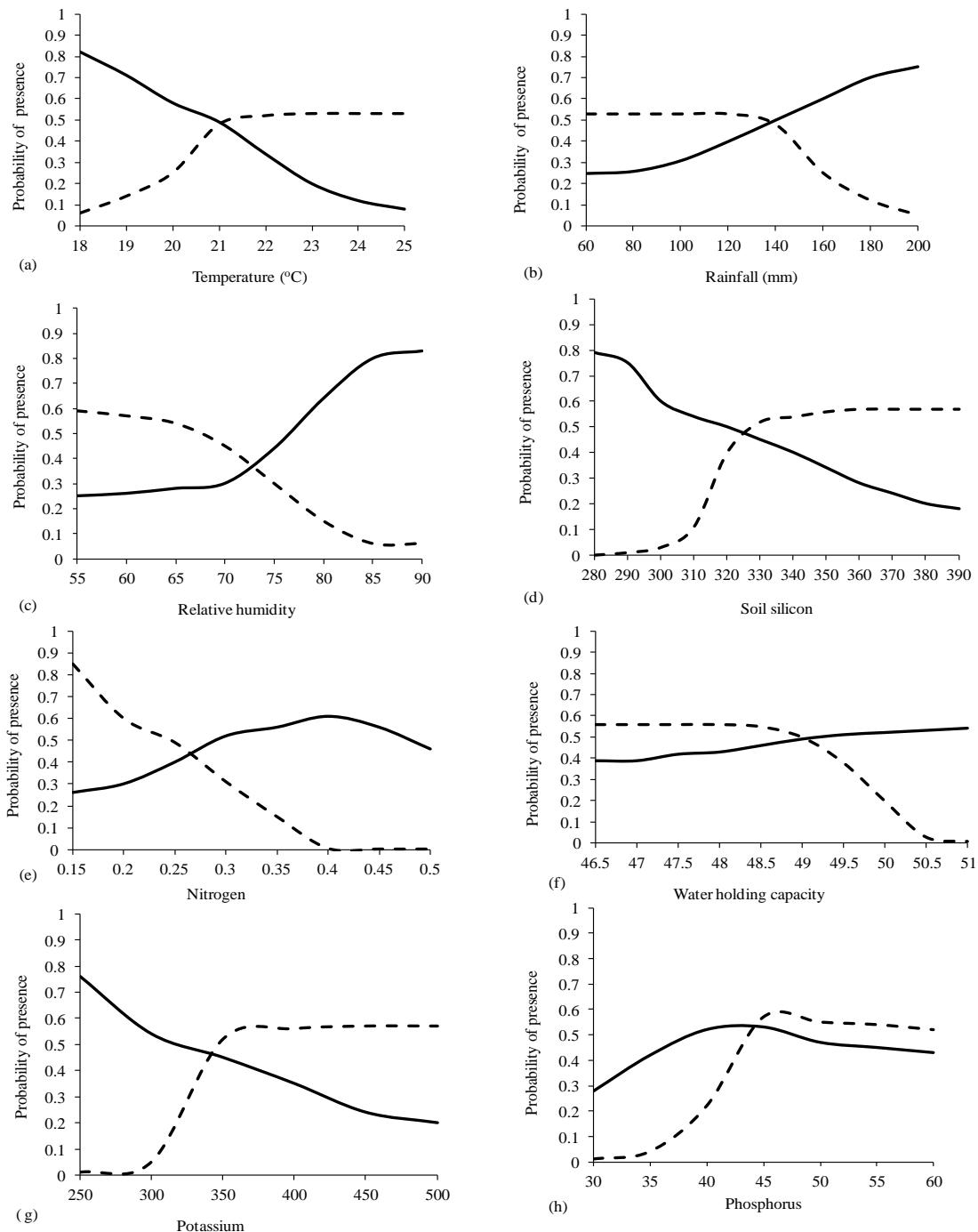


Figure 6.3: Response curves illustrating relationship of probability of presence to environmental variable in Mount Kilimanjaro transects. The dotted line represents *Chilo partellus* and solid line represents *Busseola fusca*.

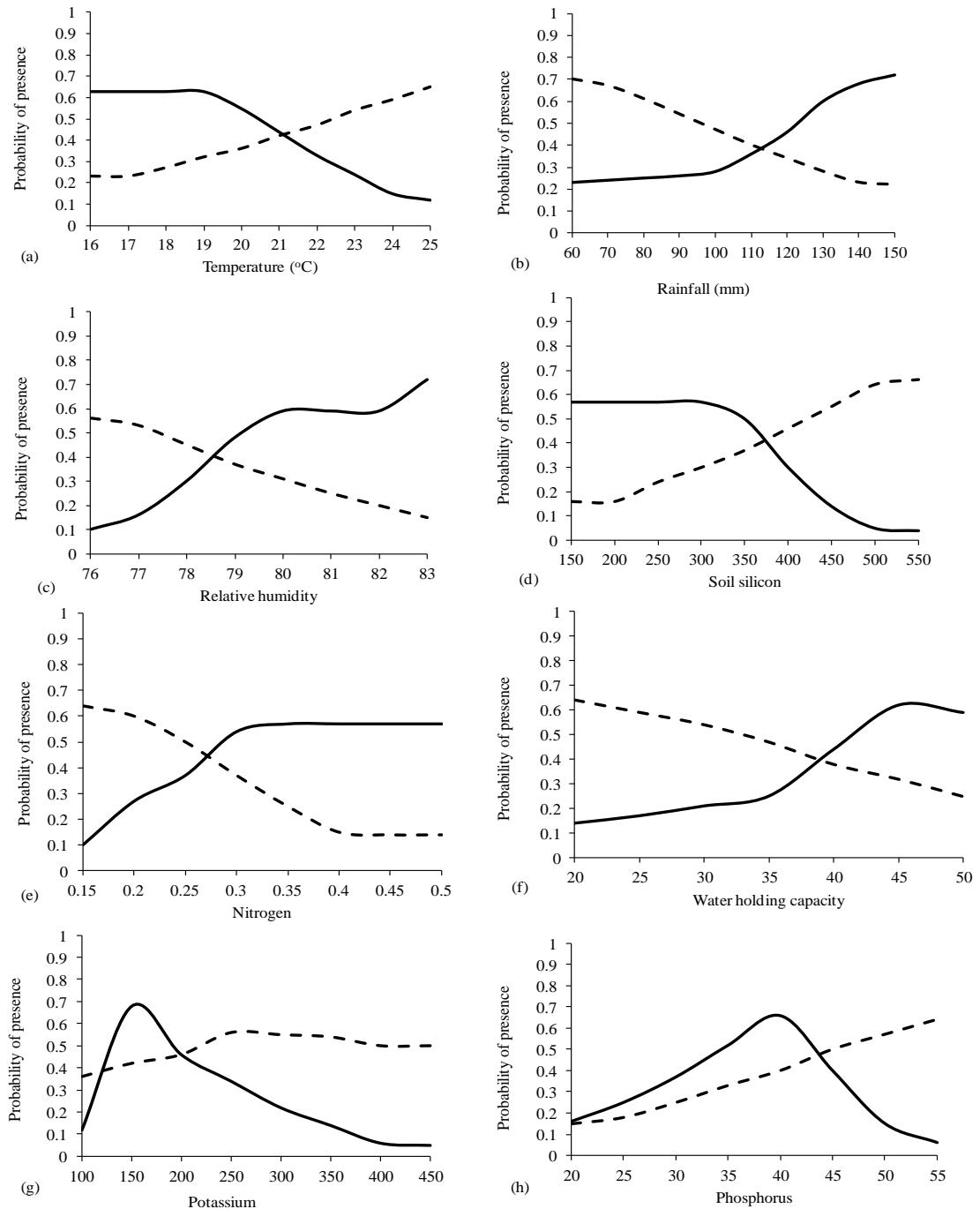


Figure 6.4: Response curves illustrating relationship of probability of presence of the species to environmental variable in Taita hills transects. The dotted line represents *Chilo partellus* and solid line represents *Busseola fusca*.

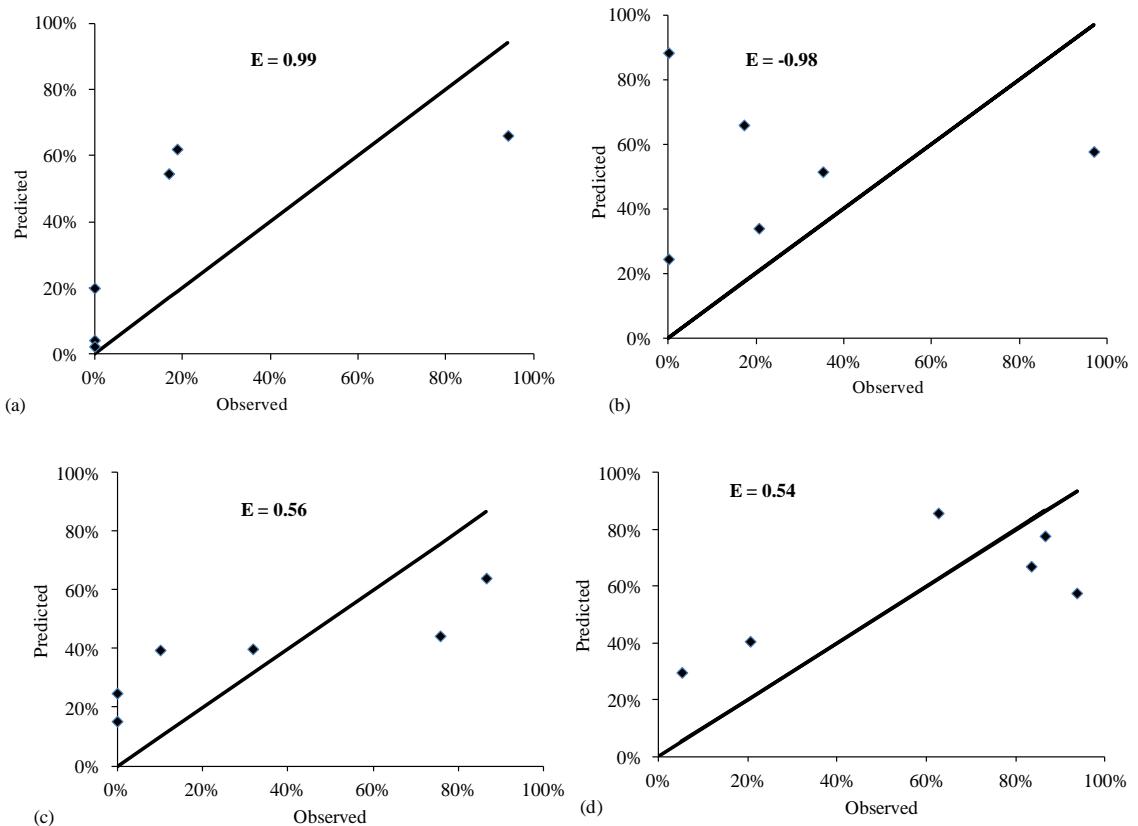


Figure 6.5: Relationship between observed and predicted for species distribution when all environmental variable are included; Mount Kilimanjaro transect: (a) *Chilo partellus*; (b) *Busseola fusca*; Taita hills transect, (c) *Chilo partellus* and (d) *Busseola fusca*.

6.4 Discussion

In this chapter, the potential distribution of maize stem borers with environmental variables along East Africa, Mountain gradients were conducted. The study was based on known species occurrence records with suites of environmental variables that can reasonably be expected to affect the species physiology and probability persistence. The inductive approach modelling was employed through maximum entropy distribution modelling to assess which factor most influence insect pest's distribution. The results revealed that both environmental factors were important in influencing the geographical distribution of *C. partellus* and *B. fusca* across the study areas. These results agree with Sithole *et al.* (1989) who argued that other environmental factors such as rainfall and relative humidity affect *C. partellus* distribution. Similar studies by Abraham *et al.* (1972), found that there was combined contribution of climatic factors on the stem borer infestation. In contrast, with Bohf *et al.* (2000) observed that significantly small larvae had disappeared from exposed plant to rainfall than from protected plant. In addition, Lowe (1970) described that lack of rain may cause larva dessication, and heavy rain and floods may wash the larvae from the plants. Conversely, these findings contrast with the present study, where *B. fusca* survived better at the higher rainfall. Similar results by Gupta (1959) reported that high rainfall is also regarded as a contributory factor for greater multiplication of the stem borers. In other studies, precipitations have been found to be most important in determining the distribution of white coffee stem borer (Kutywayo *et al.* 2013). Moreover, the stem borer lifecycle can last up to 50 days; hence the biotic factors that are related to its distribution have to be conducive for maize stem borers. In light of this, the seasonality of rainfall becomes important as it determines the variation of the supportive environment of the pest over a longer time period. This could

be a reflection of changing climatic conditions or differing farming practices, which create additional suitable conditions for these species. Temperature was not important in determining *C. partellus* distributioninalong along both Mount Kilimanjaro and Taita hills transects when all environmental variables are combined. Interestingly, previous studies found that temperature variability is the most important factor for the distribution of other important pests of maize such as stem borers (Khadioli *et al.* 2014, Mwalusepo *et al.* 2015). This is likely due to the fact that the studies considered only one environmental variable in their predictions. In contrast, for *B. fusca*, this study found that temperature contributes significantly in potential distribution. These results agree withthe a priori notion that temperature is the main environmental factor (Khadioli *et al.* 2014, Mwalusepo *et al.* 2015). The areas highly suitable for stem borer obtained from this study do not necessarily translate into a measure of field infestation. In addition, to the biotic factors used in this study, multiple other physical and socio-economic factors determine stem borer incidence and infestation.

Additionally, the results confirm that soil characteristics play important roles in species distribution. The soil nutrient status is an indicator of host plant quality, which plays an important role in the population dynamics of many herbivores (Sarwar 2011). The study by Ali *et al.* (2006) shows that increasing nitrogen increases the number of borers, while plant damage decreased, resulting in higher maize yields. Through correlation studies (Setamou *et al.* 1995, Chabi-Olaye *et al.* 2005) concluded that increasing nitrogen not only increases maize yields but also pest infestation. Furthermore, a study by Jiang and Schulthess (2005) indicated that nitrogen can also increase the performance of the parasitoids. In contrast, Archer *et al.* (1987) reported that some other plant nutrients have negative effects on the herbivorous insects such as phosphorus. Further still, most

attention has been paid to the relationship between potassium content in host plant and change in performances of herbivores. Tiwari (2002) reported that potassium improves rice plant tolerance to adverse climatic conditions, lodging and insect pests. Further, noted that although potassium is one of the major plant nutrients underpinning crop yield and quality, the use of potassium for pest suppression has not been so popular among farmers. Slansky and Scriber (1985) studies had indicated that the amount, rate and quality of food consumed by immature herbivores influenced their fitness, growth rate, developmental duration, final body weights, dispersal abilities and probabilities of survival, and influenced adults performance in mating success as well timing and extent of reproduction and disposal ability. However, potassium effects on pest population can be offset by other factors in the altitudinal gradient. These factors may include natural enemies, the health and defensive responses of the plant to insect herbivore (Hacker and Bertness 1995). The present study suggests that silicon, potassium and phosphorus application should be emphasized for high-yielding maize production. This could reduce the input of fertilizers, and decrease the application of pesticides due to lower occurrence of pests, reduce losses of yield and finally increase farmer's income to sustainable development of maize protection and production.

However, discrepancies exist between the degree to which these environmental variables contribute in potential distribution of stem borers; they nevertheless, provide a starting point for planning adaptation strategies to respond to the impact of future climate change, to minimize the negative impacts not only on the stem borers but also for other insect pests.

In conclusion, East African mountain gradients at local scale provide different ecological conditions with variation of biotic and abiotic ecological factors (CEPF 2012), they allow

determining response of insect pest to the environmental variables, the present prediction at local scale confirms results from studies at large scale (Setamou *et al.* 1993, Bale *et al.* 2002, Hodkinson 2005). It confirms that although many studies (Bale *et al.* 2002, Hodkinson 2005, Deutsch *et al.* 2008, Tylianakis *et al.* 2008, Garibaldi *et al.* 2011, Khadioli *et al.* 2014, Mwalusepo *et al.* 2015) demonstrated that temperatures is an important factor in distribution of insect pests, there are other environmental factors such rainfall, relative humidity, and soil characteristics that may affect the potential distribution of stem borers. Thus, the results obtained from this study could be useful in responding to climate change challenges especially in the agricultural sector in East Africa, which is projected to be the most vulnerable (Waithaka *et al.* 2013). Policy makers and managers might use the information to improve national pest management and quarantine measures, such as cultural, biological control, and host plant resistance. Finally, the presented and discussion in this chapter considered only environmental variables in current climatic conditions, however, future studies should also consider both climatic conditions and the effects of land cover change.

6.5 Chapter summary

Understanding of the factors that influence maize stem borers' distribution is crucial in predicting their response to future climate change. The fundamental hypothesis of the present chapter is that the potential distribution of maize stem borer depends not only on temperature but also on other environmental variables along East African mountain gradients. Potential species distribution was implemented by using maximum entropy application with three climatic variables and five soil factors. We evaluated the model accuracy by AUC values based on test data and training data. Results indicate that other

available environmental variables namely; rainfalls, relative humidity, and soil characteristics in both Mount Kilimanjaro and Taita hills transects are important in determining species range for *C. partellus* and *B. fusca* potential distribution. The study concludes that understanding how environmental variables potentially affect maize stem borer distribution will help to improve communication with the general public and design-makers, and develop adaptation mechanism to reduce maize yield losses and increase farmer's incomes, particularly for smallholders and substance farmers in the region.

CHAPTER SEVEN

SUMMARY, CONCLUSIONS AND RECOMMENDATIONS

7.1 Introduction

Food production must be increased in order to meet the needs of a growing population, projected to increase to over 9 billion by the year 2050 (UN 2013). During this time, climate is changing creating higher temperatures over most of the world and likely to increasing heat waves and drought, shifts in timing and distribution of rainfall, excess rainfall and flooding severity (IPCC 2014). It has been anticipated that the impacts of climate change will be greater in developing countries with predominant small land holders and subsistence farmers (Ito and Kurosaki 2009). Changes in climate and extreme events could have significant effects on agricultural pests and disease distribution and magnitude. These changes could thus have major impacts on crop production and food security in East African countries, and will be particularly profound for smallholder maize farmers, who depend on agriculture (Thornton *et al.* 2009b, Mwalusepo *et al.* 2015). These effects are occurring on top of rapid population growth, socio-economic problems, fast-paced unurbanization, land-use change and conflict. Yet none of the major assessments of the impact of climate change on food security included maize stem borers at local scale on maize crop, despite maize being one of the most important staple food crops in most of East African countries (Smale *et al.* 2001, Mwalusepo *et al.* 2015), maize is mainly cultivated by subsistence farmers for human consumption, but damage caused by maize stem borers is one of the most important constraints to maize production in region. Therefore, improved understanding on the influence of climate change on

agricultural production is needed to cope with expected changes in temperature, precipitation, and an increasing number of undernourished people due to food insecure.

The goal of this study was to explore the impact of climate change on maize stem borer communities and their main natural enemies along two altitudinal gradient localized on Mount Kilimanjaro (Tanzania) and Taita hills (Kenya). The specific objectives were: (1) To investigate the impact of temperature changes to the maize stem borers and their natural enemies along altitude gradient on the two mountains using temperature based phenology models; (2) To establish a resource based mathematical model which can determine the impacts of temperature changes on the insect communities and determine stability of the equilibrium points ; and (3) To model the impact of different factors (temperature, rainfall,relative humidity and soil characteristics) in predicting the potential distribution of maize stem borers at local scale in East Africa. All of the above objectives have been achieved in this study.

7.2 Summary

In chapter one, the significance of the theoretical investigation of the combined impact of climate change and maize borer species distribution on the maize crop production were highlighted. Relevant literatures were reviewed to buttress the significance of the investigation in chapter 2. This is followed by a general material and methods including the field survey data collection approach in chapter 3. Model problems were presented and tackled in chapter 4 to 6 and the results were graphically presented and dicussed. Chapter four presented the finding reporting the impact of temperature changes to the maize stem borers and their natural enemies along altitudinal gradients in two mountains of East Africa by using phenology modelling. The temperature-dependent phenology

models of *C. partellus*, *B. fusca*, *C. flavipes* and *C. sesamiae* were used in geographical information system for mapping. The three risk indices namely; establishment, generation, and activity index were computed using current temperature data record from local data logger and predicted future (year 2055) climatic conditions based on downscaled climate change data from AFRICLIM database. All the calculations were carried out using the index interpolator, a sub-module of Insect Life Cycle Modelling (ILCYM) software. The thin plate algorithm was used for interpolation of the indices. The results confirm that temperature is a key factor in explaining the distribution of stem borer pests and their natural enemies but to point the likely important role played by other climatic factors and the related top-down regulation of pest by parasitoids. Furthermore, the results revealed that the distributions of *C. partellus* and *C. flavipes* will expand into higher altitude areas; whereas *B. fusca* and *C. sesamiae* will more spread at high and middle altitude under future temperature. Chapter five describes establishment of a resource based mathematical model and stability analysis of the equilibrium points on the model. In this chapter, the models explored the effects of resource and temperatures on competition between insect species were proposed and analysed qualitatively using stability theory. A local study of the models was performed around trivial, axial, planar and interior equilibrium points to successively estimate the effect of: (i) one species interacting with a resource; (ii) two species competing for a single resource; and (iii) three species competing for a single resource. The local stability analysis of the equilibrium is discussed. Numerical simulation of the models was performed to investigate the sensitivity of certain key parameters. The models are used to predict population dynamics in the selected cases studied. The results showed that when a single species interact with a resource, the species will be able to establish and sustain a stable

population. However, in competing situation it is observed that the combinations of three parameters (half-saturation, growth rate and mortality rate) determine which species wins for any given resource. Moreover, the results indicate that each species is a superior competitor of a resource for the range of temperatures for which it has the lowest equilibrium resource.

In chapter six, the potential distribution of maize stem borer with other environmental variables were presented. A maximum entropy (Maxent) distribution modelling was applied on current climatic conditions, soil characteristics and occurrence species data collected from maize farms. The results indicate that both climatic factors and soil characterists were more important in regulating *C. partellus* and *B. fusca* potential distribution.

In addition, chapter's four to six of this thesis has resulted into published or submitted papers in the International peer-reviewed Journals (see Mwalusepo *et al.* 2014, Mwalusepo *et al.* 2015).

7.3 Conclusions

In East Africa countries, maize production is the most important agricultural activity and is considered as the main economic driver in the region. As temperatures rise due to future climate change take marginally suitable regions will be brought into the fold of maize stem borer incidence and spread. Moreover, being highly phytophagous pests, the chances for spread and establishment of maize stem borers in the new areas are greater and most likely lead to higher maize yield losses. The predictions in this study at small scale confirmed and completed the results recorded at country scale, and confirm that the impact of the projected changes in global temperature on the prediction of the future

distribution and abundance of the most important cereal pests in East Africa will worsen the stem borer impact on maize production along the two gradients. Thus, this thesis brings valuable contributions to the understanding how climate change will potentially affect maize crop production and will help undertaking response adapted on maize pests in the two transects. Therefore, it would be interesting to conduct further quantitative and qualitative studies for all kind insect communities in different small-scale areas in East Africa. Also, future research must be carried out in the direction of insect thermal adaptation in order to assess the species reproduction potential and related evolutionary properties as the respond to long and short term temperature change. The development of more sophisticated models, such as demographic system models and ecological niche models is also an imperative essential to improve and complete all current models. Thus models that are based on weather and other factors can more reasonably estimate the spatiotemporal population evolution and invasive potential of native and non-indigenous species in new areas. Finally, each of the modelling approaches either inductive or deductive approaches used in different computer packages and models presents advantage and disadvantage. Referring to the fact that the errors and uncertainties in pest risk mapping are unavoidable, the focus and emphasis should be on combining several tools and methods in conjunction with expert opinions, for better predictions of establishment risk and population growth potential of species of interested.

7.4 Recommendations

Decisionmakers and others concerned with adapting East African agriculture to climate change can take the following steps:

- i. Invest in cultural control measures of maize stem borers; these measures include, host plant resistance, crop rotation, intercropping, biological control, cultural practices by removal of crop residues. However, an efficient pest management system will only become a reality if a participatory approach is used in the development thereof and political support for enforcement of regulatory mechanisms.
- ii. Protection of natural enemies (parasitoids and predators) from pesticides and conservation and restoration of their habitats in the crop areas and surroundings are essential for pest management.
- iii. Provide drought-tolerant maize varieties, could play an important role in the adaptation to climate change. Other management changes of maize cropping systems like date of planting and cultural association should also be considered . Further, cassava, sorghum, pearl millet and green grams are better adapted to higher temperatures and sporadic rainfalls; they could be alternative crops to maize as an adaptation response to climate change in lowland areas. Other elements of adaptation include making use of agrobiodiversity diversifying livelihoods (beekeeping).
- iv. Public policy should ensure that small farmers have opportunities to increase their productivity and income. Investments by national governments, as well as global and regional institutions, should focus on improved smallholder accesss to inputs such as seeds and fertilizer through lower transport and marketing costs, improved market infrastructure, and greater competition, as well as financial and extension services and weather-based crop insurance.

- v. Promotion of research on the relationship between climate change and agriculture; facilitation of interaction among multiple stakeholders such as bringing together users of climate information (that is farmers) and producers (climate scientists).
- vi. Planning for climate change adaptation must focus on both short term (the springboard) and long term solutions (transformative actions) that take account of inherent capacities of an environment and its inhabitants.
- vii. Building of human and institutional capacity, particularly in the areas of climate change modelling, remote sensing, and developing climatic early warning systems. Further, models, particularly simple mathematical models, should be constructed using empirical crop and pest data.

7.5 Limitation of the study

This research had some limitations, including;

- i. This study was primarily limited by sample size, field survey were carried in maize fields only, because of limited resources including time and finance that is why land cover changes and alternative wild host plant infestations were not included in the modelling. In addition, climate data equipment such as Data loggers and Rain gauges, were expensive, some Data loggers were stolen in the field, compensation to the farmers who always asked for more when their maize plants were cut for the destructive sampling and Care taker for Data loggers and Rain gauges, unpredictable time for maize planting (season) because of climatic variability. Regrettably there were delays in equipment and data loggers and rain

gauges at the beginning of the field survey because of logistic importation from abroad.

- ii. Insect life cycle Modelling approach requires data input in appropriate quantity and quality and collecting this is quite demanding and time consuming, and might constitute an important factors for the massive use of the program. When using this proram for determining species environmental suitability, the program specifically guides the user to understand the temperature effects that limit the geographical distribution of the species and identify the temperature optima that favor population growth. The approach therefore takes temperatures as the only influence variable on insect phenology, because the effects of this climate factor are well assessed through laboratory experiment. However, further effects of other abiotic factors such as rainfall, light and humidity as well as species specific limiting factors and environmental stress, should be quantified and included in the concept for better accuracy. Furthermore, the effect of temperature on the induction of diapause in maize stem borer larvae was not included in modelling.
- iii. Uncertain of prediction climate data; Global climate models (GCMs) attempt to describe the earth's climate and are used in a variety of applications. These include the investigation of the possible causes of climate change and the simulation of past and future climates. But these models are limited in important ways, including: an incomplete understanding of the climate system, an imperfect ability to transform our knowledge into accurate mathematical equations, the limited power of computers, the models' inability to reproduce important atmospheric phenomena, and inaccurate representations of the complex natural

interconnections. These weaknesses combine to make GCM-based predictions too uncertain to be used as the bases for public policy responses related to future climate changes. Furthermore, in local scale a long term climate data are not available, which make it difficult to analyse the climate data in a small area of study.

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APPENDECES

APPENDIX A: SAMPLE COMPUTER PROGRAM IN R SOFTWARE

Programe 1: R program for three species and one resource model

```

library(deSolve)

sia <- function(t,y,parms){
  with(c(as.list(y),parms),{
    y0 = alpha1*exp(-(beta33-beta4)^2/(2*beta5^2))
    y1 = alpha*exp(-(beta33-beta6)^2/(2*beta5^2))
    y2 = alpha4*exp(-(beta33-beta7)^2/(2*beta5^2))
    dN1dt <- N1*((y0*I)/(gamma1+I)-beta1)
    dN2dt <- N2*((y1*I)/(gamma+I)-beta)
    dN3dt <- N3*((y2*I)/(gamma3+I)-beta3)
    dRdt<-beta2*(gamma2-I)-((y0*alpha2*I*N1)/(gamma1+I))-
      ((y1*alpha3*I*N2)/(gamma+I))-((y2*alpha5*I*N3)/(gamma3+I))
    list(c(dSdt,dS1dt,dS2dt,dIdt))
  })
}

time <- 0                      # set initial time
N1 <- 10                      #total population size
N2 <- 10
N3 <- 10
R <-60
initial.SI <- c(N1 = 10,N2 = 10, N3 = 10,R = 60)
Values <- c(beta1 <- 0.02,
            beta <- 0.02,

```

```

beta2 <- 0.01,
beta3 <- 0.02,
beta33 <- 10,
beta4 <- 21.78,
beta5 <- 7,
beta6 <- 20.0,
beta7 <- 23.0,
gamma <- 0.9,
gamma1 <- 0.8,
gamma2 <- 100,
gamma3 <- 0.7,
alpha <- 0.17,
alpha1 <- 0.2,
alpha2 <- 3,
alpha3 <- 0.5,
alpha4 <- 0.2,
alpha5 <- 0.4)

time.out <- seq(0,50,by = 5)

ts.sia <- data.frame(lsoda(
  y = initial.SI,           # Initial conditions for population
  times = time.out,         # Timepoints for evaluation
  func = sia,               # Function to evaluate
  parms = Values            # Vector of parameters
))

plot(ts.sia$time, ts.sia$N1, type="l", col="red", lwd="2",)
lines(ts.sia$time, ts.sia$N2, type="l", col="green", lwd="2", pch=15)

```

```
lines(ts.sia$time, ts.sia$N3, type="l", col="yellow", lwd=2, pch=15)
lines(ts.sia$time, ts.sia$R, type="l", col="blue", lwd=2, pch=15)
```

Program 2: R program for data interpolation in Taita hills

```
setwd("c:\\")
CoordTaita<-read.delim("C:/Users/smwalusepo/Desktop/TaitaDataMax/CoordTaita.txt")
RainTaita      <-read.table("C:/Users/smwalusepo/Desktop/TaitaDataMax/RainTaita.txt",
header=T, quote="")
RhTaita       <-    read.table("C:/Users/smwalusepo/Desktop/TaitaDataMax/RhTaita.txt",
header=T, quote="")
SilicaTaita   <-read.table("C:/Users/smwalusepo/Desktop/TaitaDataMax/SilicaTaita.txt",
header=T, quote="")
TempTaita     <-read.table("C:/Users/smwalusepo/Desktop/TaitaDataMax/TempTaita.txt",
header=T, quote="")
soil          <-  read.table("C:/Users/smwalusepo/Desktop/TaitaDataMax/soil.txt", header=T,
quote="")
Water.holding.capacity<-read.table("C:/Users/smwalusepo/Desktop/TaitaDataMax/Water
holding capacity.txt", header=T, quote="")
Organic.Matter <-  read.table("C:/Users/smwalusepo/Desktop/TaitaDataMax/Organic
Matter.txt", header=T, quote="")
Potassium     <-  read.table("C:/Users/smwalusepo/Desktop/TaitaDataMax/Potassium.txt",
header=T, quote="")
library(fields)
library(raster)
library(rgdal)
set.panel(2,2)
fit4<- Tps(CoordTaita,TempTaita)
out.p4<- predict.surface (fit4)
image(out.p4)
```

```

sur4<-raster(out.p4)

surface(out.p4)

writeRaster(sur4, "Temp_Taita", format = "GTiff")

set.panel( 2,2)

plot(fit4)

summary(fit4)

```

Program 3: R program for data interpolation in Kilimanjaro

```

setwd("c:\\\\")
Coords <- read.delim("C:/Users/smwalusepo/Desktop/KiliDataMaxent/Coords.txt")

Waterhc   <-  read.table("C:/Users/smwalusepo/Desktop/KiliDataMaxent/Waterhc.txt",
header=T, quote="\"")

Organic   <-  read.table("C:/Users/smwalusepo/Desktop/KiliDataMaxent/Organic.txt",
header=T, quote="\"")

Potassium <- read.table("C:/Users/smwalusepo/Desktop/KiliDataMaxent/Potassium.txt",
header=T, quote="\"")

KiliSoil   <-  read.table("C:/Users/smwalusepo/Desktop/KiliDataMaxent/KiliSoil.txt",
header=T, quote="\"")

pho1 <- read.table("C:/Users/smwalusepo/Desktop/KiliDataMaxent/pho1.txt", header=T,
quote="\"")

library(raster)

library(rgdal)

set.panel( 2,2)

fit4<- Tps(Coords,pho1)

out.p4<-predict.surface(fit4)

image(out.p4)

out.p4<-raster(out.p4)

```

```
surface(out.p4)
res(out.p4)
writeRaster(out.p4, "pho1", format = "GTiff")
set.panel( 2,2)
plot(fit4)
summary(fit4)
```

APPENDIX B: SAMPLE COMPUTER PROGRAM IN ArcGIS

Program 4: Confusion matrix program for two species interactions in Kilimanjaro

Need two species maps of presence and absence (zeroes and ones), species one called *Chilo partellus* called and species two *Busseola fusca*

Determine binary maps from continuous MaxEnt predictions using 'Max sens+spec'

Con("chilo2015" > 0.4752, 1, 0)

Save output map as chilo2015_pa

Con("busseola2015" > 0.4267, 1, 0)

Save output map as buss2015_pa

Con(("chilo2015_pa" == 1) & ("buss2015_pa" == 1), 1,

Con(("chilo2015_pa" == 1) & ("buss2015_pa" == 0), 2,

Con(("chilo2015_pa" == 0) & ("buss2015_pa" == 1), 3, 4)))

Con(("chilo2015_pa" == 1) & ("buss2015_pa" == 1), 1, Con(("chilo2015_pa" == 1) & ("buss2015_pa" == 0), 2, Con(("chilo2015_pa" == 0) & ("buss2015_pa" == 1), 3, 4)))

Save output map as Cp_Bf_matrix

Program 5: Confusion matrix program for two species interactions in Taita hills

Need two species maps of presence and absence (zeroes and ones), species one called *Chilo partellus* called and species two *Busseola fusca*.

Determine binary maps from continuous MaxEnt predictions using 'Max sens+spec'

Con("chilo2015" > 0.352, 1, 0)

Save output map as chilo20155

Con("busseola2015" > 0.321, 1, 0)

Save output map as buss20155

Con(("chilo20155" == 1) & ("buss20155" == 1), 1,

```
Con(("chilo20155" == 1) & ("buss20155" == 0), 2,  
Con(("chilo20155" == 0) & ("buss20155" == 1), 3, 4)))  
Con(("chilo20155" == 1) & ("buss20155" == 1), 1, Con(("chilo20155" == 1) &  
("buss20155" == 0), 2, Con(("chilo20155" == 0) & ("buss20155" == 1), 3, 4)))  
Save output map as Cpt_Bft_matrix
```