POTENTIAL EFFECTS OF CLIMATE CHANGE ON TRITROPHIC INTERACTIONS IN CRUCIFER FARMING SYSTEMS OF MOUNT KILIMANJARO AND TAITA HILLS

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DECLARATION

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To my late dad Valentine Ngowi, mum Winnie Ngowi, and Tumaini, my wife. Your love and unwavering support helped me realize my potential.

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ABSTRACT

Diamondback moth (DBM) (*Plutella xylostella* L.), a pest of cruciferous vegetables worldwide, is resistant to major groups of insecticides, and attention has shifted to biological control using parasitoids. However, DBM and its parasitoid species have individual climatic requirements which, when not met adequately due to climate change, will potentially disrupt biological control of the pest. The response of this pest and its parasitoids to climate change at a local scale is less documented than in international scale and is largely ignored in a region where climate patterns have been changing in a way that is likely to interfere with the insect life history and the pest incidence. This study was therefore conducted to determine the likely changes in DBM abundance, the parasitic interaction between the pest and its key parasitoid species *Diadegma semiclausum* and *Cotesia vestalis*, and the feeding relationship between the pest and host plants, in response to climate change along altitudinal gradients. Potential effects of climate change on future distributions of the three insects were investigated to establish possible future trend of the pest levels necessary for developing adaptive pest control strategies.

Field surveys were conducted for two years on two transects laid along the altitudinal gradients of Mount Kilimanjaro and Taita hills. Based on altitude, each transect was sub-divided into low, medium and high zones within which farmer-owned crucifer vegetable farm plots were identified for the study and marked by Global Positioning System (GPS). Thermohygrometers and rain gauges were installed on farms for recording daily values of temperature, relative humidity and rainfall. The crucifer plants were sampled for larvae and pupae of DBM which were all collected and taken to laboratory for parasitism assessment and life table studies. The pest abundance and parasitism were subjected to analysis of variance (ANOVA) to determine differences among seasons. Biodiversity.R, a statistical package for community ecology, was used to calculate the diversity of parasitoid species. Generalized linear models and regression analyses were adopted for assessing the weather effects on crop damage and parasitism. Colonies of DBM, *D. semiclausum* and *C. vestalis* were initiated in laboratory for generating life history datasets at 10, 12.5, 15, 20, 25, 30 and 35°C. Temperature-driven phenology models for the pest and its respective parasitoid species were developed based on laboratory experimental data obtained at constant temperatures and validated through life table data collected outdoor under field temperature conditions. All model development was implemented through the Insect Life Cycle Modeling (ILCYM) software version 3. The generated phenology models, the recorded baseline (2013) field temperatures and future temperatures (2055) downscaled from AFRICLIM database; and the digital georeferenced topographical maps of the transects, were loaded in index interpolator, a sub-module of ILCYM for calculating, interpolating and mapping potential population growth of the insects, through establishment, generation and activity indices.

The results showed that DBM abundance was least during long rains and highest during hot dry and short rainy seasons in the two transects. Besides *D. semiclausum* and *C. vestalis,* other parasitoid species emerged from parasitized DBM. *Cotesia vestalis* and *Oomyzus sokolowskii,* a parasitoid, contributed significantly to DBM parasitism (*O. sokolowskii*: F = 32.69, df = 1, 101, P < 0.0001***; *C. vestalis*: F = 27.74, df = 1, 101, P < 0.0001***) compared to other parasitoids in the low zone of Mt. Kilimanjaro, at 43% and 40.7%, respectively. *Diadegma semiclausum* was the most dominant parasitoid in medium and high zones of both transects. Diversity of parasitoid species declined considerably from low to medium zones of Taita hills probably because of great competitiveness and dominance of *D. semiclausum* released from 2002 to 2004 in Taita hills. Crop damage increased with DBM abundance in the two transects and declined with rainfall. The DBM parasitism by *C. vestalis* varied significantly with temperature (F =

1.322; df = 3, 56; P = 0.0496*) in the medium zone of Taita hills. The *D. semiclausum*-caused parasitism varied significantly with temperatures in both high zones (Mt. Kilimanjaro: F = 11.68, df = 3, 56, P = 0.0021**; Taita hills: F = 6.546, df = 3, 56, P = 0.0049**). The life history phenology showed optimal oviposition of *D. semiclausum* occurs between 15°C and 20°C and that of *C. vestalis* at 20-25°C. Spatial simulations indicated increased survival and establishment of the insects at high zones of both transects. The models predicted a future decline of DBM in the low zone of Mt. Kilimanjaro; and in low and medium zones of Taita hills due to increased temperatures, which will lead to less DBM-damaged crop in these zones. However, such increased temperatures could be more favourable to new pests which call for pest monitoring programs to equip crop protection authorities with sound knowledge for preparedness before new pest outbreaks. Increased temperatures are predicted to weaken the parasitic interaction between *D. semiclausum* and DBM in the low zones but strengthen the *C. vestalis*-based parasitism. Therefore, adoption of location-specific altitudinal gradients in studying potential effects of climate change rather than utilizing the regional and global climate change scenarios provided the insights necessary for improvement of future biological control of DBM in a local context.

CHAPTER ONE: GENERAL INTRODUCTION

1.1 Background information

Climate change is a global phenomenon evident from the increase in global average temperatures, extreme weather events and changes in rainfall patterns (Karuppaiah and Sujayanad, 2012). The passage of the tropical cyclone referred to as the "Great Bhola Cyclone" in Bangladesh in 1970 claimed an estimated 300,000 lives (World Meteorological Organization, 2017). Different regions are often associated with particular adverse weather events. In Africa, the most dreadful extreme weather events are droughts and floods. The severe drought spell of 2010 – 2011 claimed lives of about 50,000 people in Somalia, killed over 80% of the livestock and necessitated relief aid to approximately 13 million people (Osman-Elasha, 2012). The gradual but considerably long changes in weather patterns also contribute to climate change. The fifth assessment report of the Intergovernmental Panel on Climate Change (2013) predicted the likelihood of increase in numbers of warm days and nights and decrease in numbers of cold days and nights on a global scale. In its summary for policy makers, the report concluded that there has been clear warming of climate systems. This warming is felt across different sectors. However, the magnitude of potential impacts varies between regions and across sectors. In the agricultural sector, the global warming is already imposing severe and costly effects on different communities. The increased frequency of drought spells is predicted to cause direct famine on farming communities due to crop failure. This will most likely be intense in Africa, whose inhabitants depend primarily on agriculture for earning their livelihood (Intergovernmental Panel on Climate Change, 2007; McIntyre *et al*., 2009).

Climate change can however, on the other hand, reduce crop productivity directly through drought and indirectly through increased pest populations. On different occasions, Lockwood (1999) and Brumbelow and Georgakakos (2001) showed that an increase in the rate of evaporation by two to three percent is adequate to signal the slightest change of crop loss under the warm climate areas of the United States. Increased temperatures and drought have been recorded to expand the geographical range of varied insect pests, increase chances of their survival during winters and support a growing number of their generations in India (Rao *et al*., 2009). Potentially indirect effects of climate change are many. In one laboratory study, a long term increase of temperature raised nitrogen levels in the leaves, resulting in enhanced plant nutritional quality (Zvereva and Kozlov, 2006). The increased quality made the plants more favourable to the green peach aphids (*Myzus persicae,* Sultzer). The overall result was a greater rise of the pest population than at ambient temperature. Moisture stress, another key factor slowing down crop performance, limits the photosynthetic rates and causes premature leaf abscission (Kozlowski *et al*., 1991) and thereby deprives insect pests of the available foods. Temperature and moisture content have usually been kept at optimum requirement levels when studying the effect of carbon dioxide in plants. Under these conditions, decreasing the carbon dioxide supply has been shown to decrease the grain yield in wheat (*Triticum aestivum* L.) and tuber yield in potato (*Solanum tuberosum*, L.), with further losses compounded by insect pests attacking the respective grains and tubers (Kimball *et al*., 2002). In multitrophic interactions, climate change affects relationships between insect pests, their natural enemies and host plants through complex mechanisms (Tylianakis *et al*., 2008; Gillespie *et al*., 2012) which can bear impacts in the present agroecosystems. Several studies have reported that elevated temperature can negatively affect the survival of temperature-sensitive parasitoid wasps (Voigt *et al*., 2003; Bannerman, 2011; Gillespie *et al*., 2012) through decreased rates of development with a potential of causing phenological mismatch between insect hosts and their parasitoids (Klapwijk *et al*., 2011). The decline of parasitoid population can lead to lower plant biomass resulting from increased potential of pest outbreak.

Several direct effects of climate change onthe diversity and abundance of insects have been recorded (Fand *et al*., 2012). The insect diversity in an agroecosystem may present a healthy status of the system as different insects play important roles in food chains (Ingram *et al*., 1996), pollinate many critical crops (Klein *et al*., 2007; Ricketts *et al*., 2008), contribute to human economy through valuable products like honey (Murugan, 2006); and are good indicators of climate change because of their high sensitivity to surrounding environmental conditions like temperature (Gregory *et al*., 2009). Adverse effects of climate change on insects which provide essential ecosystem services risk the food security and socio-economic livelihood, especially so when some ecologically important insect species fail to adapt to the changes and get eliminated in the course of time (Thomas *et al*., 2004).

Gaining the knowledge of potential effects of climate change on population dynamics of insect pests is of paramount importance to improving agricultural productivity. As temperature is the key factor regulating population dynamics of insects, the increase in temperature within certain favourable range will shorten the length of life cycles of the insect pests but lead to increased numbers of generations and associated crop damage (Yamamura and Kiritani, 1998). Across a given spatial scale of climate change that involves increased temperatures, elevated carbon dioxide and moisture stress, the potential of expanding the geographic range of insect pests and, in temperate regions, increasing survival during winters, is great (Fand *et al*., 2012). More importantly, the changes can destabilize the ecological balance because of unpredictable changes in populations of insect pests and their natural enemies (Intergovernmental Panel on Climate Change, 2014).

Natural enemies of insect pests provide a vital ecosystem service of controlling insect pests on crops in an ecological-friendly and sustainable manner. Most natural enemies (e.g. parasitoids, predators and entomopathogens) are density-dependent in action and their effectiveness is subject to thresholds of both biotic and abiotic components (Fand *et al*., 2012). Parasitoid species form an important group of natural enemies that spends part of its developmental stages on or inside the bodies of the host insects. Climate change can therefore affect parasitoids adversely through its indirect unpleasant effects on their host insects (Thomson *et al*., 2010). Inside the body of a host insect, the larval and pupal stages of an endoparasitoid are subject to the climate surrounding the host insect. However, adult parasitoids are free and when such adults and their respective vulnerable host insects respond differently to the same environmental conditions, the parasitoid populations could be impacted adversely from the declined survival of the host insects. Some studies have shown that quick development of the vulnerable stages at high temperatures deprive some adult parasitoids enough window for oviposition which risks their very survival and multiplication (Petzoldt and Seaman, 2010).

Different crop plants, insect pests and natural enemies live in communities that are subject to the same climate parameters at any given time. Such groups of organisms interact in various ways which ensure communities thrive. To understand the role of global climate change on insect communities, studies on the effects of different environmental parameters on species interactions are becoming critical in enhancing our knowledge on the realistic dynamics of communities (Harrington *et al*., 1999; Araujo and Luoto, 2007). Studying the combined effects of these environmental parameters on species interactions provides more insights for expanding this knowledge base (Hoover and Newman, 2004; Tylianakis *et al*., 2008). A study on the combined effect of temperature and nitrogen levels on insect trophic interactions found that rising levels of the two factors contributed in changing the size and availability of host insects to parasitoids (de Sassi *et al*., 2012). Responding to such changes, parasitoids focused on the more abundant and larger host insects (de Sassi *et al*., 2012). In a similar set up, Bezemer *et al*. (1998) studied the effects of elevated temperature and carbon dioxide on a tritrophic interaction involving host plants, green peach aphid *Myzus persicae* and parasitoid *Aphidius matricariae*.

The researchers found that the aphid populations increased under both increased temperature and carbon dioxide but the associated parasitism increased only when temperature increased. In other instances, the effects of environmental parameters on insect interactions may not be direct but still equally destabilize the insect host-parasitoid interaction. Atmospheric pollution through elevated ozone gas has been reported to disrupt attraction of female *Cotesia vestalis* (Haliday) (Hymenoptera: Braconidae) to the damaged crucifer crops, resulting into limited parasitism of diamondback moth (DBM) (*Plutella xylostella* L.) (Lepidoptera: Plutellidae) (Himanen *et al*., 2009).

Climate change is alteration in the state of climate that can be identified (e.g. using statistical tests) by changes in the mean and/or the variability of its properties and that persists for an extended period, typically decades or longer (Intergovernmental Panel on Climate Change, 2014). Interactions between organisms depend on climate, their position in the food chain and the physical and chemical soil properties in the ecosystems (Maes *et al*., 2012). Tritrophic interaction is a three – way association between plants, insect pests and their natural enemies. This is exemplified by the interactions of DBM with crucifer crops and parasitoid species in tropical crucifer agroecosystems. The family Cruciferae is large and made up of both cultivated and wild plant species. Common cultivated crucifers in the region include the head cabbage (*Brassica oleraceae* var. *capitata*), kale (*B. oleracea* var. *acephala*) and Chinese cabbage (*B. rapa* var. *pekinensis*). Others include cauliflower (*Brassica oleraceae* var. *botrytis*), broccoli (*Brassica oleraceae* var. *italica*) and Ethiopian mustard (*Brassica carinata*). Climatic factors influence the biology of each species involved in the interactions differently, with the possibility of destabilizing the population dynamics of each trophic level (Van der Putten *et al*., 2010). When the host insect and its natural enemy respond differently to the extreme low or high temperatures, a potential disruption of the insect pest – natural enemy synchrony may lead to pest outbreaks (Dosdall *et al*., 2012).

Besides temperature, water stress, for example, can also limit photosynthetic rates and causes premature leaf abscission (Kozlowski *et al*., 1991) which deprives insect pests of food. Enhanced summer rainfall and drought have been shown to promote a rapid increase in the population of soil-dwelling root-chewing wireworms, *Agriotes lineatus,* prompting the pest epidemics (Easterling *et al*, 2007). Following heavy rainfall in the temperate regions, the combined high relative humidity and poor sunlight create a favorable condition that supports the germination of fungal spores which penetrate the insect's integument (Ferron, 1985). In contrast, drought is known to provide a more favourable thermal environment for the growth of phytophagus insects (Mattson and Haack, 1987) and mutualistic microorganisms but not natural enemies of the phytophagous insects (Brock *et al*., 1984).

Crucifers present a family of plants which host several climate-sensitive species interactions. Smallholder farmers grow about 90% of all the crucifer vegetables in East Africa (Grzywacz *et al*., 2010). Crucifer production provides a major source of income and contributes to poverty alleviation of women and youths in peri-urban areas (Kahuthia-Gathu, 2007). Cultivated crucifers are grown under varied agroecologies which extend from the coastal lowlands to the interior highlands of East Africa (Nyambo and Löhr, 2005). Most farmers grow vegetables during the rainy seasons but where irrigation is available, crucifer vegetables are grown throughout the year. In Kenya, most cabbage production occurs between 800 and 2000 metres above sea level (m.a.s.l.), of which the central and rift valley provinces then produced about 80% of the total national production (Macharia *et al*., 2005). Crucifer vegetables are grown in about 35,000 hectaresof the highlands, which produced approximately 550,000 tons and 562,681 tons in 2007 and 2014, respectively (FAOSTAT, 2007; 2014). A significant production is gaining ground in the semi arid lowlands (Nyambo, 1995).

Wild crucifers include some of the weeds found in crucifer farms such as wild radish (*Raphanus raphanistrum*), Ethiopiankale (*Erucastrum arabicum*), garden cress (*Lepidium sativum*) and the shepherd's purse (*Capsella bursa*). The weeds serve as alternate hosts of crucifer pests and provide refugia to both DBM and its natural enemies particularly when cultivated crucifer vegetables get old, have been harvested, uprooted or destroyed till the next growing cycle (Landis *et al*., 2000; Kahuthia–Gathu, 2007). Several wild crucifer plants in the region e.g. wild radish, hedge mustard (*Sysimbrium officinale*) and crambe (*Crambe kilimandscharica*) provide refuge to some hymenopteran wasp parasitoids, namely *Diadegma semiclausum* Hellen (Hymenoptera: Ichneumonidae), *Diadegma mollipla* Holmgren (Hymenoptera: Ichneumonidae) and *C. vestalis* (Kahuthia–Gathu, 2007). These plants provide such parasitoids the alternate nectar sources for feeding (Fitton and Walker, 1992; Idris and Grafius, 1995).

Presence of glucosinolate compounds is characteristic of crucifer plant species. Glucosinolates are secondary, non-volatile chemical compounds whose toxic hydrolysis products are used to defend crucifers against many unadapted insect pests. Glucosinolates powerfully stimulate the feeding and oviposition behavior of DBM on its host plants (McCloskey and Isman, 1993; Renwick, 2002). The compounds are present in varying and dynamic quantities in different tissues, growth stages, cultivars and species (Hopkins *et al*., 2009). Verkerk and Wright (1996) demonstrated that the moth preferred the young chinese cabbage, cauliflower, Indian mustard (*Brassica juncea*) and pak-choy (*Brassica rapa*) over the matured head cabbage. Twelve years later, Gols (2008) reasoned this is because the succulent bodies supported desirable levels of glucosinolates, making them more attractive to the larvae. It is worth noting that when a plant tissue is damaged, the glucosinolate compounds undergo a series of reactions which form toxic hydrolysis products (Li *et al*., 2000) that impart broad-spectrum toxicity to many bacteria and fungi (Van Etten and Tookey, 1979) and several insects feeding on crucifers (Feeney, 1976).

Diamondback moths feed exclusively on crucifer plant species (Talekar and Shelton, 1993) because their bodies have developed a mechanism to neutralize these toxic products (Ratzka *et al*., 2002). Specifically, secretion of glucosinolate sulphatase in the gut lumen gets rid of sulphur from the compounds, the action which stops myrosinase hydrolysis and obstruct formation lethal compounds (Ratzka *et al*., 2002). This enables DBMto consume crucifer plants with no or little effect on its larval performance (Li *et al*., 2000). In contrast to glucosinolate comppounds, which are volatile, when DBM forages on such plants, the bitten leaves release volatiles which serve as clues for parasitoids to locate their hosts (Whitman and Eller, 1992).

Many insect pests attack crucifer crops in East Africa. Diamondback moth is the lead insect pest of crucifer crops in East Africa (Löhr, 2001) followed by aphids (Nyambo and Löhr., 2005). The cabbage aphid (*Brevicoryne brassicae* L.) sucks cell sap from the leaves and rob plants of the nutrients needed for their growth. The pest feeding behavior is further associated with transmission of the turnip mosaic virus (TuMV) and its honeydew associated with encouraging the growth of black sooty mold fungus. Besides cabbage aphids, the mustard aphid (*Lipaphis erysimi* Kaltenbach) and green peach aphid are other aphids commonly available in crucifer fields in East Africa. The onion thrips (*Thrips tabaci* Linderman), webworm (*Crocidolomia binotalis* Zeller), sawfly (*Athalia rosae* Linnaeus) and cutworm (*Agrotis ipsilon* Hufnagel) are also common types of insect pests. Sporadic insect pestsinclude the harlequin bug (*Bagrada cruciferarum* Kirkaldy) that attacks crucifer crops especially in the lowlands where temperature levels are relatively high. It is common to find different insect pest species simultaneously in crucifer crops.

The DBM is attacked by a wide range of natural enemies. These include parasitoids, predators, viruses, pathogenic fungi and bacteria (Furlong *et al*., 2013). Parasitoids have so far proved to be the most effective natural enemies of DBM in crucifer agroecosystems (Furlong *et al*., 2013). An estimated 60 parasitoid species have been documented to limit population growth of DBM in the fields (Delvare, 2004). Diamondback moth parasitism caused by species of genera *Diadegma, Cotesia, Apanteles* and *Diadromus* species, and *Oomyzus sokolowskii*Kurdjumov (Hymenoptera: Eulophidae) and *Microplitis plutellae* Muesbeck (Hymenoptera: Braconidae) is the most effective in controlling DBM populations (Furlong *et al.*, 2013). These parasitoids respond to various attributes of host plants when searching for their host insects. Once on plant, Lim (1982) noted that consumption of food from the floral nectars increased significantly the length of oviposition period and female longevity of parasitoids. Talekar and Yang (1991) found that different host plants somehow contributed to different rates of parasitism. While it may not be possible to know all the reasons behind the different parasitism rates impacted by parasitoids on the host insects, it has been known that the host plant quality affects the development time, weight and longevity of the specialist parasitoids (Golizadeh *et al.*, 2009).

1.2 Classical biological control program of diamondback moth in East Africa

The control of DBM in East Africa has primarily focused on insecticide applications. In vegetable-producing areas of north eastern Tanzania, Ngowi *et al*. (2007) reported most farmers made applications of insecticides on routine basis. Under the same observations, more than 15% of farmers reported applying insecticidesat least 16 times per season. In the Taita hills, Nyambo *et al*. (2006) observed kale and cabbage farmers applied 12 rounds of sprays per season against DBM alone besides other pests. Intensive applications of insecticides over a period of time have contributed to development of insecticide resistance by DBM (Liu *et al.*, 1995; Kibata, 1996; Zhao *et al.*, 2002; Sarfraz and Keddie, 2005; Heckel *et al.*, 2007; Santos *et al.*, 2011), raising production costs and increased human and environmental health problems. It is against this background, along with the relative ineffectiveness of the local parasitoids (Seif and Löhr, 1998; Löhr, 2001), that the International Centre of Insect Physiology and Ecology (ICIPE) partnered with national agricultural research systems to initiate a biological control program for DBM in Kenya, Uganda and Tanzania. *Diadegma semiclausum* was imported from Taiwan and introduced to farmers' fields located in selected highlands of Nyamira and Taita hills in Kenya, Kabale district in Uganda and Mount Meru in Tanzania, between 2003 and 2007 (Löhr *et al*., 2007; Gichini *et al*., 2008). The year-round availability of crucifer crops and the relatively cool temperatures of the highlands provided prime conditions for the growth, development, survival and reproduction of *D. semiclausum*. Approximately eight months immediately following the release, *D. semiclausum*had largely out-competed and displaced the native parasitoids: *O. sokolowskii*, *D. mollipla*, *Apanteles sp*. and *Itoplectis sp*. and was responsible for > 80% of DBM parasitism (Gichini *et al*., 2008). The parasitoid dispersal over the same period reached 16 km radius (Gichini *et al*., 2008). *Cotesia vestalis,* another larval parasitoid of DBM, was imported from South Africa for controling DBM populations in the lowland areas of Kenya. The wasp completes its development successfully over a temperature range from 21 – 33°C (Nofemela, 2004). A number of surveys carried out before its release revealed existence of a small population of local *C. vestalis* (Löhr *et al*., 2007). The imported *C. vestalis* was introduced and released in the semi arid regions of Yatta valley and Athi River in March 2004 and in Loitoktok in 2006. Kale was the dominant crop and was grown mostly under irrigation. Two years after its release however, a few individuals were recovered in Yatta valley and Athi River (Kahuthia-Gathu, 2011). Post release surveys conducted from September 2011 to April 2012 in Loitoktok revealed *C. vestalis* established and spread successfully. The parasitoid contributed an average of 50% of total parasitism in Loitoktok (Kahuthia-Gathu *et al*., 2017).

1.3 Altitudinal gradients as indicators of potential climate change trends

Comparative studies of insect ecology along altitudinal gradients provide a forum for observing the likely response to climate change (Hodkinson, 2005). Steep altitudinal gradients are characterized by rapid environmental change over short distances (Beniston *et al*., 1997). The main changes in local climate along an altitudinal gradient involve temperature, rainfall, relative humidity, wind speed and radiation (Barry, 1992). Studying altitudinal gradients provides an option for conducting experiments when examining climate change (Williams *et al*., 2003, Chen *et al*., 2009). The other option may include studying species development and reproduction under different climate settings in a laboratory. The predictable changes in abiotic conditions can be associated with the corresponding biotic patterns, which when matched with physical parameters associated with climate change, can provide a powerful predictive tool (Strong *et al*., 2011). A growing body of evidence suggests that high mountainous regions experience more rapid temperature changes than environments at lower elevations (Pepin *et al*., 2015). Impacts of climate change on insect species' richness and distribution are therefore more profound in mountains than lowlands as insects track the changing climate over relatively short distances (Critical Ecosystem Partnership Fund, 2012). This is despite the fact that changes in some climatic variables might be locally influenced by extreme varying local topography and exposure (Pepin *et al*., 2015).

Partial pressures of atmospheric gases e.g. oxygen and carbon dioxide decrease linearly with the increasing altitude (Peacock, 1998), reducing the amount of oxygen gradually (Hodkinson, 2005). On rainfall, another influential environmental variable, its amount and frequency generally rises along altitudinal gradients in the tropics which can be evidenced in the increased productivity and distribution of moisture-sensitive host plants (Egger and Hoinka, 1992). However, an accurate prediction of rainfall patterns over complex topography of a mountain range is less precise and often subject to long term change compared to a rather free standing mountain (Weltzin *et al*., 2003). On the other hand, while the wind speed increases with altitude, it may vary locally depending on the surface topography. Sustained high speed winds are known to disperse beneficial insects (Hodkinson *et al*., 2002). Soil properties contribute in influencing vegetation along altitudinal gradients. Soil moisture gradient is critical in determining the quantity and structure of vegetation. On the other hand, changing the structural diversification of vegetation has shown to influence the oviposition behavior (quantity and pattern) and distribution (spatial and temporal) of insects.

Manipulating crop habitats, timing the companion plants, integrating non-host plant species, the use of plant volatiles and inclusion of trap crops affect insect herbivores and natural enemies in several ways (Hooks and Johnson, 2003). The egg distribution of cabbage looper, *Trichoplusia ni* Hubner on cabbage farm plots which were surrounded by candy tuft *Iberis umbellata* changed relative to monocultural cabbage, with the number of eggs laid increasing with increased distance away from *I. umbellata* (Bigger and Chaney, 1998). The researchers attributed this to the disrupted movement and oviposition behavior of the *I. umbellata* border. Dover (1986) argued the herb sage *Salvia officinalis* L. physically disrupted the searching behavior of DBM. Besides the physical disruption, decades ago Tahvanainen and and Root (1972) found that non-host odors from tomato plants created the chemical barrier to *Plutella cruciferae*. In all instances of manipulating the habitat to control insect pest damage, attention should be paid to ensuring competition effects do not mask the adverse effect on pest populations (Dempster, 1969). The disruption or sustenance of insect pest – natural enemy relationship in diversified cropping system is subject to strength of their association. The strong relationship between *Diadegma semiclausum* and DBM was not deterred by different habitat manipulation. On the other hand, soil moisture is influenced strongly by the microclimate and topography (Wilcke *et al*., 2008).

Mount Kilimanjaro and Taita hills are some of the several regions rich in biodiversity in the Eastern Afromontane Biodiversity Hotspot (EABH). Endowed with numerous endemic plant and animal species, the EABH provides ecosystem goods and services which include water for irrigation and fertile land for production of food and cash crops (CEPF, 2012). Taita hills consist of three compact blocks of undulating mountains in contrast to Mt. Kilimanjaro, a free standing mountain. However, both are characterized by steep elevational gradients which present an opportunity of investigating the corresponding relationships between the changing weather and population dynamics of insect species in the context of climate change. Altitudinal changes have long been associated with varying climatic conditions which interfere with species performance along the elevation. Declining temperature levels upward the altitude are likely to slow down the development and spatial distribution of high temperature-tolerant insect species (Hodkinson, 2005). Randall (1982) observed that declined temperatures along the altitude reduced parasitic interaction significantly between the moth *Coleophora alticollela* Zeller and its parasitoids *Euderus viridis* Thomson (Hymenoptera: Eulophidae), *Elachertus olivaceus* Thomson (Hymenoptera: Eulophidae) and *Scambus brevicornis* Gravenhorst (Hymenoptera: Ichneumonidae).

1.4 Problem statement

Crucifer vegetables are grown throughout altitudinal gradients of agroecological zones of East Africa. Diamondback moth is the main pest of these vegetables and it is resistant to most insecticides because of intensive and frequent application (Talekar and Shelton, 1993). The hymenopteran parasitoids *Diadegma semiclausum* and *Cotesia vestalis* provide the most effective control of DBM populations in the region. However, the weather requirements differ among insect species and populations and can modulate their survival, abundance, development, reproduction, distributionand diversity. The current DBM – parasitoid equilibrium may no longer remain stable under the changing climate. This can lead to a mismatch of the DBM – parasitoid activity, leading to increased crop damage and yield loss. This is especially so because rapid effects of climate change in montane ecosystems are likely to influence the phenology of DBM and its parasitoids (Pepin *et al*., 2015) thereby increasing ability of the pest to infest and damage crops as well asdecreased ability of parasitoids to search and oviposit in their host. The magnitude of climate variation in East Africa is unpredictable and so is the DBM response. This study seeks to address the knowledge gap on sustainability of the DBM biological control service under changing climate and its potential implications on crucifer production and new pest management strategies.

1.5 General and specific objectives

1.5.1 General objective

The overall objective of this study was to investigate changes likely to occur in interactions among crucifer plants, diamondback mothand its key parasitoid species, in response to changes in climate along altitudinal gradients of Taita hills and Mount Kilimanjaro.

1.5.2 Specific objectives

The study specifically sought to:

(i) Establish baseline seasonal abundances on population dynamics of diamondback moth and its key parasitoid species; *Diadegma semiclausum* and *Cotesia vestalis*, along altitudinal gradients of Mt. Kilimanjaro and Taita hills.

(ii) Investigate weather-related change ininteractions among crucifer plants, diamondback moth, *D. semiclausum* and *C. vestalis*, along altitudinal gradients of Mt. Kilimanjaro and Taita hills.

(iii) Establish temperature-dependent phenology models for predictions of the impacts of climate change on diamondback moth, *D. semiclausum* and *C. vestalis*.

1.5.3 Research Questions

(i) Do diversity and densities of crucifer plants, DBM and key parasitoid species differ at spatial and temporal scale along altitudinal gradients of the Taita hills and Mt. Kilimanjaro?

(ii) How do temperature, rainfall and relative humidity influence herbivory and parasitic interactions among crucifer plants, DBM and the key parasitoid species?

(iii) How does temperature influence different stages in the life cycle of DBM and key parasitoid species and how can such changes be predicted?

(iv) Which is the most influential climate factor and how does it affect the likely changes in distribution and abundance of DBM and key parasitoid species?

(v) How can the abundance and distribution of DBM and key parasitoid species be predicted along the altitudinal gradient of Taita hills and Mt. Kilimanjaro?

(vi) How much reliable from the reality are phenological models in establishing the population growth response of DBM and its key parasitoids to climate change in Taita hills and Mt. Kilimanjaro?

1.5.4 Hypotheses

1. Climatic change along altitudinal gradients affects tritrophic relationships among DBM, its host plants and key parasitoid species.
2. Climate change affects the potential population growth and mismatch between DBM and its key parasitoid species.

CHAPTER TWO: LITERATURE REVIEW

2.1 Overview of climate change

Climate change can refer to extensive and extraordinarily huge variations in weather conditions ranging from a few decades to several millennia. The Earth's climate has always been changing as a result of natural causes, including volcanic eruptions, solar radiations and the Earth's orbital change (Intergovernmental Panel on Climate Change, 2013). In 'Climate Change 2001', a body of research compiled for IPCC (Houghton *et al*., 2001), it has been demonstrated how the emission of sulphur dioxide and ash following volcanic eruptions increases the Earth's reflectivity and cools the atmosphere. Other natural causes can include small changes in the output of solar energy (Baede *et al*., 2001; Folland and Karl, 2001) and tilting of the Earth (Sciencing, 2017) which causes the temperate regions to experience warmer summers and colder winters. The advent of industrial revolution in 18th century amplified the climate change with introduction of new technologies. The extensive burning of fossil fuels releases greenhouse gases into the atmosphere (Intergovernmental Panel on Climate Change, 2014), namely carbon dioxide, methane and nitrous oxide, which trap the radiated heat within the atmosphere and warm the planet (Environmental Protection Agency, 2007; Climate Action, 2018). Between 1750 and 2015, the industrial revolution is estimated to have increased carbon dioxide production by approximately 40% despite uptake of large portions of the emission by forests which act as natural 'sinks' (Centre for International Forestry Research, 2017; Earth System Research Laboratory, 2017). Such carbon dioxide increase is predicted to have contributed to a temperature rise of 0.8°C in the last century and is expected to rise between 1.1°C and 4.8°C by 2100 (Intergovernmental Panel on Climate Change, 2014). This temperature rise matters because small changes can upset the delicate balance of living organisms in ecosystems. Climate change can directly affect crop productivity through inadequate rainfall and floods, and indirectly through the changed dispersal behavior of crop damaging insects, to mention a few. Closer to the East Africa region, Reliefweb, (2017) recorded significant contribution of the severe and recurrent droughts in causing far reaching implications in national food security and human livelihoods in Somalia and Ethiopia.

2.1.1 Climate change in East Africa and its implication in agriculture

East Africa is characterized by diverse climate patterns. Some patterns change with the local topography, particularly the altitude. Thornton *et al*., (2014) observed that variability of the regional climate has always led to different lengths and intensity of rainfall, temperature levels and unpredictable seasons. In mountainous Nepal, Dorji *et al*., (2016) noted that locations spaced just tens of kilometres apart could have very different rainfall patterns, quantities and frequencies which may result in contrasting vegetation types over short distances. Extreme cases of excessive and deficient rainfall have repeatedly caused floods and droughts in 2000s (Webster *et al*., 1999; Hastenrath *et al*., 2007). Shongwe *et al*., (2009) showed growing incidences of hydrometeorological extreme events: < three events/annum during 1980s, about seven events per year in 1990s and approximately ten events annually from 2000 to 2006. Extreme drought cases have been reported during 1983/84, 1991/92, 1995/96, 1999/2001, 2004/2005. Effects of variability of the local topography on the regional rainfall get compounded by warming of surface temperatures of the south-west Indian Ocean (Plisnier *et al*., 2000; Rowe, 2001). The inter-annual climate variability of El Niño Southern Oscillation (ENSO) in 1998 intensified the local adverse weather effects by causing excessive rainfalls and floods which led to hundreds of deaths, crop damage, household asset losses, extensive infrastructural damage and water-borne disease outbreaks in Somalia and Kenya (CARE, 1998). However, long - term recorded climatic patterns in the region show a general reduction of precipitation. The precipitation has decreased for about 11% or 177 mm/annum (2.6 mm/year) since 1935, in Mount Kilimanjaro (Agarwala, 2003).

The extraordinary rise of surface temperature of the Indian ocean contributed immensely in rising the water level of Lake Victoria to about two metres from 1961-1962 (Flohn and Nicholson, 1982). A study on temperature changes in East Africa found that there has been a steady rise of the daily mean minimum temperature since 1905 but fairly stable daily maximum temperatures (Christy *et al*., 2009). This rise of mean minimum temperature levels has contributed greatly to changing the local climatic patterns in the mountainous regions (Pepin *et al*., 2015). Hay *et al*., (2002) indicated an increase in the average spatial temperatures in Kilimanjaro between 1951 and 1960, slight decrease between 1960 and 1981 and the raise again between 1981 and 1995. In Amboseli, just north of Mt. Kilimanjaro, the daily mean maximum temperatures increased at a rate of 0.275^{o}C/annum. Such temperature changes have been projected to being harmful or beneficial to some crop production. The rising mean minimum daily temperature levels have long been predicted to interfere with the optimal growth of maize in East Africa (Jones and Kiniry, 1986) but forecasted to favour cotton yields, particularly in Tanzania (Tanzania Initial National Communication, 2003).

Climate change has been identified as one of the principal contributors to the declining snow of Mt. Kilimanjaro. Agarwala *et al*., (2003) showed precipitation has generally been declining around Mt. Kilimanjaro since 1880. The weather records from Lyamungo Agriculture Research Station (currently Tanzania Coffee Research Institute) showed the number of dry months with < 30 mm. increased between 1937 and 2000 (Lyamungo Coffee Research Institute, 2000). In the same region, temperature, another important climatic factor, has also been recorded to increase gradually since 1950 (Kruss, 1983). Such climate change conditions have also been associated with some land use changes, for example the growing incidence and extent of wild fires, particularly in the last century. Land cover changes, extensive agricultural activities and encroaching human settlement have dwindled forest coverage and hence, precipitation (Altmann et al., 2002; Agarwala *et al*., 2003). In addition to glacier retreat from 4.2 km^2 in

1976 (Hastenrath and Greischar, 1997)to 2.6 km^2 in 2000 (Thompson *et al*., 2002), it has been recorded to thin as well (Thompson *et al*., 2002). The glacier and forest changes have considerable implications in the agriculture sector over time in Kilimanjaro.

2.1.2 Effects of climate on species distributions

Insect species are ectothermic but various species differ in their physiological thermal tolerance, life – history strategies and dispersal abilities across latitudes and altitudes (Parmesan, 2006). Long term changes in climate affect the response and direction of some of these attributes (Olfert and Weiss, 2006; Sutherst *et al*., 2007), even to species that live in the same climatic region (Parmesan and Yohe, 2003). Numerous studies have documented various latitudinal range shifts of insects from the temperate to the North Polar Region in response to increased warming (Mikkola, 1997; Parmesan *et al*., 1999; Hill *et al*., 2002; Hickling *et al*., 2005). Some cool temperature – tolerant insect species shift latitudinally northwards where the thermal suitability still supports their optimal development and reproduction (Hickling *et al*., 2005). The sachem skipper butterfly expanded its range northwards from California to Washington State (420 km) in 35 years, with 75 km covered within a single year of 1998, which was the warmest (Crozier, 2003; 2004). Further south, the warming trends in low latitudes are associated with movements of tropical insect species into the temperate areas (Parmesan, 2006). The African plain tiger butterfly (*Danaus chrysippus*), prevalent in North Africa, established in southern Spain in 1980 and by the 1990 it had built into multiple, large populations (Haeger, 1999). The expanding ranges and insect shifts across latitudes can disrupt the coordinated timing between life cycles of predators and their prey, parasitoids and host insects, herbivorous insects and host plants; and pollinators and flowering plants, and ultimately resulting to adverse effects in ecosystem functioning (Harrington *et al*., 1999). Responding to hot dry spells, the butterfly *Euphydryas editha*shifts to the cooler microclimate for better phenological timing of emergence of its offspring when the nectar resources are widely available (Weiss *et al*., 1988). On the other hand, under extreme weather conditions, severe summer frost kills the host plant *Collinsia torreyi*, starving the butterfly and driving some populations to extinction (Thomas *et al*., 1996).

Distribution of many plant and insect species along altitudinal gradients can also be used to reflect the changing local climate (Strong *et al*., 2011). Temperature, precipitation, relative humidity, wind speed and radiation constitute the main environmental factors observed in changing climate along altitudes (Barry, 1992). Change of altitudinal gradients shows mixed responses in population distributions of different insects. In central Spain, the lower elevational limits of 16 species of butterfly rose by an average of 212 m in 30 years, concurrent with a 1.3°C rise in mean annual temperatures (Wilson *et al*., 2005). Descimon *et al*. (2006) showed the ability of the cool – adapted Apollo butterfly (*Parnassius apollo*) to disperse to higher elevations where suitable habitats exist. However, several insect populations decline with altitude e.g. ermine moth *Yponomeuta mahalebella* and delphacid bug *Ditropis pteridis* (Lawton *et al*., 1987; Alonso, 1999) while the common sawfly *Strongylogaster lineata* stands among a few which show no definite trend (Lawton *et al*., 1987). Variations in populations of herbivorous insect species along altitudinal gradients change the apparent levels of feeding damage to their host plants (Reynolds and Crossley, 1997; Alonso, 1999).

2.1.3 Climate change impacts on insect populations in agroecosystems

Optimal production of crops is subject to suitable climate conditions and timely availability of adequate input. Heat stress, evaporation and pest populations are some of common constraints affecting crop production (Thompson *et al*., 2010). Experiments demonstrate availability of high levels of carbon dioxide results into increased crop productivity (Long *et al*., 2004) but the increase is countered by the effects mediated by reduced moisture (Thompson *et al*., 2010). There is growing evidence that climate influences distributions of insect pests (Parmesan *et al*., 1999; Batalden *et al*., 2007; Trnka *et al*., 2007). Quick changing climate triggers a behavioral change in insect species that can prompt them to migrate and colonize new areas (Intergovernmental Panel on Climate Change, 2007) and/or shift expansion ranges (National Research Council, 2008). Huge climate change might even expose species to the risk of extinction (Thomas *et al*., 2004; Visser and Both, 2005). Climate also influences the phenology of insect pests (Parmesan, 2007) and their emergences (Dewar and Watt, 1992; Whittaker and Tribe, 1996). While the climate effects on insect pests will potentially lead to emergence of new pests and disappearance of others (Jepsen *et al*., 2008), natural enemies of insect pests will be affected in numerous ways and reshape the delicate insect pest-natural enemy dynamics (Stireman *et al*., 2005). To adapt to a changing climate, different species populations take hundreds or thousands of years to evolve but a few species can adapt relatively rapidly (Hendry *et al*., 2008). Changes in the cover patterns, as exemplified by forest clearing for agriculture, have exacerbated the temperature rise due to the lowered surface albedo and evapotranspiration rates (Pepin *et al*., 2015). The rising temperatures contribute to the global warming which is already disrupting insect populations by increasing the rate of growth and development and change the emergence patterns of insect pests, including diamondback moth (Dosdall *et al*., 2012).

2.1.4 Implications of climate change on insect interactions

Tritrophic interactions offer valuable insights into complex changes along altitudinal gradients. Examined individually, the levels of host insect parasitism by various host-specific insect parasitoids generally appear to decline with increasing altitude (Hodkinson, 2005). Coulson and Whittaker (1978) suggested that the searching efficiency and thus the efficacy of parasitoids is impaired under the cooler and misty conditions of higher elevations. The autumnal moth *Epirrita autumnata* Borkhausen (Lepidoptera: Geometridae) which feeds on mountain birch, is controlled by two main parasitoids: braconid wasp *Cotesia jucunda*in the low and eulophid wasp *Eulophus larvarum*in the highaltitudes (Virtanen and Neuvonen, 1999). Different species within or between different trophic levels do not necessarily react to climate change in a similar way (Schweiger *et al*., 2008).

2.2 Climate change and key natural enemies attacking diamondback moth

2.2.1 General life cycle of diamondback moth under different climates

The diamondback moth (Fig. 2.1) lays eggs singly or in small groups along veins in the leaf surface (Varela *et al*., 2003). The female may deposit close to 190 eggs in her life time (Harcourt, 1954).

Figure 2.1: Adult diamondback moth on a young cabbage plant

The newly hatched larvae penetrate the epidermis underside of the leaves and mine through it. During the early stages, the first instar larvae consume the succulent spongy mesophyll tissues inside the leaves (Varela *et al*., 2003). The second instars emerge out of the leaves and continue cutting round holes through the epidermis and scratch off the tissue (Talekar and Shelton, 1993). As the larvae grow further, they feed from the lower leaf surface and usually consume all tissue except the wax layer on the upper surface, forming windows in the leaves (Seif and Nyambo, 2013). Older larvae will eventually tear the leaves (Fig. 2.2). Once matured, a fourth instar larva spins a loose open lacework white cocoon which is attached to the leaves or stems of plants for pupation (Guo and Qin, 2010). Adults feed on pollen and nectars from flowers, honeydew secreted by aphids and water drops or dew (Talekar and Shelton, 1993).

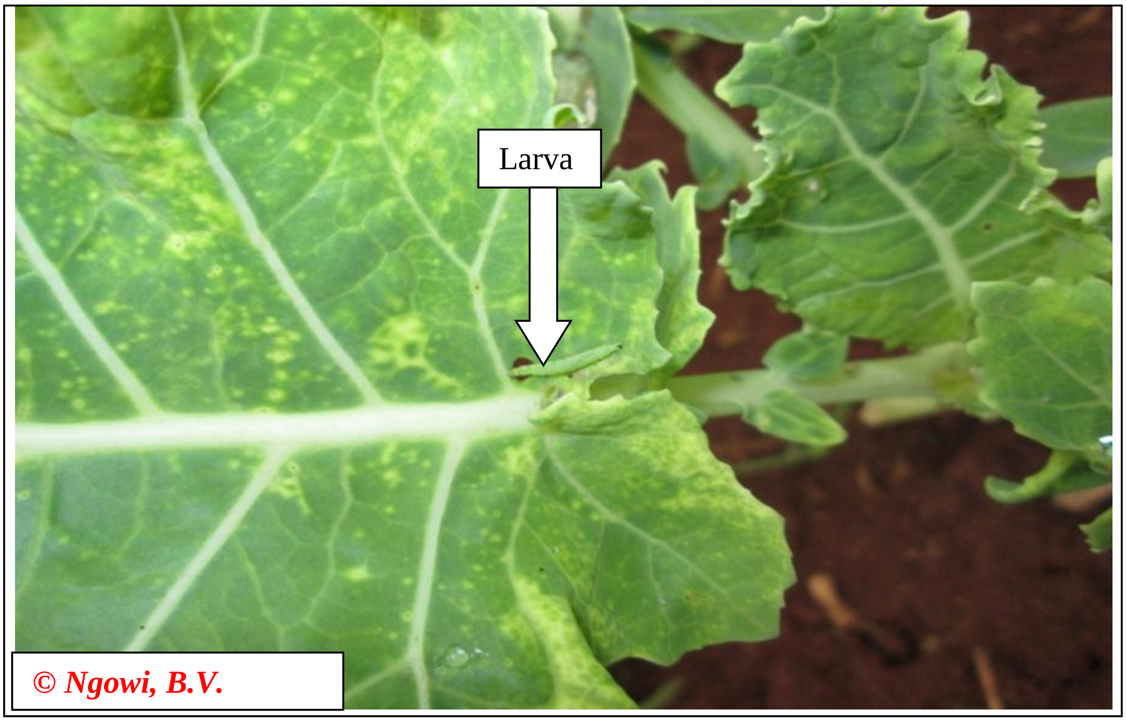

Figure 2.2: Larva of diamondback moth (see arrow) tearing a kale leaf when feeding

Temperature is known to increase the rates of development and reproduction of insects, which often results into added number of generations in a given time (Bale *et al.*, 2002). This can have negative implications on the yield of cultivated crucifers in lower parts of altitudinal gradients due to increased damage (Rasmann *et al.*, 2013). The ability of crops to compensate for the tissue loss after insect damage has also been shown to be affected by climate change (De Lucia *et al.,* 2012).

2.2.2 Natural enemies of diamondback moth

Various predacious arthropods, namely ground beetles, fire ants, syrphid fly larvae, lacewing larvae and spiders as well as parasitoids and entomopathogens can be important factors in controlling DBM. Of these, parasitoids are the main natural enemies of DBM in the region (Löhr, 2001a). Parasitoids are of enormous importance in natural and agricultural systems as they influence population densities of host insects (Godfray, 1994). The genus *Diadegma* (Hymenoptera: Ichneumonidae) which represents a group of about 200 parasitic wasps is known to occur worldwide (Yu and Horstmann, 1997) and is considered to be very effective in attacking the DBM larvae. It has been introduced to many parts of the world due to its superior performance in limiting the DBM populations (Waterhouse and Norris, 1987; Fitton and Walker, 1992; Khatri, 2011).*Cotesia vestalis* is another effective solitary larval parasitoid that is most widely distributed (Nofemela, 2004).

2.2.2.1 General life cycle of *Diadegma semiclausum* under different climates

The *D. semiclausum* is a solitary and specialist larval parasitoid of DBM which lays around 164 eggs during its lifetime (Abbas, 1988). Inside the host insect, the parasitoid larva consumes the host tissues and leaves the cuticle before pupation (Huang *et al*., 2008). The adult gnaws a small circular hole at the anterior end before emerging (Talekar and Lin, 1998). Emerged adults (Figure 2.3) mate immediately after eclosion (Abbas, 1988).

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Figure 2.3: *Diadegma semiclausum* adult male

During its life cycle, the development rate of *D. semiclausum* may varies with different agroecological gradients (Pellisier *et al*., 2012). Varying crop assemblages are common along altitudinal gradients due to different optimal climate requirements of the individual crop species. Different crops therein can interact with climate factors to affect the developmental performance of *D. semiclausum* (Dosdall *et al*., 2012). Extreme limits of climate play a big role in adversely affecting the parasitoid populations. Yang *et al*. (1993) reported sex ratio gets biased towards males as temperature exceeds 28°C, an observation which can translate into lower population growth and DBM parasitism in warm areas.

2.2.2.2 General life cycle of *Cotesia vestalis*

Unlike *D. semiclausum*, adult *C. vestalis* (Fig. 2.4) has many lepidopteran hosts besides DBM, including the green garden looper *Chrysodeixis eriosoma,* cotton bollworm *Helicoverpa armigera* and rice moth *Corcyra cephalonica* (Khan *et al*., 1991). However, DBM is the preferred host (Cameron and Walker, 1997; Cameron *et al*., 1997a). Oviposition in the second instar host larvae usually results into female offspring (Nofemela, 2004). Nofemela observed that each female lays an average of approximately 10 eggs/day during the first 2 days and a totalof 42 eggs in the first 5 days. The author further noted that the second and third instar host larvae warrant optimal development of the parasitoid, guarantee the best possible size and maximized physical fitness of adults. The parasitoid larvae feed on the host tissue and pupate mostly when the host larva is in the fourth instar stage (Wang and Keller, 2002). The eclosed adultsmate immediately and look for potential hosts for oviposition.


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Figure 2.4: *Cotesia vestalis* adult

Climate affects population dynamics of *C. vestalis* directly through pupae and adults and indirectly through DBM because the egg and larval stages develop inside bodies of the host larvae. Studies have shown that development time of the parasitoid is directly proportional to temperature between 13°C and 33°C, implying the parasitoid could be widely distributed in moderately warm to warm areas of the tropics. At a constant temperature of 35°C, both the parasitoid pupae and DBM larvae fail to complete development which points to a coevolutionary relationship between *C. vestalis* and DBM (Htwe *et al*., 2008). The response of organisms to changing climate can be different: extending life cycles, fewer numbers of instars and reduced temperature thresholds for developmentare some of common phenomena. The observations can get well pronounced onsteep altitudes because of rapid change of the weather patterns. The collembolan *Isotomurus alticola* develops a lesser number of instars in response to unfavourably short growing season in the high altitude.This is reported to affect the body size and fecundity adversely (Zettel, 2000).

2.3 Tritrophic interactions involving diamondback moth in crucifer agroecosystems

2.3.1 Altitudinal distributions of diamondback moth

Several biotic and abiotic factors, including plant phenology (Hodkinson, 1997), plant secondary compounds (Louda and Rodman, 1983), natural enemies (Koptur, 1985), temperature and rainfall (Hodkinson, 2005) affect the developmental performance of insect pests along elevational gradients. Diamondback moth occurs over wide agroclimatic conditions (Talekar and Shelton, 1993). The upper and lower altitudinal distribution limits of DBM are largely determined by ability to match its thermal tolerance range to altitudinal temperatures of the habitats (Hodkinson *et al*., 1999). In the laboratory, Bahar *et al*., (2014) demonstrated that DBM can survive and develop at temperature range from 4°C to 38°C, a range which is wider than one which is commonly found along altitudinal gradients of East Africa where crucifer vegetables are grown. Under changing climate, the pest is thus likely to shift its distribution towards more favourable temperature conditions. Despite their relevance as 'natural experiments' for studies investigating potential role of climate change on insect dynamics (Rasmann *et al*., 2013), very few studies have investigated the influence of altitudes in studying population dynamics of DBM. Two studies comparing the DBM performance between the lowland and highland agroecological systems in the region found the DBM population is more widely distributed in the highlands (Ayalew and Ogol, 2006; Kahuthia-Gathu, 2011).

2.3.2 Seasonal weather influence on diamondback moth population and parasitism

The life cycle of DBM is greatly influenced by weather variations in different seasons. This is particularly evidenced during hot and rainy seasons when the moth population sizes differ markedly (Harcourt, 1986). However, in temperate regions where crucifer vegetables are not grown all year round, it is not established very clearly whether the moth hibernates or not during the cold season (Talekar and Shelton, 1993). A few early studies (Miles, 1924; Theobald, 1926) suggested the perennial occurrence of DBM in this region could only be possible from hibernation of the pupae and/or adults in host plant debris during winter. However, in the two studies no moths were collected during the coldest month and brought out of hibernation to confirm the idea, which implies the DBM does not hibernate. In Honda (1993), it was demonstrated that DBM could not hibernate in Japan. The author observed that the moth migrated from the southern to northern parts to attack the crucifer vegetables during summer. Besides hot and cold temperatures, high humid conditions affect the pupation, hatching and emergence rates in DBM negatively (Ahmed and Ansari, 2009). The effects are profound on the emergence pattern of DBM in an environment where temperature is relatively stable (Guo and Qin, 2010).Of various environmental factors, rainfall remains a key mortality factor of the moth in the field (Talekar *et al*., 1985, Annamalai *et al*., 1988; Sivapragasam *et al*., 1988; Kobori and Amano, 2003). Rainfall interrupts the flight and mating activities of the moth which contribute to dwindling DBM populations (Talekar and Shelton, 1993).

Seasonal changes impose diverse effectson parasitoid populations, DBM and crucifer plants. Developmental rate of the host larva decreases with low quality of plant tissue available for consumption (Lindroth *et al*., 1993; Soufbaf *et al*., 2014). Host plant quality affects the fitness of adult parasitoids (Nofemela, 2004: Khatri, 2011). A similar phenomenon can be observed in the forest insect community where quality of the foliage increases when the buds get close to burst and any late hatching long after budburstwill deny the larval herbivores adequate food supply (Dewar and Watt, 1992), starving some of them to death and eventually decreasing the number of hosts available to parasitoids. Thomson *et al*. (2010) noted that the ability of adult parasitoids to withstand extreme seasonal changes relative to DBM; along with their movement rates, can be used to determine ability of parasitoids to track their hosts. However, very often DBM population travel long distances when favorable climate conditions deteriorate in search for new crucifer plantings. Uncorrespondingly low numbers of resident parasitoid population will likely not manage to limit the DBM population accordingly and in so doing, paving way for the build up of DBM populations, at least in the short term (Talekar and Shelton, 1993). Studying the seasonal incidence of DBM parasitoids in the region, Kahuthia–Gathu (2011) observed parasitoid populations decline during the rainy season but peakup during the dry season.

Climate gradients observed along the altitudes can present significant changes in observed seasonality of insects. Investigating seasonal incidence of DBM and its parasitoids in Kenya, Kahuthia-Gathu (2011) observed insect populations in the medium altitudinal zones varied from the high zones. Regardless of the season, the author reported increased incidence of DBM in the high zone but decreased incidence of parasitoid species in the same zone. This could have resulted from temperature variation along the altitude which limits the upper distributional limits of most warm-adapted parasitoid species (Hodkinson *et al*., 2005). The distribution of cold and warm-adapted insect species are largely determined by ability to match their thermal tolerance range with that available in their habitats (Hodkinson *et al*., 1999).

The effect of climate variability on seasonal phenology of host plants and its associated impacts on insects have been well documented (Hodkinson, 1997; Virtanen and Neuvonen, 1999; Hodkinson *et al*., 2001). The shifted timing of phenological events have been recorded to adversely affect productivity of host plants. Elevating the temperature levels around a biennial herb *Oenothera biennis* reduced herbivory rate from Japanese beetle *Popillia japonica* and resulted to increased seed biomass under warm conditions (Lemoine *et al*., 2017). The individual size of British bug *Craspedolepta nebulosa*, an insect pest of fireweed *Epilobium angustifolium*, is comparatively smaller upward the high altitudes of Haugastøl, Norway, than in the low altitudes. Such smaller size enables it to complete life history successfully under temperature-limiting conditions (Hodkinson and Bird, 2004).

The ability of DBM to thrive under wide temperature conditions and agro-ecology subjects it to varied parasitoid species. Its immature stages are attacked by about sixty parasitoid species worldwide (Delvare, 2004), fewer than over ninety previously suggested by Goodwin (1979). However, only about a dozen of parasitoid species have been found to be of economic significance in controlling DBM populations (Furlong *et al*., 2013). The parasitoid species attack all developmental stages of DBM (Delvare, 2004). Several relatively effective parasitoids have been introduced to different parts of the world: *D. semiclausum* and *Diadromus collaris* into the Far East, South East Asia and Kenya (Vos, 1953; Wilson, 1960; Ooi, 1992; Talekar and Shelton, 1993; Löhr *et al*., 2007); *D. semiclausum* into the Far East (Ventura, 1997; Talekar, 2004); India (Chandramohan, 1994) and Kenya (Löhr *et al*., 2008); *C. vestalis* into different parts of the world (Delvare, 2004; Talekar, 2004); and *Oomyzus sokolowskii* into China and Taiwan (Talekar, 2004). Successful colonization of parasitoids in a new habitat depends on several factors, including the surrounding environmental conditions. The DBM parasitism by *Diadegma mollipla* and *D. semiclausum* is more prevalent in the relatively cool areas (Manyangarirwa, 2009; Kahuthia-Gathu, 2011) than hot areas where *C.*

vestalis, *Apanteles sp*. and *Brachymeria sp*. are among the predominant parasitoids (Kahuthia-Gathu, 2011).

Change in climate indirectly influences diversity of insect pests and the respective parasitoid species across time and space (Van der Putten *et al*., 2004). Temperature and carbondioxide changes present some of the global environmental changes which contribute to increased frequency of herbivory on plants and destabilize incidences of parasitoids (Tylianakis *et al*., 2008). During cold spells, the *Epirrita autumnata*, a polyphagous defoliator, continues to feed while activities of its parasitoid species cease, resulting to extensive plant damage (Virtanen and Neuvonen, 1999). High summer temperature therefore increases the number of parasitoid species and enhances their mobility to new areas as opposed to cooler temperatures. Also, the increase in rainfall sustains the availability of soil moisture content which in turn supports the emergence of many host plants from seed bank in the soil. The resulted plant richness avails abundant food supplies for insect pests and adult parasitoid species (Petermann *et al*., 2010).

The degree of DBM parasitism is determined by several factors, including nutritional content of the host plant species (Wakisaka *et al*., 1992; Syed and Abro, 2003; Sarfraz *et al*., 2006; Golizadeh *et al*., 2009), availability of quality moth stages and weather (Godfray, 1994; Nofemela, 2004; Khatri, 2011). The quality of host plants influences directly the growth, survival and development of DBM and indirectly, the fitness of parasitoids through the unhealthy host larvae. The moth larvae that feed on young plants attract more parasitism than those feeding on old plants probably because of the high nutritional component (Talekar and Yang, 1993). The authors further observed that the DBM parasitism by *D. semiclausum* increased when the larvae fed on the head cabbage *B. oleracea* var. *capitata* than on cauliflower *B. oleracea* var. *botrytis*, broccoli *B. oleracea* var. *italica* and Chinese cabbage *B. pekinensis*. In the same experiment, the *C. vestalis*–caused DBM parasitism peaked when the larvae foraged on Chinese cabbage compared to the other three host plants. In separate investigations, other researchers have linked such different performances to different quality of the host plants (Singh and Singh, 1982; Golizadeh *et al*., 2009).

To limit the DBM population effectively, the individual parasitoid species have to forage in a habitat which is ecologically suitable for their survival, development and fecundity. However, most parasitism rates of insect pests, including DBM, decline with altitude. The parasitism rate of common rush case bearer *Coleophora alticolella* by parasitoid wasp *Scambus brevicomis* declines to zero before the maximum altitudinal range limit is reached (Randall, 1982).

2.4 Temperature-dependent phenology of insects

Insects are poikilotherms with very limited ability to control external temperatures, hence temperature remains an important factor determining their life cycles (Fand *et al*., 2014). Below the maximum thermal limit, temperature increases the rate of growth, development and fecundity. When insects sense temperature levels change and approach the lower or upper limits, they may switch behavior and physiology to adapt to the changes (Furlong *et al*., 2013). Phenology, which refers to timing of life cycle in relation to weather, becomes increasingly apparent with seasonal change. Several authors have demonstrated phenology change of species with respect to seasonal change during the last six decades (Parmesan, 2006). Temperature-dependent phenologies of insects often change with huge temperature variations (Cornelissen, 2011). Many insects initially respond by shifting to areas deemed favourable with temperature ranges (Chapman *et al*., 2002; Hodkinson, 2005; Parmesan, 2006).

Phenology models refer to mathematical expressions which portray the physiological pattern of insect development, fecundity and growth under a varying climate to mimic and forecast population dynamics in the field (Marchioro and Foerster, 2011; Kroschel *et al*., 2013; Fand *et al*., 2014; Tonnang *et al*., 2014). Developing temperature-dependent phenology models can provide fresh insights needed for better preparations against potentially serious pest outbreaks (Fand *et al*., 2014). The generated information can be used in designing and implementing location-specific pest control strategies in the context of predicted climate change (Khadioli *et al*., 2014a).

The temperature-dependent phenology models of DBM have been studied in different parts of the world, including Iran, Brazil and United States (Golizadeh *et al*., 2007, 2009; Marchioro and Foerster, 2011, 2012; Bahar *et al*., 2014). Studies on temperature-based phenology of natural enemies of DBM are comparatively fewer and have focused on a small number of key parasitoid species, namely *D. semiclausum* (Yang *et al*., 1993; Dosdall *et al*., 2012), *C. vestalis* (Lim, 1982, Nofemela, 2004, Htwe *et al*., 2008) and *O. sokolowskii* (Talekar and Hu, 1996). Life table studies have shown DBM can survive and develop at 19 different constant temperatures tested in laboratory, ranging from 8°Cto 32°C and over 14 outdoor temperatures, ranging from 4°C to 38°C (Liu *et al*., 2002). Studies on *D. semiclausum* under laboratory conditions have shown its fecundity is impaired at > 30°C (Yang *et al*., 1993) contrary to *C. vestalis* and *O. sokolowskii* which have demonstrated to thrive better under the relatively hot conditions (Talekar and Hu, 1996; Htwe *et al*., 2008). Temperature-dependent phenology of insects developed at constant temperatures in laboratory can be linked to outdoor field temperatures and Digital Elevation Model (DEM) in Insect Life Cycle Modeling (ILCYM 3.0) tool to generate insectactivity indices, which can be mapped for depicting the insect abundance and distribution (Kroschel *et al*., 2013).

2.5 Stability of pest-natural enemy interaction

Stability of pest-natural enemy interaction contributes greatly to success of any biological control program. However, there are a number of factors, including temperatures, which have been recorded to be capable of destabilizing such interaction (Parmesan, 2006). In one study, Van Nouhuys and Lei (2004) showed that by basking in the sun during the cool air temperatures, the larvae of butterfly *Melitaea cinxia* escape parasitism from the parasitoid wasp *Cotesia melitaearum*. The parasitoid cocoons develop in the shade and become adults long after the butterfly larvae have pupated and are no longer available for parasitism. In another observation, Visser and Both (2001) found that the rising minimum temperatures in northern Europe prompt the tropical pied flycatcher to migrate northwards in search of resident caterpillar prey. The timing of emergence of natural enemy offspring and abundant availability of foods is crucial for successful control of pests (Hoover and Newman, 2004). The insectivorous bird, the great tit (*Parus major*) feeds its nestlings on caterpillars of winter moth (*Opheroptera brumata*) available mainly during a short period in the spring (Visser and Both, 2005). Such a narrow window of availability pressures the great tit to time its reproductive cycle such that the needs of the nestlings match the peak abundance of caterpillars to avoid development of fewer and weak offspring (van Noordwijk *et al*, 1995; Verboven *et al.*, 2001). Montane studies on the effects of elevation-driven climate change on host insect-natural enemy interaction are very scarce and less documented (Parmesan, 2006). Few studies have been conducted in the region to address the influence of climate change on insect pest-host plant and insect pest-natural enemy interactions along elevations. Okonya and Kroschel (2013), found the consistent decrease of crop damage upward the altitudinal transect in Kabale district in Uganda corresponded to the declining population of sweet potato butterfly. Some findings from a more comprehensive study in Tanzania have predicted potential disruptions on the distributions of maize stem borers *Chilo partellus* and *Buseola fusca* and their respective parasitoids *Cotesia flavipes* and *C. sesamiae.* Such interruption will weaken the biological control in the medium altitude (Mwalusepo *et al.*, 2015).

Different plants have evolved direct and indirect defence mechanisms against insect pest damage. Direct plant defences obstruct or reduce the performance and damaging behavior of insect pests on crops. Development of spines and thick wax layers are examples of direct defences which interfere with establishment and movement of pest on the plant (Schoonhoven *et al*., 2005). Other defence adaptations include development of toxins and digestibility reducers which lessen the growth and survival of the pests. Indirect defence traits refer to plant behaviors that enhance the effectiveness of natural enemies of the pest. Development of evolutionary adaptation of natural enemies to such indirect defence traits by crucifer plants presents the interface between the two trophic levels which are fundamental in tritrophic interactions. Provisioning of alternative food and habitats, and attraction to insect Herbivore-Induced Plant Volatiles (HIPV), are some of the common indirect plant defences (Gols, 2008). Parasitoid species can use HIPV to locate plants infested with their host insects (Sabelis *et al*., 1999; Turlings *et al*., 2002). Development of direct defence is also associated with production of secondary chemical compounds which impair development and survival of insect pests. Glucosinolates are non-volatile chemical compounds, for instance, common in all cruciferous plants and serve to protect them against several insect pests (Hopkins *et al*., 2009; Textor and Gershenzon, 2009). The compounds have been shown to adversely affect the fitness and survival of many insect pests that attack crucifers and other plant species (Feeny, 1976) but not DBM. Specialized to attack crucifer plants, DBM has evolved a glucosinolate detoxification mechanism in the gut (Ratzka *et al*., 2002) that renders it harmless on its larval performance (Li *et al*., 2000; Gols *et al*., 2008; Muller *et al*., 2010). On the other hand, when DBM damage host plants during feeding, the damaged parts emit HIPV which attract its parasitoids (Dicke, 1999; Turlings *et al*., 2002). The HIPV therefore play an active role in the host-searching behavior of parasitoids against DBM larvae (Turlings *et al*., 2002) by providing clues for them to locate their hosts. As a result, the parasitoid oviposition to DBM helps to limit the pest population and hence relieve crucifer plants from the pest load. The silk thread secreted by DBM to suspend it on air immediately after it has been disturbed has also been shown to serve as a visual clue to DBM parasitoids, notably *D. semiclausum*, when searching for DBM (Wang and Keller, 2002).

Diamondback moth also attacks wild crucifer species which very often are some of the weeds commonly found in crucifer vegetable farms in East Africa (Kahuthia-Gathu*et al*., 2008). Most weeds have higher amounts of glucosinolate compounds than in cultivated crucifers. Such high amount is thought to contribute to poor development and survival of the generalist and a few specialist insect pests along with their parasitoids (Gols *et al*., 2008). The author suggested that centuries of domestication of cultivated crucifers may have disorientedthe chemical componentof cultivated crucifers and lowered the amount of glucosinolates. When present on farm, the population density of DBM is therefore frequently higher in the cultivated than wild crucifers. Nonetheless, wild crucifer weed species offer the moth with substitute hosts for feeding and oviposition; and its parasitoids for nectar resources, when the cultivated crucifers get old or are no longer available (Kahuthia-Gathu*et al*., 2008). The author also observedthat significant numbers of DBM return to crucifer vegetables once a new crop is replanted in the subsequent growing season.

The cultivated crucifer species are grown under different agroecological conditions in the region which are characterized by varying climate. The altitudinal landscape of the crucifer agroecosystems presents an opportunity to investigate the role of climate change on crucifer-DBM-parasitoid interactions. A few studies have used altitudinal gradients to model the potential effects of climate change on insect interactions (Rasmann *et al*., 2013; Mwalusepo *et al*., 2015). The parasitic interaction of stem borer *Chilo partelus* and hymenopteran wasp *Cotesia sesamia* is predicted to weaken under the increasing altitude due to their growing discrepancy in response to altitudinal change (Mwalusepo *et al*., 2015). The researchers noted the opposing changes in the altitudinal distributions might also signal the phenological asynchrony between the pest and its parasitoid by 2055. Under this climate change scenario, the insects are predicted to shift distributions in opposing directions with a potential of weakening their phenological match and thereby resulting in increased pest outbreaks. On the other hand, a study has linked decreased crop damage upward the altitude when the pest is subjected to increased unfavourable climate conditions and plant resistance (Rasmann *et al*., 2013).

2.6 Cost benefit analysis of biological and chemical control

The level of crop damage imparted by agricultural pests and invasive weeds differs with insect species, crop stage, weather variability, pest behavior and management measures. The annual global costs of insecticide applications against DBM alone in crucifer vegetables amount to US$ 1.4 billion. The cost increases to US$ 2.7 billion if yield losses are considered (Zalucki *et al*., 2012). The pest is reportedly to have contributed a cabbage yield loss of 31% in Kenya, which is translated to 6.8 tons/ha (Macharia *et al*. 2005). Intensive applications of insecticides have resulted to significant resistance in the region (Kibata, 1996). A report by Jankowski *et al*. (2007) has shown that the application of insecticides against DBM in Nyeri County in Kenya is higher than that applied in Arumeru and Lushoto districts in Tanzania altogether, and yet the Nyeri farmers collected much fewer revenues compared to their counterparts. A mango mealy bug *Rastrococcus invadens* Williams (Homoptera: Pseudococcidae) caused direct devastative losses in mango yields in Benin, Ghana and Togo (Agounke *et al*., 1988). The authors further noted the pest secreted honeydew which attracted black sooty mould that interfered with photosynthesis. In water bodies, prolific multiplication of water hyacinth in Lake Victoria destroyed extensively the fish breeding sites, interfered with navigation and clogged irrigation canal and fresh water sources (Makhanu, 1997). Chemical control of agricultural pests by application of insecticides in the developed nations is extensive and generally favoured because of its immediate effects, particularly because it seems economically practical when the pest scouting exercises are inadequate and being there is little work force (Nansen and Ridsdill-Smith (2013). Several methods have been adopted to address problems triggered by the intensive application of pesticides, including insecticide resistance. Biological control has been one of the very effective methods used against DBM. Introduction of *D. semiclausum* in Kenya reduced the yield loss by 30%, production costs by 7.9% which resulted to increased yields by 6.8 tons/ha and a benefit-cost ratio of 24:1 (Macharia *et al*., 2005). The introduction of *Gyranusoidea tebygi* against the mango mealy bug in Benin resulted to the recovery of mango productivity from 26 kg/tree 84 kg/tree and a benefit-cost ratio of 145:1 (Bokonon–Ganta *et al*., 2002). Efforts to control water hyacinth in southern Benin led to benefit – cost ratio of 124:1 (De Groote *et al*., 2003). The benefit-cost calculations in DBM biological control focused on yield loss reduction in cabbage only and do not quantify the accrued benefits from the increased safety of farmers and consumers (Macharia *et al*., 2005).

2.7 Implications of chemical and biological control of pests on biodiversity

Application of pesticides in agriculture has been rising steadily since the World War II. Pesticide application is very intensive and forms an integral part of crop production in Europe and North America (Isenring, 2010). The numbers of pesticide-treated farmlands in the United Kingdom expanded by 30% from 1990 to 2016 (Fera, 2009). Intensifying crop production methods by including pesticides have largely been responsible for the decline of weed and not-target plant species by half, insect species by a third and bird species by four-fifths (Robinson and Sutherland, 2002). Several factors account for the decline of plant insect species populations including the level of pesticide toxicity, quantity applied, frequency, timing, application method, weather and vegetation structure (Isenring, 2010). Broad-spectrum herbicides are particularly threatening because they deprive the quantity of weeds eaten by the pests which form important part in food webs. In Canada, intensive insecticide applications have been linked to sixty two species which are at low populations and near extinction (Gibbs *et al.*, 2009). Intensive insecticide use has also been reported to account for 85% of death cases of honey bees reported from 1995 to 2001 in United Kingdom (Fletcher and Barnett, 2003). Non-regulated insecticide applications in the new agricultural lands bordering the Amazon forests in Brazil destroyed more natural enemies than insect pests of new established crops (Schiesari *et al.*, 2013).

The implication of the classical biological control on biological diversity rests mainly on a scenario whether the practice increases or lessens the biodiversity in a target location. Huffaker and Messenger (1964) argued that introduction of different natural enemies provide a stronger and stable containment of pests. The successful containment stems from the cumulative stress model whereby the pest activity is controlled because of the integrated actions of different natural enemies from diverse functional groups (Denoth *et al.*, 2002). The ecological concepts of niche partitioning and complementarity underline the model (Evans, 2016). However, validity of the cumulative stress model has been subject to scrutiny when the introduction of one natural enemy has proved to be able to suppress the target pest (Louda, 2003, McEnvoy and Coombs, 2000). Cases of the ignorance of potential effects of natural enemies on non-target pests; and competition among themselves, which can lead to killing each other, have been cited to demonstrate shortcomings of multiple introductions of natural enemies (Ehler and Hall, 1982; Polis and Holt, 1992; Cardinale *et al.*, 2011) and emphasize on limiting the pest population (Evans, 2016).

CHAPTER THREE: SEASONAL ABUNDANCE OF DIAMONDBACK MOTH AND DIVERSITY OF ITS PARASITOIDS ALONG ALTITUDINAL GRADIENTS OF MOUNT KILIMANJARO AND TAITA HILLS

3.1 Introduction

Weather influences variability of diamondback moth (DBM) field population. Rainfall is a key variable capable of destabilizing such field populations (Mosiane *et al*., 2003; Ahmad and Ansari, 2010; Sow *et al*., 2013). The DBM populations respond to seasonal variability, agroecological structures and natural enemies (Kahuthia-Gathu, 2011). The survival and reproduction rates of DBM have been recorded to be influenced strongly by temperature and host plants (Shelton *et al*., 1991; Syed and Abro, 2003; Golizadeh *et al*., 2007; Golizadeh *et al*., 2009).

Seasonal changes modify the temporal and spatial population dynamics of insects (Menzel and Dose, 2005). A change in diversity of the natural enemy community due to different response to seasons can hamper temporarily the effectiveness of biological control of a pest to the detriment of crops. Along a spatial agroecological scale, when an insect pest and its natural enemies react to a changing climate by shifting into different directions and patterns, they might end up colonizing dissimilar ranges (Hodkinson, 2005). Very often, such shifts have been recorded to lead to pest out breaks and increased yield losses (Parmesan, 2006). It is in this view an assessment was undertaken to establish the degree of dispersal and spread of *Diadegma semiclausum* and *Cotesia vestalis* 11 years after their first field release for controlling DBM in Kenya (Löhr*et al*., 2007) and a decade after releasing *D. semiclausum* in Tanzania (Nyambo and Löhr, 2005). Investigation on the influence of seasonal changes on population dynamics of these insects along the altitudinal gradients of Mount Kilimanjaro and Taita hills can help evaluate the current status of biological control of DBM by the parasitoids. It is especially important to know the fate of *C. vestalis* because the preliminary surveys in Mt. Kilimanjaro indicated presence of *C. vestalis* although there are no documented records for its release in Tanzania.

Diamondback moth has been reported worldwide. The pest has been recorded throughout the year in Pathum Thani province in central Thailand but its population size differs among seasons and between regions with routine and infestation – based insecticide spraying regimes (Kuwahara *et al*., 1995). In Kenya, crucifer damage from DBM is reportedly serious during hot dry season than in the rainy season (Kahuthia-Gathu, 2011). However, variability of the moth population is also subject to its natural enemy population and the local environmental conditions, including topography, weather and crucifer plants. Information on the seasonal population dynamics of DBM is essential for determining the appropriate timing of management strategies e.g. insecticide application to reduce the moth population in the field (Kuwahara *et al*., 1995). Adoption of the augmentation strategy in biological control of pests, one which requires information on the abundance of insect pests beforehand, can be very effective after knowing the seasonal incidence of insect pests. This is even more important in the lowland areas of Mt. Kilimanjaro and Taita hills where farmers apply insecticides as the main method of controlling the pest. Further to this, although DBM causes significant yield losses in crucifer vegetables, its status has not been established, at least in Kilimanjaro.

In this regard, the main objective of this study was to establish changes in the seasonal population dynamics of DBM and its parasitoids, as well as the diversity of its parasitoids along altitudes of the eastern Afromontane region of Mt. Kilimanjaro and Taita hills. The generated knowledge will likely shed light towards improvement of the integrated pest management (IPM) package of DBM under different seasons and agroecology.

3.2 Materials and methods

3.2.1 Study sites

Two sites were chosen for this study: Mt. Kilimanjaro located in north-eastern Tanzania and Taita hills in the southern Kenya. The field work was conducted along the slopes of south eastern Mt. Kilimanjaro in Moshi rural district – Tanzania and Taita hills located in Taita – Taveta County, in southern Kenya. Mount Kilimanjaro is a large dormant stratovolcano estimated to have been formed during formation of the Great Rift Valley about three million years ago. The location of Mt. Kilimanjaro is between 03°378'S, 37°450'E and 03°481'S, 37°456'E. Several crops are cultivated on its adjacent plains at the base of the mountain at around 700 metres above sea level (metres a.s.l.) to 1800 metres a.s.l. at the edge of the montane forest. The forest is protected under the Kilimanjaro National Park. Taita hills form the northern-most tip of the Eastern Arc Mountains, a chain of ancient geologic mountains which extend from the south-eastern Kenya to Udzungwa in the south-western Tanzania (Bennun and Njoroge, 1999). The mountains are rich in flora and fauna and many species are endemic (Newmark, 2002). Taita hills are characterized bythree compact groups of massifs: Sagalla in the southern region of Voi town, Kasigau towards the Tanzanian boundary and Dabida in south west of the county. Dabida is the largest and tallest of the three, with the peak in Vuria. The steep elevation and closeness of Mt. Kilimanjaro and Taita hills to the coast provide the southern and south eastern parts of the two areas withthe warm Indian ocean currents which cool down upward the mountains and avail precipitation for most crop production (Hemp, 2006), including crucifer vegetables. The moisture-loaded winds also sustain the moist tropical forests and rich biodiversity in the high altitudes contrary to the low altitudes. The high altitudes of Mt. Kilimanjaro and Taita hills form water tower catchment areas for the lowland areas of Moshi and Voi towns.

This study was conducted along two 1 km wide altitudinal transects, located along the south-eastern windward side of Mt. Kilimanjaro in Tanzania (700 metres a.s.l. to1,692 metres a.s.l. (Fig. 3.1) and along the southern windward side of the Dabida massif for the Taita hills in Kenya; (700 metres a.s.l. to 1,785 metres a.s.l.) (Fig. 3.2). The transects were sub-divided into three smaller blocks, termed altitudinal zones, based on the mean annual temperature and microclimate: low (700 metres asl. to 1,200 metres asl.), medium (1,201 metres asl. to 1,600 metres asl.) and high (> 1,600 metres asl.) as previously defined by Ngowi *et al*. (2017a, b). Each altitudinal zone was composed of four farms. Inside each farm, a diagonal transect was established for further studying wild crucifer weed species.

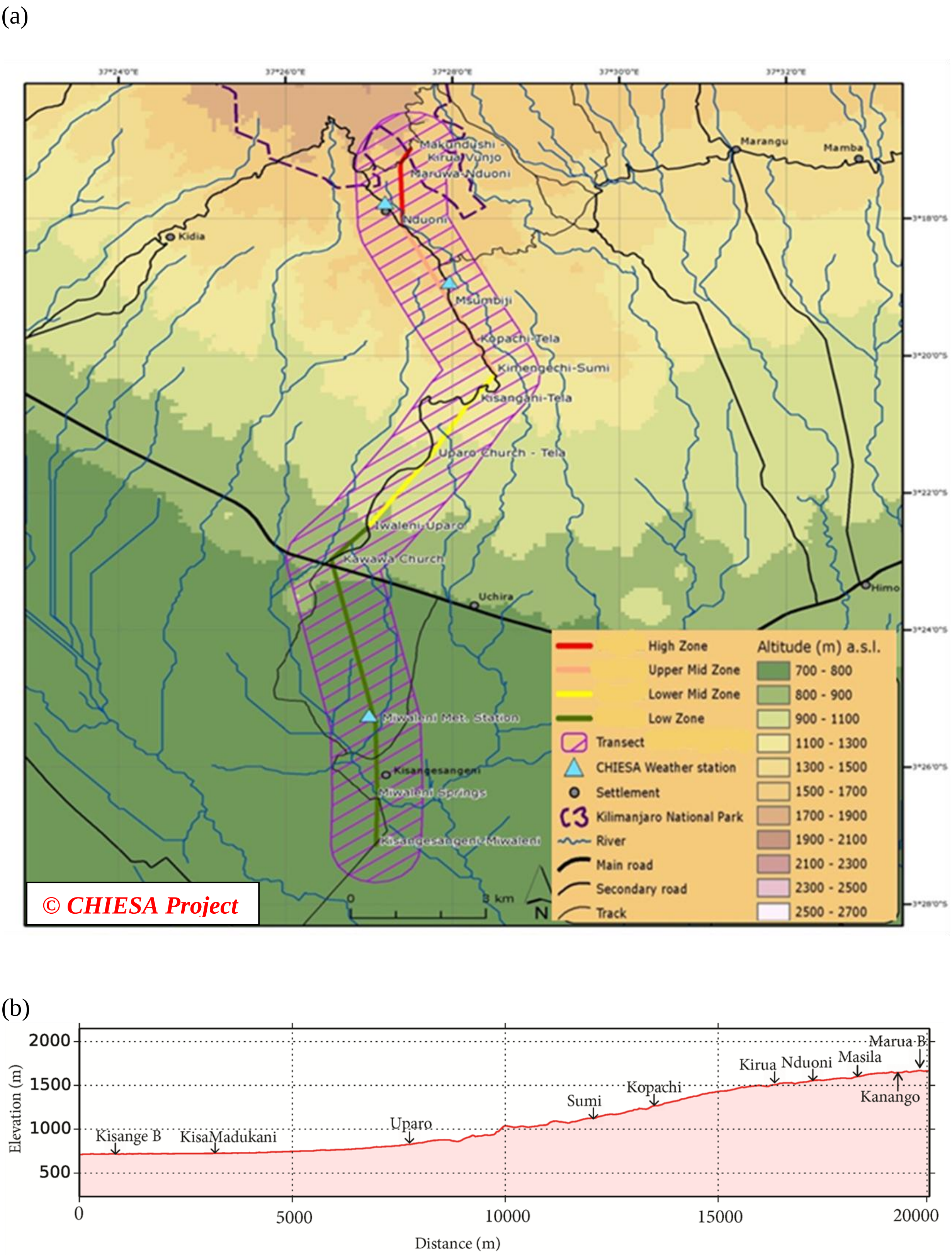


Figure 3.1: Locations of representative farms on Mount Kilimanjaro altitudinal transect in Tanzania**:** (a) topographical map showing physical features along the altitude; (b) cross-sectional altitudinal profile of Mt. Kilimanjaro transect

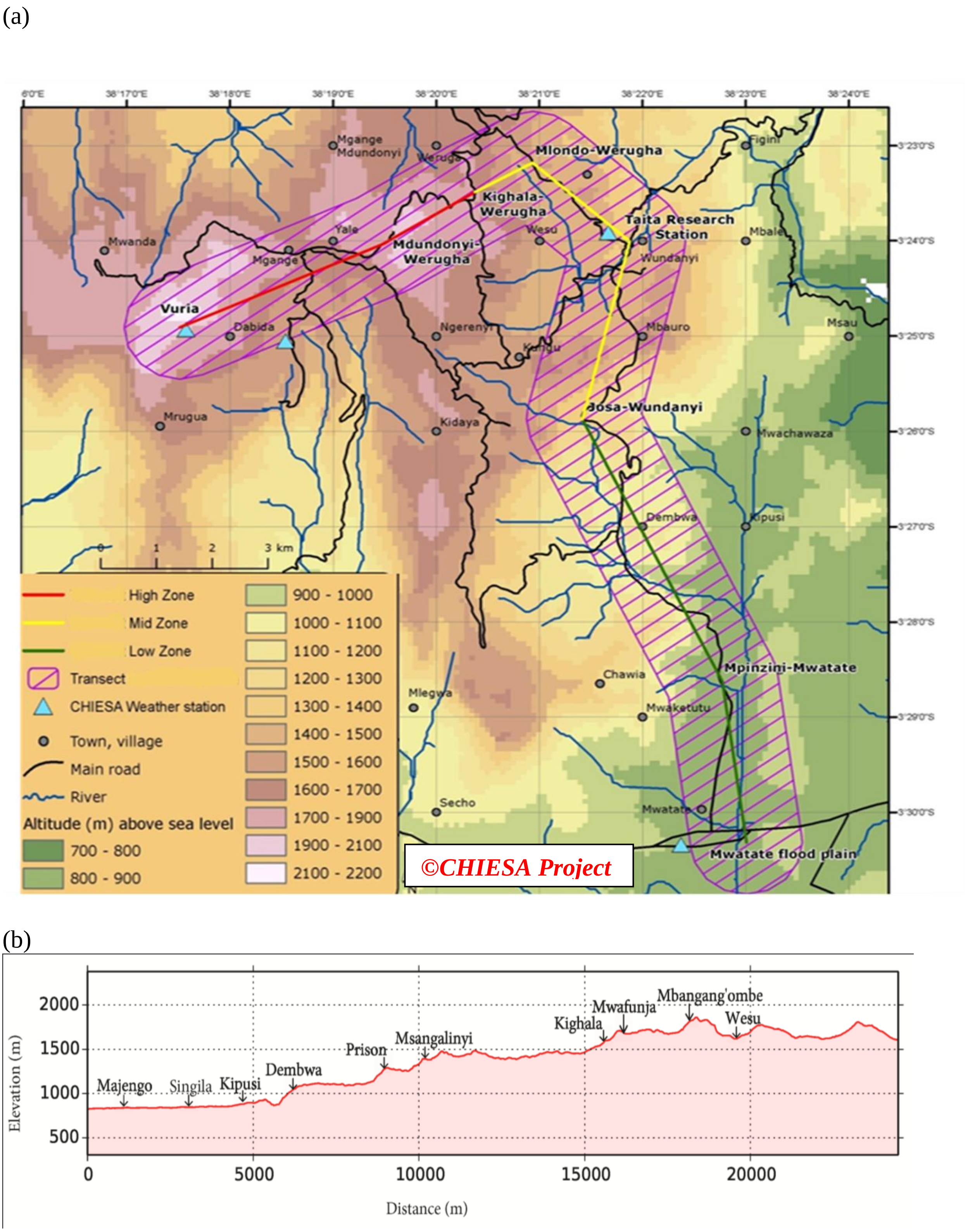


Figure 3.2: Locations of representative farms on Taita hills altitudinal transect in Kenya**:** (a) topographical map showing physical features along the altitude; (b) cross-sectional altitudinal profile of Taita hills transect

3.2.1.1 Mount Kilimanjaro transect

The lowland area of the altitudinal transect is composed of open crop lands and small fragments of bush lands. The soil is normally young and chiefly constituted of eutric fluvisols (De-Pauw, 1984). The average annual temperatures have been recorded to be 33°C below 900 metres a.s.l. (United Republic of Tanzania Kilimanjaro Region Socio-Economic Profile, 1998). The rainfall pattern is unpredictable and ranges from 400 mm to 900 mm/ annum (Soini, 2003). Supplementary irrigation is widely practiced during the dry season, utilizing water from wells built on several farms and from the nearby Miwaleni springs. Vegetational complexity of the crop and bush lands altered gradually to Chagga homegardens in the medium zone, where the mean annual temperature is around 26°C (Hemp, 2006). Majority of the soil is haplic phaeozem (De-Pauw, 1984). Rich with humus on the surface layer, the soil is permeable with well aggregated structure. According to Fernandes *et al*., (1984), the homegarden is an agroforestry-based cropping system whose vegetational complexity is characterized by distinct vertical pattern: food crops and fodder herbs (less than 1 m), coffee (from 1 m to 2.5 m), bananas (from 2.5 m to 5 m), fodder and firewood trees (from 5 m to 20 m) and multipurpose trees (more than 20 m). Furrow irrigation and application of farmyard manure constitute some of key components in sustenance of the homegardens (Fernandes *et al*., 1984). The structural complex of vegetation in the homegardens gets richer with increasing altitude in the high zone (Hemp and Hemp, 2008). Two distinct rainy seasons exist in the medium and high zones: long rains from March to May and short rains from October to December. The amount of rainfall in the medium zone is lower (1000 mm – 1500 mm) than in the high zone (1400 mm to 2000 mm) (Zongolo *et al.,* 2000a, b). The amount and frequency of rainfall rise with increasing altitude (Zongolo *et al*., 2000 a,b). With the average annual temperature of 24°C (Hemp, 2006), this is the least in the three zones. The soil is dominated by humic nitisols (De-Pauw, 1984), which are characterized by deep, well-drained and most fertile soils. The number of farmers growing crucifer vegetables in the low zone is small and they are widely dispersed but the number increases and distance between farmers shrink towards the high zone. Population density is high (650 people / km^2 in the high zone and 250 people / km^2 in the low and medium zones (Zongolo *et al*., 2000)). Farming activities are extensively diversified and are the main means for earning the livelihood. Maize and beans are often intercropped in the low and medium zones. Other crops commonly grown in the zones include bananas, fingermillet, sunflower, sweet potatoes and assorted vegetables and fruits (Aminu-Kano *et al*., 1992). Besides banana and coffee in the homegardens, beans, potatoes, yams, taro, cabbage, tomatoes and eggplant are common crops, to mention a few (Fernandes *et al*., 1984). Crucifer vegetables are grown for household consumption and income generation. Livestock keeping system is normally zero grazing. Fodder grasses are grown in the homegardens, along the contours, on the borders and also some are transported from the low zone (Mlambiti, 1985). Many farmers in the medium and high zones also keep bees traditionally (Fernandes *et al*., 1984).

3.2.1.2 Taita hills transect

Undulating hills form the main topography pattern of the Taita hills. The low zone is fragmented into bush lands with dryland agriculture widely practiced. The mean annual temperature is about 27.3°C (Njuguna *et al*., 2015). Largely constituted by red weathered soils resulted from metal oxides, rhodic ferralsols constitute most of the low zone (Njuguna *et al*., 2015). Sisal farming, maize, millet, sorghum and livestock grazing is dominant in the foot hills and adjacent plains (Maeda, 2011; Boitt *et al*., 2014). Crucifer cultivation during the dry season is sustained largely by supplementary irrigation from wells. The altitudinal gradient gets steep closer to the medium zone, along with the increased tree vegetation. The mean annual temperature lowers to about 21.4°C in the medium zone, and further down to 19.4°C in the high zone (Njuguna *et al*., 2015). With many undulating hills, most valley bottoms retain moisture for long intervals after the rainfall sessions. Cultivation of crucifers is common in these valleys. The soil is largely composed ofhumic cambisols and nitisols, particularly in the medium zone (Njuguna *et al*., 2015). Such soil has got aggregate structure with a good drainage and clay content, attributes which are deeply exploited for agriculture.The high zone is largely characterized of cambisols. The transect receives bimodal rainfall: long rains from March to Mayand short rains from October to December. Maeda (2012) recordeda rainfall range of 500 mm-1000 mm in the low zone; 1000 mm-1400 mmin the medium zone and over 1400 mm in the high zones. Most rivers in the low and medium zones have dried up and remain seasonal. Agriculture is the main stay of the economy with maize, beans, peas, potatoes, cabbage, tomato and banana being some of the most common crops (Soini, 2005). Crucifer vegetables are grown for household consumption and alternative source of income. The population growth shows a steady increase from 110,742 in 1969 to 147,597, 207,273, 246,671 and 284,657 people in 1979, 1989, 1999 and 2009, respectively (The Population and Housing Census, 1999; Kenya National Bureau of Statistics, 2009). The population growth increases at a rate of 1.8% per annum. The population density varies extensively from 3 people per km^2 to as high as 800 people per km^2. The average population density in 1999 was 14 people per km^2 (Kenya National Bureau of Statistics, 2009). The least population is found in the erosionally-sensitive dry lowlands and the highest in the rich and fertile rainy highlands.

3.2.2 Selection of farms

Four farms were selected purposively in each of the three altitudinal zones along the two transects. A total of twelve farms were therefore selected in Mt. Kilimanjaro transect and twelve other farms in Taita hills transect. The selection based on whether either a crucifer vegetable crop species e.g. kale, cabbage or Ethiopian mustard, was present on farm, and with adequate abundance for sampling. When different crucifer vegetable crops were present, only one crop species was selected for sampling DBM and its parasitoids. Another criterion for farm selection includeddistance between farms (≥ 100 m) and the random occupation of the farms within the 1 km width of the transect. A portable Global Positioning System (GPS) receiver, Garmin eTrex 30 brand, produced byGarmin International Inc. Taiwan, was positioned in middle of the individual surveyed farms for recording on site the latitudes, longitudes and altitudes.

3.2.3 Sampling of the diamondback moth and its parasitoid species

Crucifer vegetables and wild crucifer weed species in the two study transects were observed for DBM and its parasitoid species every month for two consecutive years (from January 2013 to December 2014). The monthly observations were grouped into four seasons: hot dry season (January to February), long rainy season (March to May), cold dry season (June to September) and short rainy season (October to December). A purposive sampling of twenty infected plants from one crucifer vegetable species (either kale, cabbage or Ethiopian mustard) was conducted from each individual farm and all the leaves physically checked, both undersides and uppersides, for presence of the larvae and pupae of DBM. A mini transect of 2 m wide going diagonally from one corner of the farm to another corner in the opposite edge, was established for surveying twenty wild crucifer species under purposive sampling. Wild crucifer species were identified with the help of plant taxonomist and a field identification guide as a reference material (Flora of Tropical East Africa, 2012). Several specimens of wild crucifers were collected from Mt. Kilimanjaro and taken to the National Herbarium of Tanzania for correct identification. Each individual leaf of the purposively selected wild crucifer plants was also physically checked for DBM. The number of the larvae and pupae observed on the individual plantswas recorded. Transparent plastic containers, measuring 12 cm X 10.2 cm X 6.5 cm, were utilized to pack the larvae and pupae collected from the individual farms. Samples which were collected from crucifer vegetables were separated from those collected from wild crucifer weed species. Lined with paper towels at the bottom, which were inserted to absorb excess moisture, all containers were closed with perforated lids. The perforations contained fine muslin clothes for ventilation. The larvae were supplied with fresh leaves of kale, cabbage or Ethiopian mustard for those collected from cultivated crucifers and wild crucifer weed leaves for those collected from wild crucifer species. All samples were then taken to laboratory and reared on fresh cabbage leaves in laboratory for assessing DBM parasitism.The leaves were grown from potted cabbage plants in a greenhouse. The DBM parasitism in the current context referred to presence of parasitoid egg or larva inside the host larva, where the parasitoid larva fed on the host tissues such that the pest remained alive until the larval development of parasitoid was complete. Figure 3.3 depicts some steps adopted for maintainance of the insect culture to deduce parasitism in laboratory.

Figure 3.3: Maintained culture for parasitism assessment**:** (a) greenhouse containing cabbage for rearing diamondback moth in laboratory; (b) Potted cabbage; (c) Experimental container with cabbage leaf for feeding larvae; (d) Developed cocoons of diamondback moth; (e) Cocoons of *C. vestalis*; (f) Cocoons of *D. semiclausum*

In the laboratory, each larva was reared individually on a fresh 7 – 8 week old cabbage cut-leaf inside a petri dish under standard temperature conditions of 25 ± 2°C and relative humidity of 50 – 70% in laboratory. The cut-leaf was replaced daily. The developmental stage of larva was observed consistently after every 24 hours. When the larva pupated, the pupa was relocated to the individual but ventilated plastic vial and observed daily till eclosion of either adult DBM (if the egg, larva or pupa was not parasitized in the field) or parasitoid (if the egg, larva or pupa had already been parasitized in the field when the insect was collected). For fresh pupae brought directly from the field, they were transferred into the individual labeled vials and observed daily. When a parasitoid species emerged, it was identified using a dichotomous key (Wahl and Sharkey, 1993) and morphometric measurements based on protocol developed by Azidah *et al*., 2000 (Appendix 1). A morphological comparison between the collected parasitoid species and reference specimens preserved in the Biosystematic Unit of ICIPE was conducted. The parasitoid specimens collected from the field were preserved in 95% ethanol for identification at the Plant Protection Division of Tropical Pesticides Research Institute (TPRI) and the Arthropod Pathology Unit of ICIPE.

3.2.4 Data analysis

The DBM abundance was derived from a ratio of the total numbers of DBM collected on farm and the total numbers of surveyed plants on the farm (Number of DBM/plant). The data were subjected to analysis of variance (ANOVA) to determine whether there were any significant differences in the abundance of DBM and the pest parasitism across the seasons. When significant differences were detected, a Tukey HSD ($P < 0.05$) test was adopted to find out which specific abundance and parasitism means (when compared with each other) were significantly different. Alphabetical letters were utilized to denote significant differences or similarities. Three different letters were adopted where there were similarities of some but not all compared means. Numbers ofparasitoid species eclosed from parasitized DBM collected from individual crucifer vegetable farms; and numbers of wild crucifer species from each farm, were individually summed up. The proportions of individual parasitoids and wild crucifer species were calculated from these sums and were used to compute Shannon Wiener index (Shannon, 1948; Magurran, 2004) for studying diversity of the two, respectively. The percentage abundances of parasitoid species were ranked. Rank abundance linear plots were developed with rank number on the horizontal axis and abundance on the vertical axis to illustrate the patterns of diversity. A steeper linear plot indicated species were less evenly distributed and gentle plot implied the species were more evenly distributed. On the horizontal axis, species richness is provided by the width of the curve. A plot rising way high above the x – axis and extending widely from left to right indicated high species richness.

The DBM parasitism values from solitary parasitoids were calculated from the equation:

$$Parasitism = \frac{sum\, of\ emerged\ parasitoids\, out\, of\ DBM\ collected\ on\ farm}{sum\, of\ collected\ DBM\ on\ farm} \times 100$$

For gregarious parasitoids, the parasitism values were calculated from

$$Parasitism = \frac{sum\, of\ parasitized\ cocoon\, out\, of\ all\ developed\ cocoons}{sum\, of\ developed\ cocoons} \times 100$$

Before analyses, the data were subjected to Shapiro – Wilk test for normality and Bartlett test for homogeneity of variances. The analyses were implemented using R statistical program version 2.15.1 (R Core Team, 2012).

3.3 Results

3.3.1 Abundance of diamondback moth on crucifer vegetables

The DBM abundance was generally low. The abundance was least during the long rains in Mt. Kilimanjaro (0.11 and 0.2 DBM/plant in medium and high zones, respectively) and Taita hills (0.05, 0.18 and 0.33 DBM/plant in the respective low, medium and high zones).This abundance increased in thehot dry season in the two transects but peaked during the short rainy seasons:0.62DBM/plant and 0.71 DBM/plant in lowand high zones of Mt. Kilimanjaro and 1.04DBM/plant, 0.80 DBM/plantand 0.59 DBM/plant in low, medium and high zones of Taita hills, respectively. Thevariation was significant between short and long rains in the high zone of Mt. Kilimanjaro (F = 2.814, df = 3, 56, P < 0.047). In Taita hills, the pest abundance varied significantly between the short and long rains in the low zone (F = 3.189, df = 3, 56, P < 0.031) and between short rains and all other seasons in the medium zone (F = 9.366, df = 3, 56, P < 0.001). The annual average of DBM abundance peaked in high altitudinal zones of both Mt. Kilimanjaro and Taita hills transects. Table 3.1 summarizes the DBM abundance along the altitudinal zones and across seasons.

Table 3.1: Seasonal abundance of DBM in crucifer vegetables along altitudinal zones

		Number of DBM/Plant		
Transect	Season	Low	Medium	High
Mt. Kilimanjaro	Hot dry	0.59 ± 0.16a	0.38 ± 0.11a	0.56 ± 0.18a
	Long rains	0.29 ± 0.12a	0.11 ± 0.04a	0.20 ± 0.06ac
	Cold dry	0.19 ± 0.09a	0.38 ± 0.06a	0.33 ± 0.08a
	Short rains	0.62 ± 0.28a	0.30 ± 0.08a	0.71 ± 0.14ab
	Average	0.42 ± 0.09(a)	0.31 ± 0.04(a)	0.47 ± 0.07(a)
Taita hills	Hot dry	0.35 ± 0.07a	0.31 ± 0.07ad	0.56 ± 0.01a
	Long rains	0.05 ± 0.02b	0.18 ± 0.05ac	0.33 ± 0.15a
	Cold dry	0.30 ± 0.08a	0.30 ± 0.06ad	0.39 ± 0.08a
	Short rains	1.04 ± 0.1c	0.80 ± 0.14ab	0.59 ± 0.13a
	Average	0.43 ± 0.21(a)	0.41 ± 0.05(a)	0.47 ± 0.06(a)

Unbracketed mean values (within a zone but between seasons) with standard errors within the same column followed by the same letter do not differ significantly at P<0.05, ANOVA (Tukey test). The means in brackets (between transects) within a column followed by the same letter do not also differ significantly at P<0.05, ANOVA (Tukey) test
Letters a-d were adopted to denote significant mean differences as generated from Tukey test

3.3.2 Parasitoid species and DBM parasitism on crucifer vegetables

Eight (8) and six (6) parasitoid species emerged from DBM collected in Mt. Kilimanjaro and Taita hills transects, respectively (Table 3.2). Of all the parasitoid species, *C. vestalis*was the most abundant parasitoid species collected in the low zone and *D.semiclausum*in the medium and high zones of Mt. Kilimanjaro and Taita hills. Diamondback moth parasitism caused *Diadromus collaris*,*D. mollipla*,*Apanteles sp*. and *Brachymeria sp*.,and reached10% as maximum limit. In addition, the DBM parasitism caused by these parasitoids was only observed during the hot dry season in Taita hills. A few parasitoid species were collected only occasionallyduring the two-year survey period. When no parasitoids were collected during most part of the monthly two-year survey period, the standard errors remained close to the mean. A hyperparasitoid of *C. vestalis*, *Eurytoma sp*. (Hymenoptera: Eurytomidae), wascollected in medium zones of Mt. Kilimanjaro and Taita hills.

Table 3.2: Parasitoid species and seasonal variation of parasitism on DBM collected from crucifer vegetables along the three altitudinal zo**nes**

Zone	Parasitoid species	DBM parasitism in Mt. Kilimanjaro (%)				DBM parasitism in Taita hills (%)			
		Hot dry	Long rains	Cold dry	Short rains	Hot dry	Long rains	Cold dry	Short rains
Low	*D. semiclausum*	2.7 ± 2.7ab	0	0	0	24.0 ± 7.5a	0	25.8 ± 13.9a	9.9 ± 3.5ab
	C. vestalis	40.7 ± 5.8a	3.1 ± 3.1a	11.1 ± 7.9a	14.7 ± 11.9a	17.6 ± 7.8a	50 ± 50	34.8 ± 0.9a	16.3 ± 1.7a
	O. sokolowskii	14.8 ± 5.6a	28.1 ± 28.1a	43.0 ± 14.7b	17.2 ± 16.5a	5.9 ±2.7a	0	1.3 ± 1.3b	3.0 ± 2.1b
	D. collaris	1.54 ± 1.5b	0	0	0	0	0	0	0
	Brachymeria sp.	0	0	0	0	3.5 ± 2.8a	0	0	0
	Apanteles sp.	0	3.1 ± 3.1a	0	0	5 ± 5a	0	0	0
Medium	*D. semiclausum*	38.9 ± 8.6b	0	29.1 ± 8.1a	37.1 ± 10.3a	49.8 ± 14.0a	65.2 ± 9.7	59.3 ± 5.43	33.6 ± 9.1a
	C. vestalis	2.2 ± 1.3a	0	2.1 ± 2.1b	3.5 ± 2.5b	0	0	0	1.2 ± 0.7b
	O. sokolowskii	1.1 ± 1.1a	0	0	4.5 ± 4.5b	0.9 ± 0.9b	0	0	0
	D. mollipla	10 ± 10ab	0	3.2 ± 3.2b	0	0	0	0	0
	A. aethiopicus	0	0	0	3.2 ± 2.1b	0	0	0	0
	Brachymeria sp.	0	0	0	3.2 ± 3.2b	0	0	0	0
High	*D. semiclausum*	31.2 ± 4.8a	3.5 ± 3.5a	32.1 ± 7.7a	35.0 ± 3.5a	46.0 ± 10.2b	47.2 ± 13.9	40.3 ± 2.8	25.9 ± 10.0
	C. vestalis	3.7 ± 2.2b	0	0	0	5.5 ± 3.7ab	0	0	0
	O. sokolowskii	3.8 ± 3.4b	50 ± 50a	0	0	0	0	0	0
	D. mollipla	1.2 ± 1.2b	0	2.8 ± 2.8b	0.6 ± 0.6b	0.8 ± 0.8a	0	0	0
	Brachymeria sp.	6.7 ± 6.7b	0	0	0	0.8 ± 0.8a	0	0	0
	Apanteles sp.	0	0	0	0	0.9 ± 0.9a	0	0	0

Mean values with standard errors within the same column followed by the same letter do not differ significantly at $P<0.05$, ANOVA (Tukey test)Letters a-b were adopted to denote significant mean differences as generated from Tukey test

Parasitism levels changed with seasons and zones. *Cotesia vestalis* dominated parasitism levels during the hot dry season (40.7%) in the low zone of Mt. Kilimanjaro, which was significantly different from that caused by other parasitoids (F = 22.19, df = 7, 32, P < 0.001). However, the observed parasitismdeclined substantially duringthe short rains (14.7%), cold dry (11.1%) and long rainy (3.1%) seasons. In contrast, parasitism by *O. sokolowskii* increased during short rains (17.2%), long rains (28.1%) and cold dry (43%) seasons. Compared to low zone of Mt. Kilimanjaro, the *C. vestalis*– caused DBM parasitism in the low zone of Taita hills was conspicuously higher than that of *O. sokolowskii*during the cold dry season (F = 7.601, df = 5, 18, P < 0.007). *Diadegma semiclausum*provided more effective parasitism rates during hot dry (24%) and cold dry (25.8%) seasons in the low zone of Taita hills compared to Mt. Kilimanjaro (2.7% during hot dry and none during cold dry). Regardless of the season, 6and 3 parasitoid species were collected in the medium zones of Mt. Kilimanjaro and Taita hills, respectively (Table 3.2).*Diadegma semiclausum* was the most effective parasitoid in this zoneduring short rains, and it causedDBM parasitism of approximately 28 times that of *C. vestalis*. *Diadegma mollipla* was collected in the hot and cold dry seasons. Acrosshigh zones of the two transects, *D. semiclausum* was observed throughout thefour seasons, inflicting parasitism ratesranging from 3.5% - 35% in Mt. Kilimanjaro and from 25.9% to 47.2% in Taita hills. The DBM parasitism differed significantly during the hot dry season in high zones of Mt. Kilimanjaro (F = 22.33, df = 7, 32, P < 0.001) and Taita hills (F = 16.69, df = 5, 24, P < 0.001).In the two zones, *D. semiclausum* accounted for most of parasitism (31.2% in Mt. Kilimanjaro and 46% in Taita hills). Parasitism of DBM by *C. vestalis*, *O. sokolowskii* and *D. mollipla* wasalso recorded in various seasons (*C. vestalis*: hot dry; *O. sokolowskii*: hot dry and long rains; *D. mollipla*: hot dry, cold dry and short rains) in Mt. Kilimanjaro. Except for *D. semiclausum*,which was collected across seasons in the high zone of Mt. Kilimanjaro, other parasitoid species were collected only during the hot dry season in this zone. In general, the

DBM parasitism caused by *C. vestalis* decreased from 40.7% in the low zone, to 3.5% in the medium zone and 3.7% in the high zone of Mt. Kilimanjaro. Likewise, the *C. vestalis*-caused parasitism declined from 50% in the low zone to 5.5% in the high zone low. In contrast, the peak DBM parasitism rate by *D. semiclausum* generally increased with altitude from 2.7% in the low zone to 38.9% in the medium and eventually 35% high in the high zones. Over the Taita hills, The DBM parasitism rose from 25.8% in the low zone, to (low), 65.2% in the medium zone and 47.2% high in the high zone. The peak parasitism of DBM by *D. semiclausum* occurred in the medium zone.

3.3.3 Diversity of parasitoids emerged from DBM collected on crucifer vegetables

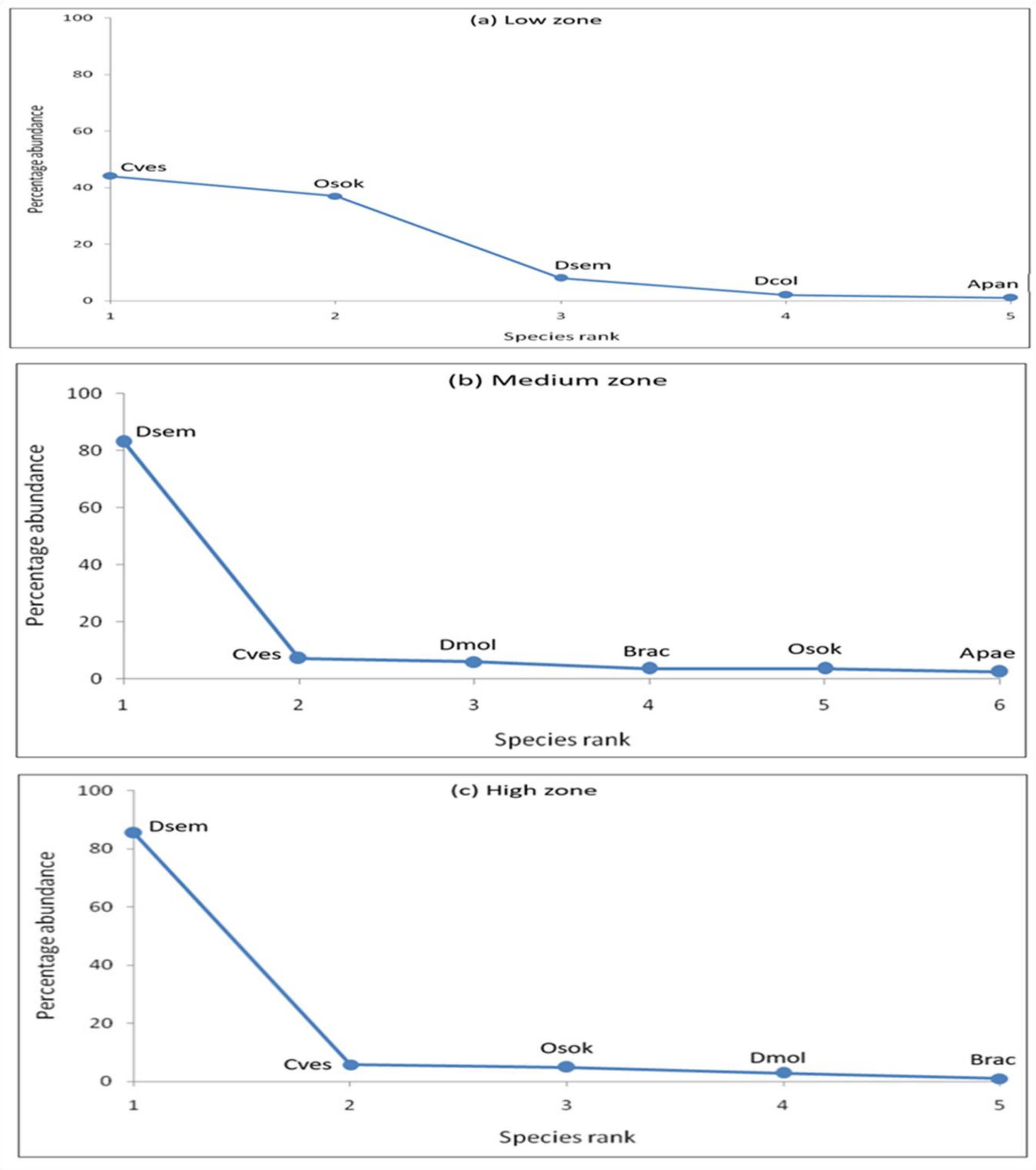
Low zones of the two transects boasted the rich parasitoid diversity than the medium and high zones. (Table 3.3). The level of diversity reduced with increasing altitude in the two transects.

Table 3.3: Estimated diversity of parasitoid species that emerged from DBM collected on crucifer vegetable farms

Mt. Kilimanjaro		Taita hills	
Altitudinal zone	Shannon index	Altitudinal zone	Shannon index
Low	1.06	Low	1.10
Medium	0.86	Medium	0.22
High	0.60	High	0.29

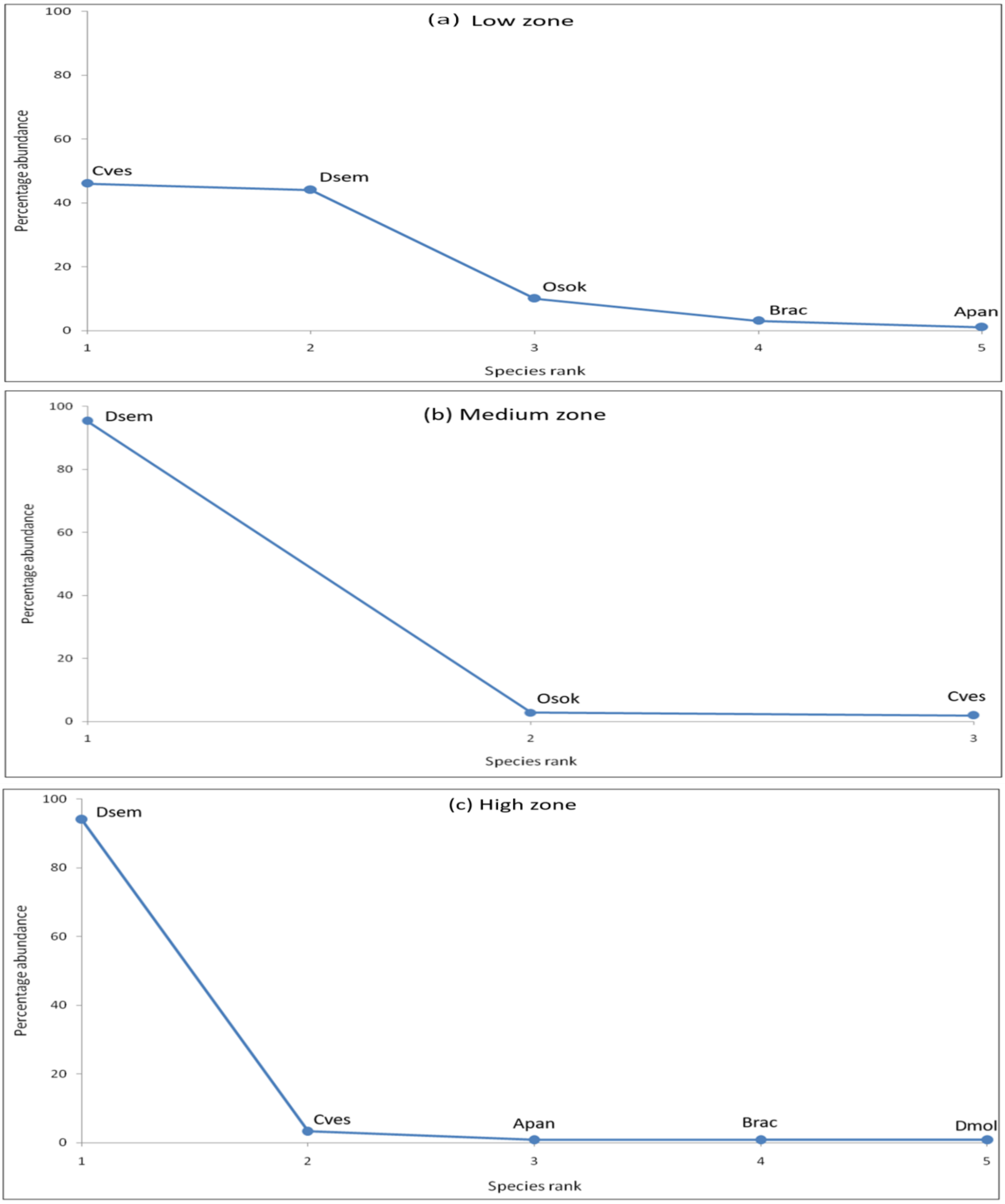
For Mt. Kilimanjaro: n = 92 (low zone), n = 88 (medium zone) and n = 103 (high zone)
For Taita hills: n = 104 (low zone), n = 106 (medium zone) and n = 121 (high zone)

A steeper rank abundance linear plot indicated parasitoid species were less evenly distributed and gentle linear plot implied the species were more evenly distributed. Distribution of the parasitoids was more even in the low than in the subsequent upper zones of Mt. Kilimanjaro (Fig. 3.4) and Taita hills (Fig. 3.5). This implies the parasitoids in the low zone had closer proportional relationship than they did in the medium and high zones. The proportional relationship of *D. semiclausum* and other parasitoids showed the ichneumonid was far more abundant in the medium and high zones of both study sites, and hence the most dominant parasitoid species.



Dsem =*Diadegma semiclausum*; Cves =*Cotesia vestalis*; Osok = *Oomyzus sokolowskii*; Dmol = *Diadegma mollipla*; Brac = *Brachymeria sp.*; Dcol = *Diadromus collaris*; Apae = *Apanteles aethiopicus*; Apan = *Apanteles sp.*

Figure 3.4: Rank abundance linear plots for parasitoid species that emerged from DBM collected on cultivated crucifer vegetables in Mt. Kilimanjaro



Dsem =*Diadegma semiclausum*; Cves =*Cotesia vestalis*; Osok = *Oomyzus sokolowskii*; Dmol = *Diadegma mollipla*; Brac = *Brachymeria sp.*; Dcol = *Diadromus collaris*; Apae = *Apanteles aethiopicus*; Apan =*Apanteles sp.*

Figure 3.5: Rank abundance linear plots for parasitoid species that emerged from DBM collected on cultivated crucifer vegetables in Taita hills

3.3.4 Diversity of parasitoid species emerged from DBM collected from wild crucifers

The types and numbers of parasitoid species which emerged from DBM collected on wild crucifer species were quite a few to warrant proper diversity analysis. *Diadegma semiclausum* and *C. vestalis* were the only two parasitoids that emerged from DBM which was collected on wild crucifer weed species. Diamondback moth collected from wild crucifers in Mt. Kilimanjaro was parasitized by both two parasitoids but the host population collected from Taita hills was parasitized by *D. semiclausum* only (Table 3.4).Wild crucifer weed species were not found in low zones of the study region and hence, neither DBM nor parasitoid species were observed correspondingly in the zone. The pest was observed only during hot dry season in the medium zone. The DBM abundances across different seasons in high zones of Mt. Kilimanjaro and Taita hills were not substantially different. The DBM parasitism rates by *D. semiclausum* were observed more frequently in high zones of the two altitudinal transects but likewise the rates were not substantially different across seasons.

Table 3.4: Seasonal abundance and parasitism of DBM in wild crucifer species

		Mt. Kilimanjaro			Mt. Kilimanjaro		
		Abundance	Parasitism (%)		Abundance		Parasitism (%)
Zone	Season	Number of DBM/Plant	*D. semiclausum*	*C. vestalis*	Number of DBM/Plant	*D. semiclausum*	*C. vestalis*
High	Hot dry	0.14 ± 0.12a	7.5 ± 5.09a	0	0	0	-
	Long rains	0.08 ± 0.06a	20.82 ± 13.99a	0	0.008 ± 0.008a	16.67 ± 16.67a	-
	Cold dry	0.03 ± 0.01a	7.24 ± 4.03a	0	0.03 ± 0.01a	5.83 ± 3.26a	-
	Short rains	0.11 ± 0.04a	10 ± 10a	25 ± 25	0.07 ± 0.05a	6.25 ± 6.25a	-
Medium	Hot dry	0.03 ± 0.03	16.65 ± 9.61	-	0	0	-
	Long rains	-	-	-	0.05 ± 0.05a	0	-
	Cold dry	-	-	-	0.06 ± 0.03a	7.69 ± 5.21	-
	Short rains	-	-	-	-	-	-
Low	Hot dry	-	-	-	-	-	-
	Long rains	-	-	-	-	-	-
	Cold dry	-	-	-	-	-	-
	Short rains	-	-	-	-	-	-

Mean values with standard errors within a column followed by same letter do not differ significantly at P<0.05 ANOVA (Tukey test)
Zero (0) means wild crucifer weed species were observed and sampled for DBM and its parasitoids but no insects were found
Hyphen (-) means no wild crucifer were observed during the survey

3.3.5 Diversity of wild crucifer weed species

Eight wild crucifer species in Mt. Kilimanjaro and four in Taita hills were observed and sampled for DBM and parasitoid species during the surveys. The recorded wild crucifer species in Mt. Kilimanjaro included hairy bittercress (*Cardamine trichocarpa*), Ethiopian kale (*Erucastrum arabicum*), hedge mustard (*Sysimbrium officinale*) and wild radish (*Raphanus raphanistrum*) and shepherd's purse (*Capsella bursa*). Yellowcress (*Rorippa micrantha*), peppercress (*Lepidium bonariense*) and African bittercress (*Cardamine africana*) were also observed. Conspicuously lower than Mt. Kilimanjaro, only four species were observed and recorded in Taita hills. The list included Ethiopian kale, wild radish, hedge mustard and peppercress. The number of species observed along the altitude of Mt. Kilimanjaro includes five in the medium and seven in the high zones. Diversity of the wild crucifers decreased downward the altitude in Taita hills. Diversity of wild crucifers in the medium zone of Mt. Kilimanjaro was higher than that in the high zone. The two-year monthly surveys could not find wild crucifers in low zones of the two study sites. The observed wild crucifer species in the medium zone of Mt. Kilimanjaro were three times more diverse than that in the medium zone of Taita hills (Table 3.5).

Table 3.5: Diversity estimates of wild crucifer species

Mt. Kilimanjaro		Taita hills	
Altitudinal zone	Shannon index	Altitudinal zone	Shannon index
Low	0	Low	0
Medium	1.23	Medium	0.38
High	1.07	High	0.51

For Mt. Kilimanjaro: n = 0 (low zone), n = 688 (medium zone) and n = 568 (high zone)
For Taita hills: n = 0 (low zone), n = 205 (medium zone) and n = 477 (high zone)

3.4 Discussion

Diamondback moth abundance dwindled in the long rainy season largely due to mortality. Rainfall interfered with flight, mating and foraging of adults and indirectly caused a poor population growth during the rainy season. These findings agree with previous field reports of Asian Vegetable Research and Development Centre (1988), Ahmad and Ansari (2010) and Sow *et al*., (2013) who related rainfall to the lowest abundance of DBM populations. Little amounts of rainfall in the low zones necessitated crucifer cultivation through irrigation from wells or downstream water. The practice was conspicuous during the hot dry season. Provision of irrigation often aided in consistent supply of fresh host plants and hence abundant food and oviposition sites. The short rainy season experienced uncharacteristically high pest abundance. Availability of long dry intervals relative to that during long rains probably allowed some substantial buildup of the DBM populations. However, the generally low levels of the pest abundance may imply the pest might have not been a big problem during the field work as compared to closely two decades ago (Löhr, 2001).

Distribution of DBM abundance varied across seasons and altitude. The seasonal changes are associated with changes in weather conditions which impacted on the DBM abundance in the altitudinal zones. The DBM populations increased upward the altitude. The rising altitude and the increasingly varying topographical features, which includes the growing density of vegetation, probably contributed to slowing down the temperatures which made medium and high zone agroecological landscapes more attractive and supportive to the moth activity than the low zones. The moth population is reportedly capable of growing favorably between 12°C and 28°C and unfavourably beyond 36°C because of declining egg development (Liu *et al*., 2002). The survival rate of DBM was therefore better in the mid and high zones than low zones. The findings in the high zones are also supported by laboratory studies (Marchioro and Foerster, 2011; 2012) which showed the highest percentage of egg survival to adult occurs at

20°C (96.7%) and that females undergo maximum oviposition at 20°C. However, some occurrence of low abundance in the medium zone of Mt. Kilimanjaro, which contrasted some of these findings, could partly be attributed to abrupt emergence of many wild crucifer weed species which attracted DBM by providing alternative refuge to the pest especially when farmers uprooted the old crop or switched to other crops. Furthermore, the increased incidence of parasitoid populations, which resulted from a wide availability of nectar resources in the medium zone, could have further limited the DBM population.

The total *D. semiclausum*-caused parasitism of DBM in Mt. Kilimanjaro (42.9%), along with that caused by *C. vestalis* (16.6%), were both lower than that in Taita hills (*D. semiclausum*: 74.4%, *C. vestalis*: 21.8%). *Diadegma semiclausum* was introduced and released in the highlands of Taita hills from the early to mid 2000s (Löhr *et al*., 2007; Gichini *et al*., 2008) undoubtedly contributed to its strong establishment. The parasitoid was also released on the slopes of Mount Meru in Tanzania, which is close to 70 km away from Mt. Kilimanjaro, between 2002 and 2003 (Gichini *et al*., 2008).The parasitoid population has since dispersed to the slopes of Mt. Kilimanjaro. Whether there was a local strain of *D. semiclausum* in Kilimanjaro before this release, is yet to be established. Regardless of this, *D. semiclausum* is a specialist parasitoid of DBM, and has largely outdone and displaced other parasitoid species for oviposition of the available DBM larvae in the high altitudes. The favourably cool climatic conditions of the medium and high zones attracted establishment and colonization of the parasitoid. Except for the reportedly biotype of *D. semiclausum* which thrives relatively better under hot conditions of Syria (Kadirvel *et al*., 2011), the observed parasitoid was very effective under the cool climate conditions of the mid and high zones. Some similar findings on the spread and colonization of *D. semiclausum* in East Africa were gathered by Momanyi *et al*., (2006) and Löhr *et al*., (2007).On the contrary, *Cotesia vestalis* has been recorded to tolerate high temperatures better the *D. semiclausum* (Nofemela, 2004, Htwe *et al*., (2008), which go in line with its high presence in the warmer low zones of the two altitudinal transects. *Cotesia vestalis* has been the most reliable natural enemy of DBM over areas characterized by high temperatures and humid environmental conditions in Zambia since 1979 when it was introduced from Pakistan (Ministry of Agriculture and Rural Development of Zambia, 1984; Sohati, 2012; Chipabika, 2014). The *C. vestalis* populations observed in Mt. Kilimanjaro could either be a native population or might have originated from the population released about a decade earlier in Loitoktok and dispersed over a period of time. Application of molecular tools can further help in establishing the true identity and origin of the parasitoid.

The parasitoid diversity was high in the low zone for several reasons. The low zones are presumably warmer than the subsequent upward zones which make their climate more suitable for the survival, development and fecundity of most insect species, including parasitoids. High temperature conditions during the hot dry seasons likely accelerated physiological activities which translated to rapid growth, development and increased generation of new offspring. A field study in Senegal demonstrated a positive relationship between high temperatures and proliferation of DBM parasitoids (Sow *et al*., 2013).*Cotesia vestalis* populations built up overtime in response to the growing DBM populations. However, the parasitoid diversity declined gradually towards the high altitude due to declining temperatures which favored the more competitive, hot temperature-sensitive *D. semiclausum*. The high efficiency of *D. semiclausum* in foraging crucifer plants, searching for and parasitizing DBM is reported to contribute greatly to displacement of many local parasitoids like *Diadegma mollipla* in Kenya (Löhr, 2001; Kfir, 2003; Löhr *et al*., 2007; Kahuthia-Gathu *et al*., 2009; Kahuthia-Gathu, 2011).

Comparing the agroecological landscapes of Mt. Kilimanjaro and Taita hills, different food sources and host insects for oviposition were widely available higher up the Mt Kilimanjaro.

This attracted a multitude of parasitoid species, from the complex cropping system of the Chagga homegardens (Ngowi *et al*., 2017a). The homegardens provided suitable environment to support more host insects and natural enemies, including parasitoid species, than the less diverse cropping systems practiced in Taita hills. The rich vegetation structure nurtures the host-parasitoid relationships (Liu *et al*., 2000). An increase in diversity of plant species increases the structural diversity of agroecosystems which attracts different insects, including pests and parasitoids (Marino and Landis, 1996). Owing to homegardens, the increased diversity of parasitoids was more evident in the mid and high zones of Mt. Kilimanjaro than Taita hills.

The observed wild crucifer weed species provided DBM with alternative foods inside and outside the farm. In addition, availing the oviposition and refuge sites is an important ecological resource to sustain DBM particularly during off-season. The weeds sprouted where there was adequate moisture condition to support their growth. The low zones of both transects were relatively dry and growing of crucifer vegetables was only possible under supplementary irrigation. The relatively dry conditions in the low zones likely could not support the growth of wild crucifers. No wild crucifer species were found in these low zones. Moving upward the altitude, increased moisture levels and improved microclimate resulted from increased tree vegetation most likely created conducive environment for the growth of wild crucifers, notably in Mt. Kilimanjaro (personal observation). As a result, the crucifer cropping systems of Mt. Kilimanjaro were also more resilient to harsh climates than Taita hills. Conducting a study on the role of homegarden – based microclimate on performance of wild crucifers can enrich the knowledge on conservation of wild crucifers as trap crops for controlling diamondback moth in different agroecological landscapes.

Development of resistance to synthetic insecticides has renewed efforts on the application of biological control methods for limiting DBM populations. The use of parasitoid species has so far proved to be the most effective method. However, the seasonal and altitudinal changes can trigger different behavioral responses on the abundance and distribution of DBM and its parasitoids. In the studied regions studied, the pest population occasionally climaxed during the rainy seasons instead of declining. This might suggest the potential of DBM outbreak when it is least expected. Although farmers can do little to influence the seasonal variability, they can play a vigorous role in sustenance of biological control methods through diversifying the cropping systems to enrich the gene pool of parasitoids. Besides incorporating other crops on farm, farmers can be advised to select multipurpose wild crucifer species, and with assistance of the local agricultural extension officers, evaluate their agronomic practices. Deliberate integration of wild crucifer species trap crops for controlling DBM is advocated. A particular attention can be paid in the low zones where insecticide application is relatively extensive. *Oomyzus sokolowskii* is reportedly more tolerant to insecticide applications than *C. vestalis* (Ayalew and Ogol, 2006) and its populations can therefore be manipulated to complement *C. vestalis* where the braconid does not thrive well. Mass rearing, introduction and release of *O. sokolowskii* into the other hot lowland areas is advised. Finally, on-farm continuous assessment and monitoring of parasitoids are recommended.

CHAPTER FOUR: EFFECTS OF WEATHER VARIABILITY ON CRUCIFER DAMAGE AND DIAMONDBACK MOTH PARASITISM ALONG ALTITUDINAL GRADIENTS

4.1 Introduction

Weather is one of the major factors influencing the local population dynamics and distributions of insect pests. Several studies have demonstrated that temperature heavily influences the field population dynamics of insects through its effects on development and fecundity (Talekar and Shelton, 1993).However, studying combinations of different weather variables and biotic factors like pathogens (Vezina and Peterman, 1985; Bowers *et al*., 1993), parasitoids and foliage (Berryman, 1996) have proved to offer a more reliable approach in investigating the cyclic abundances of pest populations (Mantyka-Pringle *et al*., 2012) and their possible implications to the host plants.

Several studies have established that weather variability affects the survival, development, fecundity and mortality of field populations of DBM (Wakisaka *et al*., 1992; Ahmad and Ansari, 2010; Sow *et al*., 2013; Ahmad *et al*., 2015). Emergence of female diamondback moth (DBM) happens earlier than males at a combination of high temperature (33°C) and relative humidity (90%) in contrast to moderate temperatures of 25°C and high relative humidity of 90% (Guo and Qin, 2010). Besides the moth, weather variability affects the whole arthropod complex interacting with DBM (Nyambo *et al*., 2005). Investigations on the response of DBM and its parasitoids to the same weather conditions have demonstrated weather variability can affect ability of the pest to infest and damage crops and that of parasitoids to search and oviposit on the host (Nofemela, 2004; Ayalew *et al*., 2005; Emana, 2007; Van der Putten, 2010; Dosdall *et al*., 2012; Bahar *et al*., 2014).

The extent of crucifer damage and DBM parasitism at a local scale can be subject to weather variability. Understanding the survival, developmental and ovipositional response of DBM and these parasitoids from weather variability is crucial for maintaining effective biological control of the pest (Van der Putten *et al*., 2004; Schweiger *et al*., 2008).

The crop types, insect pests and parasitoid populations do not necessarily respond the same way to weather. Productivity of cabbage declines substantially under hot temperatures (Mulekee*t al*., 2014; Callaway *et al*., 2004).In contrast, the development rate of thrips (*Thrips tabaci*) population, one of key insect pests of cabbage in East Africa, increases with temperatures. Distinct thermal requirements by insect pests and their natural enemies can lead to a temporal or long term mismatch of their activities (Read, 1962) through unchecked population growth. Besides temperature, other weather variables can also influence the insect pest-parasitoid interactions. In cassava (*Manihot esculenta* Crantz) fields, the parasitism of mealybug (*Phenacoccus herreni* Cox and Williams) (Hemiptera: Pseudococcidae) byencyrtid parasitoid *Apoanagyrus diversicornis*Howard (Hymenoptera: Encyrtidae) declines under increased drought due to immune response of the host insect (Catalayud *et al*., 2003). The parasitism success declines when the oviposited egg or thedeveloping embryo is encapsuled by the mealybug physiological defence mechanism (Nenon *et al*., 1988).The concentrationof plant nutrients in amino acids or amino acid profiles (Catalayud *et al*., 2000) under moisture-deprived ecological conditionsintensifies the encapsulation (Mattson and Haack, 1987). Understanding implications of the weather variability on interacting trophic levels is important for assessment of dynamics of ecological communities. In recent decades, an increasing number of studies have addressed the effects of combined weather variables e,g, temperature and precipitation; and gases e.g. carbon dioxide, on trophic interactions and food chain dynamics (Bezemer *et al*., 1998; Newman, 2004; Jamieson *et al*., 2012; Dyer *et al*., 2013).

Studies of insects along altitudinal gradients can present the opportunity to generate knowledge on potential effects of climate change (Williams *et al*., 2003; Hodkinson, 2005; Strong *et al*., 2011; Rasmann *et al*., 2013). This is accomplished by linking the weather changes along the altitude with the associated changes in the local populations. After successful establishment following their introduction and release in East Africa, *Diadegma semiclausum* and *Cotesia vestalis*populations limited the field DBM populations fairly well, leading to reduction of insecticide use was reduced (Löhr *et al*., 2007; Kahuthia-Gathu, 2007). However, the sustainability of this biological control in the face of increased weather variability remains uncertain. This may well be pronounced in the local population dynamics and distributions of the insects. The objective of this chapter therefore was to investigate the effects of weather variability on crucifer vegetable-DBM-parasitoid interactions in order to shed light on its implications to crop damage and the pest parasitism. The findings are used to draw recommendations aimed at safeguarding the ecological-friendly cultivation of crucifer vegetables in the region.

4.2 Materials and methods

4.2.1 Measurement of weather variables

Thermohygrometers were used for recording temperature and relative humidity throughout the survey period. They were in form of data loggers (iButton®, Maxim Integrated Products Inc.) which were installed on each of the 24 farms spread long the altitudes of the Mt. Kilimanjaro and Taita hills transects. The data loggers were erected on wooden pegs at about 30 cm. high. The loggers were calibrated to record average measurement values after every 24 hour cycle. The records were downloaded from the loggers and uploaded in computer during each field survey visit. Twelve GENERAL^{R} wireless rain gauges were installed in six altitudinal zones of Mt. Kilimanjaro and Taita hills transects (two gauges/altitudinal zone) to keep track of rainfall. Daily values of rainfall in each zone were taken and recorded.

4.2.2 Sampling for crop damage

Twenty kales or cabbage or Ethiopian mustard, depending on the availability and adequate quantity, were randomly sampled for the larvae and pupae of DBM on each farm during the field surveys conducted from 2013 to 2014. The two insect stages were collected following the procedure described under section 3.2.3. The damage inflicted by DBM was assessed visually and the specific percentage of damaged leaves was recorded and grouped using a score of 1 – 5 whereby 1 = no damaged leaves, 2 = 1 – 25% of leaves are damaged, 3 = 26 – 50% of leaves are damaged, 4 = 51 – 75% of leaves are damaged and 5 ≥ 76% of leaves are damaged (Appendix 2).

4.2.3 Sampling for diamondback moth parasitism

The DBM larvae and pupae collected from individual farms along the two altitudinal transects were packed in plastic containers and taken to laboratory for assessment of parasitism. The larvae were reared on fresh cabbage cut-leaves which were replaced after every one or two days. The dichotomous keys were adopted for identification of parasitoid species. The total numbers of individuals of *D. semiclausum* and *C. vestalis* that emerged from parasitized DBM were recorded. The parasitism values of DBM by *D. semiclausum* and *C. vestalis*, both solitary parasitoids, were calculated as detailed under section 3.2.4.

4.2.4 Data analysis

The number of DBM and its abundance recorded from the individual farms during the monthly surveys were clumped and zero-inflated particularly during the rainy season. The data were therefore subjected to negative binomial, generalized linear models (NB GLMs) for assessing the weather effects on DBM population at 5% significance level, and the associated relationships plotted. Relationship between pest abundance and leaf damage was explored for key assumptions under linear regression: linearity and homoscedasticity (through scatter plots), multivariate normality (by histogram) and autocorrelation (using Durbin-Watson test).The relationship between DBM abundance and leaf damage was established through a linear equation:

$$Y = \beta_0 + \beta_1 A$$

Where Y is the percentage of leaf damaged per plant, A is the DBM abundance representing potential infestation, and β_0 and β_1 the intercept and slope of the regression relation, respectively. The linear regression equation was adopted because all the dependent variable data ranged between 10% and 90%, a range which covers all the section that demonstrates linearity of the curve. From this, no predicted values were obtained below 0 and above 100%.

Besides fulfilling the assumptions held under the simple linear regression, the independent weather variables, namely temperature, relative humidity and rainfall, were tested for multicolinearity through correlation matrix and no correlation with each other was established. Using the recorded monthly temperature, relative humidity and rainfall, which provided independent variables, and DBM parasitism which presented dependent variables, the effect of weather on parasitism was described under a multiple linear regression equation:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \alpha$$

where Y is the estimated DBM parasitism by either *D. semiclausum* or *C. vestalis*, β_0 the constant, β_1, β_2 and β_3 the coefficients, X_1, X_2 and X_3 the temperature, relative humidity and rainfall values respectively, and α the residual error. The multiple linear regression method was chosen to determine the influence of the independent weather variables on DBM parasitism, forecast effects of changes and predict trends and future values. In addition, the independent variables were not highly correlated with each other and the residuals were normally distributed. A multivariate regression analysis was adopted to determine and plot the effect of individual weather variables on DBM parasitism by *D. semiclausum* and *C. vestalis* when both parasitoids were present in the same zone.

4.3 Results

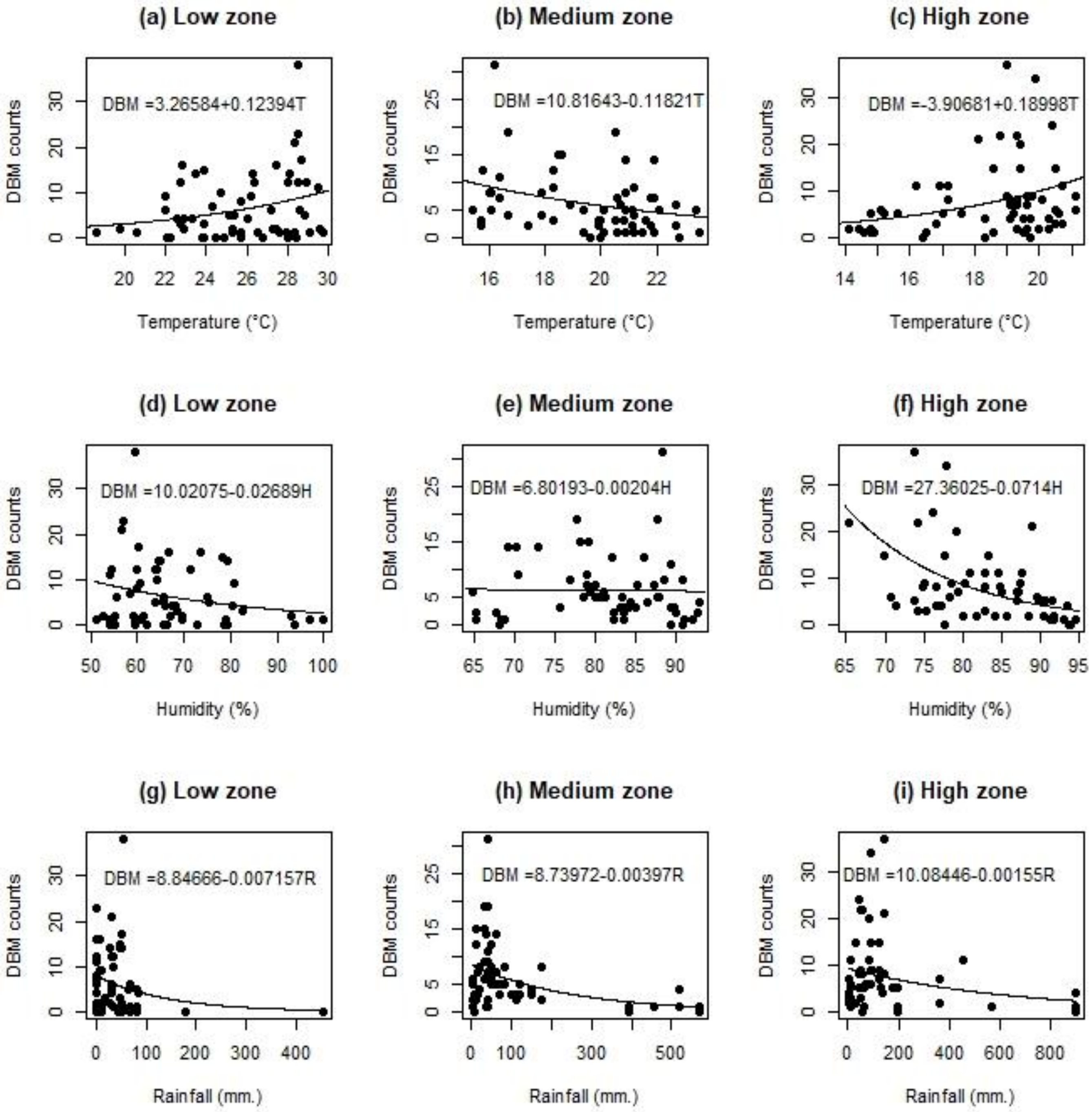
4.3.1 Effects of weather on DBM abundance along altitudinal zones

Temperature had a significant positive effect on DBM abundance (t = 2.129, df = 1, 59, P = 0.0377) in the low zone of Mt. Kilimanjaro. A unit increase in temperature increased the log expected abundance by 0.2477 (Table 4.1). Upward the subsequent medium zone, it had a significant negative relationship with the pest abundance (t = -2.054, df = 1, 59, P = 0.0446). Rainfall and pest abundance presented a highly significant negative relationship (t = -3.509, df = 1, 59, P = 0.0009). Every unit increase in rainfall resulted in a decreased log expected abundance of the pest by 0.0032.

Table 4.1: Negative binomial regression model estimates on DBM abundance as affected by weather variables along altitudinal zones of Mt. Kilimanjaro and Taita hills

	Mt. Kilimanjaro								
	Low zone			Medium zone			High zone		
Variable	Estimates	t-value	P-value	Estimates	t-value	P-value	Estimates	t-value	P-value
Temperature	0.2477	2.129	0.0377	-0.1459	-2.054	0.0446	0.0669	0.704	0.4841
Humidity	0.0252	0.822	0.4145	-0.0229	-1.012	0.3157	-0.0539	-1.935	0.0581
Rainfall	-0.0079	-1.495	0.1406	-0.0032	-3.509	0.0009	-0.0007	-0.991	0.3259
	Taita hills								
	Low zone			Medium zone			High zone		
Variable	Estimates	t-value	P-value	Estimates	t-value	P-value	Estimates	t-value	P-value
Temperature	-0.2297	-1.508	0.1370	0.0379	0.43	0.6690	-0.0178	-0.175	0.8618
Humidity	-0.0365	-0.56	0.5780	-0.0286	-0.915	0.3640	-0.0193	-0.585	0.5613
Rainfall	-0.0015	-0.273	0.7860	-0.0005	-0.242	0.8100	-0.0013	-1.841	0.0717

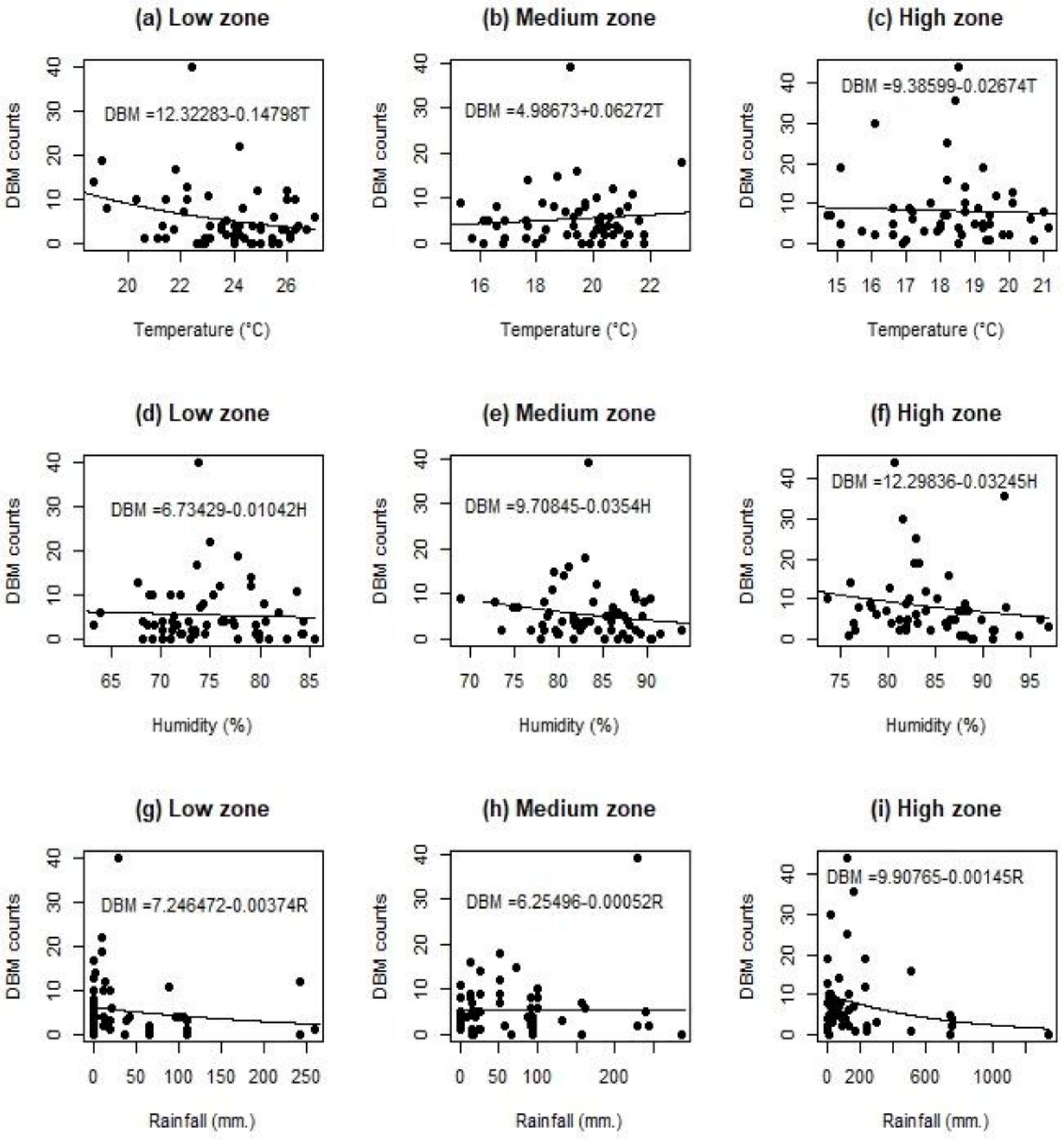
Effects of the three weather variables on DBM population varied with altitudes. As temperature rose, DBM populations declined. The pest population varied inversely proportional to rainfall throughout the altitude (Fig. 4.1g-i). At lower temperature ranges, the pest abundance increased with increasing temperature in the high zones (Fig. 4.1c). The population decreased gradually from 20 to 0 DBM with increasing relative humidity in the low zone (Fig. 4.1d). However, the population increased from 0 to 30 DBM with decreasing relative humidity in the high zone (Fig. 4.1f).



*DBM = diamondback moth, T = temperature, H = relative humidity, R = rainfall

Figure 4.1: Relationship between weather variables and DBM population along the three altitudinal zones of Mt. Kilimanjaro transect

The pest population decreased with increasing temperatures in the low zone of Taita hills (Fig. 4.2a) but increased in the medium zone (Fig. 4.2b). The average monthly temperature levels ranged from 18.7°C to 27.0°C in the low zone and 15.3°C to 23.1°C in the medium zone. The population decreased with decreasing relative humidity levels in high altitudes (Fig. 4.2e-f). Increased amount of rainfall reduced the pest population in Taita hills transect (Fig. 4.2g-i), particularly in the high zone where the amount of the rainfall was the highest (Fig. 4.2i).

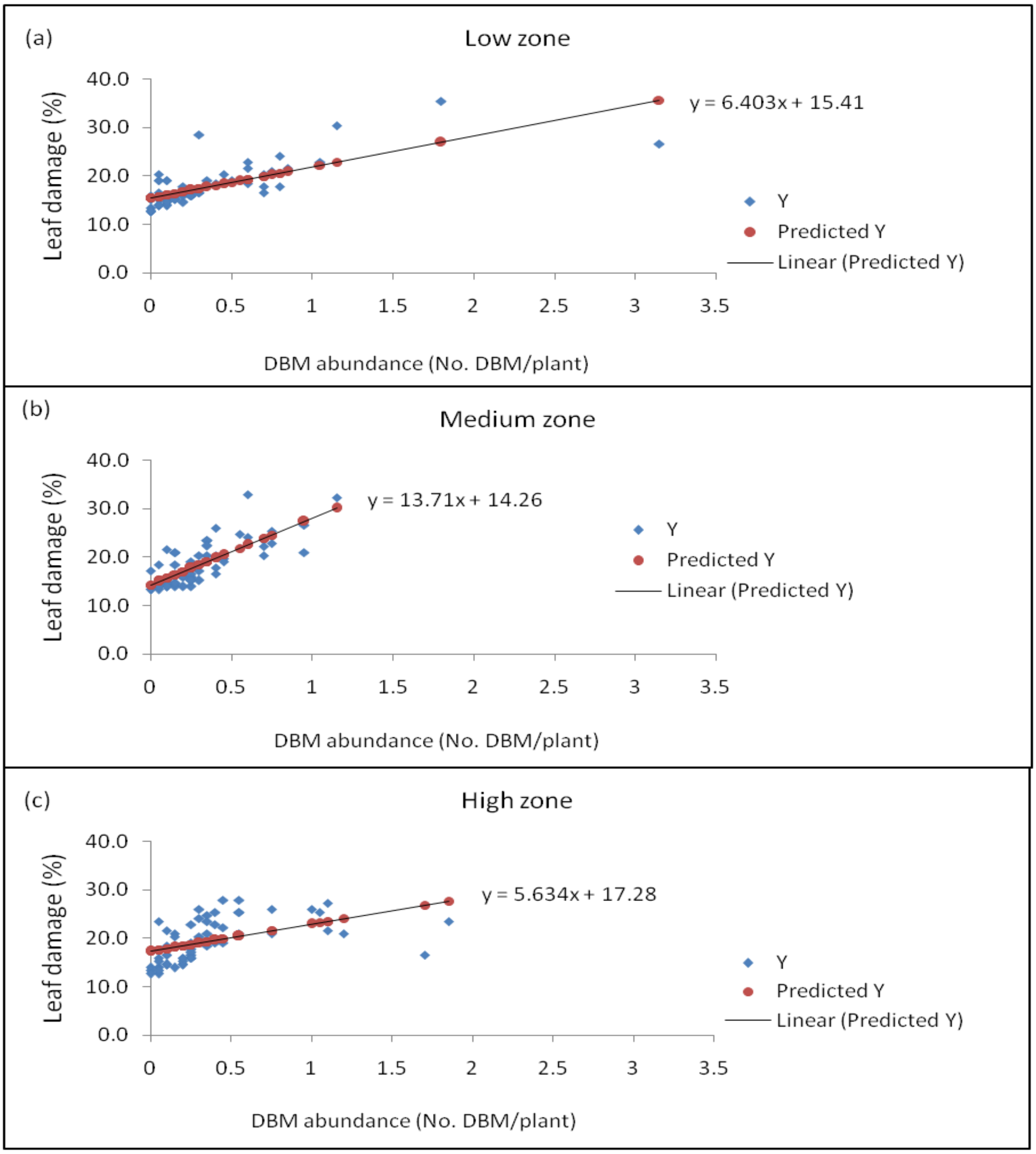


*DBM = diamondback moth, T = temperature, H = relative humidity, R = rainfall

Figure 4.2: Relationship between weather variables and DBM population along the three altitudinal zones of Taita hills transect

4.3.2 Crop damage along the altitude

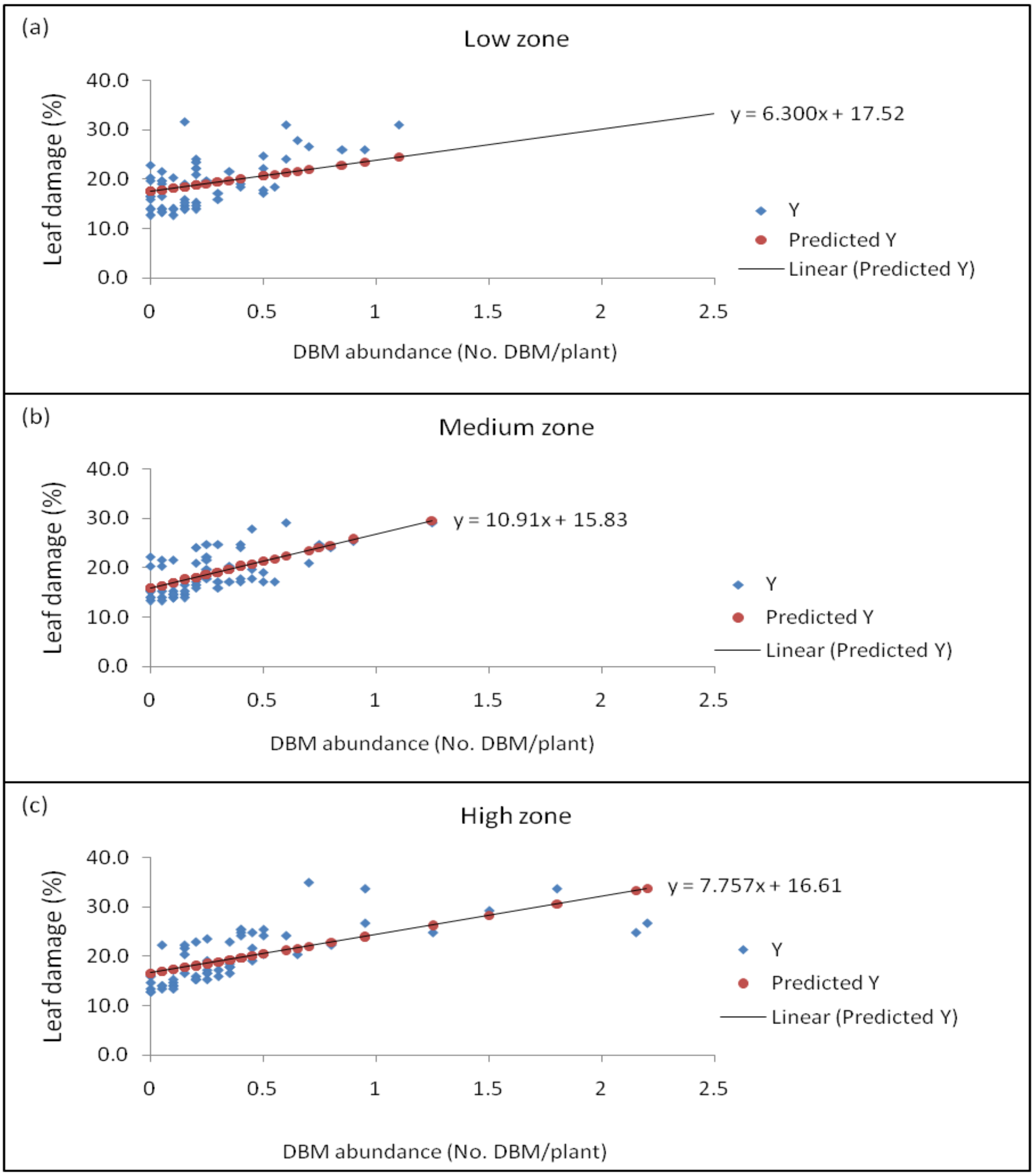
The leaf damage reached 35.5% in the low zone of Mt. Kilimanjaro. In this zone, the DBM abundance reached 3.2 DBM/plant (Fig. 4.3a). The pest abundance in high zone reached 27.9% (Fig. 4.3c). The observed leaf damages are marked by blue diamond-shaped objects in Figs. 4.3a-c. Regression models are presented by red circles.



* Y = leaf damage (percentage leaf consumed), x = dbm abundance (No. DBM/plant)

Figure 4.3: The relationship between leaf damage and DBM abundance in Mt. Kilimanjaro

The leaf damage reached 33% in the low zone of Taita hills. In this zone, the DBM abundance reached 1.2 DBM/plant (Fig. 4.4a). The pest abundance in the high zone of Taita hills accounted for 34.8% of crop loss through the leaf damage (Fig. 4.4c).



*** Y = leaf damage (percentage leaf consumed), x = dbm abundance (No. DBM/plant)**

Figure 4.4: The relationship between leaf damage and DBM abundance in Taita hills

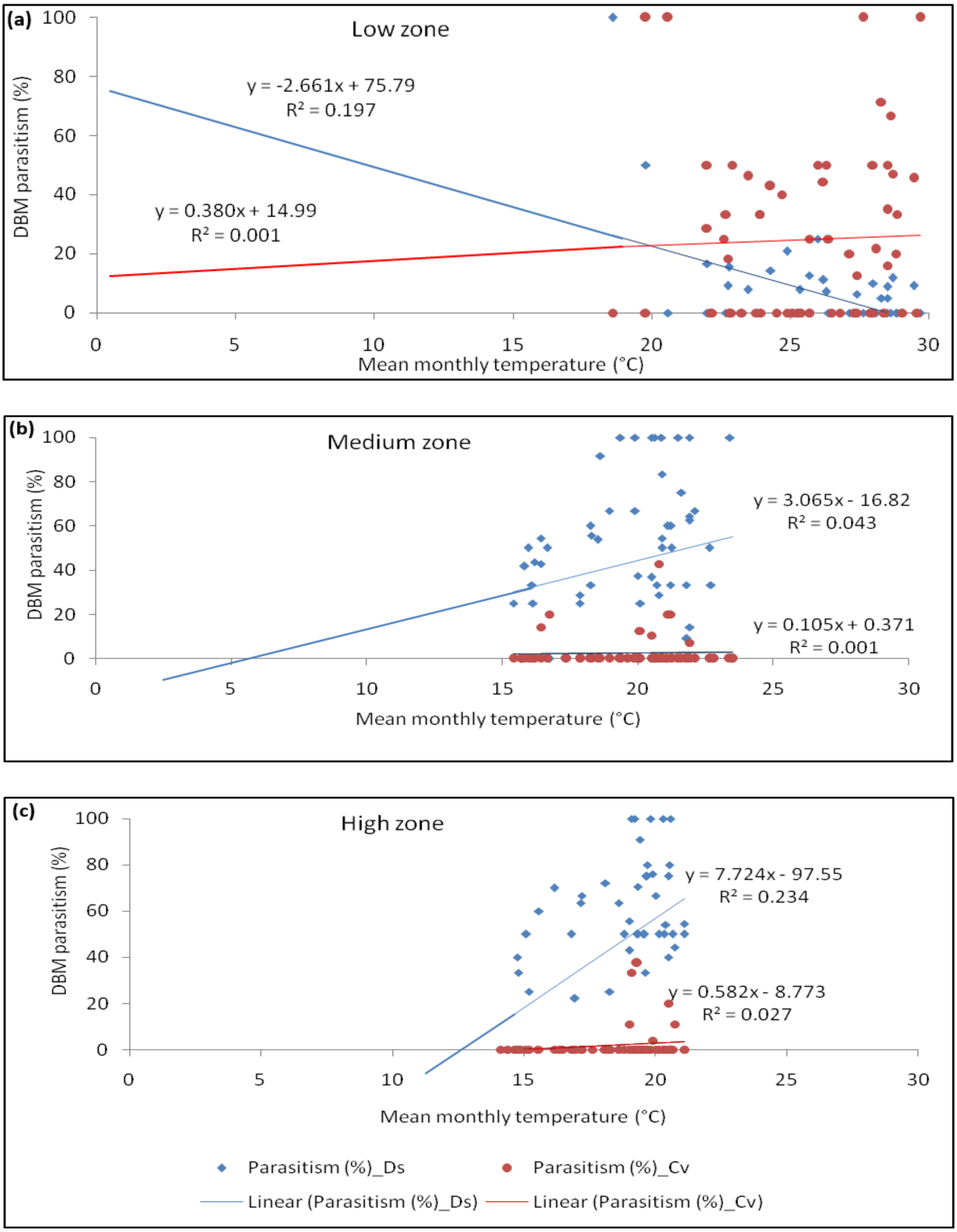
4.3.3 Effects of weather on DBM parasitism

The DBM parasitism by *D. semiclausum* varied significantly with relative humidity in the low zone (F = 6.942, df = 3, 56, P = 0.0435), and temperature (F = 11.68, df = 3, 56, P = 0.0021) and rainfall (F = 11.68, df = 3, 56, P = 0.0052) in the high zone of Mt. Kilimanjaro (Table 4.2). For every additional unit of rainfall in the high zone, the parasitism rate caused by *D. semiclausum* declined by 0.0627% provided the temperature and relative humidity levels remain unchanged. The DBM parasitism by *C. vestalis* decreased with increasing temperatures in the medium and high zones in contrast to *D. semiclausum*-based parasitism (Fig. 4.5 b and c).

Table 4.2: Multiple linear regression model estimates for DBM parasitism as affected by weather variables along altitudinal zones of Mt. Kilimanjaro

		Mt. Kilimanjaro								
		Low zone			Medium zone			High zone		
	Predictor	Coefficient	t-value	P-value	Coefficients	t-value	P-value	Coefficients	t-value	P-value
D. semiclausum	Temperature	-0.9682	-0.903	0.3703	-0.0143	-0.005	0.996	8.9756	3.227	0.0021
	Humidity	0.5766	2.066	0.0435	-1.1879	-1.209	0.232	0.2086	0.252	0.8019
	Rainfall	-0.0646	-1.955	0.0555	0.0424	1.217	0.229	-0.0627	-2.908	0.0052
C. vestalis	Temperature	-0.5823	-0.267	0.791	0.1108	0.153	0.879	0.2389	0.309	0.758
	Humidity	-0.3206	-0.564	0.575	-0.0008	-0.004	0.997	-0.1216	-0.529	0.599
	Rainfall	-0.0094	-0.14	0.89	-0.0019	-0.241	0.81	0.0037	0.622	0.537

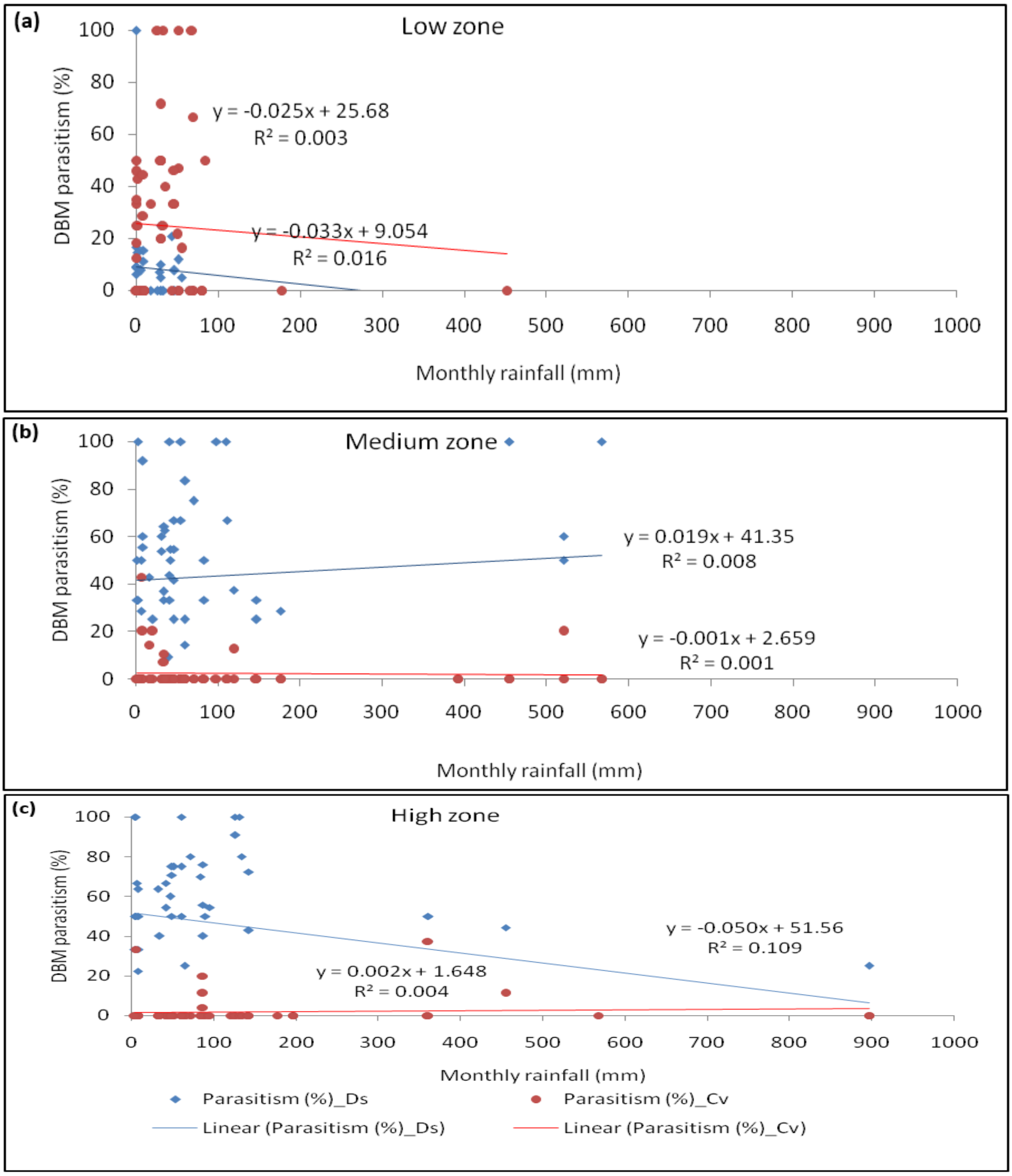
The t-value evaluates the significance of the coefficient of each term in the model in presence of other terms



**Ds = Diadegma semilcausumCv = Cotesia vestalis*

Figure 4.5: Influence of mean monthly temperature on DBM parasitism caused by *D. semiclausum* and *C. vestalis* along altitudinal zones of Mt. Kilimanjaro

However, the pest parasitism by the two parasitoids generally declined with increasing rainfall in the three altitudinal zones (Fig. 4.6 a, b and c).



**Ds = Diadegma semilcausumCv = Cotesia vestalis*

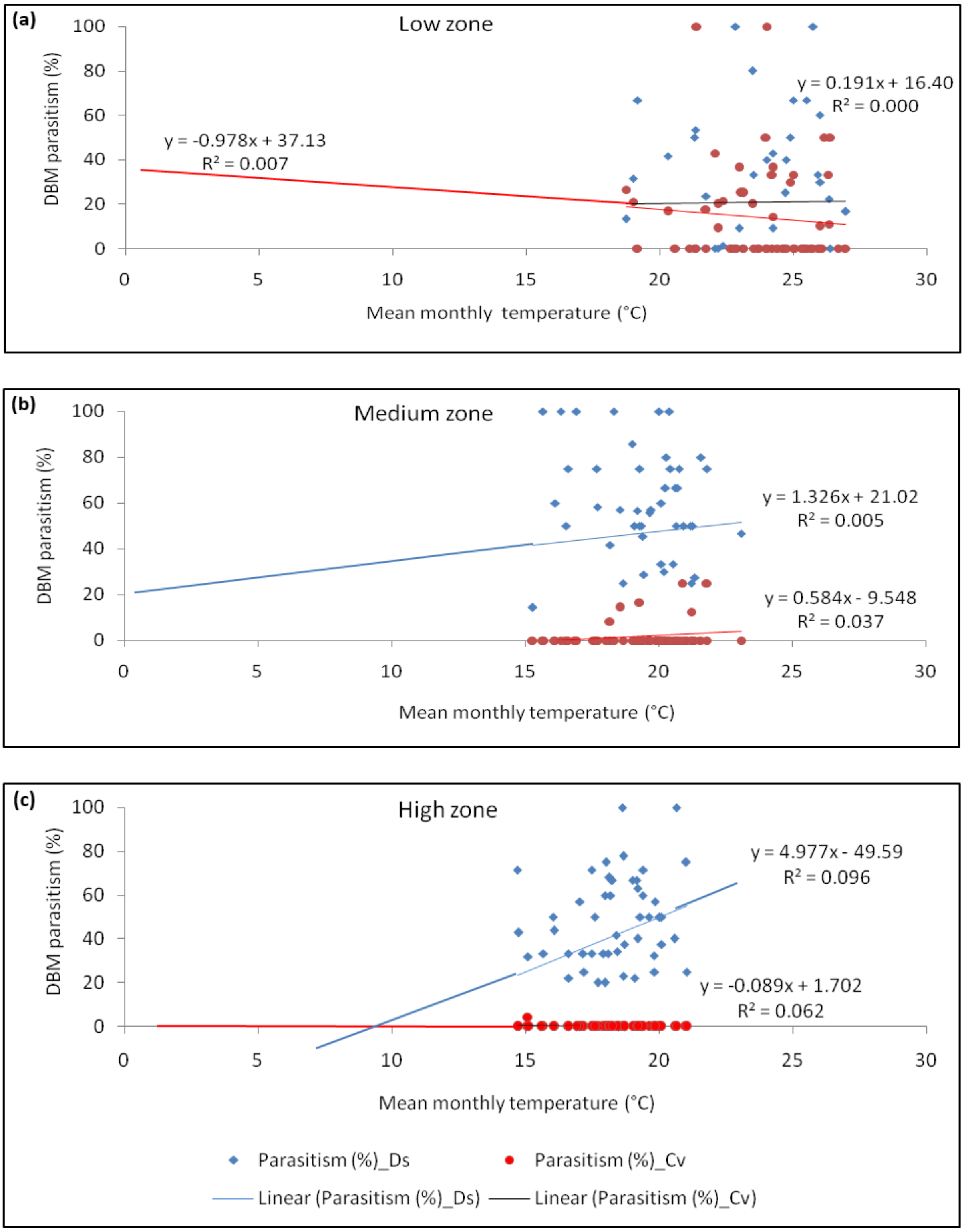
Figure 4.6: Influence of monthly rainfall on DBM parasitism caused by *D. semiclausum* and *C. vestalis* along altitudinal zones of Mt. Kilimanjaro

The *C. vestalis*-caused parasitism varied slightly with temperature in the medium zone of Taita hills (F = 1.322, df = 3, 56, P = 0.0496). However, variation of the DBM parasitism by this parasitoid was significant in the high zones (F = 1.589, df = 3, 56, P = 0.0416) (Table 4.3).The DBM parasitism by *D. semiclausum* also varied significantly with temperature in the high zone (F = 6.546, df = 3, 56, P = 0.0049).Like in Mt. Kilimanjaro, the DBM parasitism by this ichneumonid wasp increased with increasing temperature in the medium and high zones (Fig. 4.7 b and c). In this transect, *D. semiclausum*-caused parasitism declined with increasing rainfall in the medium (F = 2.062, df = 3, 56, P = 0.0483), with significant decline occurring in the high zone (F = 6.546, df = 3, 56, P = 0.0012) (Table 4.3). The DBM parasitism rates by the two parasitoids declined with increasing rainfall in the medium and high zones (Fig. 4.8 b and c).

Table 4.3: Multiple linear regression model estimates for DBM parasitism as affected by weather variables along altitudinal zones of Taita hills

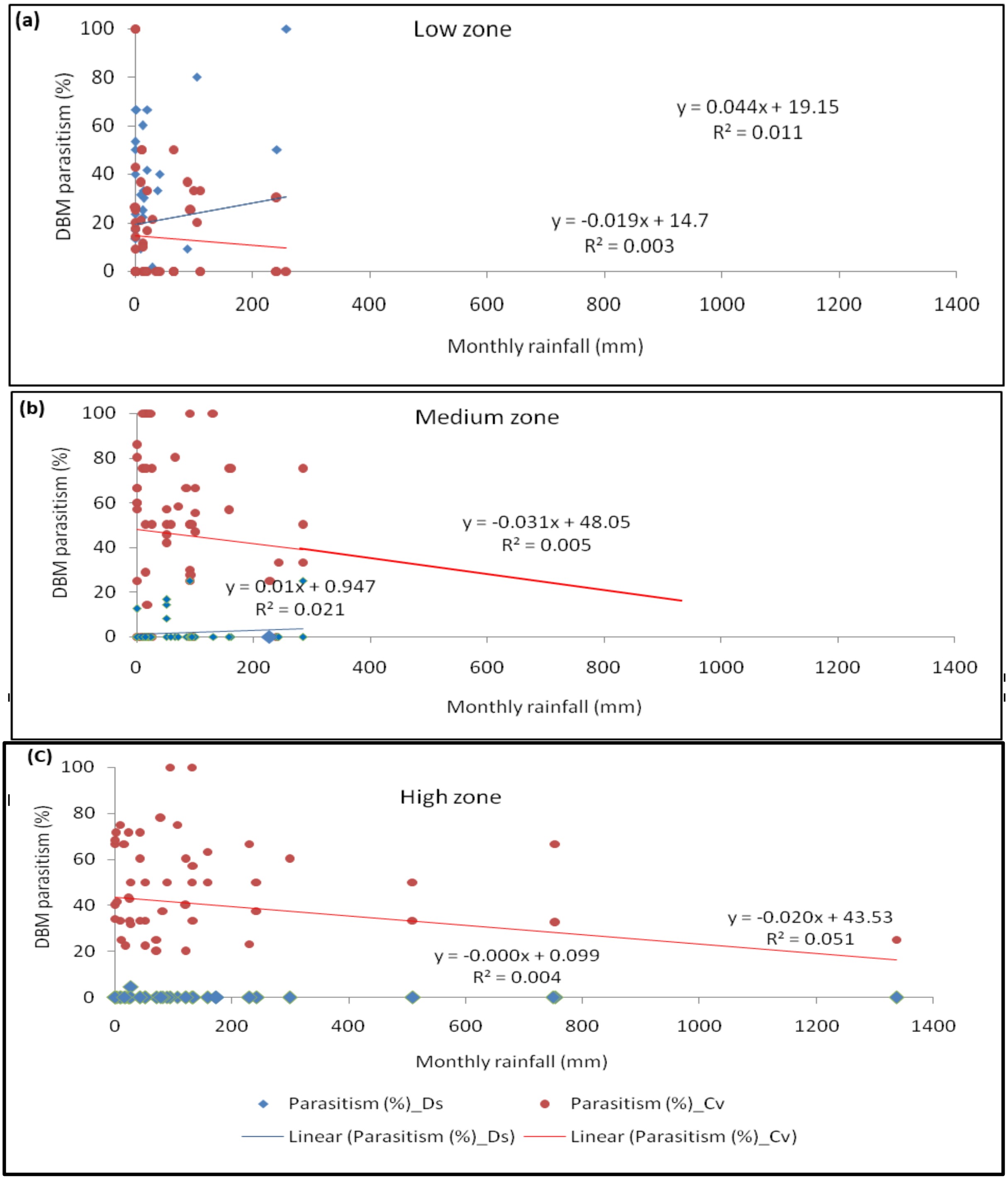
Taita hills										
		Low zone			Medium zone			High zone		
	Predictor	Coefficients	t-value	P-value	Coefficients	t-value	P-value	Coefficients	t-value	P-value
D. semiclausum	Temperature	0.9245	0.471	0.64	2.6563	0.951	0.3456	5.7936	2.933	0.0049
	Humidity	1.1737	1.417	0.162	-0.1401	-0.14	0.8888	0.3634	0.595	0.5539
	Rainfall	-0.0077	-0.115	0.908	-0.1231	-2.019	0.0483	-0.0378	-3.421	0.0012
C. vestalis	Temperature	-1.2746	-0.777	0.44	0.9759	1.998	0.0496	-0.0103	-2.086	0.0416
	Humidity	-0.4256	-0.616	0.541	0.1923	1.102	0.2751	-0.013	-0.852	0.3979
	Rainfall	0.0052	0.093	0.926	-0.0135	-1.266	0.2108	0.0001	-0.145	0.8851

The t-value evaluates the significance of the coefficient of each term in the model in presence of other terms



**Ds = Diadegma semilcausum, Cv = Cotesia vestalis*

Figure 4.7: Influence of mean monthly temperature on DBM parasitism by *D. semiclausum* and *C. vestalis* along altitudinal zones of Taita hills



*Ds = *Diadegma semilcausum*, Cv = *Cotesia vestalis*

Figure 4.8: Influence of rainfall on DBM parasitism by *D. semiclausum* and *C. vestalis* along altitudinal zones of Taita hills

4.4 Discussion

A reliable interpretation of how biotic and abiotic factors determine different species populations is imperative for predicting potential effects of global change on dynamics of insect species. The findings gathered in this study show the DBM population is presently available throughout agricultural lands of Mt. Kilimanjaro and Taita hills but its concentration differed with variability of weather conditions. The DBM population could not thrive extensively under the relatively hot temperature conditions in the low zones possibly because of physiological disturbances which impair its development and reproduction. The observation coincides with several studies whose findings concluded that the pest survives better at lower temperatures (< 20°C) than at higher temperatures (> 25°C) (Yang *et al*., 1993; Liu *et al*., 2002; Smith, 2002). Furthermore, due to the sparse tree vegetation structure, hot period intervals were undoubtedly longer in the low zones than in subsequent higher zones. The DBM populations on farms adjacent to Miwaleni springs at the lower end of the transect were greater than on other farms in the low zone. The springs possibly provided suitable microclimate to DBM in an area which is usually hot. Rainfall affects DBM population directly by disrupting the life cycle and indirectly by providing the moisture content needed for host plants, both the cultivated and wild crucifer plants. However, heavy rain droplets probably killed the tender eggs, and the first and second instar larvae. In addition, long sessions of intensive rainfall particularly during the long rainy season likely dislodged the second, third and some fourth instars from the infested plants to the soil, subjected them to the running water sheet and kill them in the process. In Asia, numerous studies have documented the mortality effect of rainfall on DBM (Annamalai *et al*., 1988; Sivapragasam *et al*., 1988; Wakisaka *et al*., 1991; Kobori and Amano, 2003). To adults, rainfall likely disrupted the mobility associated with mating and oviposition activities. Undoubtedly, these reduced the DBM population and the associated leaf damage as observed during the rainy season.

The observed weather-related population dynamics of DBM had profound implications on leaf damage which resulted to yield loss. The pest abundance was relatively huge in ecologically-fragile areas of the low zones e.g. nearby the Miwaleni springs in Mt. Kilimanjaro and where insecticides application was widely practiced. Resistance of DBM to many synthetic insecticides and probably considerable elimination of many of its natural enemies from extensive application of insecticides might have also contributed to the buildup of DBM population in such areas of the low zones. However, the widespread lower temperature conditions up the altitude were expected to increase the favourable environment for the pest to thrive. Several insect pests adapted to cool and moderate temperature conditions are reported to shift upward the altitudinal gradients in response to the warming climate in the low and midlands of the tropical ecosystems (Parmesan, 2006; Pepin *et al*., 2015).

The parasitic efficiency of *C. vestalis* in the low zone could be associated with its adaptability to hotter temperature conditions relatively common in the zone. Comparatively, *Diadegma semiclausum* is more sensitive to hot temperatures. Such observations can partly be explained from the findings by Talekar and Yang (1991) which established that the optimal temperatures for DBM parasitism by *D. semiclausum* ranges from 15°C to 25°C and for *C. vestalis* from 20°C to 30°C. The pest parasitism by *D. semiclausum* was also found to drop sharply when the temperature approaches 30°C (Talekar and Yang, 1993). Field observations in Mt. Kilimanjaro and Taita hills showed temperature levels in the low zones were distinctly higher than in the mid and high altitudinal zones. Two studies in the region have reported the parasitism rates of DBM by *D. semiclausum* in low altitudinal-based fields are lower than on fields based in the high altitudes (Kahuthia-Gathu, 2007; Kahuthia-Gathu *et al*., 2011). Contrary to temperature and rainfall, a moderately high level of relative humidity (60%-80%), prevalent in the zones, was needed for optimal pupation of DBM and parasitoid development. This humidity level was abundant in the two transects. In China, Guo and Qin (2010) noted two peak adult emergences occurred when a relative humidity of 50% or 70% combined with a temperature of 20°C and three peaks when 90% relative humidity combined with 20°C.

In conclusion, temperature plays a big role in shaping the interactions between DBM, its host plants and parasitoid species. The vulnerability of *D. semiclausum* to hot temperature conditions might suggest a potentially declining DBM – *D. semiclausum* parasitic interaction under long periods of growing or high temperature conditions. Under the same scenario, the DBM – *C. vestalis* parasitic interaction, which remains strong under the relatively hot conditions, is likely to become more important in biological control systems under global warming. According to United Nations Environmental Program (2009) report, temperature has increased by approximately 1.5°C in the drylands of eastern Kenya since 1960s. Geographically, Taita hills and Mt. Kilimanjaro are not very far from this area and any more temperature rise in the vicinity of the study site will likely affect the stability of the temperature-sensitive biological control systems of DBM in Mt. Kilimanjaro and Taita hills. Restricting applications of broad spectrum insecticides, controlling the use and frequency of selective insecticides and adopting organic farming methods are necessary for maintaining the favourable environmental conditions for *C. vestalis*.

CHAPTER FIVE: TEMPERATURE-DEPENDENT PHENOLOGY OF DIAMONDBACK MOTH AND ITS KEY PARASITOIDS

5.1 Introduction

The timing of life cycle events of insect pests can be directly influenced by climate. Diamondback moth responds to climatic variability in several ways, including long range migration (Xing *et al.*, 2013). In this context, the pest can disperse to and from between areas that allow them to thrive throughout the year and into areas that are only seasonally suitable for its growth and development. Climate variability affects the pest's phenology. Leith (1974) defined phenology as the study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species. A lot of researches have been conducted to investigate climate change-driven species' phenologies, particularly in the cool temperate regions (Beebee, 1995; Crick *et al*., 1997; Gibbs and Freisch, 2001; Forister and Shapiro, 2003; Huppop and Huppop, 2003; Both et al., 2004; Parmesan, 2006). Most of these studies have related temperature variations strongly with not only the timing of developmental stages but also the length of the growing season.

Temperature rise across the higher latitudes is recorded to contribute substantially in shortening the unfavourably long winter seasons and thus lengthening the growing seasons of different crops, including crucifer vegetables (Parmesan, 2006; Pepin *et al*., 2015). The length of the growing season for different vegetables in northern United States has increased (Parmesan, 2006). Between 1959 and 2003, such growing season for different vegetables has lengthened by one week and a half (Menzel and Fabian, 1999; Menzel, 2000). To different species, a consistent rise of mean monthly temperature up to 2.8°C in Wisconsin in the United States, between 1940s and 1990s, has been associated with arrival of the migratory birds 7.3 days earlier during spring (Bradley *et al*., 1999).In another study, Crick *et al*. (1998) associated consistent temperature rise in United Kingdom with the increasingly common earlier laying dates of 20 bird species.

Insect population dynamics have always been used as indicators of climate change due to their short life cycle and strong vulnerability to temperature changes. A few researches have linked climate change to biological dynamics of insect species along altitudinal variations (Pounds *et al*., 1999; Penuelas *et al*., 2002). One of such studies was conducted in the Mediterranean lowland California using data collected for thirty one years, and demonstrated butterflies have advanced their first flight dates by around 24 days (Forister and Shapiro, 2003).Climate change – related research in the eastern and southern Africa is not extensive. Such research has so far largely focused on short term field surveys, laboratory studies and modeling (Kahuthia-Gathu, 2011; Khadioli *et al*., 2014a, b; Mwalusepo *et al*., 2015).

Several DBM parasitoids have been introduced and established successfully in different parts of the world. However, a few could not establish fully due a number of factors related to host density dependence and reproductivity (Stiling, 1990; Lane *et al*., 1999), weather conditions (Norris *et al*., 2002) and structure of habitat (Tscharntke *et al*., 2005).The DBM and parasitoid populations are dynamic and are affected by both biotic and abiotic factors. *Diadegma semiclausum*, one of the key parasitoids of DBM in the region, initially could not control the DBM population in New Zealand and Australia due to weak adaptation (Beck and Cameron, 1992; Cameron *et al*., 1997b). *Cotesia vestalis*, another key parasitoid, is widely distributed over large areas of lowland. However, a few DBM outbreaks have been reported in several areas of the lowland in south-east Asia where *C. vestalis* is reportedly present and synthetic insecticides are less sprayed (Verkerk and Wright, 1997). Generally, insects respond to temperature rise under global warming by reducing the time taken to acquire enough energy to complete the life cycle (Zalucki *et al*., 2012; Bahar *et al*., 2013). However, rising temperatures can affect biological control of the moth if such a rise leads to a mismatch of life cycles of DBM and its parasitoids (Bahar *et al*., 2012).

Different timings of their biological events in the life history with respect to temperature may result in the phenological mismatch of DBM and its parasitoids. This can spell a potential DBM outbreak if parasitoids responded unfavourably to temperature and to DBM favourably. Any parasitoid response resulting to lower numbers of added generations and disruption of the host search efficiency can impair the control of DBM population. A recent modeling study has predicted climate change-based shrinkage of ecological niche of some invasive species (Hill *et al*., 2016), which is also possible to parasitoids. Thus, the coevolution of thermal tolerance of DBM and its parasitoids is of paramount importance for keeping the pest population in check. Without such coevolution, crop damage would likely rise from the increased feeding and reproduction of pests (Chidawanyika *et al.*, 2012). The current study builds on the role of temperature on influencing the life history of DBM, *D. semiclausum* and *C. vestalis* for better understanding its implication on biological control along altitudinal gradients.

5.2 Materials and methods

Temperature change may directly affect the biology of DBM, *D. semiclausum* and *C. vestalis*. The effect can lead to corresponding behavioral change of the insects which might result into some fundamental ecological or agronomical consequence e.g. increased or decreased crop damage, pest outbreak, species dispersal or even extinction. The life cycles of the three mentioned insects were therefore studied under some constant temperature conditions in laboratory to understand the behavioural change which could give light to population changes and their potential implications in species interactions. The study focused on the egg, larva, pupa and adult stages of the insects. Experiments on the development and mortality of the immature stages (egg, larva and pupa), life span and reproduction of adults under constant temperatures were conducted in laboratory. The experiments were repeated under outdoor fluctuating temperature conditions following the same procedure. Outputs from the two experimental set ups (laboratory and field) were compared for validation. The numbers of days taken by a cohort of insect stage to develop into subsequent stage, number of days lived, numbers of eggs laid, age of females and the proportion of female offspring were randomized several times under 'Stochastic simulation' tool (Kroschel *et al*., 2013)to estimate the population growth parameters, namely intrinsic rate of natural increase (r_m), net reproduction rate (R_o), gross reproduction rate (GRR), mean generation time (GT), finite rate of increase (λ) and doubling time (Dt). The parameters were used to draw the demographic trends of DBM, *D. semiclausum* and *C. vestalis*.

5.2.1 Establishment of diamondback moth and parasitoid colonies

Samples of the DBM population obtained from the field surveys in Taita hills were brought to laboratory for establishment of the life tables. The conditions stipulated in the research permits issued by the governments of Tanzania (reference letter FA/191/228/01/61) and Kenya (reference letter RESEA/1/KFS/5) did not allow transportation of DBM across the border. In addition, the life history study in laboratory could not be conducted in Tanzania because of limited facilities. The pest colony was therefore initiated and maintained at ICIPE in Nairobi, Kenya, and the DBM was reared on common cabbage (Gloria, F1 hybrid), as described by Kahuthia-Gathu *et al*. (2008). To acclimatize to laboratory conditions, the collected population was raised for one generation.

The *C. vestalis* and *D. semiclausum* populations that were utilized for setting the life table experiments were collected from the emerged adults in the laboratory. The insects were reared on two separate DBM (host insect) colonies in the laboratory, one for each parasitoid species. Both colonies were placed inside a clear, ventilated cubic perspex container (60 cm X 45 cm

X 45 cm) and maintained at a room temperature of 25°C. The parasitoids were fed on 10% honey solution moderately absorbed in small, cotton balls, which were replaced daily.

5.2.2 Experimental procedures

5.2.2.1 Development of temperature – dependent life tables of diamondback moth

A life table was constructed by tracking the life history of 1872 eggs till eclosion of all progeny of these individuals. Development of DBM life stages, which includes oviposition and mortality, was recorded daily. Eggs that were laid within the past 24 hours were positioned on fresh cabbage cut-leaves and placed in glass or plastic vials (7.5 cm length and 2.5 cm diameter). The vials were lined with paper towels for absorbing excess moisture and covered with a fine mesh sieve ventilated lid. The lids of containers were perforated and the holes were covered by muslin cloth for ventilation as described by Ngowi *et al*. (2017b). The experimental set ups were placed in six separate incubators of, Sanyo MIR – 554, manufactured by Sanyo Electric Co. Limited of Japan. Each incubator was calibrated at a constant temperature (10°C, 15°C, 20°C, 25°C, 30°C and 35°C, each ± 1°C). For the life history study at 35°C, the eggs were individually positioned on young leaves whose stipule ends were enfolded in soaked cotton wool to delay dehydration of the leaves. This set up at 35°C was carefully put inside ventilated plastic container (12cm X 10.2 cm X 6.5cm). About a third of the total number of eggs used (670 eggs) were utilized at the lowest and highest temperatures (10°C and 35°C) to ensure adequate availability of samples following increased mortality. In each life table, at least thirty surviving females were kept for assessment of fecundity. The experiments were conducted at 60% – 80% relative humidity and a photoperiod characterized by 12 hours of daylength. Morphological change associated with egg development was observed daily and if no egg had hatched by the time of observation, an ‘Egg’ was recorded in the life table dataset record. Eggs which could not hatch were supposed to have failed. Larvae that emerged from eggs were kept under daily observations. Everyday a larva was observed, a ‘Larva’ was recorded in the life table. Morphological development of the pupa was observed daily and a 'Pupa' was recorded in the life table if the life stage did not change to adult. Emerged males were recorded in dataset. Some steps undertaken are illustrated in Fig. 5.1.

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Figure 5.1: Rearing and maintanance of DBM colony for life tables: (a) Ventilated perspex container for rearing adults; (b) Eggs laid on aluminium foil have been inoculated on cabbage plant leaves; (c) Cabbage cut-leaf inside a ventilated glass vial for feeding the larva; (d) A batch of larvae in vials is placed and reared at a constant temperature in the incubator; (e) Tray holding a batch of immature stages in vials; (f) Plastic containers for adult DBM for oviposition data

A day when an egg failed or other stages died was recorded as 'Dead'. The 'Dead' was recorded repeatedly along the column till all the life stages died. The insects were labeled with numbers and the life stage of each insect in a column was observed closely and recorded. The numbers were marked on top of columns when recording development of insects in the life table datasets. The total number of columns equaled the number of insects involved for life table dataset. The 'Model Builder' tool in ILCYM sums up the total number of days taken by the insect to pass a particular stage and utilizes such information for modeling its development. The numbers of eggs laid daily during the evaluation interval were filled in the dataset to serve two folds: to denote the females in the life table dataset, and to include oviposition data. A day the female could not lay eggs was filled with zero (0). Table 5.1 exemplifies an experimental procedure used for developing a life table dataset at a given constant temperature.

Table 5.1: Exemplified experimental design for developing and recording temperature-dependent life table dataset

Time period		Track number labels assigned to individual insects							
Date	Day	1	2	3	4	5	6	7	8
1/1/2014	1st	Egg	Egg	Egg	Egg	Egg	Egg	Egg	Egg
2/1/2014	2nd	Egg	Egg	Egg	Egg	Egg	Egg	Egg	Egg
3/1/2014	3rd	Egg	Larva	Egg	Larva	Egg	Egg	Egg	Egg
4/1/2014	4th	Egg	Larva	Egg	Larva	Egg	Larva	Larva	Egg
5/1/2014	5th	Larva	Larva	Egg	Larva	Larva	Larva	Larva	Egg
6/1/2014	6th	Larva	Larva	Larva	Pupa	Larva	Larva	Larva	Larva
7/1/2014	7th	Larva	Pupa	Larva	Pupa	Larva	Pupa	Pupa	Larva
8/1/2014	8th	Larva	Pupa	Larva	Pupa	Pupa	Pupa	Pupa	Larva
9/1/2014	9th	Pupa	Pupa	Larva	0	Pupa	Pupa	Pupa	Larva
10/1/2014	10th	Pupa	17	Pupa	69	Pupa	27	52	Pupa
11/1/2014	11th	Male	44	Pupa	82	Male	77	36	Pupa
12/1/2014	12th	Male	51	Male	18	Male	19	25	0
13/1/2014	13th	Male	17	Male	4	Male	21	18	6
14/1/2014	14th	Male	Dead	Male	Dead	Male	9	23	14
15/1/2014	15th	Dead	Dead	Male	Dead	Dead	3	6	4
16/1/2014	16th	Dead	Dead	Dead	Dead	Dead	Dead	Dead	Dead

*The insect stage and numbers of eggs filled are hypothetical

A fresh supply of cabbage cut-leaves were provided to the larvae after every 1 – 2 days. The daily progress of the larvae and pupae on whether they metarmophosized into subsequent stages or not was checked daily and the observed stages recorded accordingly. The time (in days) taken for the immature life stages to develop and metarmophosize into subsequent stage was recorded. The numbers of eggs, larvae and pupae that died at different temperatures were recorded daily.

The procedure for generating oviposition data followed the description of Ngowi *et al*., (2017b). The eclosed males and females were paired at a sex ratio of 1:1. These insects were then placed inside ventilated plastic containers, measured 12 cm X 10.2 cm X 6.5 cm, and fed with 6% sugar solution which was soaked in cotton wool balls in lieu of nectar which was difficult to obtain. The balls were replaced after every 1 or 2 days to provide a fresh supply of feed. Cabbage leaf extract was prepared and coated on aluminium foil which was then hanged inside each container attract oviposition on it. The number of eggs laid were recorded every 24 hours, after which the foil was replaced by a fresh one. The total life span (in days) of individual adults at different temperature treatments was recorded.

5.2.2.2 Development of temperature – dependent life tables of parasitoid species

A total of 3,384 second and third instar DBM larvae which had just spent the past 24 hours exposed to adult parasitoids in the parasitoid colony, were picked and individually placed in glass vials (diameter of 2.5 cm and height of 7.5 cm high) for construction of life tables. Specifically, the larvae were attended as described under section 5.2.2.1 with a little modification to suit parasitoids: if the host larvae were parasitized, the individual egg and larval stages of parasitoids could not be observed visually except through morphological observation of the host larvae. These stages were thus considered together and were denoted as the combined Egg + Larva (E + L). Moreover, an extra constant temperature (12.5°C) was accorded to *C. vestalis* after failing to develop at 10°C. The emerged adult parasitoids were paired at a sex ratio of 1:1 and kept inside ventilated plastic containers (12 cm X 10.2 cm X 6.5cm) for mating. The insects were fed with 10% honey solution in lieau of nectar absorbed in small cotton balls which were replaced after every 1 to 2 days to provide fresh supply of feed. A fresh batch of twenty five second and third instar larvae of DBM (host insect) was daily placed in the plastic containers for parasitization by *D. semiclausum* or *C. vestalis.* The exercise was repeated daily till the death of the female. The larvae were exposed to parasitoids for 24 hours. Afterwards, they were picked and reared inside the improvised, sieve-ventilated plastic boxes. The larvae exposed to *D. semiclausum* were reared separately from those exposed to *C. vestalis* to avoid mixing the oviposition data. The larvae were supplied with fresh pieces of cabbage leaves after every 1 or 2 days. During this time, their morphological development was observed closely and recorded daily. The numbers of cocoons featuring the development of *D. semiclausum* and *C. vestalis* were recorded and taken for the oviposition data. A total of 52,025 host larvae were exposed to *C. vestalis* at constant temperatures for recording oviposition (12.5°C = 625; 15°C = 23,300; 20°C = 10,600; 25°C = 11,350; 30°C = 6,025; 35°C = 125). For *D. semiclausum*, 67,325 host larvae were used (10°C = 31,275; 15°C = 20,975; 20°C = 8,725; 25°C = 3,800; 30°C = 2,550).

5.2.3 Development of phenology models and analysis

The Insect Life Cycle Modeling (ILCYM version 3.0) software (Sporleder *et al.*, 2012) was employed to produce phenology models. The software is an open-source computer tool developed to capture the information on age stage-structured insect populations obtained at different temperatures and utilize it for modeling insect phenology, validation and mapping potential distributions. Insects undergo through immature stages of egg, larva and pupa (or egg and nymph) before emerging as adults. These insects may die when in immature stages or may produce new generations when adults. Insect populations are therefore under continuous reproduction and overlapping generations. ILCYM was adopted because of its ability to capture this information. The tool describes the development and mortality of immature stages, taking into consideration the variations of individuals in a population. Furthermore, the tool is used to describe the life span and reproduction of adults with respect to temperature.

The life table datasets developed were saved in .txt format and uploaded in ILCYM. Generated at different constant temperatures, the life table datasets were uploaded in the software through the ‘Upload Data’ window for phenology modeling. Three separate work folders (referred to as ‘New Project’ in ILCYM software) were created. Each folder was named after the individual insect species. The life table data set of each species was placed in its respective folder. The insect life stages recorded in the datasets were filled in the ‘Creating New Project’ window. The sex ratio was selected as 1:1. The ‘Development’, ‘Mortality’ and ‘Senescence’ tools in the ‘Model Builder’ module were activated to count the total number of days a life stage passes through a given temperature and use the information for modeling the development, mortality and adult life span at constant temperatures. The ‘Total Oviposition’ tool was turned on to pick the number of eggs in the life table dataset and model the reproduction of insects. The ‘model builder’ module present under ‘Tools’ window, was activated to develop the temperature-dependent phenology models. The coefficient of determination (R^2) and Akaike’s Information Criterion (AIC) (Akaike, 1973), the statistics inbuilt in ILCYM, were included in the criteria for selecting thebest fitted mathematical expression describing each life stage of the insect pest and parasitoids. Knowledge of the ecological behaviour of the insect with regard to temperature was also considered in the criteria. The AIC was adopted to measure the relative quality of phenological models where a model with the lower AIC value was judged to be better and was selected. The coefficient of determination was used to denote the degree by which temperature predicted the variance in the life stage. A model with a higher value of coefficient of determination was considered to be better than one with a lower value.

5.2.3.1 Analysis of development time of life stages

The time (in days) taken to complete a specific life stage at different temperatures were recorded. The temperature values were regressed against the developmental times in the generalized linear model (GLM) to establish the effect of temperature on development times of the insect life stages. Significant differences in developmental times obtained at different temperatures were established through application of Tukey HSD test ($P < 0.05$).The chi-squared test ($P < 0.05$) was adopted to test whether the observed and model-predicted developmental times corresponded. A contingency table made of six rows (developmental times of life stages at six given constant temperatures) and two columns (observed and predicted developmental times) was used in this study.

5.2.3.2 Analysis of development rate of immature stages

Development rates of DBM and its parasitoids were obtained by taking inverse of the median development time (development rate = 1/development time) as described in Kroschel *et al.* (2013). The individual non-linear models were assessed against the life tables to determine the best functions which fit closely to development rates of the immature life stages of DBM and its key parasitoids. Because the rates skewed towards the low and high extreme temperatures, the data were log-transformed to obtain a normal distribution and tested for homogeneity by Bartlett test before being subjected to ANOVA for comparison of the development rates under different temperature treatments. The Shapiro test was used to test for normality. The ANOVA was followed by a multiple range test to determine where the differences exist and in this case, the Tukey HSD test ($P < 0.05$) was employed.

A linear regression model was further fitted to determine the theoretical lower development threshold temperatures for immature life stages. These were estimated from the intercept and slope of the model through intercept/slope ratio as described in Zajack *et al.* (1989).The low threshold temperatures were developed from the linear regression equation,

$$r(T) = a + bT$$

where $r(T)$ is the development rate at temperature T, a is the intercept and b the slope of the equation. All statistical tests were conducted in R (R Core Team, 2012). The upper threshold temperatures were estimated from ILCYM.

5.2.3.3 Analysis of mortality of immature stages

The numbers of eggs, larvae, the combined egg + larva and pupae stages of DBM and its parasitoids which died daily when conducting experiments at different temperatures were counted and percentage mortality calculated. Using 'Mortality' tool in ILCYM, the experimental temperatures were regressed against the percentage mortality to produce non-linear relationships which described mortality pattern of the individual life stages against the tested temperatures. The mean mortality rates under different temperatures were compared using ANOVA and where significant difference in mortality existed, they were classified using the Tukey HSD test ($P < 0.05$).

5.2.3.4 Analysis of adult life span

The survival time periods of adult DBM, *D. semiclausum* and *C. vestalis* were recorded for both sexes. The data collected on the numbers of days lived by adults were regressed against the respective experimental temperatures using negative binomial generalized linear model (NB GLM) to establish the effect of different temperatures on the life span of DBM and its parasitoids. The differences in life spans among the given temperatures were compared using ANOVA and classified using Tukey HSD test ($P < 0.05$).

5.2.3.5 Analysis of reproduction of DBM, *D. semiclausum* and *C. vestalis*

Using the ‘Total oviposition’ tool, the total numbers of eggs laid daily by DBM were regressed non-linearly against the constant temperatures because the number of eggs laid skewed towards the lower and upper end temperatures. The reproductive capacity of parasitoids was measured in terms of fecundity and not fertility. This is because practically, not all eggs laid hatched to adults. However, some parasitoid eggs developed successfully to the pupal stages and killed their hosts. Though no adult parasitoids emerged, the host mortality contributed to decline of its population, which was vital for understanding dynamics of the field populations of DBM and its parasitoids. The number of cocoons developed was thus considered to be synonymous with the number of eggs laid. The total number of eggs laid per day was calculated.

The average numbers of eggs laid at different temperatures were compared using ANOVA. Where significant differences among such means existed, the Tukey HSD test was applied to establish where such differences exist under/between different temperatures.

5.2.3.6 Analysis of population growth parameters

The ‘stochastic simulation tool’ in ILCYM was employed to approximate the population growth parameters. These parameters were helpful in determining the survival, size and timing of insect populations necessary for predicting the population dynamics. The intrinsic rate of natural increase of DBM and its parasitoids, referring to a statistic derived from subtracting the daily number of deaths from the number of births per sum of the individuals in a generation, was computed from the life tables using cohorts of insects. Therefore, the intrinsic rate of natural increase is always given as a ratio. The average lifetime reproduction of this population, as revealed from the life tables, considering there were no diseases and starvation, was related to the gross reproduction rate. The number of female offspring produced by a female parent over a generation was calculated to establish net reproduction rate of the DBM, *D. semiclausum* and *C. vestalis* population. ILCYM software was employed to link the intrinsic rate of natural increase at different temperatures for prediction of the future population. The finite rate of population increase is equally important in predicting the population growth size over time.

The development, mortality, senescence and reproduction rates of the individual life stages of DBM and its parasitoids were calculated in ILCYM. By activating the ‘Stochastic simulation tool’ the software aided in generating an average number of days it took a cohort of insects to develop, survive and produce eggs. Nine hundred and sixty DBM eggs, 960 host larvae parasitized by *D. semiclausum* and 793 host larvae parasitized by *C. vestalis* were used for generating population growth parameters. For each species, the individual insects were assigned consecutive numbers from 1 to N (DBM: 1 – 960; *D. semiclausum*: 1 – 960; *C. vestalis*: 1 – 793). Out of these numbers, a list of random numbers was generated by ILCYM and the first 100 different life stages were sampled and utilized for simulating the rates and cohort updates. The DBM population was simulated repeatedly 10 times and either of the parasitoids 5 times under constant temperatures to estimate the population growth parameters. The mean differences in the parameter values at different temperatures were compared using ANOVA. The differences between means were separated by Tukey test at 95% significance level.

5.2.3.7 Phenology model validation

Testing ability of the phenology models developed in reproducing closely the same insect behavior under fluctuating temperature conditions in the field is essential for model validation. This was implemented by comparing the model outputs generated from the life table studies under the given constant temperatures in the laboratory with the outputs from the life table studies conducted under the outdoor fluctuating temperature conditions. Complete life table experiments for DBM, *D. semiclausum* and *C. vestalis* were thus conducted in the open at

ICIPE (S 01.22051°; E 036.89563°; altitude 1619 metres above sea level (metres asl.)) following the same procedure used in the laboratory, between 2ndNovember and 31st December 2014 (DBM) as described in Ngowi *et al*. (2017b). For *D. semiclausum*, the life table experiments for validating the phenology models were conducted from 21st November to 22nd December 2014 and for *C. vestalis*; from 24th November to 26th December 2014. One hundred individuals of each insect species were used in validation experiment. A thermohygrometer (iButton®, manufactured by Maxim Integrated Products Inc.) was erected outdoor on a wooden peg raised at about 30 cm high for recording the minimum and maximum daily temperatures throughout the period of conducting validation experiments. The loggers were placed 1 m away from where the experiments were conducted. The life tables generated and temperature datasets were loaded in ILCYM through the 'Model validation' tool and activated for generation of phenology models depicting the life history of insects under different temperatures.

5.3 Results

5.3.1 Effect of temperature on development time

Increasing the temperatures reduced the mean development times of all life stages but in contrast, decreasing the temperatures lengthened the mean development times. The mean developmental time of egg of DBM decreased from 20.6 days (10°C) to 2.5 days (35°C). The mean development time of larva was nine times longer at 10°C than at 35°CThe pupal development followed the same trend (Table 5.2).The mean development times of the life stages varied significantly with temperatures (egg: $\chi^2 = 321.6$, df = 5, P < 0.001; larva: χ^2= 178.63, df = 5, P < 0.001, pupa: $\chi^2 = 254.27$, df = 5, P < 0.001).

Table 5.2: Mean development time of DBM life stages in laboratory

Temperature (°C)	Mean development time (no. of days ± SE)		
	Egg (n = 936)	Larva (n = 747)	Pupa (n = 517)
10	20.64 ± 0.20a	25.55 ± 1.65a	27.45 ± 1.04a
15	8.68 ± 0.27b	19.30 ± 0.62b	14.84 ± 0.35b
20	5.40 ± 0.10c	11.78 ± 0.20c	7.51 ± 0.09c
25	3.47 ± 0.07de	7.89 ± 0.21d	4.84 ± 0.10d
30	3.43 ± 0.09e	5.51 ± 0.12e	3.79 ± 0.0.07ef
35	2.55 ± 0.05f	2.71 ± 0.24f	2.86 ± 0.20f

Mean values within a column followed by a different letter differed significantly at $P<0.05$, Poisson and negative binomial GLM (Tukey test).
n = number of immature stages observed
Letters a-f were adopted to denote significant mean differences as generated from Tukey test
SE = Standar Error

Like their host insect pest, the mean development times of parasitoids varied significantly with temperature: *D. semiclausum* (egg + larva: χ^2 =1953.5, df = 5, $P < 0.001$; pupa: χ^2 =425.89, df = 5, $P < 0.001$); *C. vestalis* (egg + larva: χ^2 =2403, df = 6, $P < 0.001$; pupa: χ^2 =1392, df = 6, $P < 0.001$). The development times of the combined egg + larval stage of *D. semiclausum* at 10°C was approximately half that of *C. vestalis* at the same temperature (Table 5.3).

Table 5.3: Mean development times of parasitoid life stages in laboratory

	Mean development time (no. of days ± SE)			
	D. semiclausum		*C. vestalis*	
Temperature (°C)	Egg + Larva (n = 1233)	Pupa (n = 915)	Egg + Larva (n = 1151)	Pupa (n = 807)
10	28.93 ± 0.62a	47.65 ± 0.34a	52.15 ± 1.35a	31.25 ± 1.43a
12.5	NA	NA	35.48 ± 0.62b	28.87 ± 0.79b
15	12.22 ± 0.29b	20.85 ± 0.29b	20.32 ± 0.31c	17.45 ± 0.43c
20	8.38 ± 0.13c	11.37 ± 0.16c	11.79 ± 0.28d	8.28 ± 0.14d
25	5.96 ± 0.15d	7.76 ± 0.16d	7.86 ± 0.09e	4.73 ± 0.12e
30	4.89 ± 0.05e	7.88 ± 0.17ed	5.71 ± 0.17f	3.72 ± 0.21f
35	5.38 ± 0.10cf	4.37 ± 0.10f	3.19 ± 0.10g	6.67 ± 0.33g

Mean values within a column followed by different letter differed significantly at P<0.05, Poisson and negative binomial GLM (Tukey test).
NA = Development time of *D. semiclausum* was not tested at 12.5°C
Letters a-g were adopted to denote significant mean differences as generated from Tukey test

5.3.2 Effect of temperature on development rate

Development rates of the egg, larva and pupa of DBM varied significantly with temperatures (F = 420.09, df = 2, 3, P = 0.0024). The optimal development rate of egg, larva and pupa occurred at 32.5°C,33.5°C and 33°C, respectively (Fig. 5.2). The model predicted declining development rates above these temperature values. The approximated lower threshold temperature for development were 3.76°C for egg, 4.79°C for larva and 4.21°C for pupa. Development rates of the egg, larva and pupa at different temperatures differed significantly (Egg: F = 273.1, df = 1, 4, P < 0.001; Larva: F = 355.5, df = 1, 4, P < 0.001; Pupa: F = 305.7, df = 1, 4, P < 0.001). The approximated upper threshold temperatures were 40.6°C (egg), 40.7°C (larva) and 38°C (pupa).

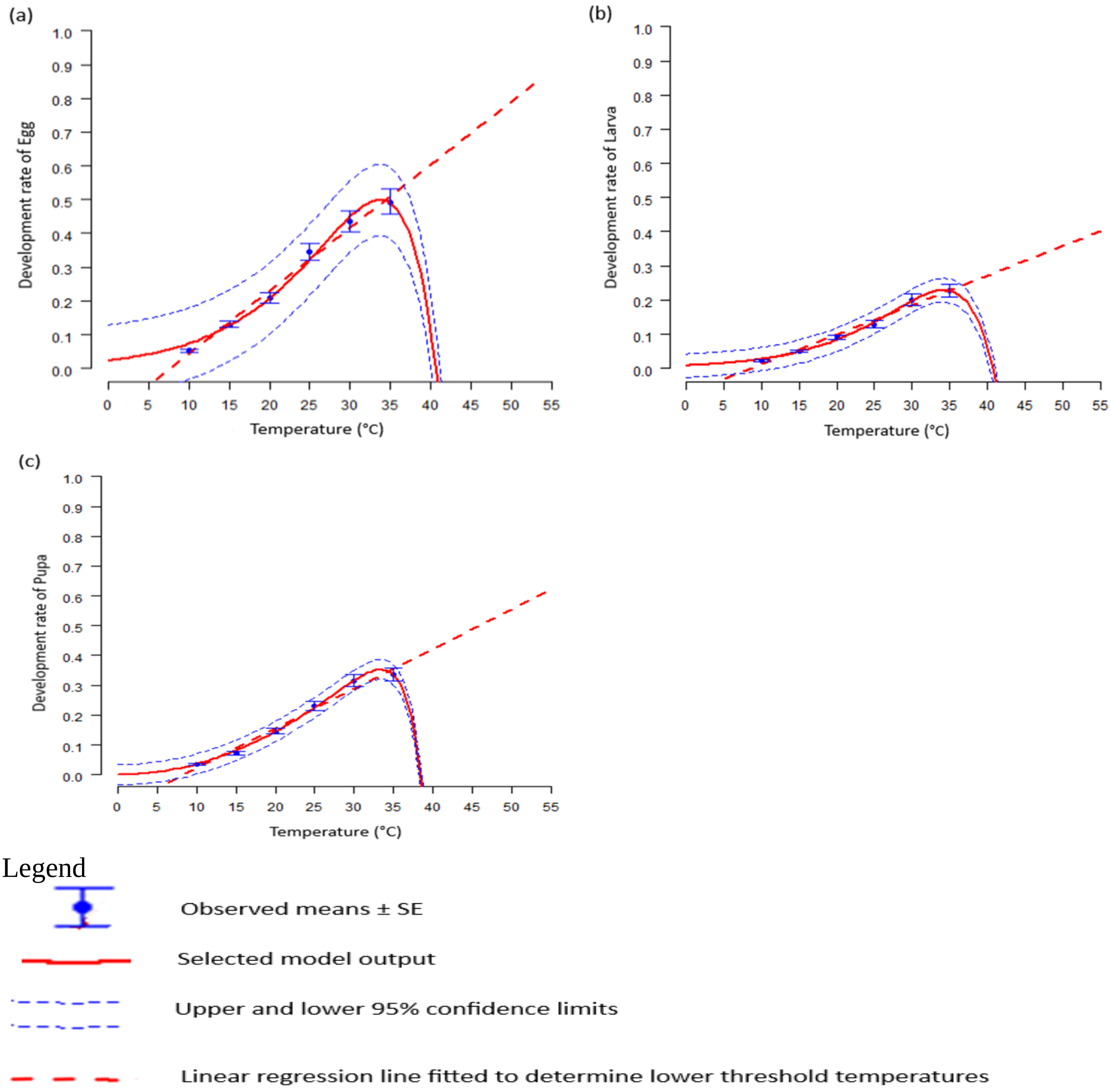

Figure 5.2: Development rates of DBM immature stages: egg (a), larva (b) and pupa (c)

The combined E + L and pupa stages of *D. semiclausum* developed at all the tested temperatures. The fitted linear regression model estimated 3.05°C, 3.76°C and 6.69°C to be the lower development threshold temperatures for E + L (F = 18.87, df = 1, 4, P = 0.0122), pupa (F = 15.45, df = 1, 4, P = 0.2817) and adult (F = 0.16, df = 1, 4, P = 0.7084), respectively. Development rates of the combined E + L differed significantly between temperature values

(F = 107.67, df = 3, 2, P = 0.0092). The lower temperature limits for *C. vestalis* were estimated to be 13.85°C (F = 173.00, df = 1, 5, P < 0.001) for E + L; 12.5°C (F = 5.89, df = 1, 5, P = 0.0595) for pupa; and 12.6°C (F = 3.37, df = 1, 4, P = 0.1405) for adults. The selected non linear models estimated the upper threshold limits for development of immature stages: *D. semiclausum* (E+L: 37.93°C, pupa: 32.79°C); *C. vestalis* (E + L: 41.62°C, pupa: 36.53°C) (Fig 5.3). The development rates differed significantly with temperature values (F = 92.84, df = 4, 3, P = 0.0004).

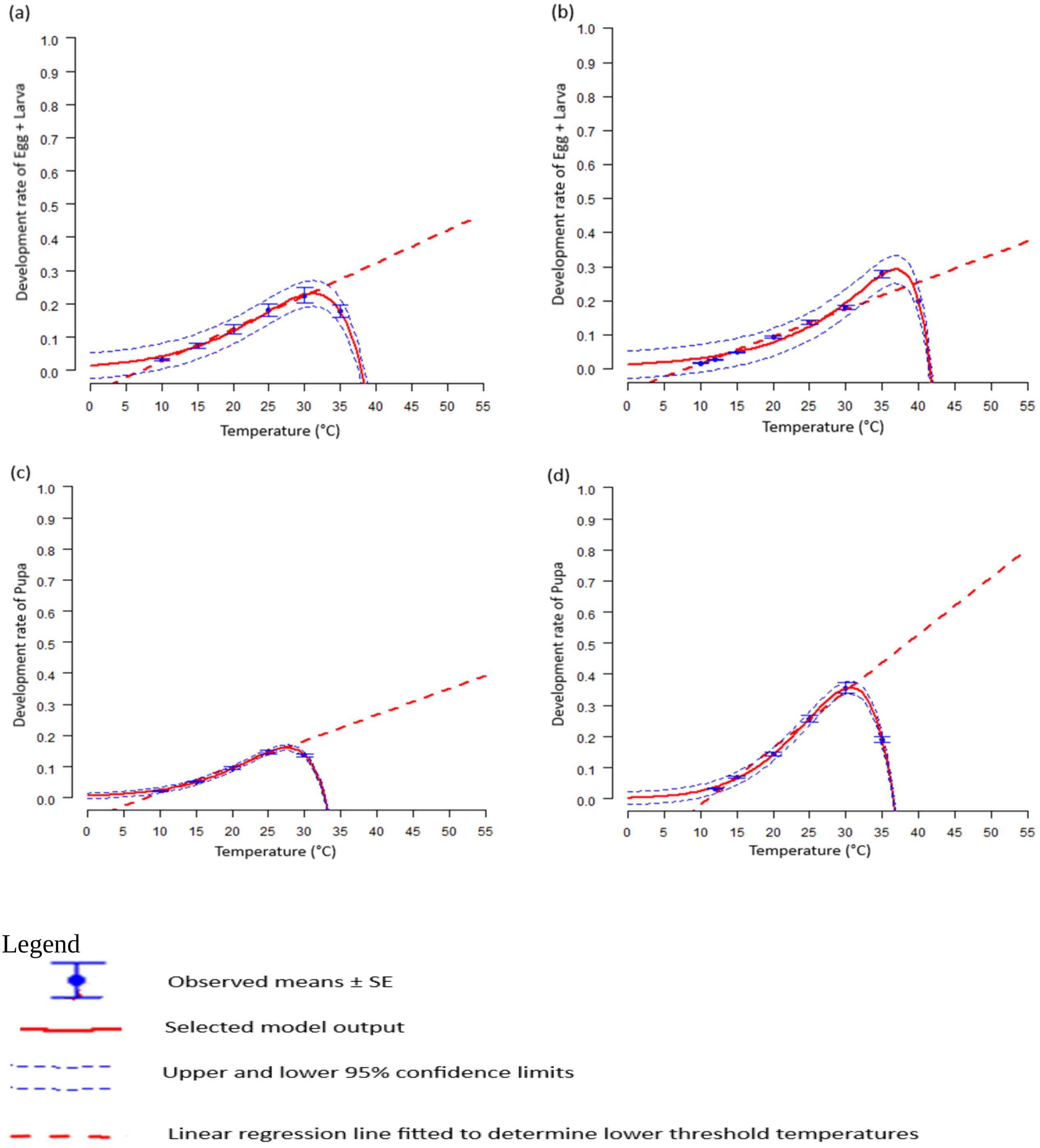

Figure 5.3: Development rates of immature stages of parasitoids at constant temperatures**.** *D. semiclausum*: combined egg and larva (a), pupa (c). *C. vestalis*: combined egg and larva (b), pupa (d)

5.3.3 Effect of temperature on mortality

Mortality rates of DBM, *D. semiclausum* and *C. vestalis* varied with temperature. For DBM, mortality of the immature stages differed significantly with temperatures (Egg: F = 151.85, df = 3, 2, P = 0.001; Larva: F = 38.39, df = 3, 2, P = 0.0073; Pupa: F = 167.28, df = 3, 2, P = 0.0008). The least percentage of eggs and larvae died at 20°C and the pupae at 15°C (Fig. 5.4). The mortality rates of egg, larva and pupa peaked at extreme low and high temperatures.

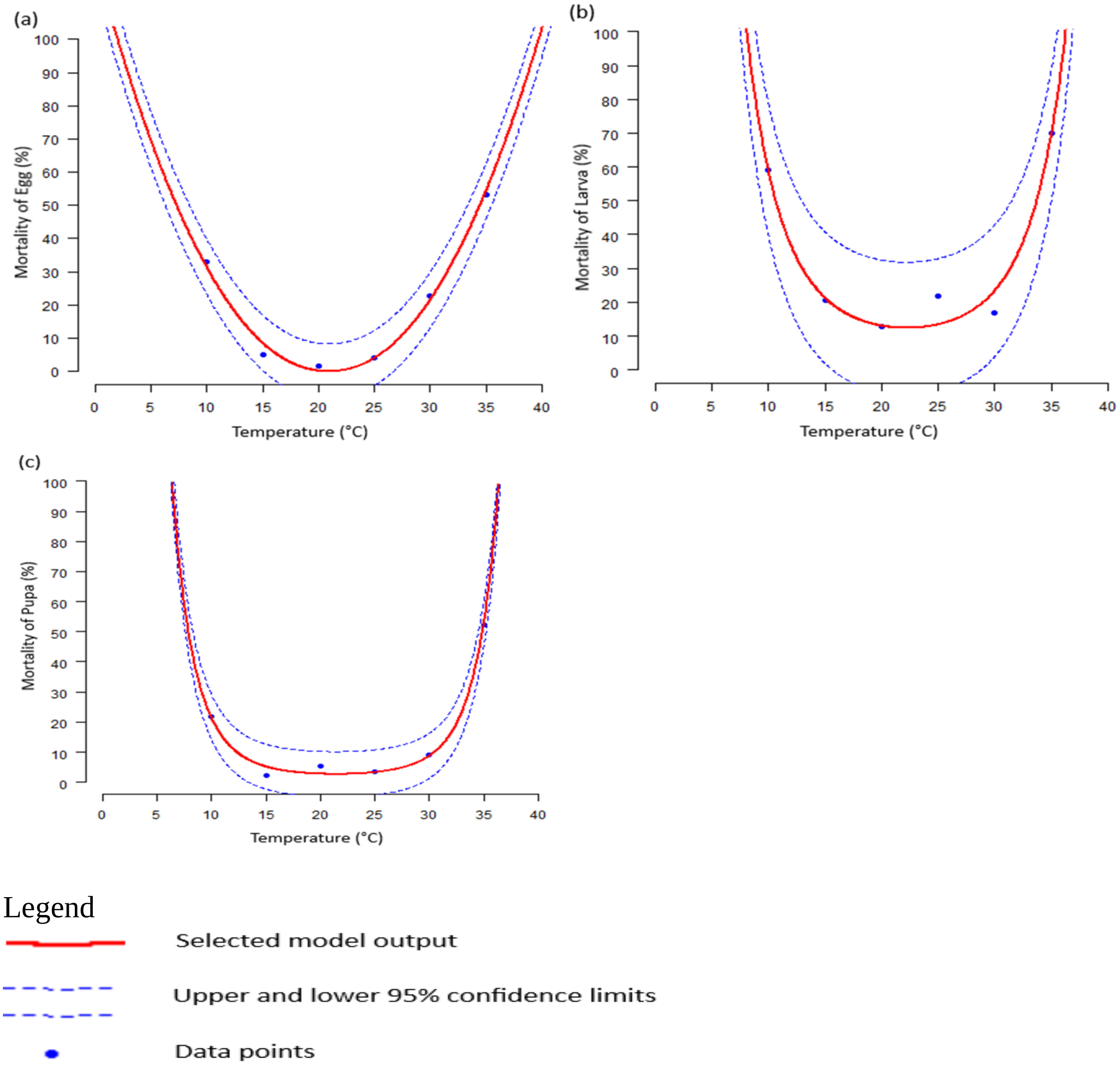

Figure 5.4: Temperature-dependent mortalities of immature life stages of DBM: egg (a), larva (b) and pupa (c)

The mean mortality rates of the pupa stage of *D. semiclausum* and *C.vestalis* differed significantly with temperatures (*D. semiclausum*: F = 147.20, df = 3, 2, P = 0.001; *C. vestalis*: F = 14.31, df = 4, 2, P = 0.015). The combined E + Lstage of *D. semiclausum* had increased mortality at 35°C (50%) and the lowest mortality at 20°C (12.2%). Mortality of the combined E + L stage of *C. vestalis* was relatively higher at 35°C (78.2%) and the lowest at 25°C (6.5%). The pupal stages of *C. vestalis* could not survive the low extreme temperature (10°C) but its mortality decreased with increasing temperature range from 10°C - 30°C. Mortality of the pupa stage of *D. semiclausum* increased with temperature from 25°C to 30°C but all the pupae died at 35°C (Fig. 5.5).

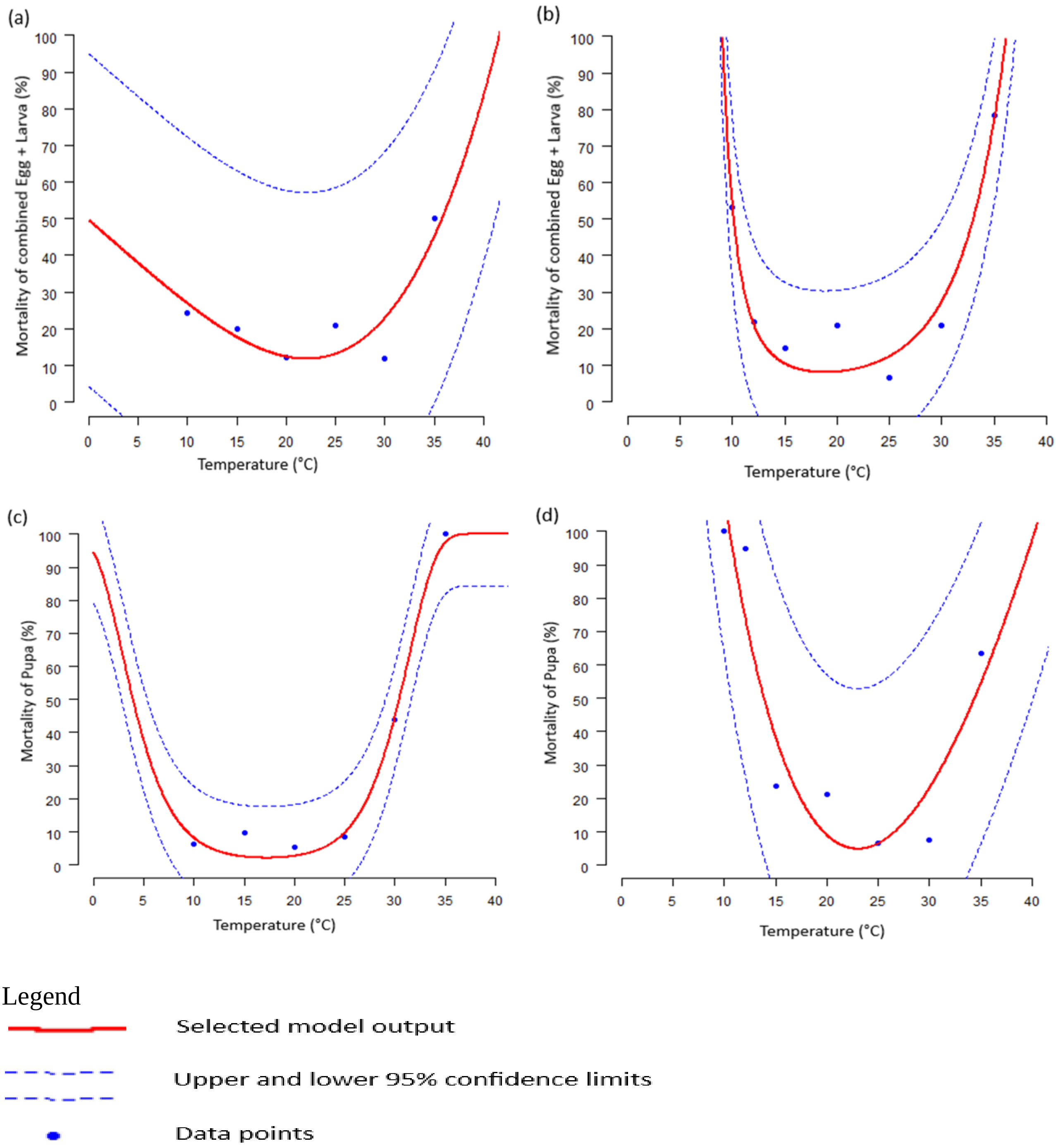

Figure 5.5: Mortality rates of the immature stages of parasitoids: (a) Combined egg and larval stage of *D. semiclausum*, (b) Combined egg and larval stage in *C. vestalis*, (c) Pupa of *D. semiclausum* and (d) Pupa of *C. vestalis*

5.3.4 Effect of temperature on adult life span

The adult life spans of the male and female moths declined with increasing temperatures. The life span of both sexes differed significantly at extreme temperatures of very low (10°C) and very high (35°C): (male: $F = 20.26$, $df = 1, 29$, $P < 0.001$; female: $F = 50.91$, $df = 1, 29$, $P < 0.001$). The life span of males and females differed significantly between the lower temperatures (10°C and 15°C) and the rest of the temperatures ($F = 6.15$, $df = 1, 41$, $P = 0.0173$). Females outlived males at the lowest experimental temperature (Female: 58.46 days; Male: 44.73 days). However, female life span got comparatively smaller as temperatures increased (Table 5.4).

Table 5.4: Life span of DBM and its key parasitoids at constant temperatures

Temperature (˚C)	Life span (in days)					
	DBM		*D. semiclausum*		*C. vestalis*	
	Male (n = 246)	Female (n = 229)	Male (n = 459)	Female (n = 193)	Male (n = 307)	Female (n = 186)
10	44.73 ± 3.82a	58.46 ± 3.89a	26.19 ± 0.98a	33.24 ± 3.22a	None	None
12.5	NA	NA	NA	NA	6.4 ± 0.8124a	12.5 ± 1.5a
15	44.09 ± 2.68a	31.89 ± 1.84b	14.89 ± 0.63b	17.04 ± 0.74b	16.49 ± 0.71b	19.19 ± 1.73ab
20	31.97 ± 1.21b	22.61 ± 0.84c	6.21 ± 0.27c	9.40 ± 0.58c	9.55 ± 0.38ac	10.09 ± 0.46ac
25	21.34 ± 1.6cd	14.04 ± 0.91de	3.62 ± 0.26d	4.08 ± 0.22de	7.25 ± 0.22ad	8.55 ± 0.43acd
30	20.17 ± 1.03d	13.90 ± 0.79e	2.12 ± 0.11e	3.32 ± 0.15e	5.15 ± 0.34ae	6.05 ± 0.43aef
35	7.33 ± 2.03e	6.43 ± 0.78f	None	None	1.44 ± 0.24f	2.5 ± 1.5f

Mean values within a column followed by different letter differed significantly at $P<0.05$, Poisson and negative binomial GLM (Tukey test).

n = number of adults observed

NA = Life table experiments were not conducted for DBM and *D. semiclausum* at 12.5°C
Letters a-f were adopted to denote significant mean differences as generated from Tukey test

Temperature affected the life spans of both sexes of *D. semiclausum* significantly (Male: F = 217.65, df = 3, 2, P = 0.0046; Female: F = 8.91, df = 5, 12, P = 0.001) and for *C. vestalis*, only the female (F = 20.58, df = 4, 2, P = 0.0469).Contrary to the host insect, females of both parasitoid species lived longer than males at all the tested temperatures (Table 5.4). Except for 10°C which was physiologically disruptive to the life span of *C. vestalis*, the ages of both parasitoid species declined with rising temperatures.

5.3.5 Effect of temperature on reproduction

The three insects laid fewer eggs around extreme temperatures. The numbers of eggs laid per female by DBM (fecundity) varied significantly under different temperatures (F = 51.59, df = 3, 2, P = 0.0191) (Table 5.5).

Table 5.5: Mean number of eggs laid by DBM and key parasitoids at constant temperatures

Temperature (°C)	Fecundity (no. of eggs/female)		
	DBM (n = 220)	*D. semiclausum* (n = 193)	*C. vestalis* (n = 186)
10	26.83 ± 10.09a	21.57 ± 4.45a	None
12.5	NA	NA	2.5 ± 0.5a
15	155.64 ± 18.72bde	84.26 ± 7.91b	40.63 ± 4.06b
20	265.21 ± 13.24cd	89.38 ± 7.52b	78.86 ± 5.18c
25	197.83 ± 14.39d	41.39 ± 4.68c	51.45 ± 2.89d
30	101.54 ± 11.80e	0.42 ± 0.13d	30.10 ± 2.54e
35	None	None	1 ± 1a

Mean values within a column followed by different letter differed significantly at P<0.05, ANOVA (Tukey test). n = number of adults observed

NA = Life table experiments were not conducted for DBM and *D.semiclausum* at 12.5°C

Letters a-e were adopted to denote significant mean differences as generated from Tukey test

The fecundity trend of DBM was best described by a simple Gaussian model. The optimal temperature for oviposition was near 20°C, around which the female laid an average of 265.2 eggs. Females which were reared at 35°C could not lay eggs (Fig. 5.6).

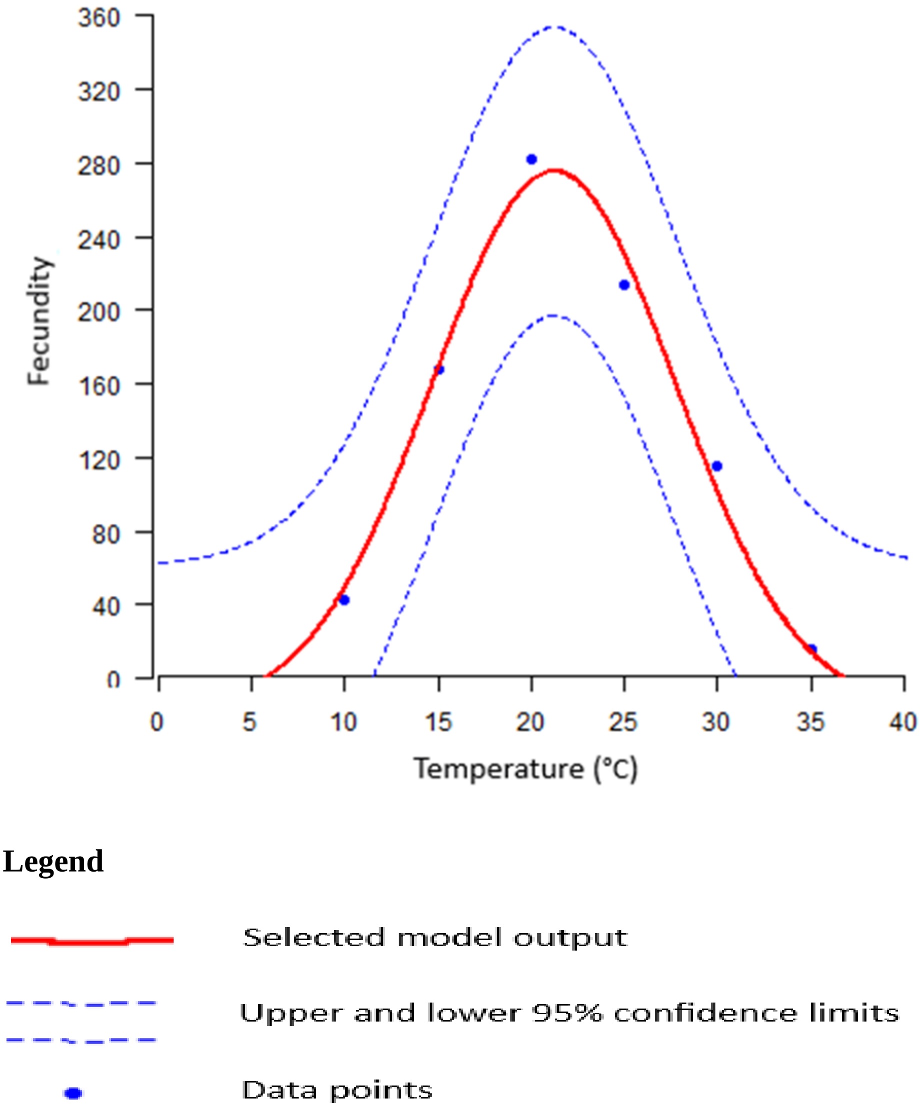

Figure 5.6: Temperature-dependent egg production of DBM

The numbers of eggs laid by the two parasitoids varied significantly at different temperatures: (*D. semiclausum*: F = 87.10, df = 3, 2, P = 0.0114; *C. vestalis*: F = 45.85, df = 3, 3, P = 0.0053). Only 1 out of the 186 female *C. vestalis* laid eggs at 35°C. A Simple Gaussian model predicted a temperature range of 15°C–20°C asthe most favourable for oviposition of *D. semiclausum*.

The female laid an average of 89.38eggs at 20°C but could not lay eggsat 35°C. *Cotesia vestalis* produced a comparatively fewer numbers of eggs at low temperatures but a greater number of eggs at high temperatures (Fig.5.7).

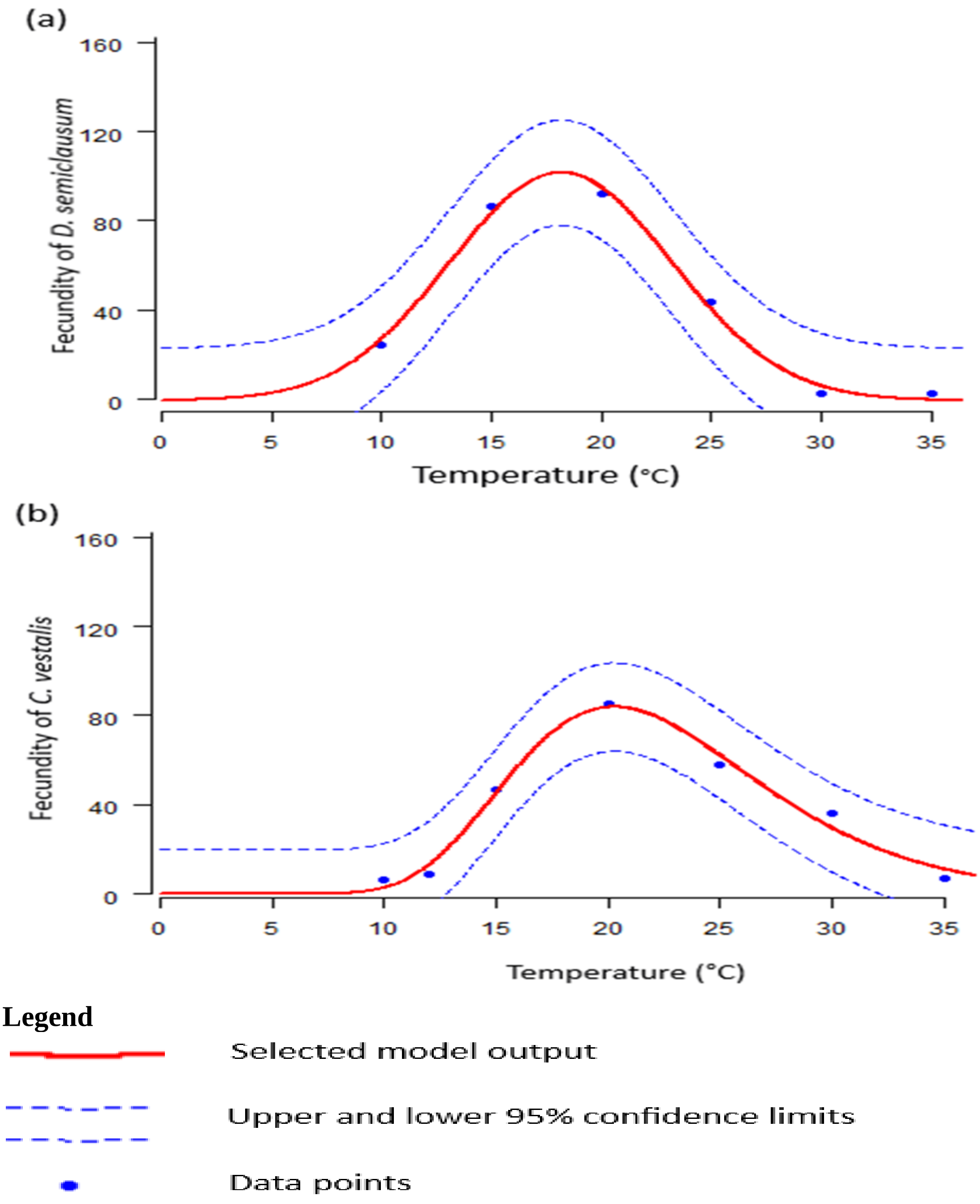

Figure 5.7: Temperature-dependent egg production of *D. semiclausum* (a) and *C. vestalis* (b)

5.3.6 Estimation of population growth parameters

The DBM population grew at a fraction of 0.21 individuals/day at the optimal temperature of 25°C. At this temperature, the pest population was growing because the number of the younger, vigorously reproducing individuals was higher than that of the older, less reproductive individuals. The pest population reproduced 87.38 female offprings /female/generation at 20°C which is more than half of the estimated1 136.12 individuals produced per female per generation. The time period taken from one life stage to the same life stage in subsequent generation reduced with increasing temperature. The finite rate of population increase started to decline at temperatures above 25°C. The temperatures between 10°C and 25°C reduced the time period taken by the population to double its size (Table 5.6).

Table 5.6: Estimated population growth parameters of DBM under constant temperatures

Temperature	Population Growth Parameters					
(°C)	r_m (n = 50)	Ro (n = 50)	GRR (n = 50)	GT (n = 50)	λ (n = 50)	Dt (n = 50)
10	0.01 ± 0.001a	3.31 ± 0.36a	32.44 ± 4.15a	86.92 ± 0.75a	1.01 ± 0.001a	56.96 ± 5.57a
15	0.07 ± 0.001a	41.22 ± 1.25b	110.77 ± 2.91bcd	54.31 ± 0.29b	1.07± 0.001a	10.14 ± 0.11b
20	0.13 ± 0.001a	87.38 ± 3.19c	136.12 ± 4.41c	33.67 ± 0.18c	1.14 ± 0.001a	5.23 ± 0.05cde
25	0.21 ± 0.002a	72.59 ± 3.28d	102.8 ± 3.37d	20.63 ± 0.09d	1.23 ± 0.003a	3.35 ± 0.04de
30	0.20 ± 0.004a	17.08 ± 1.03e	38.35 ± 2.31a	14.11 ± 0.08e	1.22 ± 0.005a	3.48 ± 0.08e

Mean values within a column followed by different letter differed significantly at $P<0.05$, ANOVA (Tukey test). r_m = intrinsic rate of natural increase; R_o = net reproduction rate; GRR = gross reproduction rate; GT = mean generation time; λ = finite rate of increase; Dt = doubling time (days).

Adult female DBM failed to reproduce at 35°C.

Letters a-e were adopted to denote significant mean differences as generated from Tukey test

The population growth patterns of DBM parasitoids were also influenced by temperatures. The *D. semiclausum* population size grew by approximately 0.12 individuals per day within a range of 20°Cto 30°C. The estimated average maximum number of offsprings produced by each female over a generation ranged from 37.73 to 39.16 individuals at 20°C. The approximate number of female offprings emerged out the host larvae oviposited by the same female parasitoid in one generation ranged from 16.51 to16.90 over a temperature range of 15°C – 20°C (Table 5.7). As in the host insect, the mean time periods between two successive generations reduced with rising temperature. The doubling time of the parasitoid population differed significantly when reared at 10°Ccompared to other experimental temperatures (F = 1238, df = 4, 45, P< 0.0001).

Unlike *D. semiclausum*, the *C. vestalis* population grew favourably under relatively high temperatures. The female reproduced approximately 8.18 individuals/generation at 30°C, which is approximately six times higher thanthe 1.3 individuals/generation added by *D. semiclausum* under the same temperature conditions (Table 5.7). By activating the population growth rate at 0.13 individuals/day, 25°C was the most favorable among the evaluated constant temperatures. The daily finite rate of population increase rose steadily with increasing temperature between 12.5°C and 25°C. This rate peaked at 1.14 females/female/day at 25°C before dropping once this temperature was surpassed. Each female was estimated to have produced 17.94 female offsprings in its lifetime when reared at 20°C.

Table 5.7: Estimated population growth parameters of *D. semiclausum* and *C. vestalis* under constant temperatures

Parasitoid	Temperature (°C)	Population growth parameters					
		r_m	Ro	GRR	GT	λ	Dt
D. semiclausum	10	0.02 ± 0.001a	3.6 ± 0.2a	8.44 ± 0.33a	73.16 ± 0.55a	1.017 ± 0.001a	40.07 ± 1.72a
	15	0.07 ± 0.002a	16.90 ± 1.02b	39.16 ± 2.27b	41.66 ± 0.17b	1.07 ± 0.002a	10.26 ± 0.26b
	20	0.12 ± 0.002a	16.51 ± 0.67b	37.73 ± 1.04b	23.10 ± 0.05c	1.129 ± 0.002a	5.72 ± 0.09b
	25	0.12 ± 0.003a	6.46 ± 0.25a	16.24 ± 0.58c	14.96 ± 0.15d	1.327 ± 0.004a	5.58 ± 0.14b
	30	0.12 ± 0.011a	0.19 ± 0.02c	1.30 ± 0.35d	13.72 ± 0.18d	0.884 ± 0.009a	5.76 ± 0.47b
C. vestalis	12.5	0.02 ± 0.001a	3.30 ± 0.22a	17.40 ± 2.11a	48.56 ± 0.21a	1.02 ± 0.001a	28.87 ± 1.89a
	15	0.07 ± 0.001a	15.79 ± 0.80bc	48.09 ± 2.24b	40.74 ± 0.28ab	1.07 ± 0.001a	10.26 ± 1.39bc
	20	0.09 ± 0.002a	17.94 ± 1.37b	47.15 ± 3.23b	30.77 ± 0.18b	1.1 ± 0.003a	7.43 ± 0.19cd
	25	0.13 ± 0.004a	10.51 ± 0.59c	25.69 ± 1.78c	17.45 ± 0.16c	1.14 ± 0.004a	5.17 ± 0.16d
	30	0.10 ± 0.006a	3.00 ± 0.21a	8.18 ± 0.25d	10.84 ± 0.12d	1.10 ± 0.006a	6.99 ± 0.40cd

Mean values within a column followed by different letter differed significantly at $P<0.05$, ANOVA (Tukey test). r_m = intrinsic rate of natural increase; R_o = net reproduction rate; GRR = gross reproduction rate; GT = mean generation time; λ = finite rate of increase; Dt = doubling time (days)

Letters a-d were adopted to denote significant mean differences as generated from Tukey test

5.3.7 Output from validation of phenology model

The minimum temperature ranged from 13.1°C to 18.6°C and the maximum temperature from 22.6°C to 38.6°C. The average temperature throughout the validation period was 21.8°C. The values generated from simulation of finite rate of population increase (λ), intrinsic rate of natural increase (r_m), doubling time (Dt) and mortality of the pest were nearly the same as the observed values (Table 5.8), demonstrating reliability of the phenology models developed in estimating insects' demography. For parasitoids, the simulated values of the r_m, λ, Dt and development times were comparable to the observed values (Table 5.9).

Table 5.8: Phenology model validation of DBM life stages

Population growth parameters				Phenology model			
Parameter	Simulated	Observed	P-value	Mortality	Simulated	Observed	P-value
r_m	0.16(0.01)	0.16	0.31	Egg	0.12(0.05)	0.12	0.5712
λ	1.18(0.01)	1.17	0.3054	Larva	0.17(0.08)	0.18	0.2611
Dt	4.28(0.32)	4.34	0.3734	Pupa	0.55(0.13)	0.54	0.8497

Standard errors areshown in brackets
n = 100

Table 5.9: Phenology model validationof *D. semiclausum* and *C. vestalis* immature stages

	Population growth parameters				Phenology model			
Parasitoid	Parameters	Simulated	Observed	P-value	Development time	Simulated	Observed	P-value
D. semiclausum	r_m	0.102(0.017)	0.138	< 0.0001	Egg + Larva	5.734(0.25)	8.687	< 0.0001
	λ	1.108(0.019)	1.148	< 0.0001	Pupa	11.187(0.112)	10.049	< 0.0001
	Dt	6.838(1.228)	5.023	< 0.0001	-	-	-	-
C. vestalis	r_m	0.116(0.014)	0.138	< 0.0001	Egg + Larva	8.256(0.175)	10.646	< 0.0001
	λ	1.123(0.015)	1.147	< 0.0001	Pupa	5.904(0.148)	6.286	< 0.0001
	Dt	6.028(0.786)	5.04	< 0.0001	-	-	-	-

Standard errors are shown in brackets.
n = 200

5.4 Discussion

The development and reproduction of DBM population occurred within the lower and upper temperature thresholds of the immature stages. The observations of threshold temperatures for oviposition and survivorship of DBM agree with findings reported by Bahar *et al*. (2014) who demonstrated 4°C to be the lowest threshold temperature of eggs for the north Americam DBM population and 38°C the highest for survival of the larvae. As to the optimal temperature for oviposition and population growth, Marchioro and Foerster (2012) reported that the moth laid the highest number of eggs at 20°C. The authors further noted that the intrinsic rate of natural increase of moth population was rapid between 20°C and 25°C. All observations suggest that although increasing temperature stimulates development and growth of insect populations, such development and population will decline beyond the optimum temperature level, regardless of geographic origin of the insect pest. To increase the chances of survival and perpetuation of the species, the moth lays the highest number of eggs in the early days following emergence and fewer eggs as it ages (Chelliah and Srinivasan, 1986). In these findings, the female laid 50% of eggs in the first 36.4% of its life time, as reported earlier by Ngowi *et al*. (2017b). *Diadegma semiclausum* laid the highest number of eggs within a temperature range of 15°C – 20°C, implying the parasitoid was better positioned to control DBM population under the cool temperature conditions. Several studies in the study site have documented a wide prevalence of this parasitoid in the relatively cool climatic conditions, in contrast to *C. vestalis* (Grzywacz *et al*., 2011, Kahuthia-Gathu, 2011).

Extreme temperatures interfered adversely with the pest development and growth. Of the DBM individuals which survived at 35°C, none could lay eggs. Marchioro and Foerster (2012) observed earlier that long exposure of the eggs above 32.5°C damages the viability of eggs of DBM and consequently lead to decline of the field population. At lower temperatures, the insects developed slowly resulting in fewer generations over a given time. The situation gets worse under freezing temperatures in temperate countries like Japan because of increased possibility of hibernation (Honda, 1992). On the contrary, increased warming conditions result into shorter development times which could easily be interpreted to imply more number of generations added into the population per unit time. Nonetheless, this is not always true as high temperatures can disrupt the enzyme functioning (Trugill et al., 2005) which will eventually deprive the pupae and adults the required weight for proper cellular growth and differentiation (Trudgill *et al*., 2005; Bahar *et al*., 2014). High temperature could also favour the population build up of *C. vestalis* which may point to further deterioration of DBM population. Drawing from the laboratory findings, the high temperature levels during hot dry season over most areas in the low zone likely contributed to the relatively fewer DBM collected in the zone compared to the high zone. However, the DBM population on fields with ample irrigation resources likely built up because of the abundant food supplies. Guilloux *et al*. (2003) observed that the DBM outbreaks during hot dry season in the lowland tropical Brazil often occurred after a rainy season.

Temperature fluctuates under field conditions due to diurnal variations. Periodical stresses due to unfavourable temperature conditions can limit the insect activity temporarily (Petavy *et al*., 2004; Bahar *et al*., 2012). A study found that DBM eggs could still be incubated for thirty six hours at 38°C and yet developed safely when transferred to 28°C (Liu *et al*., 2002). The life stages used for conducting experiments in this study were not shifted between temperatures but their performance can still be compared with species performance under field temperature conditions. A few studies have been conducted on the role of environmental temperature on mortality and population and demography of DBM (Ahmad *et al*., 2008; Bahar *et al*., 2012; Xing *et al*., 2015). In a study conducted under 25°C ± 10°C,57% of eggs of DBM perished at 35°C (Liu *et al*., 2002), which is close to 53.3% observed mortality under this study. Likewise, 5.6% of the recorded pupae which died at 20°C in this study is comparable to 8.5% pupae which died under the field temperature conditions (from 15°C to 27°C, average: 22°C) reported earlier (Bahar *et al*., 2012). Apparently, research on comparative responses of the life histories of *D. semiclausum* and *C. vestalis* with constant and fluctuating temperatures is still at infancy stage. The models projected the moth population had a better chance of staying alive in the moderate temperatures. This is supported by the field surveys which showed the mid and high zones were more suitable for growth of the moth population.

Two studies in the study site have documented a wide prevalence of *D. semiclausum* under the cool climate conditions in the field (Grzywacz *et al*., 2010; Kahuthia-Gathu, 2011). The temperature ranging from 15°C – 20°C turned out to be the optimal range for carrying out the key biological processes which contributed to its demographics. The models predicted *D. semiclausum*c ould not develop below the minimum threshold of 6.61°C for the combined egg + larva stage. This finding contrasted observations reported byYang *et al*. (1993) who demonstrated the minimum threshold temperatures for the egg and larva to be 5.74°C and 3.8°C, respectively. Such a discrepancy from the findings presented in this work could stem from temperature effects imposed on the combined egg + larva stage (developing inside the host) as compared to those imposed on the individual egg and larva stages. In addition, the adaptation to the local climate among geographically-different species is vital in explaining the differential thermal tolerance (Honek, 1996). The current study utilized species collected from the tropical climatic conditions of Kenya as opposed to that collected in the temperate climatic conditions of Chinaused by Yang *et al*. (1993). Adaptation to local climate has enhanced the physiological fitness of *D. semiclausum* in Kenya to survive better under the relatively hotter climate conditions in the region than in China.

The skew towards more male populations' after eclosion of *D. semiclausum* at ≥ 30°C can be translated to further reduction of DBM parasitism rates under the hot temperature conditions. Capable of surviving under hotter temperature range than *D. semiclausum*, the DBM populations can forage crucifer plants located in the hot range margins and through that escape from parasitism. The escape can be quite effective if the moth population utilize substantial amount of time in colonizing the new habitat. The temperature-driven, male-biased sex ratio and higher life spans of female *D. semiclausum* have been reported earlier (Yang *et al*., 1993; Dosdall *et al*., 2012). A study has established that females reabsorb eggs to allow additional energy for survival when the host larvae are not available (Heimpel *et al*., 1997). This is conspicuous when the DBM population density is low and fragmented. Several studies have reported substantial populations of *D. semiclausum* in the moderately cool climates of East Africa where it remains the most effective parasitoid of DBM (Löhr*et al*., 2007; Gichini *et al*., 2008; Kahuthia-Gathu, 2011). Inability of this East African strain of *D. semiclausum* to survive and reproduce at 35°C differentiates it from the rare Syrian strain which is reportedly capable of surviving under the relatively hot field conditions (Kadirvel *et al*., 2011).

Contrary to *D. semiclausum*, the temperature – dependent phenology of *C. vestalis* showed the braconid can withstand high temperatures better than *D. semiclausum*. The high survival of its immature stages within a range of 20°C – 30°C and the rapid development of pupa at 30.2°C can equally suggest this to be the optimal range for physiological performance of *C. vestalis*. In addition, the thermal tolerance of pupa to temperatures up to 36.5°C can point to a growing potential of using the parasitoid for controlling moth populations in the relatively hot areas. This coincides with numerous field observations where the parasitoid is evidenced to have established and spread, providing effective DBM parasitism in the hot humid lowlands of Asia and Africa (Talekar and Shelton, 1993; Roush, 1997; Verkerk and Wright, 1997).The parasitoid could not develop successfully to adult stage at 10°C. Such low temperature could have immobilized the highly temperature-dependent enzyme functioning of the parasitoid.

Raising the experimental temperature to 12.5°C shortened the developmental time of *C. vestalis* compared to 10°Cbut very few individuals reached the physiological maturity. At lower temperatures, Abbas (1988) found that long time periods are needed to attain the physical fitness of adults. The temperature thresholds for effective DBM parasitism differed with geographical populations. In the present study, the predicted lower threshold (12.6°C) was way higher than the reported 8.14°C for the South African strain (Nofemela, 2004), 10.1°C for the Myanmar strain (Htwe *et al*., 2008) but lower than 13.8°C for the Malaysian strain (Lim, 1982). Adaptation to the local agroecology, experimental procedures used and climate (tropical for Kenya and Malaysia, monsoon for Myanmar and Mediterranean for South Africa) may have all contributed to the observed differences. The speedy development of the immature and adult stages may have led to building up parasitoid populations under hot temperatures. The population growth is likely to increase under fluctuating temperatures because the recurrent temperature oscillations between the moderate and extreme levels provide enough time for recovery to occur. To adversely affect the adult performance, Zhang *et al*., (2015a) illustrated that unless a stressful heat condition impacted the insect stage closest to the adult stage, the adult performance will suffer very little. Another study showed that some insects repaired and restructured their morphology and physiology through metamorphosis which reduced the damaging effects to subsequent stages (Seifert *et al*., 2012). Coinciding with the findings documented by Htwe *et al*. (2008), the immature stages of *C. vestalis* showed the ability to survive better under temperature range between 20°C and 33°C than at lower temperatures of < 15°C which is an indication that parasitoid is physiologically – adapted to survive in moderate to high temperature conditions. The reasonable capability of the parasitoid to thrive under high temperature conditions may also suggest a potential altitudinal and latitudinal expansion range of *C. vestalis* in response to global warming in the future.

A sustainable biological control of DBM using parasitoid species requires availability of suitable environmental conditions for development and growth of parasitoid populations. Subjected to the same environmental conditions, this study established that temperature could affect the survival, developmental and reproductive parameters of DBM, *D. semiclausum* and *C. vestalis* differently. The pest completed its life history over a wider range of temperatures than either of its parasitoids. The global temperature is projected to increase by a range of 1.4°C – 5.8°C over the 21st century (Karl and Trenbeth, 2003). In Kenya,it is projected to increase from 1.0°C-2.5°C between 2000 and 2050 (Jones *et al*., 2009). Added to this, several studies have projected increased warming conditions in the mountain ecosystems (Pepin and Lundquist, 2008; Pepin *et al*., 2015). These observations, along with the demonstrated ability of *C. vestalis* to survive, develop and reproduce better under the warming conditions, could be pointing to a growing potential of *C. vestalis* being a more reliable DBM parasitoid under the warming climate. This may imply less vulnerability of the ecosystem service provided by the parasitoid. To substantiate this, field studies in line with the parasitoids' ecology and global change are deemed necessary. The findings may contribute to predicting the future population dynamics of DBM and its key parasitoids across a spatial scale. Achieving this is vital for deducing mitigation measures against new introductions and spread of diamondback moth.

CHAPTER SIX: POTENTIAL FUTURE DISTRIBUTION AND ABUNDANCE OF DIAMONDBACK MOTH AND ITS KEY PARASITOIDS IN MOUNT KILIMANJARO AND TAITA HILLS

6.1 Introduction

The projected reduction of precipitation and a temperature rise of 3°C – 4°C by 2080 in most Sub-Saharan Africa (Intergovernmental Panel on Climate Change, 2014) are predicted to constrain different pest management strategies because of the favourable environmental conditions which will likely support increased pest incidence. According to the Intergovernmental Panel on Climate Change (IPCC), such increase will likely change the population dynamics and spatio-temporal distributions of pests (Intergovernmental Panel of Climate Change, 2007; 2014).Warming conditions in coffee-producing areas of East Africa may increase the infestation of coffee berry borer (*Hypothenemus hampei*) in the highlands of Burundi, Uganda, Kenya, Ethiopia and Rwanda (Jaramillo *et al*., 2011). Nicholls *et al*. (2008) indicated the risk of altitudinal range shift of the damaging burrowing nematode (*Radopholus similis*) due to increased warming in banana-producing regions of East Africa. Temperature is the key weather variable which will likely influence potential future distributions of stem borers *Chilo partellus* and *Buseola fusca* on maize grown along the slopes of Mount Kilimanjaro and Taita hills in Tanzania and Kenya, respectively (Mwalusepo *et al*., 2015).

The success of DBM as the most widely distributed pest of crucifer vegetables is greatly because of its capacity to stay alive over a wide range of temperature, being highly prolific, diversity of food sources and insecticide resistance (Shelton, 2004; Vickers *et al*., 2004). Worldwide, studies that relate simultaneously laboratory and field data for mapping the pest activity across a spatial distribution are very few (Zalucki and Furlong, 2011). Distribution models of the pest have been developed based on various factors, including occurrence/absence data (Centre for Agriculture and Bioscience International, 2012), timing of the life cycle (Zalucki and Furlong, 2011) and movement (Harcourt, 1986; Honda *et al*., 1992). The earliest distribution map was a synthesis of incomplete distribution records (Commonwealth Institute of Entomology, 1967). The latest comprehensive global distribution map of DBM was created using its suitable climatic information (Zalucki and Furlong, 2011). Hopkinson and Soroka (2010) utilized wind trajectory models to map the potential increase of DBM infestation under a 2°C temperature rise in the Canadian prairies. Closer to East Africa, distribution map of DBM based on temperature and cropping systems has been developed in Ethiopia (Ayalew *et al*., 2007).

The interface between insect pests and natural enemies has the potential to influence the distribution of pests (Agnew *et al*., 2004).Pérez-Rodríguez *et al.*, (2015) suggested that due to coevolutionary ecology, many parasitoids evolve to synchronize their distributional expansion and possibly migration with their hosts. Increased exposure of the pest to parasitoid attack can lead to movement of unattacked DBM away from the parasitoid range (Chapman *et al*., 2015).Being r-selected species, highly mobile and having a high intrinsic rate of natural increase, DBM can withstand the seasonal shortage of food resources by dispersing to locate fresh host plants, as opposed to most parasitoids. Parasitoid attack when fresh host plants for DBM are limited therefore triggers long range distribution of the moth. Under such circumstances, only strong winds can help propel parasitoid population towards DBM (Dosdall *et al.,* 2004). Here, the frequency – dependent selection by parasitoids for specific hosts results in coevolutionary cycles of herbivory and parasitism. The post-release surveys of *Diadegma semiclausum* in Werugha and Tharuni locations in Kenya revealed concurrent incidences of DBM and its parasitoid populations (Löhr *et al*., 2008). Increased incidence of DBM population was limited by the parasitoid before the pest population reached out of proportions. Labou *et al*. (2017) showed the significance of pest density, size and available crucifer farms in determining concurrent distribution patterns between DBM and its parasitoids across an agroecosystem landscape in Senegal. However, there have been several reports of insect pest-parasitoid mismatch triggered by various factors, including climate. Some field observations reported in Machekano *et al*. (2017) showed the chill and hot temperatures were more detrimental to the development of *Cotesia vestalis*than DBM in southern Africa. Building from this, the authors argued that extreme temperature change could destabilize DBM – *C. vestalis* relationship that has coevolved over time along the spatial and temporal distributions. However, this is not a general rule since some prepupae stages of *C. vestalis* populations in northwestern China undergo facultative diapause (Alvi and Momoi, 1994) which enables them to reduce metabolism and survive under harsh cold environmental conditions where DBM can't (Wei *et al*., 2017). Long distance migration of *C. vestalis* is not common. Lei and Camara (1999), however, recorded limited migration of *Cotesia melitaearum,* a close relative of *C. vestalis*.

Understanding the potential future distribution of DBM and its parasitoids at a local scale is important for making meaningful interventions for sustaining biological control under changing climate conditions. Any DBM – parasitoid mismatch in terms of distributions can interfere with the accurate pest surveillance and pest forecast, and distort the sustainable biological control with eventual effect on the overall decision-making in pest management strategies. This is especially critical in crops like crucifer vegetables which are attacked by many pests. However, information on the likely future distributions of the various pests in these agroclimatic and biodiversity hotspots is lacking. Nonetheless, the future distribution and abundance of DBM and its key parasitoids *D. semiclausum* and *C. vestalis* under the changing climate is uncertain. This chapter is seeking to address the potential effect of climate change on the distribution and abundance of DBM and its key parasitoids and the likely effect on the DBM – parasitoid interaction. The knowledge will help in understanding the associated changes in the insect populations and whether such changes will maintain or disrupt the vital biological control service provided by the parasitoids.

6.2 Materials and methods

6.2.1 Study area

The locations considered for the study were the two altitudinal transects described in detail under section 3.2.1. The geographical coordinates of latitudes and longitudes; and elevation of each farm were recorded using a portable Garmin GPS model eTrex 30 as explained under section 3.2.2 and shown in Table 6.1.

Table 6.1: Elevation and geographical coordinates of the surveyed farms

Transect	Farm	Elevation (metres a.s.l.)	Latitude	Longitude
Mt. Kilimanjaro	Kisange B	728	-3.45292	37.45203
	KisaMadukani	732	-3.41765	37.44879
	Kisa Kusini	741	-3.44002	37.43683
	Uparo	891	-3.37850	37.45020
	Sumi	1221	-3.34310	37.47420
	Kopachi	1365	-3.33170	37.47240
	Moto	1508	-3.31367	37.46042
	Kirua	1513	-3.31960	37.46586
	Pakula	1546	-3.31039	37.46430
	Nduoni	1573	-3.30812	37.46002
	Masila	1604	-3.30204	37.45708
	Kanango	1657	-3.29258	37.45049
	Marua B	1677	-3.29258	37.45282
	Marua A	1692	-3.28746	37.45496
Taita hills	Majengo	830	-3.51035	38.38246
	Singila	842	-3.50457	38.38127
	Kipusi	874	-3.47235	38.38252
	Dembwa	1107	-3.44625	38.36257
	Bura	1262	-3.45035	38.31597
	Josa	1321	-3.43291	38.36108
	Prison	1400	-3.40124	38.36454
	Msangalinyi	1461	-3.39120	38.35022
	Wesu	1628	-3.41287	38.34016
	Mwatungu	1643	-3.40462	38.34138
	Kighala	1674	-3.39057	38.33800
	Mwafunja	1693	-3.39258	38.32787
	Kishamba	1765	-3.40188	38.29395
	Mbangang’ombe	1785	-3.40123	38.30420

*Kisange B = Kisangesangeni B, KisaMadukani = Kisangesangeni Madukani, Kisa Kusini = Kisangesangeni Kusini

*Farms are arranged in order of increasing altitude

6.2.2 Inputs for development of distribution and abundance maps

Development of the distribution and abundance maps of DBM and its key parasitoids was derived from generation of three population indices: Establishment Index (EI), Generation Index (GI) and Activity Index (AI) (Kroschel *et al.*, 2013). The EI was adopted to identify areas having the favourable climate for establishment, survivorship and distribution of the pest and its parasitoid populations. Generation index referred to the estimated mean number of generations which DBM, *D. semiclausum* or *C. vestalis* could produce in a year. Activity index was employed to predict the annual population growth potential of the individual insect species. The mentioned population indices were generated through a process whose implementation required three inputs: temperature – dependent phenology of the insects to be mapped, climate data and the digital georeferenced, three – dimension topographical map. The generated phenology information of each species contained life table datasets for laboratory and outdoor testings, developed models and simulation models for population growth parameters. ILCYM software was employed for analysis because it is a software which has been designed to pick up the daily minimum and maximum temperatures collected on farms, and link these with altitudinal information from the digital georeferenced topographical maps. To predict temperature values between sample points, 'index interpolation' tool was adopted. Loading up the information in the software and engaging it linked up the recorded field and life table temperatures to map the distribution and abundance of insect species. Detailed manipulation of such inputs for generation of the distribution and abundance maps is described in detail in subsequent sections 6.2.2.1, 6.2.2.2 and 6.2.2.3.

6.2.2.1 Phenology of DBM and its key parasitoids

The temperature – dependent phenology of DBM, *D semiclausum* and *C. vestalis* developed in chapter five were used for generation of EI across the spatial scale of Mt. Kilimanjaro and Taita hills altitudinal transects. Specifically, information collected from the development time and rates were linked to suitable establishment areas, with mortality and life span linked to survivorship, and reproduction linked to distribution. The information gathered from the gross and net rates of reproduction were linked to GI. The infinite rate of natural increase (r_m), infinite rate of increase (λ) and doubling time (Dt) were linked with AI. The Insect Life Cycle Modeling (ILCYM) software was adopted to link the phenology and indices because of its ability to interpret life table datasets across a spatial scale.

6.2.2.2 Climate data

The current temperature was derived from the average minimum and maximum daily temperature data recorded in the thermohygrometer data loggers installed on the individual farms surveyed using 2013 as the base year. All the projected future temperature changes were referred to this base year. All changes in the future distribution and abundance of the insects were also benchmarked from the base year**.** To map temperatures along the altitudinal transects, temperature data files were developed for the individual farms and loaded in ILCYM. The latitude, longitude and altitude information were also recorded in the files to capture temperature variability on the terrain. Each file was saved in text tab delimited (.txt), a compatible format for analysis in ILCYM.

Climate databases projecting future temperatures are available. WorldClim is considered a reference global database (Fick and Hijmans, 2017). Several regional climate databases are available too but most have coarse resolution and are not customized to integrate details of particular ecological landscapes (Hijmanns, 2015) African Climate database (AFRICLIM) (Platts *et al.*, 2014) was chosen because it is loaded with different regional climate models (RCM) which are developed to project climate in an area as small as 1 km^2 and in addition, it is focused on particular biodiversity hotspots, including the Eastern Afromontane, where the study site is contained. The database is corrected from bias, freely available and accessible at http://www.york.ac.uk/ environment/research/kite/resources/. The RCM are made of high resolution climate projections. The regional climate models are valuable predictive tools but could not account for the local climate variability due to low resolution. Extraction of the potential future but local on-farm temperatures was therefore derived from such climate projections through downscaling. In this case, downscale referred to a process of drawing information from a large scale source of climate data for prediction at a local scale. To make this happen, the temperature and geographic coordinates of the surveyed farms were utilized as reference points for interpolations of the minimum and maximum daily future temperatures in adjacent areas with respect to RCM as described in detail by Platts *et al*. (2014).

The projected future temperature values in AFRICLIM are stored in raster format, which are made of cells that are organized into rows and columns. Each cell represents a temperature value. Such temperatures are grouped in different RCM projection folders depending on the type of modeling method used to generate them. For this study, the temperature values were stored in the RCM projection under the representative concentration pathway 8.5 (rcp 8.5) for year 2055 as described in Platts *et al*. (2015). Representative concentration pathway is a greenhouse gas concentration trajectory adopted by the IPCC for climate projection and research (Intergovernmental Panel on Climate Change, 2014). The pathway provides time-dependent projections of atmospheric greenhouse gas concentrations (Intergovernmental Panel on Climate Change Expert Meeting Report, 2007). The future temperature data in AFRICLIM are calibrated for 2055 and 2080. To obtain the temperatures, the year 2055 was selected for projections of the future climate data because first; there are more than thirty years between it and 2013 which qualifies it for a study on climate change (Intergovernmental Panel on Climate Change, 1996; 2001a; 2007) and second, there are a fewer number of years (42 years) between it and 2013 than between 2080 and 2013 (67 years), which implies a smaller room of uncertainty from potentially unpredictable factors. The temperatures were downloaded by activating the folders ‘tasmin_rcp85_2055_ensemble-max-v3_wc30s.zip’ and ‘tasmax_rcp85_ 2055_ensemble-max-v3_wc30s.zip’ for opening up the projected 2055 daily minimum and maximum temperatures covering the Eastern Afromontane Biodiversity Hotspot (EABH) region, respectively. To get specific temperature values on farm, first; the downloaded temperature raster data were transferred in Quantum Geographic Information System 2.16.2 (QGIS 2.16.2)(Quantum Geographic Information System Development team, 2009)for opening up and second, a file having names, geographical coordinates and altitudes of the surveyed farms was prepared, saved in a comma delimited (.csv) file format and loaded on such temperature raster data in QGIS for mapping the farms through ‘Add delimited text layer’ tool. By positioning the ‘Identify features’ pointer and clicking on a mapped farm, the projected temperatures were revealed and recorded.

It was necessary to understand the difference in temperature on each farm between the base years (2013) and (2055) future year in order to associate it with the potential change in distribution and abundance of the insects. Several steps were involved to load the baseline and the projected future minimum and maximum temperatures of the individual farms in the ‘raster calculator’ to establish the difference between base year and future climate conditions. Representative farms from the three altitudinal zones were selected to make clearer visualization of differences than utilizing all the farms: Mt. Kilimanjaro transect – Kisangesangeni B (low), Kirua (medium) and Marua A (high); Taita hills transect– Majengo (low), Msangalinyi (medium) and Kishamba (high).

6.2.2.3 Generation of digital georeferenced topographical maps of the study area

Development of the distribution and abundance maps was guided by the digital georeferenced topographical map of the study site. The map is a three-dimension (3D) product which was formed by reconstructing the terrain as a physical body with vertical dimensions. On the map are points of known geographic coordinates and altitude. The Shuttle Radar Topography Mission (SRTM) is a database containing a high resolution digital 3D topographic map of the Earth. The digital georeferenced topographical maps of the two transects were developed stepwise from the SRTMas described in the subsequent paragraph.

The digital georeferenced altitudinal map covering the globe was downloaded from the open-sourced Consultative Group for International Agricultural Research – Consortium for Spatial Information (CGIAR-CSI) server (http://srtm.csi.cgiar.org/SELECTION/inputCoord.asp). From the map, the focus was shifted to East Africa where EABH is found. The longitudinal coordinates covering the EABH region were selected to range from 37.10000 W to 38.60000 W. The selected latitudinal coordinates were 3.10000 S and 3.60000 S. By activating ‘Click here to begin search’, a georeferenced 3D topographical map of the EABH fitting the given geographic coordinates was generated and saved in GeoTIFF file format. However, the generated maps covered the two transects and area far beyond these transects. To focus into the altitudinal transects, the maps were transferred to QGIS 2.16.2 and trimmed to fit in the actual width and length of the Mt. Kilimanjaro and Taita hills transects and produced two ‘shapefiles’ of the transects. To put it simply, a shapefile was a 3D topographical map of the transect.

6.2.3 The projected future pest and parasitoid spatial distribution and abundance

6.2.3.1 Population growth indices of DBM and its key parasitoids

The insect phenology developed under chapter five, the base year (2013) and projected future (2055) temperature data; and shapefiles of the two transects were utilized as inputs for calculating and mapping the population growth indices (establishment, generation and activity indices) of DBM, *D. semiclausum* and *C. vestalis*. Establishment index (EI) value was settled to be 1 on condition all life stages of the insect were able to survive, spread and grow in a given geographical location throughout the year. When an EI = 0.5, it indicated an area where the insect population was able to survive and establish only during six months (6/12) out of the year. Generation index (GI) was derived from averaging the number of generations the DBM, *D. semiclausum* and *C. vestalis* produced in a year. Sporleder *et al*., (2008) described the method to obtain AI, which includes calculating a log of products of the daily finite rates of population increase. Every increase of the index by one implied the present population increased by 10-fold. An index value of 2 indicated a potential population increase by a factor of 10^2 i.e. 100 individuals in a year. The activity index was also used to illustrate the damage potential of DBM and population growth potential of parasitoids. Establishment index represented distribution of the insect population across a spatial scale because mapping it visualized ability of the insect species to establish populations based on spatial and temporal changes in temperatures. From increasing or decreasing number of generations in a population, along with the change of population size over time, the generation and activity indices addressed population growth potential of the insect species. Generation of these indices was implemented using the GIS module of ILCYM for spatial analysis and mapping as detailed in the subsequent paragraphs.

6.2.3.2 Change of DBM and parasitoid growth indices between 2013 and 2055

Predictions of the future distribution and abundance of the DBM and its key parasitoids were framed in such a way that changes were to be observed on the same zone but between the two time periods (2013 and 2055). This arrangement simplified drawing observations and conducting evaluations on the status of distribution and abundance of DBM and its parasitoids in the base year, in the projected future and on the resulted change over that period of time without confusing the time periods or altitudinal zones. In the two altitudinal transects, the distribution and abundance of the insects were thus observed for example on the same low zone but between 2013 and 2055 and between 2013 and 2055 in the medium zone.

6.2.3.3 Mapping spatial distribution and abundance of DBM and key parasitoids

The spatial distributions and abundance of DBM, *D. semiclausum* and *C. vestalis* were mapped individually through a number of steps. The ILCYM was selected because the software is designed specifically for modeling temperature-dependent life history of insects. The field climate data for the base year 2013 was uploaded and saved in index interpolator, a sub-module of ILCYM. A folder of DBM with its complete phenology was uploaded and saved separately. The shapefile of Mt. Kilimanjaro was subsequently uploaded. Starting with the EI, the index was selected under the 'Index' drop down menu and the plot button activated for plotting the distribution map. The spatially – referenced EI values was calculated using the population growth parameter values obtained by linking the loaded temperatures (for base year 2013) and DBM phenology as described in detail by Sporleder *et al*. (2008), Kroschel *et al*. (2013) and Tonnang *et al*. (2013). When plotting, the index interpolator was used to predict the EI values between the sampled farms because of the assumption that spatially distributed objects are spatially correlated. The same steps were repeated for calculating and plotting EI for Taita hills.

The plotted EI map of DBM was transferred to QGIS 2.16.2 for better visualization. Using the 'Clipper' tool under the 'Extraction' icon, the generated map was trimmed into a zone shapefile of Mt. Kilimanjaro following a number of steps described in Kroschel *et al*. (2013).To point the farms on the map, a comma delimited (.csv) file containing names, altitudes, latitudes and longitudes of farms located in Mt. Kilimanjaro transect was first created and saved. Secondly, by 'turning on' the 'Coordinate Reference System Selector' window, the GPS coordinates were picked and the sampled farms were marked on the developed EI map. To give names to the marked farms, the 'Labels' icon under 'Layer Properties' tool was checked. Development of the EI map was completed by activating the 'Add Map' icon under the 'Layout' tool to develop the scale, legend and the north bearing. Following the same steps, the exercise was repeated for mapping EI in Taita hills; and again for mapping both GI and AI of DBM in Mt. Kilimanjaro and Taita hills. To map the 2013 distribution and abundance of *D. semiclausum* and *C. vestalis* in Mt. Kilimanjaro and Taita hills transects, the procedure used for mapping DBM was repeated sequentially, using the parasitoids phenologies. The potential future distribution and abundance of DBM, *D. semiclausum* and *C. vestalis* 2055 were mapped, additionally, using the 2055 temperatures downloaded and the insect phenologies.

6.3 Results

6.3.1 Temperature changes between current and future climate conditions

The future maximum temperature was predicted to increase by 1.6°C in the low zone of Taita hills but will decline significantly towards the medium and high zones upward the transect. The minimum temperature was predicted forecasted to rise to increase from 1.9°C to 2.7°C from the low to medium zones (Table 6.2). Temperature changes were predicted to be comparatively lower along Mt. Kilimanjaro transect.

Table 6.2: Changes between 2013 and 2055 temperatures on representative farms in Mt. Kilimanjaro and Taita hills transects

Mt. Kilimanjaro						Taita hills				
Maximum temperatures (°C)										
Zone	Farm	Altitude	Year 2013	Year 2055	Difference	Farm	Altitude	Year 2013	Year 2055	Difference
Low	Kisange B	716	34.3	34.8	0.4	Majengo	830	33.8	35.4	1.6
Medium	Kirua	1513	28.3	28.6	0.3	Msangalinyi	1461	27.7	28	0.3
High	Marua A	1692	26.8	27.2	0.4	Kishamba	1765	25.9	25.9	0
Minimum temperatures (°C)										
Low	Kisange B	716	20	20.9	0.9	Majengo	830	17.3	19.2	1.9
Medium	Kirua	1513	15	15.7	0.7	Msangalinyi	1461	13.1	15.8	2.7
High	Marua A	1692	13.3	14.5	1.2	Kishamba	1765	13.1	13.8	0.7

6.3.2 Spatial changes in distribution and abundance of the insects

6.3.2.1 Future distribution and abundance of DBM in Mt. Kilimanjaro

The distributional range of DBM between Kisangesangeni B (Kisange B) and Uparo in the low zone is predicted to increase over time, with its establishment index (EI) ranging from 0.6049 – 0.6497 in the base year 2013 to 0.8150 – 0.8436 in 2055 (Fig. 6.1a and d). Nearly all changes in probable distribution between 2013 and future (2055) climate conditions in Mt. Kilimanjaro will occur in the low zone (Fig. 6.1g) whose EI ranges from 0.1860 – 0.2103. From 2013 to 2055, the moth will produce a lesser number of generations (GI= -1.9299) in the low zone (Fig. 6.1h). The predicted decline of about two generations will be felt in the population growth rate, which will reduce from the Kisangesangeni Madukani (KisaMadukani) farm upwards between 2013 (AI = 32.6075 – 28.8564) (Fig. 6.1c) and 2055 (AI = 32.2601 – 28.9272) (Fig. 6.1f).

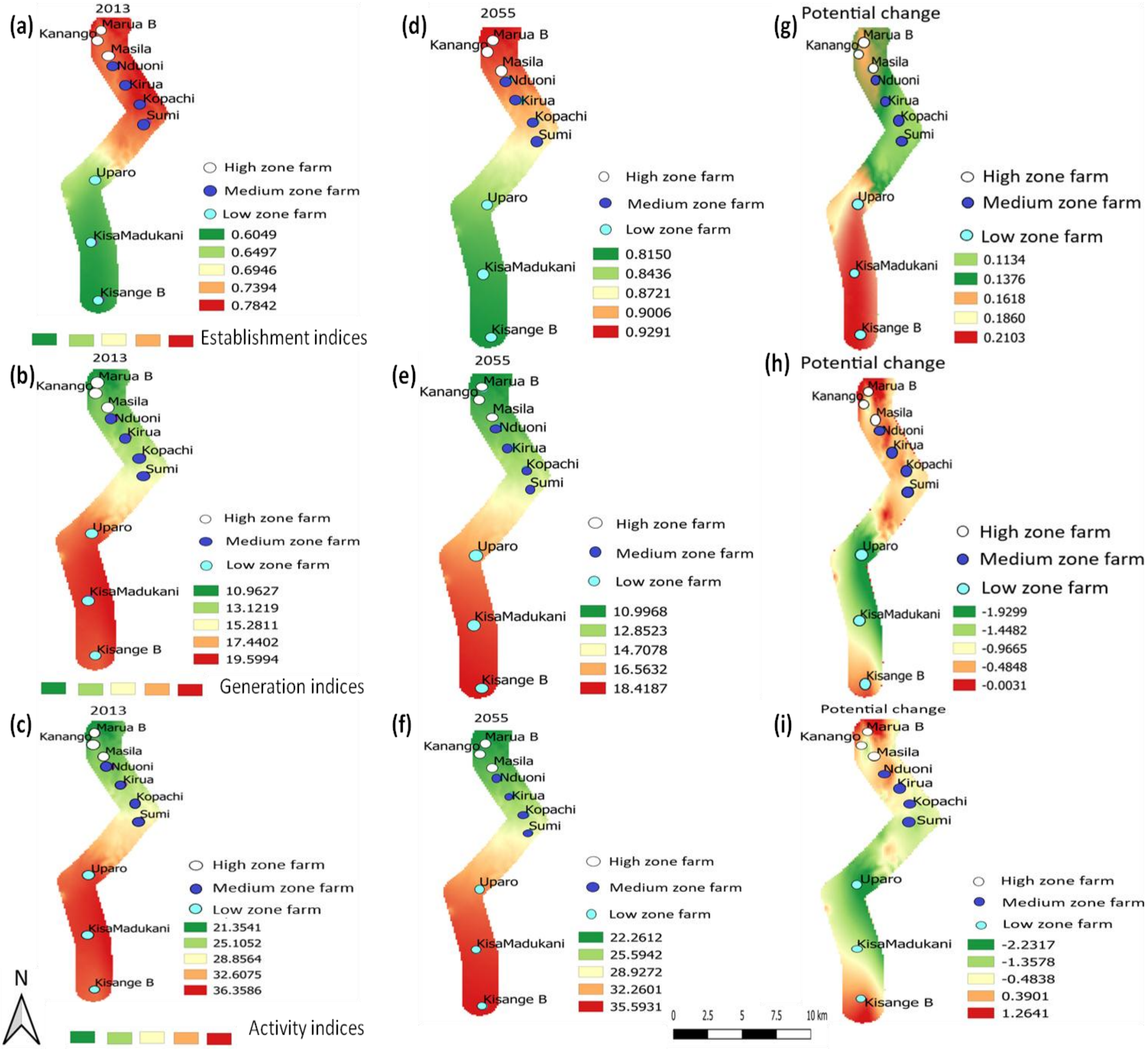

Figure 6.1: Changed population growth indices of DBM across climate change conditions of Mt. Kilimanjaro. Baseline 2013 distribution and abundance on selected farms: (a) EI, (b) GI and (c) AI; future 2055 distribution and abundance: (d) EI, (e) GI and (f) AI. Potential change in distribution and abundance between current and future conditions: (g) EI, (h) GI and (i) AI

Suitability of the medium zone of Mt. Kilimanjaro is predicted to increase from the base year 2013 to the future 2055 (EI = 0.7842 – 0.7394 to 0.8721 – 0.9291) (Fig. 6.1a and d). However, most of this zone is predicted to be less favourable to the living and thriving of the moth (EI = 0.1134) than the other zones (Fig. 6.1g), leading to decreased mean number of new generations from 0.97 – 0.48 (Fig. 6.1h). Consequently, the change will result a decline in growth rate from 13.5-fold to 4.8-fold although such variation runs short of exerting substantial change in population growth rate of DBM in the zone (Fig 6.1i).

The little increase of suitability of the high zone (increase of establishment risk index from 0.1134 – 0.1376 (Fig. 6.1g) will be derived from the growing suitable temperature conditions available for establishment of the insect pest. Such suitable areas will likely a growing number of DBM to drift into this zone. However, the change in number of generations produced will be very little, ranging from the averagely 10.96 in 2013 to 10.99 in 2055 (Fig. 6.1b and d). The corresponding overall change of 0.003 to 0.484 generations between the two time periods is almost negligible (Fig. 6.1h). The net increase of the population growth rate will rise from 3.9 – 12.6-fold only.

6.3.2.2 Future distribution and abundance of DBM in Taita hills

Some considerable changes in future temperature conditions are predicted to occur in the low zone of Taita hills. Suitability of the zone will increase over the two time periods, from establishment index range of 0.6719 – 0.7745 (2013) to that of 0.9313 – 9843 in 2055 (Fig. 6.2a and d). The changes will greatly affect the overall suitability of habitats in the zone (EI = 0.2098 – 0.2667) (Fig. 6.2g). The average number of generations produced are predicted to decline considerably, from a range of about 17.46 to 12.59 in 2013 to about 5.98 – 2.99 in 2055 (Fig. 6.2b and e) In Majengo alone, a farm located at the lower end of the transect, the pest reproductive prowess will have lost the ability to reproduce twelve generations (Fig. 6.2h). This will affect adversely the growth rate of the pest population in the zone, where it is forecasted to shrink between the two time periods (from AI = 33.1817 – 24.7361 in 2013 to AI = 24.0103 – 17.5563 in 2055) (Fig. 6.2e and f).From 2013 – 2055, The DBM population growth rate in Majengo farm is predicted to dwindle because approximately 92.2-folds of the DBM population will be lost (Fig. 6.2i).

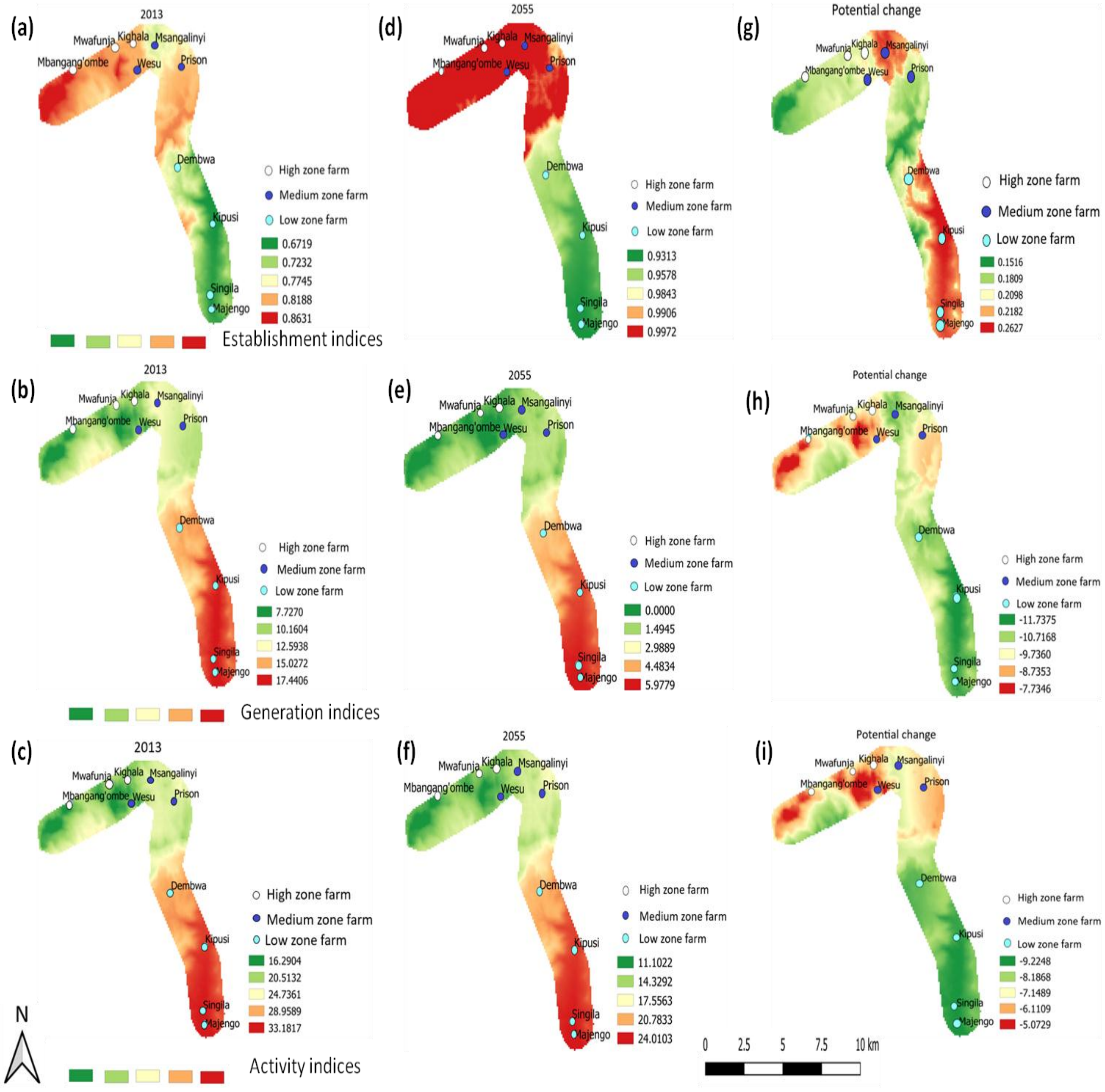

Figure 6.2: Changed population growth indices of DBM across climate change conditions of Taita hills. Baseline 2013 distribution and abundance on selected farms: (a) EI, (b) GI and (c) AI; future 2055 distribution and abundance: (d) EI, (e) GI and (f) AI. Potential change in distribution and abundance between current and future scenarios: (g) EI, (h) GI and (i) AI

The suitability of the medium zone of Taita hills will increase substantially from the base year 2013 (AI = 0.7745 – 0.8188) to year 2055 (AI = 0.9843 – 0.9906) (Fig. 6.2a and d). The overall change between the two time periods will range from establishment index of 0.1809 to 0.2667. On the contrary, the increased favourable suitability will be accompanied with a substantial decline in the reproduction prowess of DBM. The pest will add about 7.72 – 12.59 generations in the population in 2013 (Fig. 6.2b) but this capacity will decline to only about 1.49 – 2.98 in 2055 (Fig. 6.2e). The DBM population is predicted to remain stable in Wesu (Fig. 6.2e). The predicted overall reduction in the number of new generations from about 10.74 to 8.74 generations (Fig. 6.2h) can be interpreted to slow down the population growth rate. The model predicted the population growth rate will decline between the two time periods: from AI = 20.5132 – 24.7361 in 2013 (Fig. 6.2c) to AI = 14.3292 – 17.5563 in 2055 (Fig. 6.2f). Overall, the population growth rate will decline by 7 to 8-fold (Fig. 6.2i). This extensive decline can also be translated to reduced damaging potential of DBM in the zone.

The habitat suitability for survivorship and establishment of the moth in the high zone of Taita hills will change very little over time (from EI = 0.8188 – 0.8631 in 2013 (Fig. 6.2a) to EI = 0.9906 – 0.9972 in 2055 (Fig. 6.2d)). The number of new generations added in the population in 2013 ranged from approximately 7.72 to 10.16 (Fig. 6.2b) but it is predicted to lower down to 1.49 only in 2055 (Fig. 6.2e). The overall change will result to reduced ability of the moth to add about 7.73 to 9.74 generations (Fig. 6.2h). Expectedly, such a huge difference in the number of generations will impact negatively in the population growth rate, whose AI is set to range from 16.29 – 20.51 (Fig. 6.2c) to 11.10 – 14.33 (Fig. 6.2f). Overall, the population growth rate is predicted to decrease, with the greatest decrease in the low zone and the least in the high zone (Fig. 6.2i).

6.3.2.3 Changed future distribution and abundance of *C. vestalis* in Mt. Kilimanjaro

The low zone is predicted to become increasingly suitable by 2055 for establishment and distribution of *C. vestalis*. The rise of establishment index from 0.4467 – 0.5079 in 2013 (Fig. 6.3a) to 0.7184 – 0.7564 in 2055 (Fig. 6.3d) is likely to attract upward range expansion of the parasitoid. Overall, the low zone will be the most suitable for the parasitoid (Fig. 6.3g). In this zone, the parasitoid population will reproduce a range of about 18.18 – 19.47 generations in 2013 (Fig. 6.3b) and about 19.45 – 20.76 generations in 2055 (Fig. 6.3e), with a net increase of about 1.04 – 1.81 generations between 2013 and 2055 (Fig. 6.3h). The corresponding population growth rate is predicted to increase over time too, with a lower rate in 2013 (AI = 23.5734 – 25.9821) (Fig. 6.3c) and a higher rate in 2055 (AI = 27.0423 – 28.0685) in 2055 (Fig. 6.3f). Generally, between the two time periods, the population growth rate will have increased by a factor of 2.9593 – 4.3261 for most of the low zone (Fig. 6.3i).

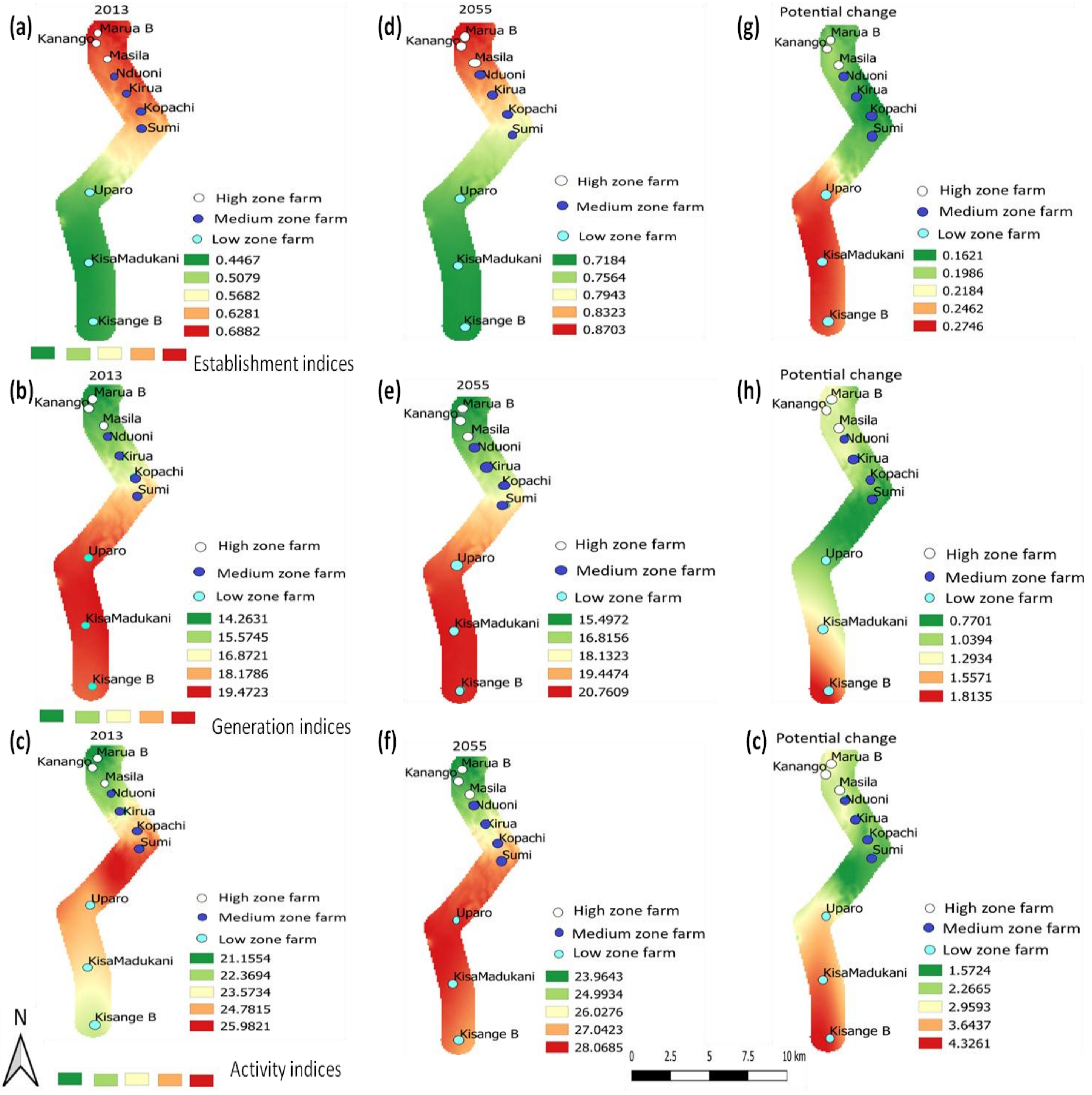

Figure 6.3: Changed population growth indices of *C. vestalis* across climate change conditions of Mt. Kilimanjaro**.** Baseline 2013 distribution and abundance on selected farms: (a) EI, (b) GI and (c) AI; future 2055 distribution and abundance: (d) EI, (e) GI and (f) AI. Potential change in distribution and abundance between current and future scenarios: (g) EI, (h) GI and (i) AI.

Suitability of the medium zone of Mt. Kilimanjaro to the survival, establishment and distribution of *C. vestalis* is predicted to increase from the baseline establishment index of 0.5682 – 0.6281 (Fig. 6.3a) to the future 0.7564 – 0.8323 (Fig. 6.3d). However, the overall change will be relatively small (EI = 0.1621 – 0.1986) (Fig. 6.3g) to call for substantial changes of new generations (GI = 0.7701 – 1.0394) (Fig. 6.3h) to the population. The potential population growth rate is predicted to increase from activity index range of 22.3694 – 24.7815 in 2013 (Fig. 6.3c) to 24.9934 – 27.0423 in 2055 (Fig. 6.3f). The overall change in potential population growth rate will result to increased population by a range of 15.7 to 22.7-fold (Fig. 6.3i).

Suitability of the high zone changed from establishment index of 0.6281 – 0.6882 in 2013 (Fig. 6.3a) to from 0.8323 – 0.8703 in 2055 (Fig. 6.3d). The overall change in the index between the two time periods ranges from 0.1621 to 0.1986 (Fig. 6.3g) and is associated with increased temperature, which is favourable to the parasitoid (Fig. 6.3g). The increased temperature is likely associated with addition of approximately 15.49 – 16.82 new generations in 2055 (Fig. 6.3e), up from 14.63 – 15.58 in 2013 (Fig. 6.3b), with the overall 1 – 1.3 new generations per annum into the existing population (Fig. 6.3h). Relative to the medium zone, the added generations are set to raise the population abundance of the parasitoid by a factor of 2.2665 – 2.9593 (AI = 2.2665 – 2.9593) (Fig. 6.3i).

6.3.2.4 Future distribution and abundance of *C. vestalis* in Taita hills

Suitability of the low zone of Taita hills to *C. vestalis* population distribution is predicted to change a little (from EI = 0.5031 – 0.6812 in 2013 (Fig. 6.4a) to 0.7545 – 0.8407 in 2055 (Fig. 6.4d), a change which will be greater than that in the medium and high zones (Fig. 6.4a and d). The predicted number of generations added by the parasitoid will range from about 15.89 – 19.54 (AI = 15.8935 – 19.5499) in 2013 (Fig. 6.4b) to 17.52 – 21.04 (AI = 17.5274 – 21.0440) in 2055 (Fig. 6.4e). Overall, the parasitoid population is predicted to add about 1 – 1.9 generations per annum between 2013 and 2055 (Fig. 6.4h). The added generations will lead to a peak population growth potential around Kipusi area (AI = 3.8344) (Fig. 6.4i).

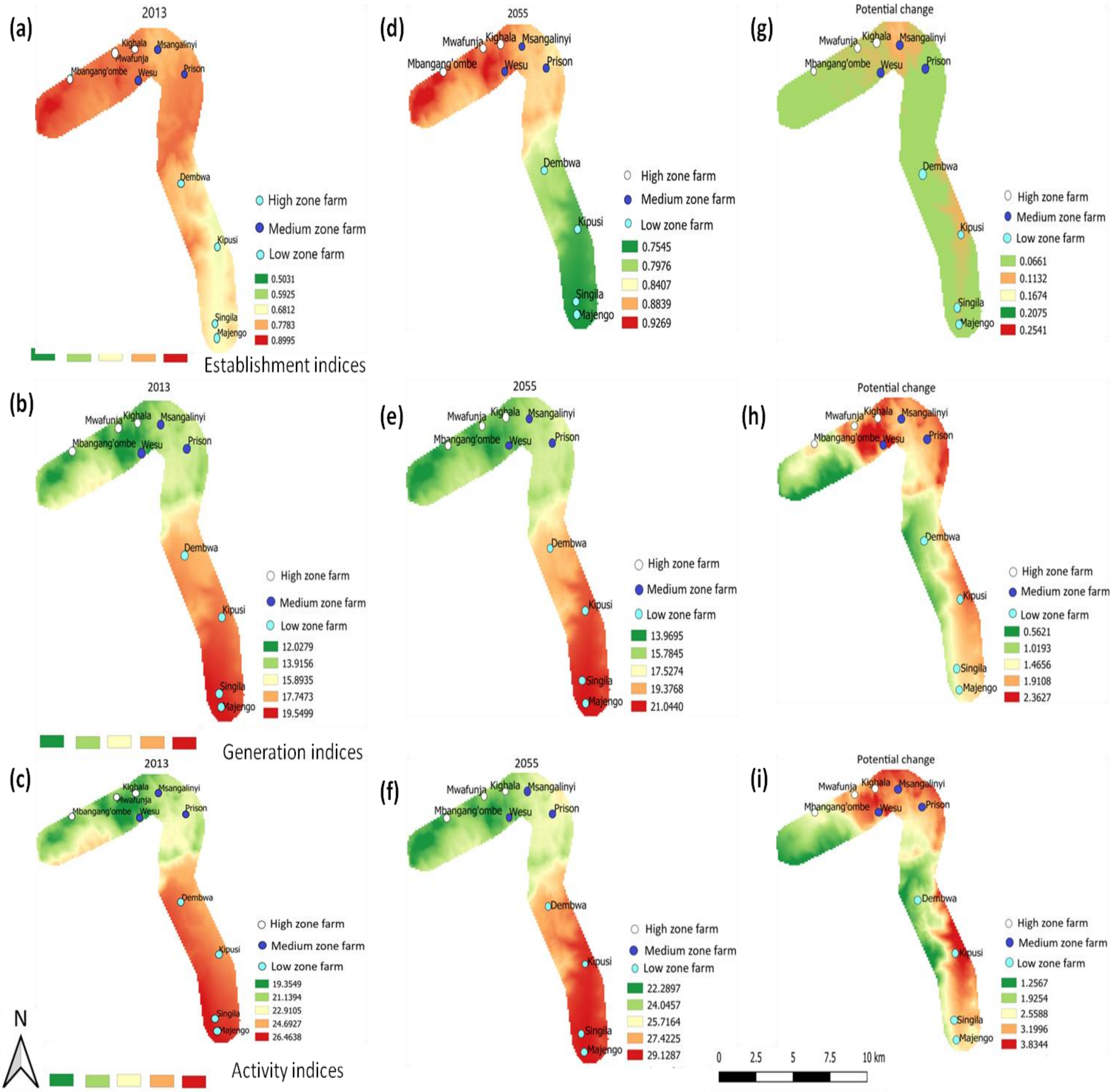

Figure 6.4: Changed population growth indices of *C. vestalis* across climate change conditions of Taita hills. Baseline 2013 distribution and abundance on selected farms: (a) EI, (b) GI and (c) AI; future 2055 distribution and abundance: (d) EI, (e) GI and (f) AI. Potential change in distribution and abundance between current and future scenarios: (g) EI, (h) GI and (i) AI

Suitability of the medium zone is predicted to increase extensively over time, as recorded from establishment index of 0.6812 – 0.7783 in 2013 (Fig. 6.4a) to 0.8407 – 0.9269 in 2055 (Fig. 6.4d). The increase corresponds to a wide overall change (EI = 0.1132 – 0.2543) (Fig. 6.4g) necessary for the survival and establishment of the parasitoid. For this reason, *C. vestalis* population is predicted to increase its generations from a range of about 12.03 – 15.89 in 2013 (GI = 12.0279 – 15.8935) along the zone (Fig. 6.4b) to 13.97 – 17.53 in 2055 (AI = 13.9695 – 17.5274)(Fig. 6.4e). Such change is associated with overall addition of approximately 1.9 to 2.4 generations per annum by 2055 (Fig. 6.4h). Predictably, the corresponding population growth is set to increase, as shown in activity index ranging from 19.3549 – 22.9105 in 2013 to 22.2897 – 25.7164 in 2055 (Fig c and e). This change is interpreted to increased population growth rate by a range of 31.9-fold to 38.3-fold (Fig. 6.4h-i).

Ranging its establishment index from 0.7783 – 0.8995 (year 2013) (Fig. 6.4a) to 0.8839 – 0.9269 (year 2055) (Fig. 6.4d), climatic suitability of the high zone-based farms is predicted to remain the most stable of all the three zones. The overall change in suitability between the two time periods will only range between 0.0663 and 0.1132 (Fig. 6.4g). With the number of generations, the overall change in this zone will involve addition of approximately 1.91 to 2.4 (AI = 1.9108 –2.3627) generations per annum between 2013 and 2055 (Fig. 6.4h). Consequently, a considerable parasitoid population growth is foreseen over most parts of the zone. The peak population growth rate is reached activity index of 19.3549 in 2013 (Fig. 6.4c) but is predicted to reach 22.2897 in 2055 (Fig. 6.4f). Such changes can be reflected on overall increase of the population growth rate by 38.3-fold (AI = 3.8344) (Fig. 6.4i).

6.3.2.5 Future distribution and abundance of *D. semiclausum* in Mt. Kilimanjaro

A large amount of changes in the possible from 2013 to 2055 in Mt. Kilimanjaro will occur in the low zone whose EI is predicted to change from 0.5945 – 0.6711 in 2013 (Fig. 6.5a) to

0.8180 – 0.8634 in 2055 (Fig. 6.5d). The net change between the two time periods is predicted to range from 0.2042 to 0.2271(Fig. 6.5g). With generation index reducing from 19.4236 – 26.3999 (2013) to 16.5306 – 22.2685 (2055) (Fig. 6.5b and e), the ability ofthe parasitoid population to reproduce and subsequently add new generations into the population is predicted to decline overtime, with a peak decline (loss of about 5.7 generations) occurring around Uparo, further away from the bottom-most farm of Kisangesangeni B (Fig. 6.5h). The population growth rate is therefore predicted to shrink, as recorded from activity index (AI = 25.4386 – 34.2203 in 2013 (Fig. 6.5c) and 23.3904 – 30.6596 in 2055 (Fig. 6.5f)). Overall, the population growth will shrink by a factor of 3.1885 at lower end of the transect and will continue to shrink up to a factor of 5.8554 in Uparo (AI = -3.1885 – -5.8554).

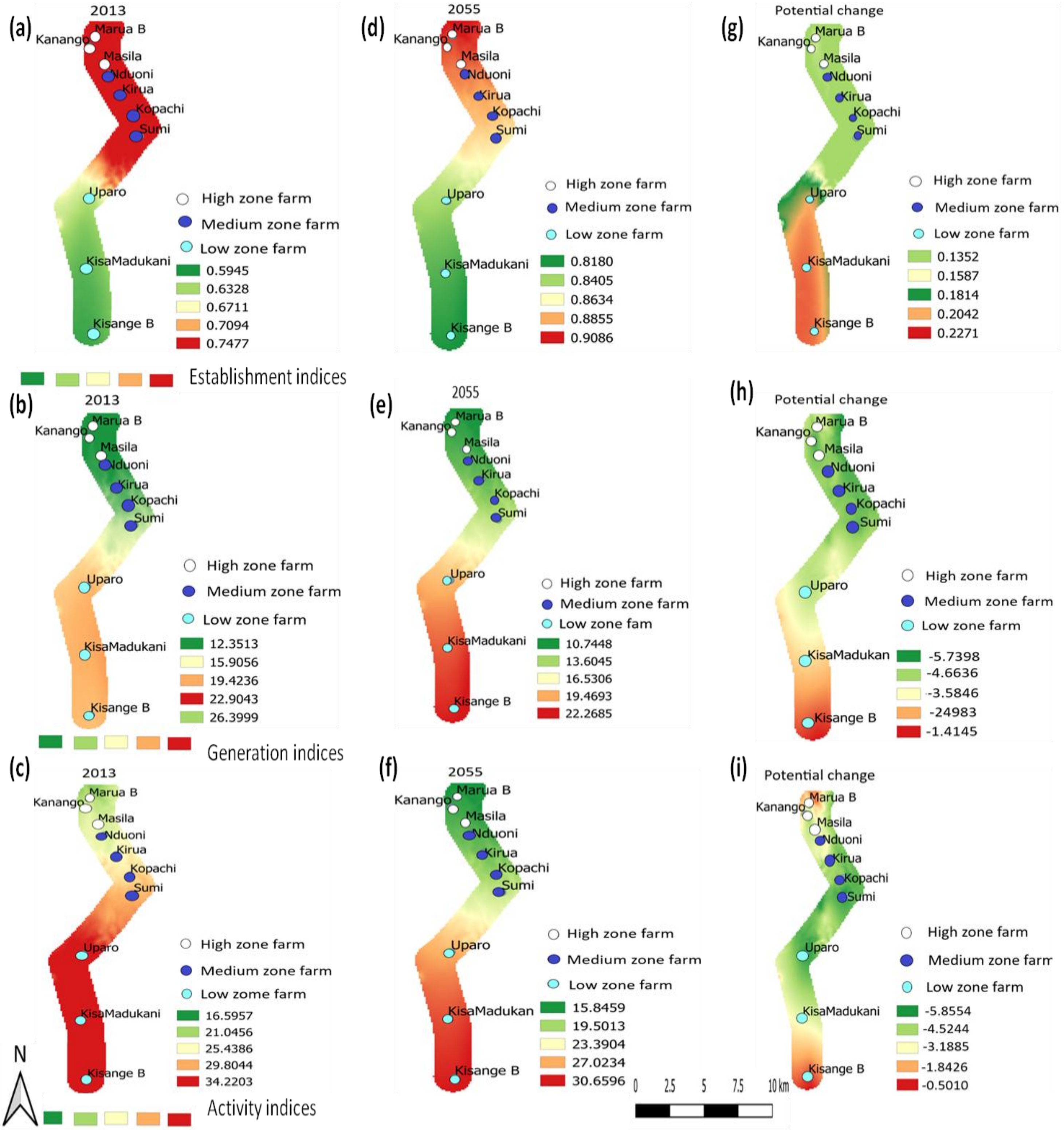

Figure 6.5: Changed population growth indices of *D. semiclausum* across climate change conditions of Mt. Kilimanjaro. Baseline 2013 distribution and abundance on selected farms: (a) EI, (b) GI and (c) AI; future 2055 distribution and abundance: (d) EI, (e) GI and (f) AI. Potential change in distribution and abundance between current and future scenarios: (g) EI, (h) GI and (i) AI

The potential of *D. semiclausum* to establish, survive and spread in medium zone of Mt. Kilimanjaro increased from the base year 2013 (EI = 0.7094 – 0.7477) (Fig. 6.5a) to year 2055 (EI = 0.8855 – 0.9086) (Fig. 6.5d). However, the prevailing environmental conditions are predicted to cause a loss of number of generations over time (GI = 15.9056 – 12.3513 in 2013 and GI = 13.6045 – 10.7448 in 2055) (Fig. 6.5b and d). The net loss will range from approximately 2.50 to 3.58 generations (GI = -3.5846 – -2.4983) but this loss is lower than in the low zone (GI = -5.7398 – -3.5846) (Fig. 6.5h).The population growth rate will therefore decline over time (from AI = 25.4386 – 21.0456 in 2013 to 23.3904 – 19.5013 in 2055) (Fig. 6.5c and f).The overall population growth is predicted to reduce in size when the activity index ranged from -3.1885 to -1.8426.

There was a narrow margin of change in suitability of the high zone to the survival and distribution of *D. semiclausum*, from establishment index of 0.7094 – 0.7477 in 2013 (Fig. 6.5a) to that ranging from 0.8855 – 0.9086 in 2055 (Fig. 6.5d). The overall change is predicted to range from establishment index of 0.1814 to 0.2042) though still the zone offered a favourable environment for future reproduction of parasitoids. The parasitoid is predicted to lose the least number of generations per annum in this zone (GI = 12.3513 in 2013 and 10.7448 in 2055) (Fig. 6.5b and e), interpreted toa net loss of about 1.4 generations (Fig. 6.5h) and therefore its population growth potential is likely to change very little (AI = -0.5010 – 1.8426) (Fig. 6.5i).

6.3.2.6 Future distribution and abundance of *D. semiclausum* in Taita hills

Suitability of the habitats of Taita hills to the establishment, survivorship and distribution of *D. semiclausum* will increase from the base year 2013 (EI = 6579 – 0.7375) (Fig. 6.6a) to 2055(EI = 0.8595 – 0.8941) (Fig. 6.6d). Over the time period, the the magnitude of changes will peak in the low zone, reaching up to 0.22 (EI = 0.2234) (Fig. 6.6g). However, the ability to produce new offsprings will decline overtime, with a range from 14.3 to 21.9 generations (GI = 14.3372 – 21.8889) recorded in 2013 (Fig. 6.6b) and from 14.2 to 18.3 generations (GI = 14.1846 – 18.2822) predicted in 2055 (Fig. 6.6e). The prevailing climatic conditions are predicted to cause *D. semiclausum* fail to produce and add into the population about 2.64 to 4.59 generations (GI = -2.6415 – -4.5893) (Fig. 6.6h). Expectedly, the population growth potential of *D. semiclausum* will decline in this zone, from generation index range of 19.8932 – 29.4949 in 2013 (Fig. 6.6c) to 20.4934 – 26.0201 (Fig. 6.6f). The overall change between the two time periods will lead to a decline of population by up to 46-fold (Fig. 6.6i).

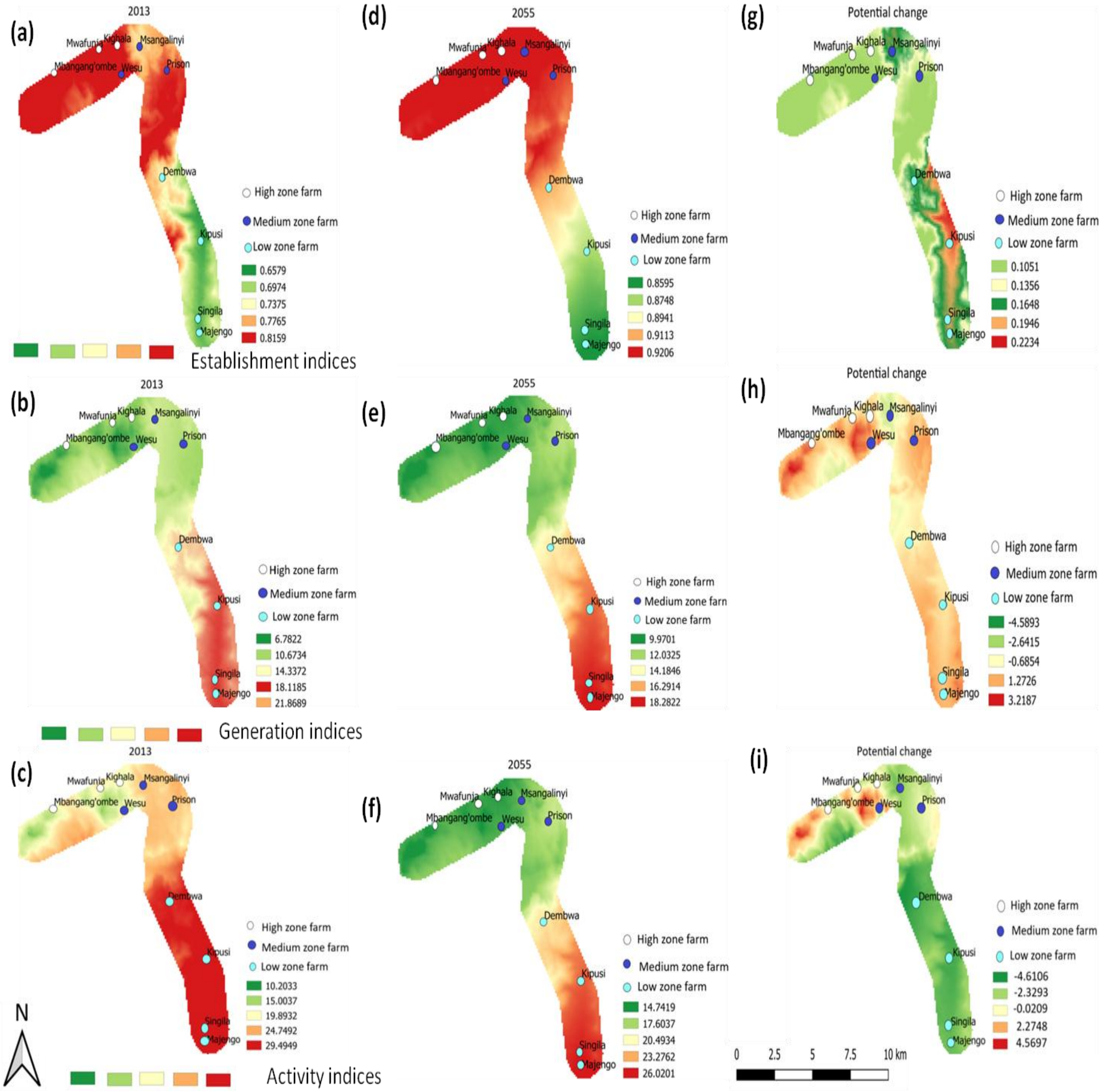

Figure 6.6: Changed population growth indices of *D. semiclausum* across climate change conditions of Taita hills. Baseline 2013 distribution and abundance on selected farms: (a) EI, (b) GI and (c) AI; future 2055 distribution and abundance: (d) EI, (e) GI and (f) AI. Potential change in distribution and abundance between current and future scenarios: (g) EI, (h) GI and (i) AI.

The changing climatic conditions of the medium zone from 2013 to 2055 will favour the establishment and distribution of *D. semiclausum* (from EI = 0.7375 – 0.7765 in 2013 (Fig. 6.6a) to EI = 0.9113 – 0.9286 in 2055 (Fig. 6.6d). The net change between the two time periods will still be favourable (EI = 0.1356 – 0.1946) (Fig. 6.6g). Nonetheless, ability of the parasitoid to add new generations in the population will have shrunk through most parts of the medium zone between 2013 and 2055, ranging between 10.7 – 14.3 generations (GI = 10.6734 – 14.3372) in 2013 (Fig. 6.6b) to 9.9 – 12.0 generations (GI = 9.9701 – 12.0325) in 2055 (Fig. 6.6e). In area around Msangalinyi, the parasitoid failed to add up to 2.6 generations per annum (GI = -2.6415) (Fig. 6.6h) into the population. On the contrary, the parasitoid population is predicted to be able to add 1.2726 new generations per annum around Prison area in Wundanyi. Overall in the zone, any gain on the parasitoid population growth in area around the Prison area is likely to be offset by the lost generations occurring in other parts of the zone (Fig. 6.6i).

There will be little variation on suitability of the high zone to the distribution of *D. semiclausum* in Taita hills between 2013 and 2055 (EI = 0.7765 – 0.8159 in 2013 (Fig. 6.6a) and EI = 0.9266 in 2055 (Fig. 6.6d).The overall change in suitability is narrow (EI = 0.1053 – 0.1356) (Fig. 6.6g). Contrary to the lower zones, where *D. semiclausum* produced a lesser number of generations over time, the parasitoid is predicted to increase number of generations from 2013 to 2055 in this zone (GI = 6.7822 – 10.6734 in 2013 (Fig. 6.6b) and GI = 9.9701 – 12.0325 in 2055 (Fig. 6.6e)). The model predicted a net increase of new generations into the existing population, ranging from approximately 1.3 to 3.2 generations per year (GI = 1.2726 - 3.2187) (Fig. 6.6h). The added number of generations will contribute greatly to the overall change in *D. semiclausum* population growth rate in the zone, which is expected to increase from activity index range of 10.2033 – 15.0037 in 2013 (Fig. 6.6c) to 14.7419 – 17.6037 in 2055 (Fig. 6.6f). With this change, the associated net increase in overall population growth rate is predicted to range from 22.7-fold to 45.7-fold (AI = 2.2748 – 4.5687) (Fig. 6.6i).

6.4 Discussion

Development and utilization of models for describing the distribution and abundance of insect species is not new. However, very often most of these models are developed at a regional, continental or global scale. These models are too generalized and utilize scarce information of the insect biology which frequently limits their applicability in improving management strategies for pests and surveillance of natural enemies with respect to a local change in climate. Some regional prediction models developed through DYMEX, a software for modeling fluctuating populations under different environmental conditions (Maywald *et al*., 2007), were utilized successfully to map population distribution of DBM in China but fell short of accurate analysis of age-structured populations. Furthermore, most models do not incorporate the local measurements of weather parameters. A proper prediction of potential effects of climate change on distribution and abundance of DBM and its parasitoids at a local spatial scale would require some information on the insect biology and ecology in order to generate meaningful insights towards improving pest management strategies. One area which is likely to benefit greatly by this is on determination of demographic parameters of insects by utilizing the upper and lower threshold temperatures during their life cycle (Kontodimas *et al*., 2004).The population growth of DBM and its parasitoids are affected substantially by weather variables, particularly rainfall and temperature.

To understand the potential change of insect distribution and abundance locally under the future climate scenario, the developed phenology models were linked with the georeferenced topographical 3D map and local temperature measurements recorded on farms on Mt. Kilimanjaro and Taita hills transects. Of the two parasitoids, *C. vestalis* has demonstrated to control DBM population growth rate more effectively in the low zone, currently and in the future. The numbers of newly added generations in *C. vestalis* population tripled those of DBM in the low zone of Taita hills and doubled that in the low zone of Mt. Kilimanjaro. This implies the braconid is poised to limit the pest populations better than *D. semiclausum* in lowland areas between the two study areas. After all, the growth rate of *D. semiclausum* was predicted to decline substantially in low zones of the study areas. However, the shorter generation lengths in the low zones could also imply a rapid increase of insect population per unit time as observed earlier by Fand *et al*. (2014). These findings indicate such population growth trends will remain viable if the DBM and *D. semiclausum* populations are not subjected to high temperatures for long periods of time, which would otherwise compromise the vulnerable immature stages. Several studies (Yang *et al*., 1993; Andrew, 2013; Nguyen *et al*., 2014) have demonstrated that when eggs and pupae are subjected to long periods of exposure to temperature above 35°C their development is disrupted.

A substantially higher increase in the mean minimum and maximum temperatures is expected in Taita hills than in Mt. Kilimanjaro. The temperature variability on mountains is subject to many attributes, including tree coverage and local topography. It is possible that shading effects of the two upward slope of Mt. Kilimanjaro was critical for local microclimate, as previously suggested by Hemp (2006) and Fernandes *et al*. (1984). The shading enhanced flexibility of the crucifer cropping systems to withstand harsh climate by providing the favorable microclimate. This will likely benefit DBM and *D.semiclausum* more than *C. vestalis* because they thrive well under moderate temperatures. A lower loss of DBM and *D. semiclausum* than *C. vestalis* is therefore expected, particularly in the medium and high zones of Mt. Kilimanjaro. A very extensive loss of forest cover due to human activities e.g. agriculture, settlement and logging in Taita hills (Pellikka *et al*., 2009) is likely to have contributed to warmer temperatures compared to Mt. Kilimanjaro (Maeda, 2011). On the contrary, only one third of the forest cover in Mt. Kilimanjaro has been degraded in the last seven decades (Hemp, 2009).

The future climate change scenarios indicated the areas around Kisangesangeni B in the low zone and most of the medium and high zones of Mt. Kilimanjaro will likely face increasing populations of DBM despite some attraction of *D. semiclausum*. Substantial changes on population growth in the low zones of Mt. Kilimanjaro underscore the probable role of Miwaleni springs, closest to Kisangesangeni B farm, at the bottom of the altitudinal transect. The springs create the microclimate needed for crucifer vegetables, DBM and *D. semiclausum* in a region that is generally hotter than the medium and high zones. Elsewhere in the low zone, the predicted declining number of generations and the resulted shrinking population growths of *D. semiclausum*could lead to future DBM – *D.semiclausum* mismatch due to higher vulnerability of the wasp to hot temperature. The mean minimum temperatures have been predicted to rise substantially in the low zones.

A sizeable decline in the number of generations due to the future increasing temperatures points to potential shrinking of DBM and *D. semiclausum* populations across Mt. Kilimanjaro and Taita hills regions. It has earlier been noted that increased temperatures do not always stimulate rapid growth of pest populations but can also impair their physiology directly or indirectly through increased killing capacity of its natural enemies (Ahmad and Ansari, 2010; Miranda *et al*., 2011; Sow *et al*., 2013). Compared to corresponding farms present in low zone of Mt. Kilimanjaro, most farms in the low zone of Taita hills are positioned at relatively higher altitudes. This may have contributed to a higher parasitic effectiveness of *D. semiclausum* in Taita hills than in Mt. Kilimanjaro. However, the projected increase of maximum temperature in this region could still point to potential decline of *D. semiclausum* population.

Compared to Mt. Kilimanjaro, the models projected a future decline in population growth rates of DBM in the low and medium zones of Taita hills due to a substantial increase of the mean minimum temperatures. Such declining population growth can be associated with potential reduction of crucifer damage in the two zones. Unlike the Chagga homegardens in Mt. Kilimanjaro, the agroecological landscape in the medium and high zones of Taita hills is less characterized by the tree component, depriving its ability to insulate the radiated temperature. The increased temperature could become favourable to hot – temperature tolerant pests and may pave way to potential outbreak of other insect pests such as thrips and aphids (Bergant *et al*., 2005; Barton and Ives, 2014).

The findings have demonstrated that *C. vestalis* can become an increasingly reliable parasitoid for controlling DBM under the warming conditions in the future. With minimum temperature values increasing gradually upward the altitudes and towards 2055, the parasitoid is likely to thrive under environmental conditions which could otherwise be relatively unfavourable to temperature-sensitive *D. semiclausum*. The increased warming upward the altitudes may also prompt expansion of colonization range upward the slope both parasitoids; *C. vestalis* in response to the favourable warming conditions and *D. semiclausum* in search for more suitably cool conditions. This signals a potentially weak DBM – *D. semiclausum* match in the low and to some extent in the medium zone. Eventually, the shifts will pave way for increasingly strong DBM – *C. vestalis* parasitic interaction in areas where it is currently weak due to differential response towards rising temperature beyond the optimum level.

In conclusion, the study has highlighted a likely DBM – *D. semiclausum* population mismatch which could lead to increased pest outbreak under the future warming conditions. However, depending on the local topography, the outbreak could be matched gradually over a period of time by *C. vestalis,* presently the key DBM parasitoid under the hot temperature conditions of the low zones. Equally important, linking phenology models with field-collected fluctuating temperature measurementsmanaged to establish more realistic and focused distribution models in a localscale than the commonly adoptedgeneral regional circulation models (RCM) andglobal circulation models (GCM). However, it is recommended to include other factors known to influence insect distribution such as relative humidity, rainfall and host plant diversityto increase validity of the models of the predicted distributions and abundance.

CHAPTER SEVEN: GENERAL DISCUSSION, CONCLUSION AND RECOMMENDATIONS

7.1 Discussion

The insect pest populations in crucifer farming systems are broadly distributed along altitudinal gradients such that populations living at the lower ends experience quite different climate conditions from those at the upper ends. This knowledge has implications for our general understanding of the biology, ecology, distribution of species and management of pests. The comparative study of species ecology along the altitudinal gradients of Mt. Kilimanjaro and Taita hills provided clues to the likely response of the interacting crucifer plants, diamondback moth and parasitoid species to climate change. The species interacted in a way partly dictated by environmental conditions along the gradient and partly by biotic factors. These findings are consistent with a study of terrestrial insect pests along elevation gradients by Hodkinson (2005) which noted that rapid environmental change along altitudinal gradients can be useful in understanding the potential effects of climate change.

Assessment of potential effect of climate change on tritrophic interactions is important for gaining a deeper understanding of the ecological community in light of changing climate. More important, the knowledge can be utilized to carefully manage the consequences of climate change at the ecosystem level (Landsberg and Stafford-Smith, 1992). Climate change is currently one of the most important issues in ecology because it has proved capable of producing far-reaching adverse implications in varied areas like agriculture and natural resource conservation and thereby risking the livelihoods of many smallholder farmers (Hillebrand and Matthiessen, 2009; Beddington, 2010). Most predictions on consequences of climate change have focused on potential effects of climatic variables on single trophic level or two interacting trophic levels. Moreover, even research on species distribution modeling has largely focused on one trophic level. Worse still, many climate change studies have examined the effects of single climatic variable on biological systems (Dyer *et al*., 2013). Development of simple models which are based on very few parameters to describe a potential community change has always risked formulating inappropriate and ineffective management strategies (Ma *et al*., 2004). A few studies have been conducted to project potential effects of climate change on tritrophic interactions involving insects (Stacey, 2003; Tylianakis *et al*., 2008; Dong *et al*., 2013; Dyer *et al*., 2013). However, most of such studies were conducted in the temperate countries e.g. United Kingdom, United States, China, New Zealand and Sweden. The current study has investigated the potential effects of climate change on tritrophic interaction involving crucifer plants, DBM and parasitoid species in agroclimatic zone of the moist tropical East Africa. The findings have contributed to building up a more comprehensive picture of potential effects of climate change which could be helpful for developing more effective adaptation measures in the region.

The findings of this study have shed light on probable changes of the insects' phenology to climate change. Low temperatures seemed to favour the phenological development and reproduction of DBM and *Diadegma semiclausum* but not *Cotesia vestalis*. Present under the relatively hot environment in lower zones of Mt. Kilimanjaro and Taita hills, differences in phenological response between DBM (resource) and *D. semiclausum* (consumer) likely affected the fitness of both, pointing to potential coevolution of their physiology and behavior to temperature. More studies have been conducted on the host plant-insect interactions than the host insect-parasitoid interactions (Van Asch and Visser, 2007), leaving a substantial gap of knowledge on the response of high trophic levels to climate change. The lower parasitic efficiency of *D. semiclausum* in the low zone could have led to increased abundance and distribution of DBM if the *C. vestalis* was not available. Naturally, a stable host insect-parasitoid interaction would require not all hosts within a population to be parasitized because this may lead to population crash (Van Nouhuys and Lei, 2004).A phenological mismatch that leads to low parasitism can help to stabilize interactions (Godfray, 1994). When the timing of parasitoid activity occurs while the suitable host insect stages are few, the host population can be subject to heavy parasitoid pressure and potentially lead to extinction of both (Jeffs and Lewis, 2013). On the other hand, a phenological mismatch due to inability of parasitoid to track a spatial shift of the host insect can lead to 'host escape' due to colonization of new habitats (Schonrogge *et al.*, 2012). Under this study, *D. semiclausum* was a dominant and specialist parasitoid of DBM in medium and high zones. On the other hand, *C. vestalis*, a generalist parasitoid, thrived under the hot climate and may have tracked DBM more effectively in the low zone because of the available alternate hosts, also since the DBM population was fragmented.

The study has further shown that the insects will likely shift their altitudinal distribution in response to changing climate. Several studies (Parmesan *et al.*, 1999; Walther *et al.*, 2002, Parmesan, 2006) have earlier documented evidence of altered climatic conditions having contributed substantially to changing species distributions. However, finding congruent populations of host insects and parasitoids is difficult (Jeffs and Lewis, 2013). In the low zone of Mt. Kilimanjaro, *Diadegma semiclausum* – based DBM parasitism was lower and could not correspond to the moth population because the parasitoid population in the range margin could not adapt very effectively to the high temperature. Contrary to the general assertion that the host insect-parasitoid populations are less well-adapted in the range margins due to short period of coevolution (Hoelmer and Kirk, 2005), the thriving *C. vestalis* population in the low zone of Mt. Kilimanjaro was efficient in limiting the moth population. Introduced from South Africa and released in Loitoktok, 85 km away from Mt. Kilimanjaro (Kahuthia-Gathu *et al.*, 2017), the parasitoid has probably dispersed to Mt. Kilimanjaro agroecological zone, adapted and established in the low zones due to the warm climate, abundant crucifer vegetables and less availability of *D. semiclausum*, its key competitor (Ngowi *et al*., 2019).

The DBM-parasitoid interactional response to climate change has also been shaped by the number of generations which were implicated in host specificity and dispersal ability. Besides speeding up development rates and increased number of generations over a unit time, the future warming conditions will likely change the generation times among DBM and its parasitoids. This can be predicted because development rates and reproduction of insects normally increase above threshold temperatures and any extension of the hot dry seasons and a delay of cold and/or long rainy seasons will result in extended population growth and breeding season. Under the circumstance, the likelihood of the physiological and behavioral response of DBM development times to the extended warmer temperatures increases when it differs from its parasitoids. If this happens, there is potential mismatch in the timing of the host insect and parasitoid generations. This was probably the reason behind the predicted substantial future population growth of DBM in the low and medium zones of Taita hills as compared to that of *D. semiclausum*.

The DBM abundance rose steadily under decreasing temperature conditions. Several studies have shown that the pest survives better at low temperatures (< 20°C) than high temperatures (>25°C) (Wakisaka *et al*., 1992; Smith, 2002). The present findings concur with this by showing increased pest abundance and the associated crop damage particularly in the higher zones. The climate condition of the two altitudinal transects was probably modified considerably by the farming systems practiced in both Mt. Kilimanjaro and Taita hills. The Chagga home gardens enhance resilience of crucifer farming systems to harsh climate in Mt. Kilimanjaro by reducing the amount of heat to the soil through the dense banana and tree component. The homegardens contributed in making the medium and high zones more favourable for moth activity than the low zones. The favourable microclimate created by the homegardens may have in turn contributed to the predicted lower loss of DBM populations by 2055. Furthermore, the homegardens largely insulate wild crucifers from moisture stress. The thriving wild crucifers avail alternate sources of food and refuge to DBM. More importantly, wild crucifers showed the potential for providing trap crops for the moth, alternative oviposition sites and refuge to parasitoid species. In contrast, the relatively poor vegetation complex of Taita hills contributes to increased vulnerability to extreme climate, particularly in the low and medium zones. Any rise in temperature in the low zones under the influence of global warming will likely prompt the insect pest to expand its range gradually upward along the gradient where temperature is relatively lower. This implies a likelihood of growing incidence of yield losses in the high altitudinal zones.

Rainfall affects crop damage indirectly through a reduction of the DBM abundance. The rain droplets kill the DBM larvae and dislodge them from crucifer plants, particularly the early instars. Frequent rainy sessions during the long rainy season experienced during this study likely interfered with fecundity through disrupting mating-related flights and oviposition particularly at dusk, confirming observations made earlier in Taiwan (Asian Vegetable Research and Development Centre, 1988; Talekar and Shelton, 1993). Rainfall therefore reduced crucifer damage rates only temporarily, as it was evident during the long rainy season. Unlike temperature, rainfall events are periodic and their contributions to overall crucifer damage were often localized and temporary.

Diamondback moth populations were controlled more effectively by *C. vestalis*and *D. semiclausum* under the hot (low zone) and cool (medium and high zones) temperature conditions, respectively. *Diadegma semiclausum* has a strong establishment and dispersal capability which makes it superior than *C. vestalis* in colonizing new ranges (Löhr *et al.*, 2007;

Gichini *et al*., 2008). The ichneumonid remains a dominant parasitoid in high altitudes and isolated areas with good microclimates. As observed previously, such areas are also very suitable to DBM. However, taking into consideration large areas under crucifer production that experience long periods of warm temperatures, this literary implies C. *vestalis* will likely remain a more reliable parasitoid species under the warming climate. In the hot and humid lowlands of Southeast Asia, where annual temperature fluctuates between 20°C and 35°C, studies have established that *C. vestalis* is the most reliable natural enemy of DBM (Talekar and Yang, 1991; Verkerk and Wright, 1997). In the current study, the *C. vestalis*-based biological control of DBM is predicted to be more effective in Taita hills where the mean minimum temperature increase along the altitude is expected to be larger (0.7°C – 2.7°C) than in Mt. Kilimanjaro (0.7°C – 1.2°C).

The population growth rate of DBM and its key parasitoids showed mixed response to the change between the prevailing climate at the beginning of the study (2013) and the future (2055) climate. The predicted sharp decline of DBM in the low and medium zones of Taita hills could be associated with the significant rise of the mean minimum temperature (1.6°C – 2.7°C) and increased incidence of *C. vestalis* in the medium zone. The predicted rise of *C. vestalis* population could offset the *D. semiclausum*-driven biological control in the low zone and perhaps lower parts of the medium zones because of the high sensitivity of *D. semiclausum* to temperature. The same response is predicted in the low zone of Mt. Kilimanjaro. Such predicted rise of temperature may also signal a growing potential for outbreaks of high temperature-tolerant insect pests such as thrips in the low zones.

The current study further harnessed the information gathered from life table experiments under constant temperatures to successfully establish phenology models. The models were run and linked with fluctuating temperatures collected in the field to establish temperature-dependent insect phenologies which are more realistic in the local context. Such phenology modeling built on field-based fluctuating temperature measurementsare likely to be more precise than the commonly adopted modeling efforts that are based on more general regional circulation models (RCM) and global circulation models (GCM).

7.2 Conclusions

This study has demonstrated how climate change contributes largely in destabilizing the herbivory and parasitic interactions involving crucifer vegetables, DBM and parasitoids. Different requirements of temperature threshold levels was the single most important attribute that influenced the direction or disruption of the interaction becauseboth the DBM, its parasitoid species and crucifer plants did not respond the same way to changing temperature.Broad changes are likely to occur in interspecific [DBM – *D. semiclausum*] interactions under the projected climate change conditions. The consequences differ but might involvethe disrupted parasitic interactions in a local scale all along the altitudinal gradients. *Cotesia vestalis* is predicted to take over from *D. semiclausum* in limiting the DBM population growth under the warming conditions but this may be gradual since the process of colonizing the new expanded range, particularly the medium zones, will also depend on other factors besides climate e.g. hyperparasitoids. This can only be observed because the developed phenology models were based on the whole life history of the insects which took account of small changes commonly overlooked by other models. However, the prediction that the DBM populations will decline in the low and medium zones of Taita hills but increase in the high zone due to rising temperatures in the low zones signalsa growing pest burden in the high zone. A new management approach should be devised including avoiding spraying the broad spectrum insecticides so as to conserve the favourable environmental conditions for *D. semiclausum*, its most effectivecontrol agent in the high zone. Increasing the structural diversity of crucifer cropping system availed the alternative sources of food and oviposition sites for DBM,nectar resources, alternate hosts and refuge for parasitoidswhich eventually led to low pest population. The knowledge can be harnessed to improve the DBM control in the study site. These observations necessitate deep understanding of the thermal biology, chemical and behavioural ecology of DBM and its parasitoids under the dynamic climate patterns to develop localized but effective control strategies of the insect pest.

7.3 Recommendations

i. The projected build up of DBM upward the altitudinal gradients signalsa growing potential of increased crop lossesin the mid and high altitudinal zones. To counter the impending losses, incorporation of ecologically friendly methods, including the locally adapted trap crops, is recommended to relieve the crucifer vegetables from the potentially abundant pest load. For example, while Indian mustard can be integrated into crucifer farming systems as a trap crop, planting tomato 30 days before planting cabbage repels the moth due to the chemical volatiles (rutin) emanating from it(Varela *et al*., 2003). Collard, another host plant, can be planted at the same time with cabbage but along the field margins to attract and pullsubstantial population of DBM away from cabbage because of its strong plant volatiles and reduced wax (Eigenbrode and Shelton, 1992; Mitchell *et al*., 2000), ability to produce foliage longer than cabbage and the tolerance to withstand varied populations of insects (Shelton and Nault, 2004).

ii. The predicted rise of temperature overtime in Taita hills heraldsadverse environmental conditions which can aggravate proliferation and expanded colonization range of new high temperature-tolerant insect pests. The Agricultural Extension Department of the Ministry of Agriculture, Livestock and Fisheries at the national and county level of Taita Taveta is advised to initiate and strengthern pest scouting and surveillance programsfor monitoring the population dynamics of new potential pests for timely decision-making inmanagement strategies. The Ministry of Agriculture can do the same in Tanzania, particularly in the lowland areas of Mt. Kilimanjaro. For already known pests, research could be conducted on potential change in behavioural patterns under climate change for advanced formulation of management strategies.

iii. Wild crucifer species can be integrated in crucifer farming systemsto provide DBM with the alternative food resources and oviposition sites. Planting them along the boundaries of the farm plots can serve to attract DBM away from the crop, and in the way reduce the pest load (Kahuthia-Gathu, 2007). Furthermore, when carefully integrated along the field margins, wild crucifers support parasitoid species when cultivated crucifer plants are unavailable, in addition to shielding them from the lethal insecticide applications. Once the cultivated crucifers are available and insecticide applications no longer available, the parasitoids will recolonize back the crop. Potential competition for nutrient resources can be reduced by timely weeding. To sensitize adoption, the departments responsible for agricultural extension under the Ministries of Agriculture in Kenya and Tanzania can organize demonstration plots displaying the technologies used for integration of wild crucifer weed species for sustainable pest control.Types of wild crucifer species, availability of quality seeds, efficiency in attracting DBM, integration in the crucifer cropping system and weeding are some of key issues for farmer training.

iv. The Ministry of Agriculture, Livestock and Fisheries in Kenya is advised to team up with Ministry of Environment and Forestry to come up with some structural diversification research-based trials of the currently practiced crucifer cropping systems to attract a wider number and different species of natural enemies of DBM for sustainable production of crucifer vegetables.The same consideration is applied to the Tanzanian respective Ministries, namely the Ministry of Agriculture and the Ministry of Union Affairs and Environment. For example, non-host crop, nectar-producing plants can be grown on the boundary surrounding broccoli farm plots to increase attraction of parasitoid species and consequently catalyze the DBM parasitism. Idris and Grafius (1995) demonstrated that manipulation of the diversity and distribution of flowers from wild plants bordering crucifer plots could enhance the life span and reproduction of *Diadegma sp*., and hence, increase DBM parasitism. The diversification can provide an added advantage of alternative crops to farmers for earning livelihoods.

v. The predicted changes of climate upward the altitudes and between the time periods have been associated with the change in insect behavior, including reproduction and distribution. To minimize the foreseen pest load and increase crucifer productivity, a call is made to responsible government organs, currently the State Department for Crop Development in Kenya and the Agricultural Training, Extension Services and Research Division under the Ministry of Agriculture in Tanzania, to foster efforts in breedingsome new crucifer vegetable varieties resistant to DBM and the other key pests. Research collaboration with international research organizations on breeding programs is recommended.

vi. It is suggested to utilize locally-collectedfield temperature as current data when modelingthe potential future distribution and abundance of insect species because of the higher precision in the local context than when utilizing the regional or global circulation models. The State Department for Crop Development, Kenya Plant Health Inspectorate Services and National Disaster Management Unit in the Ministry of

Interior and Coordination of National Government, are the key institutions in Kenya which can utilize this knowledge for designing some pest surveillance programs to generate information required for specific pest management strategies. For the same purpose, the key institutions in Tanzania to utilize this information include the Agricultural Training, Extension Services and Research Division, Plant Health Services and the National Plant Quarantine Station, both in the Ministry of Agriculture; and the Disaster Management Department in the Prime Minister's Office.

vii. The Insect Life Cycle Modeling 3.0 (ILCYM 3.0) software has shown it can be utilized to show the current distribution of insect pests but also to predict the likely trends in the potential future distribution and abundance of insect pests. Based on climate, utilization of the software to monitor potential threats and spread of invasive species of the major crops is recommended as an added tool to the national agriculture departments of Kenya and Tanzania.

7.4 Suggested areas for further research

i. The interaction of parasitoid speciesof DBM and its resulted consequence to crucifer damage under the changing climate in the region is not obvious. Such parasitoid interaction may focus onthe functional inefficiency, niche partitioning or facilitation. Conducting a study in this area may give some fresh insights on the role of an often overlooked biotic factorwhich can influence theeffectiveness of biological control of DBMunder the changing climate. The knowledge will further contribute to improving decision – making for pest control in the study site.

ii. Incorporatingother factors known to influence DBM and its parasitoids,such as rainfall, relative humidity, microclimate and food quality, into the prediction models of development, mortality, life span and reproduction of insects, could enhance validity of the derived predictions.

iii. Future experiments designed to investigate the response of multitrophic interactions to climate change should integrate the hyperparasitoids for better predictions of future population dynamics of insect pests like DBM. Information linking the hyperparasitoids to multitrophic interaction is lacking and its availability could draw some more valuable insights into the underlying insect community dynamics involving diamondback moth.

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LIST OF APPENDICES

Appendix 1: Diagnostic features of *D. semiclausum* based on morphometic measurements (Azidah *et al*., 2000)

- Female has sharp and distinct ovipositor
- The head to body end length of females is 5.00 to 7.04 mm and males 4.44 to 6.36 mm for males
- Ovipositor is approximately 0.43 to o.87 mm and 0.42 to 0.60 mm hind tibia length
- Male and female antennae consist of 23 – 27 and 21 – 25 flagellomeres respectively
- Veins of forewing are usually present; areolet connects the upper and fur end veins

Appendix 2: Modified DBM damage score scale from Dreyer (1987)

1 = No detectable damage (0%)

2 = Few to many holes but damage limited to outer or lower leaves (1-25%)

3 = Considerable damage of the outer or lower leaves, slight damage on the cabbage head, kale leaves and Ethiopin mustard leaves, crops marketable with minor leaf removal of outer leaves (26-50%)

4 = Outer or lower leaves completely destroyed, moderate attack of inner and tender leaves, heads of cabbage marketable after considerable removal of outer head leaves (51-75%)

5 = Severe attack on the cabbage heads, kale and Ethiopian mustard leaves, crops unmarketable (76-100%)