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ORIGINAL CONTRIBUTION

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Parasitism of *Hypothenemus hampei* (Coleoptera: Scolytidae) in different farming systems and altitudes of Mount Elgon, Uganda

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Abstract

Altitude and farming system play a vital role in modifying the niche for arthropods, by directly influencing microclimatic conditions, the quality and quantity of vegetative cover, which act variably on the behaviour of the pests, and their natural enemies. The objective of the study was to determine their effect on the abundance and parasitism of the Coffee berry borer (*Hypothenemus hampei*) in the Mount Elgon region. Altitude was categorized as: low (1,400–1,499 m.a.s.l); mid (1,500-1,679 m.a.s.l); and high (1,680–2,100 m.a.s.l), and farming system was categorized as: Coffee monocrop; Coffee + annual; Coffee + banana; and Coffee + banana + shade trees. For each altitudinal range, each farming system was represented three times. The study was in two districts of the Mt. Elgon, covering a total of 72 Arabica Coffee study sites. The work involved field pest infestation inventories, followed by laboratory rearing for the abundance and parasitism studies. The results revealed highly significant interactions between altitude and farming system in influencing the abundance of the pest and its four parasitoids: *Phymastichus coffea*, *Cephalonomia stephanoderis*, *Prorops nasuta* and *Heterospilus coffeicola*. *C. stephanoderis* was highest in the mid-altitudes within Coffee + banana+shade tree system; *P. nasuta* was highest at high altitude within Coffee + banana system; *P. coffea* was most abundant at mid-altitude within Coffee + banana system, whereas *H. coffeicola* was highest at high altitude within the Coffee + annual cropping system. *H. hampei* counts were highest at low altitudes, especially in the Coffee + annual system. Some of these trends can be explained by the condition of the microclimate in the Coffee fields. There was a negative relationship between temperature and abundance of all the four parasitoids. Only *C. stephanoderis* had a relationship (+) with semi-natural vegetation species counts. And only *H. coffeicola* had a relationship (+) with light intensity. These contrasted with *H. hampei*, which was positively related to temperature and negatively to light intensity.

KEYWORDS
microclimate, microenvironment, parasitoids, vegetation

1 | INTRODUCTION

Hypothenemus hampei (Ferrari; Coleoptera: Curculionidae; Scolytidae) is an important pest causing devastation of Coffee plantations in the sub-Saharan agricultural regions, especially in East Africa (Jaramillo, 2012; Jaramillo, Chabi-Olaye, & Borgemeister, 2010). Population flare-ups are exacerbated by increasing trends in temperatures and solar exposures (Jonsson, Ijala, Ekbom, Kyamanywa, & Karungi, 2014). Among the possible control measures of *H. hampei*, biological measures offer great potential, and reports of existing natural enemies, notably, *Cephalonomia stephanoderis* Betrem (Hymenoptera: Bethylidae); *Prorops nasuta* Waterston (Hymenoptera: Bethylidae); *Heterospilus coffeicola* Schemiedeknecht (Hymenoptera: Braconidae); and *Phymastichus coffea* LaSalle (Hymenoptera: Eulophidae) are available (Jaramillo, 2012; Jaramillo et al., 2010; Rutherford & Phiri, 2006). However, the pest continues to be of economic importance in the Mt. Elgon farming system in Uganda (Jonsson et al., 2014). The lack of impact of the natural enemies could be embedded in direct and indirect effects of biophysical factors in the Coffee systems in the region.

Altitude has been reported to affect insect pest regulation in mountainous ecologies, directly (Jonsson et al., 2014) and/or through its effect on the microclimates or quality, and quantity of plants that directly affect the natural enemies (Ayal, 1994; Bianchi, Booij, & Tscharntke, 2006; Patrick, Fraser, & Kershner, 2008; Siemann, 1998; Skalski, Kędzior, Maciejowski, & Kacprzak, 2011). Jonsson et al. (2014) working in the area reported a 17 per cent increase in growth rate of *H. hampei* per degree increase in temperature. There is evidence of changing thermal temperature trends due to global changes and anthropogenic influences, which create micro conditions at specific locations (Jaramillo et al., 2010, 2011, 2013; Jason et al., 2005; Seymoure, 2018).

Prevailing farming systems, at specific locations, create conditions of temperatures, humidity and light intensity, which have a selective effect on herbivores and their natural enemies (Rao, Singh, & Day, 2000; Varon, Eigenbrode, Bosque-Pérez, & Hilje, 2007). The Mt. Elgon region has Arabica Coffee farmlands with varying cropping intensities, and semi-natural vegetation that exists in mosaical patterns under variable habitat management approaches within different altitudes (Karungi et al., 2018; Liebig et al., 2016). There are reports of response of specific insect herbivores and generalist predators to cropping complexities in the region (Jonsson et al., 2014; Karungi et al., 2018, 2015). However, there is no documentation on such dynamics with regard to *H. hampei* parasitoids. As such, this study provides an understanding of the relationships of altitude, farming systems and microclimate with abundance of *H. hampei* and its parasitoids in the region.

We tested three hypothesis: (a) prevailing microclimate conditions are pushing *H. hampei* parasitoids to higher altitudes; (b) including banana and/or shade trees in Coffee can ameliorate conditions at low altitude and increase *H. hampei* parasitism, and (c) abundance of *H. hampei* parasitoids is more associated with semi-natural vegetation than microclimate.

2 | MATERIALS AND METHODS

2.1 | Study sites description

The study was conducted in the Arabica Coffee growing areas of Mt. Elgon region of Uganda within the districts of Kapchorwa and Sironko. Within these districts exist varying levels of human population (Kapchorwa = 104,580 total households and Sironko = 246,638 total households; Uganda Government National Population & housing report, 2014); and mosaical patterns of semi-natural vegetation and Arabica Coffee (*Coffea arabica*) farm lands. The altitude of this region ranges from 1,200 to 3,500 m.a.s.l. This study area lies within 1°8′43″N–1°23′04″N and 34°22′26″E–34°26′29″E, with a bimodal rainfall pattern (March–May; September–November). The average annual precipitation ranges from 1,200 to 2,200 mm (National Environmental Management Authority, 2010). Coffee is often partnered with other crops on the same field, notably: *Zea mays*, *Solanum tuberosum*, *Phaseolus vulgaris*, *Arachis hypogaea*, highland cooking banana and assorted shade trees. These annual crops are planted bi-annually while the Coffee and banana are maintained as established plantations. The soils can be described as Nitisols (International Union of Soil Science, 2007) developed on basaltic outflows (De Bauw, Van Asten, Jassogne, & Merckx, 2016).

2.2 | Research design

The study had two fixed factors: altitude and farming system. Altitude was categorized following the procedures used by Karungi et al. (2018) working in the Mt. Elgon region into three categories: low (1,400–1,499 m.a.s.l); mid (1,500–1,679 m); and high (1,680-2,100 m). Farming system as: Coffee monocrop; Coffee + annual crop; Coffee + banana; and Coffee + banana+shade trees. Within each district and for each altitudinal class, the four farming systems were replicated three times, making a total of 72 study farmlands. The localized mean microclimate readings within altitudes and farming systems are shown in Table 1. On the selected study sites, semi-natural vegetation, which included grasses, weeds, bushes, field margins and hedgerows, in and outside (5 m) the plot was scored and recorded as species counts (Table 1).

2.3 | Data collection

2.3.1 | *Hypothenemus hampei* field infestation

Five Coffee plants, spaced 10 m away from each other, were randomly selected on each sampling round from each of the 72 sites in the two districts. On the selected plants, three Coffee branches from the lower, middle and top parts were tagged (total branches sampled: five Coffee trees (three branches for each) × 4 farming systems (three farms for each) × 3 altitude levels and × 2 districts × 2 rounds = 2,160). Field infestation of *H. hampei* was calculated as a proportion of infested berries per branch, that is, the number of

TABLE 1 Parameters (means) of microclimate and semi-natural vegetation species in the study fields

Altitude	Farming system	Vegetation species counts	Temperature (°C)	Relative humidity (%)	Light intensity (foot candles)
Low	Coffee monocrop	10	26.56	58.83	187.70
	Coffee + annual	11	27.28	55.36	217.78
	Coffee + banana	10	26.68	60.28	187.95
	Coffee + banana + shade trees	20	25.08	64.71	39.83
Mid	Coffee monocrop	11	23.78	67.40	217.97
	Coffee + annual	11	25.08	64.13	180.81
	Coffee + banana	9	24.02	65.03	160.75
	Coffee + banana + shade trees	12	22.55	69.98	19.92
High	Coffee monocrop	13	24.39	56.15	281.64
	Coffee + annual	10	24.27	59.10	223.67
	Coffee + banana	10	23.84	60.38	221.89
	Coffee + banana + shade trees	17	23.01	62.45	48.44
Mean		**12**	**24.71**	**61.98**	**165.70**

[a]Bold values indicates Sample mean

infested berries in a branch/total number of Coffee berries in a branch following Jonsson et al. (2014).

2.3.2 | *Hypothenemus hampei* parasitoids counts and parasitism

In the selected Coffee fields, one hundred *H. hampei* infested berries were randomly picked per field, labelled and transferred to the Makerere University laboratory in Kampala, Uganda to rear out the pest and parasitoids. 7,200 berries in each round (100 berries × 4 farming systems (three replicate farms) × 3 altitude levels × 2 districts) were collected. The 100 berries were maintained in a round bottom jar (500 ml) under laboratory conditions, to await emergence of parasitoids (n = 72 jars for one round). The bottom of the jars was lined with absorbent materials (two parts of charcoal dust, two parts paper paste and 10 parts of crane filler); and the top cover covered with insect mesh). The jars were regularly wetted to maintain the appropriate relative humidity within the jar using water bottles with droppers. Each rearing round was maintained for 3 months, to allow for daily emergence of parasitoids, and data collected using the methodologies of Toedero and Klein (2008); Jaramillo et al. (2009). The laboratory rearing was done twice, that is, for year one and year two (N = 144 jars). The morphological identification of the parasitoids was done at the university laboratory, following the guiding descriptions of notable studies (Betrem, 1961; Espinoza et al., 2009; Evans, 1964; Feldhege, 1992; da Fonseca & Araujo, 1939; Hargreaves, 1926; Infante, 1994; Jaramillo et al., 2009; LaSalle, 1990; Le Pelley, 1968; Vergara-Olaya, Orozco-Hoyos, & Bustillo-Pardey, 2001), and the identification keys obtained from Jaramillo (2012) working with *H. hampei* parasitoids in the Coffee berry borer laboratories at ICIPE Nairobi. After the 3 months, 50 berries from each jar were opened and examined under a stereo microscope (Olympus), to count *H. hampei* individuals (dead/alive) and any un-emerged natural enemies. For the emerged parasitoids, proportional parasitism was calculated as follows: Number of parasitoids of each species/(Number of parasitoids + the number of *H. hampei*) following the guidelines of Le Pelley, (1968); Delgado and Sotomayor (1990); Echeverry-Arias (1999); Infante, Alfredo Castillo, Pérez, and Vega (2013).

2.4 | Microclimate data

Microclimatic variables (temperature, relative humidity and light intensity) were taken along the diagonal in each site, and done three times per site, for each parameter using a thermo-hygrometer pen (Model 3402, Spectrum Technologies, & Inc., 2009) for relative humidity and temperature; and foot candle metre (Model 3413F, Spectrum Technologies & Inc., 2011) for light intensity (in foot candles) following the techniques of (Dunning, 2009; Jonsson et al., 2014; Karungi et al., 2018).

2.5 | Data analysis

The effect of fixed factors (altitude and farming system) on the response variables (insect abundance and parasitism) was assessed using the generalized linear mixed models (GLMM) of Genstat version 13, making use of a binomial distribution and logit for data on proportions of *H. hampei* field infestation and parasitism, Poisson distribution with logarithm for parasitoid and *H. hampei* counts from collected berries. With parasitoid and *H. hampei* counts, the random factor was farm, and with field infestation, the random factor was the branch. Means were separated by Tukey's pairwise multiple comparisons. To establish the relationships between parasitoid/pest numbers and microclimate and vegetation species, a multiple linear regression and Pearson's two-tailed correlations were carried out. This was done on transformed data (X = 0.5)$^{1/2}$ to achieve homogeneity of variance. Relative humidity was not included in the regression model as it was found to be autocorrelated to temperature.

TABLE 2 *F* statistic for the parasitoid numbers at different altitudes and farming systems

Fixed term	*F* statistic					
	df (n.df/d.df)	*Cephalonomia stephanoderis*	*Phymastichus coffea*	*Prorops nasuta*	*Heterospilus coffeicola*	*Hypothenemus hampei*
Altitude	2,130	362.52***	435.43***	608.3***	19.89***	165.75***
Farming system	3,130	381.77***	185.45***	102.11***	40.87***	13.95***
Altitude*Farming system	6,130	11.15***	36.51***	101.92***	16.52***	17.39***

***Sig. at $p < 0.05$.

3 | RESULTS

3.1 | Effect of altitude and farming system on the abundance of Parasitoids and *Hypothenemus hampei*

The results of parasitoid abundance indicated highly significant effect of altitude, farming system and their interactions for all the parasitoids (Table 2). *Phymastichus coffea* had highest abundance under mid-altitudes, especially in the Coffee + banana, but was nonexistent in the Coffee monocrop and low altitudes (Figure 1a); *Cephalonomia stephanoderis* was highest at mid-altitudes, within Coffee + banana+shade tree and nonexistent in the Coffee + annual system at low altitude (Figure 1b). *Prorops nasuta* was highest at high altitude, within the Coffee + banana fields, but was nonexistent in the Coffee + annual system, at mid and high altitudes (Figure 1c). On the other hand, *Heterospilus coffeicola* was recorded highest, in the Coffee + annual crop system, at high altitude, but was not found in the mid-altitude levels, in the Coffee + banana+shade trees and Coffee monocrop systems (Figure 1d).

Looking at the pest, abundance from berry dissection followed the order: low altitude >mid-altitude >high altitude (Figure 2). Field infestation, of Coffee berries by *H. hampei*, was also highly significant for altitude, cropping system and their interaction. The mean proportional field infestation was highest in Coffee monocrop especially, at lower altitudes (Figure 3).

3.2 | Effect of altitude and farming system on parasitism of *Hypothenemus hampei*

Of the two factors, it was only altitude that had a significant effect on parasitism of *H. hampei* and only for *Phymastichus coffea* ($p < .05$; Table 3). *P. coffea* gave the highest parasitism in mid-altitude and the lowest in the low altitude (Table 4).

3.2 | Relationships between parasitoid/pest numbers with microclimate variables and semi-natural vegetation species

A multilinear regression showed a significant negative relationship between *C. stephanoderis* and ambient temperature, and a positive one with semi-natural vegetation species counts but no discernible relationship with light intensity (Table 5). *P. coffea* and *P. nasuta* had a similar negative relationship, with temperature but semi-natural vegetation species counts were not a significant predictor for both. For *P. nasuta*, only temperature had a significant negative relationship. Though *H. coffeicola* was also negatively related to ambient temperature, it had a unique positive relationship with light intensity (Table 5). The real contrast was with *H. hampei*, the pest, which had a positive relationship with ambient temperature, and a negative one with light intensity and no discernible relationship with semi-natural vegetation species counts (Table 5).

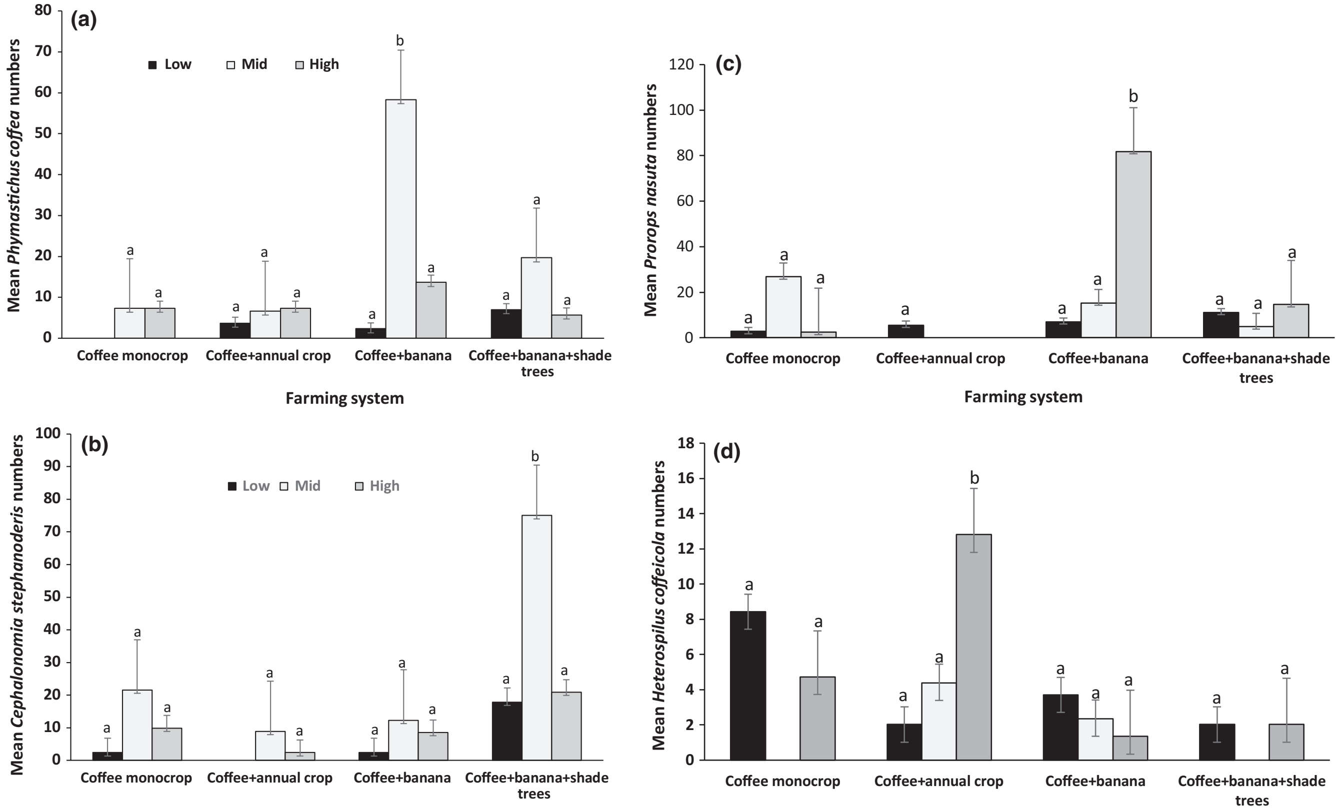

FIGURE 1 Parasitoids *Phymastichus coffea* (a), *Cephalonomia stephanoderis* (b), *Prorops nasuta* (c) and *Heterospilus coffeicola* (d) mean numbers ± *SE* reared from berries collected at different farming systems

4 | DISCUSSION

The results on parasitoid occurrence and parasitism give credence to the stated hypothesis that prevailing microclimate conditions are pushing *H. hampei* parasitoids to higher altitudes. *C. stephanoderis* and *P. coffea* were most abundant at mid-altitude and *P. nasuta* and *H. coffeicola* at high. These trends can be explained by microclimate as all four parasitoids had a negative relationship with ambient temperature, which was notably lower at mid and higher altitudes. This has implications on future regulation of *H. hampei* by the natural control agents due to the contrasting response of the parasitoids and pest to microclimate, especially ambient temperature. Theoretical models have shown that host-parasitoid relationships can be altered by environmental change. Temperature increase, for

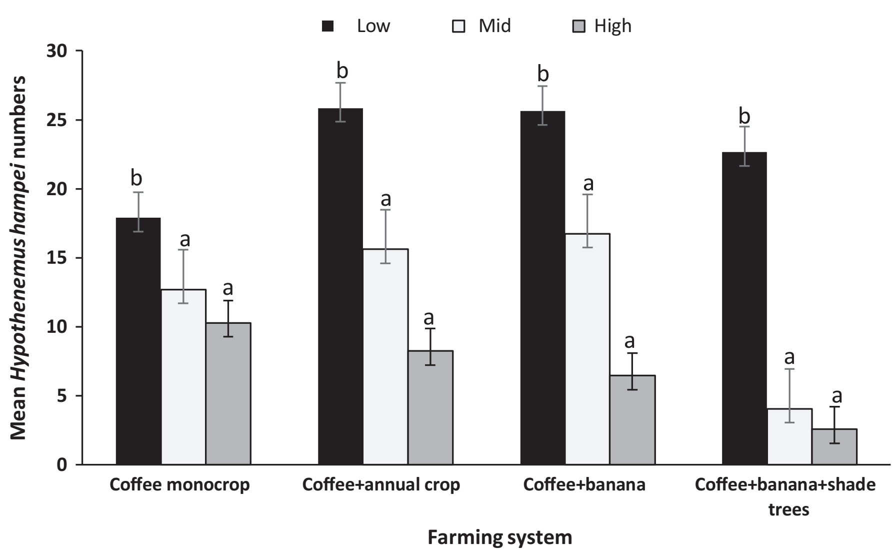

FIGURE 2 *Hypothenemus hampei* mean numbers ± *SE* reared from berries collected at different altitudes and farming systems

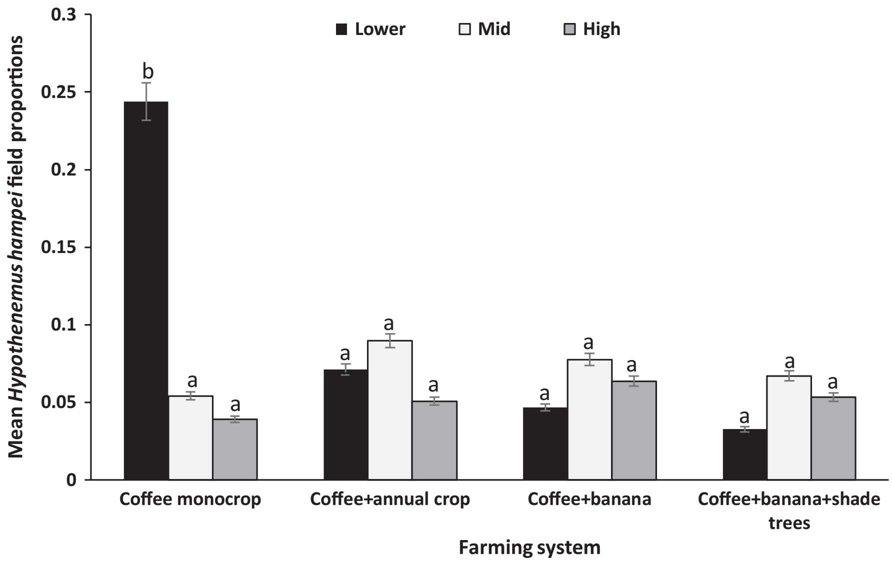

FIGURE 3 *Hypothenemus hampei* mean proportions ± *SE* from field infestation of the berries at different altitudes and farming systems

example, may differentially affect developmental cues, and rates of hosts and parasitoids (van Nouhuys & Lei, 2004). Furthermore, any climate-related changes in the development rate of the host may affect their window of vulnerability to parasitism (Klapwijk, Grobler, Ward, Wheeler, & Lewis, 2010). The resulting asynchrony can alter the fitness of both partners (van Asch & Visser, 2007; Stenseth and Atle Mysterud, 2002; Voigt et al., 2003). Jaramillo et al. (2011) indicated that a 1–2°C increase in temperature could lead to an increased number of generations, dispersion and damage by the Coffee berry borer, whereas a rise in temperature of 2°C and above could lead to shifts in altitudinal and latitudinal distribution of the pest. Yet, our results show that the opposite would be true for the parasitoids. The decoupling of the Coffee berry borer and its natural enemies could result in higher pest numbers or more serious outbreaks (Hance, Baaren, Vernon, & Boivin, 2007; Stireman et al., 2005; Walther, 2010).

The situation at low altitude is dire for *H. hampei* parasitoids if no effort is made to buffer temperature. The results showed that, including banana and/or shade trees in Coffee could indeed ameliorate conditions at low altitude, and increase abundance of *C. stephanoderis*, *P. coffea* and *P. nasuta*. It has been reported that wooded and herbaceous vegetation's provide moderate microclimates for parasitoids that would experience considerable shorter life spans at high temperatures (Hailemichael & Smith, 1994; Rahim, Hashmi, &

TABLE 3 F statistics for *Hypothenemus hampei* parasitism at different altitudes and farming systems

	F statistics				
Fixed term	*df (n.df/d.df)*	*Cephalonomia stephanoderis*	*Phymastichus coffea*	*Prorops nasuta*	*Heterospilus coffeicola*
Altitude	2,130	1.70^{NS}	3.24*	1.00^{NS}	1.18^{NS}
Farming system	3,130	2.28^{NS}	1.56^{NS}	0.24^{NS}	0.97^{NS}
Altitude farming system	6,130	0.63^{NS}	0.24^{NS}	0.74^{NS}	0.48^{NS}

Abbreviation: NS, not significant.
*Sig. at $p < .05$.

TABLE 4 Mean proportions of *Hypothenemus hampei* parasitism as affected by different altitudes

Altitude	*Phymastichus coffea*	*Cephalonomia stephanoderis ephanoderis*	*Prorops nasuta*	*Heterospilus coffeicola*	Mean	SE
Low	0.014	0.013	0.171	0.145	**0.086**	0.04
Mid	0.486	0.425	0.021	0.001	**0.233**	0.13
High	0.402	0.249	0.016	0.203	**0.218**	0.08
Mean	**0.30**	**0.23**	**0.07**	**0.12**		
SE	0.13	0.10	0.04	0.05		

Bold values indicates Grand mean

Khan, 1991), in addition to offering increased sources of pollen and nectar (Baggen & Gurr, 1998). The shade trees and banana provide both benefits.

We expected the semi-natural vegetation to play the key role in parasitoid abundance as Bianchi et al. (2006) reported greater natural enemy populations in fields associated with herbaceous habitats. In this study, it was only *C. stephanoderis* for which presence of semi-natural vegetation was crucial. This shows that microclimate, especially ambient temperature, was the general driver of occurrence of *H. hampei* and its parasitoids. Though this was also true for *H. coffeicola*, uniquely, it was the only parasitoid to show preference for Coffee + annual farming system, a system that was overall detrimental. This could be explained by its preference for high light intensity, which was relatively high in this system. This could also explain why *H. coffeicola* is challenging to culture in the laboratory (Kucel and Murphy Orozco-Hoyos (2004); Murphy, Day, Oronzo, & Kucel, 2001.

In terms of relative abundance and parasitism, *P. coffea* was the most abundant and effective parasitoid. This is in line with earlier reports showing *P. coffea* with a very high capability of lowering *H. hampei* populations in the field (Gutiérrez, Villacorta, Cure, & Ellis, 1998). *P. nasuta* though occurring in adequate numbers displayed the lowest parasitism levels. Bethylid parasitoids are reported to experience very high levels of interspecific competition, which interferes with their parasitism potential (Batchelor, Hardy, & Barrera, 2005, 2006). This could have been the case with *P. nasuta*.

As such *P. coffea*, and runner up *C. stephanoderis* show potential, and efforts should be made to provide conditions that promote their occurrence, and effect. From the results of this study and drawing on recommendations from other studies (Altieri, 1999; Jaramillo et al., 2011; Jonsson et al., 2014; Lin, 2011), we strongly recommend introduction of shade trees and/or banana intercrop as they have been confirmed to buffer microclimate and also provide additional benefits like nectar and nesting nooks that are essential for survival of parasitoids.

5 | CONCLUSION

In the Coffee farmlands of the Mt. Elgon region, there are four Hymenopteran parasitoids that collectively could regulate infestation of *H. hampei;* nevertheless, a subtle altitudinal shift of parasitoid abundance to mid and high levels could be discerned. This was mainly due to the relatively higher ambient temperature conditions at lower altitudes. Including banana and/or shade trees in Coffee systems at these levels can buffer microclimate and promote the parasitoids.

TABLE 5 Regression coefficients for microclimate variables and vegetation species occurrence as predictors of parasitoid and *Hypothenemus hampei* numbers in the collected berries

Parameter	Coefficients (unstandardized)	*SE*	*t*	Fpr.
Hypothenemus hampei				
(Constant)	−4.117	1.831	−2.249	0.026
Vegetation species	−0.059	0.353	−0.168	0.867
Temperature	0.311	0.057	5.503	0.000
Light	−0.003	0.001	−1.984	0.049
Phymastichus coffea				
(Constant)	2.257	0.493	4.575	0.000
Vegetation species	−0.065	0.095	−0.679	0.498
Temperature	−0.064	0.015	−4.209	0.000
Light	0.000	0.000	0.106	0.916
Cephalonomia stephanoderis				
(Constant)	0.738	0.481	1.535	0.127
Vegetation species	0.257	0.093	2.778	0.006
Temperature	−0.047	0.015	−3.185	0.002
Light	0.000	0.000	−0.757	0.450
Prorops nasuta				
(Constant)	0.696	0.433	1.605	0.111
Vegetation species	0.125	0.084	1.501	0.136
Temperature	−0.035	0.013	−2.620	0.010
Light	0.000	0.000	0.180	0.858
Heterospilus coffeicola				
(Constant)	0.759	0.362	2.096	0.038
Vegetation species	0.023	0.070	0.336	0.737
Temperature	−0.030	0.011	−2.707	0.008
Light	0.001	0.000	2.389	0.018

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CONFLICT OF INTEREST

We the authors of this work wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome. We further confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that the order of authors listed in the manuscript has been approved by all of us.

AUTHORS' CONTRIBUTIONS

IAR, KS and KJ conceived research. IAR, CS and SC conducted experiments. KS and KJ contributed materials. IAR analysed data and conducted statistical analyses. IAR and KJ wrote and revised the manuscript. KJ secured funding. All authors read and approved the manuscript.

DATA AVAILABILITY STATEMENT

The raw data sets generated during and/or analysed during the current study has been submitted as supporting informations (Data S1, Data S2, Data S3, Data S4, Data S5 and Data S6).

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