

# Factors Affecting Stem Borer Parasitoid Species Diversity and Parasitism in Cultivated and Natural Habitats

DUNA MADU MAILAFIYA,<sup>1,2,3</sup> BRUNO PIERRE LE RU,<sup>1</sup> EUNICE WAITHERERO KAIRU,<sup>2</sup> PAUL-ANDRÉ CALATAYUD,<sup>1</sup> AND STÉPHANE DUPAS<sup>4</sup>

Environ. Entomol. 39(1): 57–67 (2010); DOI: 10.1603/EN09196

**ABSTRACT** The effects of biotic and abiotic factors on stem borer parasitoid diversity, abundance, and parasitism were studied in cultivated and natural habitats in four agroecological zones in Kenya. Comparing habitat types, we found partial support for the “natural enemy” hypothesis, whereby, across all localities, parasitoid diversity was higher in more diverse host plant communities in natural habitats, whereas parasitoid abundance was higher in cultivated habitats. For both habitats, parasitoid richness was mainly influenced by stem borer density and/or its interaction with stem borer richness, whereas parasitoid abundance was mainly affected by stem borer abundance. Parasitoid richness was higher in localities (with bimodal rainfall distribution) with increased spatial and temporal availability of host plants that harbored the borers. Across seasons, parasitoid richness was lower in both cultivated and natural habitats in the driest locality, Mtito Andei. Overall, parasitoid diversity was low in Suam and Mtito Andei, where maize cultivation was practiced on a commercial scale and intense grazing activities persist across seasons, respectively. Across localities, habitats, and seasons, stem borer parasitism was positively correlated with parasitoid richness and abundance. Furthermore, the interaction of rainfall and altitude influenced the presence and absence of parasitoids, and consequently, stem borer parasitism. Parasitism was positively and negatively correlated with temperature in cultivated and natural habitats, respectively. Overall, natural habitats seem to serve as important refugia for sustaining parasitoid diversity, which in turn can affect stem borer parasitism in the cereal cropping system.

**KEY WORDS** biotic and abiotic factors, trophic interactions, habitat type, parasitoid diversity and stem borer parasitism

The relationships between ecosystem services and biodiversity have been a major research goal of agroecology over the past decade (Tscharntke et al. 2007). Natural pest regulation is reported to be influenced by farmland biodiversity. Thereby, diversified landscapes seem to have a high potential for the conservation of natural enemies and the sustenance of pest control functions (Tscharntke et al. 2007). The reason for differences in natural pest control between simple and diverse plant communities in agroecosystems has been explained by two main hypotheses: (1) “natural enemy” hypothesis, which predicts higher diversity and abundance of parasitoids and predators in more diverse plant communities because of availability of alternate hosts/prey and food, leading to a reduction in herbivore populations (Root 1973), and (2) “resource

concentration” hypothesis, which postulates that, in simple monocultures or homogeneous plant communities, where host plants are concentrated in time and space, herbivores will build up their populations, whereas in more diverse plant communities, a reduction in pest incidence may result from impediment of herbivore movement and colonization (Root 1973). However, increased plant diversity in agricultural systems does not always translate into increased control of herbivorous pests (Risch et al. 1983). Furthermore, because farmland biodiversity and ecosystem services are influenced by the surrounding landscape (Landis et al. 2000, Tscharntke et al. 2007), it is essential to understand their inter-relationships on a context-dependent basis at both local-site and landscape levels (Thies et al. 2003).

Parasitoid diversity and parasitism rates have been reported to be higher in structurally complex landscapes composed of arable fields intermingled with noncrop habitat than in simple landscapes composed of mainly arable fields (Thies et al. 2003, 2005). Undisturbed or perennial noncrop habitats such as field margins, fallows, hedgerows, and woody vegetation in agricultural landscapes supply parasitoids with alternative hosts, sources of food (i.e., pollen and nectar)

<sup>1</sup> Unité de Recherche IRD 072, c/o International Centre of Insect Physiology and Ecology (ICIPE), PO Box 30772, Nairobi, Kenya or Université Paris-Sud 11, 91405 Orsay Cedex, France.

<sup>2</sup> Department of Zoological Sciences, School of Pure and Applied Sciences, Kenyatta University, PO Box 43844, Nairobi, Kenya.

<sup>3</sup> Corresponding author, e-mail: dmailafiya@gmail.com and dmailafiya@icipe.org.

<sup>4</sup> Unité de Recherche IRD 072, CNRS, Laboratoire Evolution, Génomes et Spéciation, Bât 13, BP 1, Avenue de la Terrasse, 91198 Gif-sur-Yvette cedex, France.

for adults, and moderate microclimate, which increase parasitoid longevity, fecundity, population size, and spread to surrounding crops (Lee et al. 2004). These may also enhance early season abundance and parasitism rates that contribute to timely herbivore pest suppression (Landis and Menalled 1998).

In Kenya, lepidopteran stem borers are the most damaging group of cereal crop pests (Seshu Reddy 1998). Although these pests are attacked by several species of parasitoids in major cereal-growing regions (Zhou et al. 2003), no information exists on natural factors that influence parasitoid diversity/richness and its consequent effect on parasitism. However, the simplification of agricultural landscapes through deforestation, agricultural land or field size enlargement, destruction of noncrop habitat, and excessive and frequent insecticide and/or fertilizer applications and inappropriate land management practices (i.e., zero tillage and overgrazing) continue unabated with consequent decline of farmland biodiversity (Bai and Dent 2006).

In this study, we carried out field surveys in cultivated and natural habitats over 2 yr in four agroecological zones (AEZs) in Kenya to determine the effects of trophic interactions on parasitoid diversity or abundance and stem borer parasitism in different habitat types and ecological regions. The objectives of this study were to determine: (1) the effects of biotic (host plant and stem borer richness/abundance across trophic levels) and abiotic factors (altitude, rainfall and temperature across localities) on parasitoid richness and abundance during the rainy and dry seasons, and (2) the effects of parasitoid richness and abundance on stem borer parasitism during different seasons.

## Materials and Methods

**Survey Sites and Landscape Description.** Field surveys were carried out from December 2005 to December 2007 in four AEZs (characterized by different landscapes consisting of a matrix of cultivated and natural habitats) in Kenya: Suam (Trans-Nzoia District) in the highland tropics, Kakamega (Kakamega District) in the moist transitional tropics, Mtito Andei (Makueni District) in the dry mid-altitudes, and Muhaka (Kwale District) in the lowland tropics (Fig. 1).

Suam (1°11' N, 34°47' E, 1,995 masl) has a single cropping season that lasts from March to November. Average annual rainfall and temperature are 1,190 mm and 19°C, respectively. Local vegetation is characterized by a mosaic of rain forest, secondary grassland, and wetlands. Suam is a major production region, where 50% of the area is under cereal cultivation at commercial scale, mainly with an average field size of 3.4 ha. The area under natural habitats was 50%, of which the total relative cover of all potential wild host plants of stem borers was 11.2 and 10.9% during the rainy and dry seasons, respectively (Otieno et al. 2008). Human settlement was clearly separated from cultivated areas, with very few wild grass patches found mainly along field edges and road sides. Grass patch connectivity was extremely low.

Kakamega (0°13' N, 34°56' E) is 1,655 masl and has a bimodal rainfall distribution with two cropping seasons occurring from March to August and October to December. Average annual rainfall and temperature are 1,570 mm and 21°C, respectively. The vegetation is of the Guineo-Congolian rain forest type. Kakamega is a moderate production region, with 43.3% of the area under cereal cultivation. Cereals were grown at subsistence level, with an average field size of 0.28 ha located in open forest patches, or scattered around noncompact homesteads, and also along forest edges and the river bank. The area of natural habitats was 51.9%, of which the total relative cover of all potential wild host plants of stem borers was 0.5 and 0.3% during the rainy and dry seasons, respectively (Otieno et al. 2006). In addition to growing *Pennisetum purpureum* Schumacher for fodder, wild grass patches were numerous, mainly around crop fields or homesteads and along road sides and river banks, with a moderate level of connection between patches.

Mtito Andei (2°39' S, 38°16' E, 760 masl) has a single cropping season lasting from November to January. Average annual rainfall and temperature are 665 mm and 23°C, respectively. The vegetation consists of Somalia-Masai Acacia-Commiphora deciduous bushland and thicket. Mtito Andei is a minor production region with cereals grown at subsistence level. Area under cereal cultivation was 27.3%, with an average field size of 0.37 ha mainly found surrounding sparsely populated and distant homesteads. The area of natural habitats was 72.7%, of which the total relative cover of all potential wild host plants of stem borers was 13.0 and 8.0% during the rainy and dry seasons, respectively (Otieno et al. 2008). Wild grass patches were generally small and few, mainly existing in water trenches bordering crop fields or in swamps and along irrigation canals. Connectivity between grass patches was very low, and grazing activities were very high.

Muhaka (4°18' S, 39°31' E, 40 masl) has a bimodal rainfall distribution with two cropping seasons typically occurring from April to August and from October to December. Average annual rainfall and temperature are 1,210 mm and 26°C, respectively. Local vegetation is East African coastal grassy and woody mosaic bordering the undifferentiated Zanzibar-Inhambane forest type. Muhaka is a moderate growing region, with ≈10.7% of the area under cereal cultivation and an average field size of 0.15 ha. Cereals were grown at subsistence level, in fields scattered around a more compact homestead settlement. The area of natural habitats was 72.3%, of which the total relative cover of all potential wild host plants of stem borers was 2.2 and 1.0% during the rainy and dry seasons, respectively (Otieno et al. 2006). Numerous wild grass patches were available surrounding crop fields and along major roads and around ponds. The connection between grass patches was fairly high.

In Kakamega and Muhaka, cereal crops were planted during the dry season in marshy areas usually bordering streams or rivers. In localities with single cropping season only, irrigated crops were found in Mtito Andei but not in Suam.

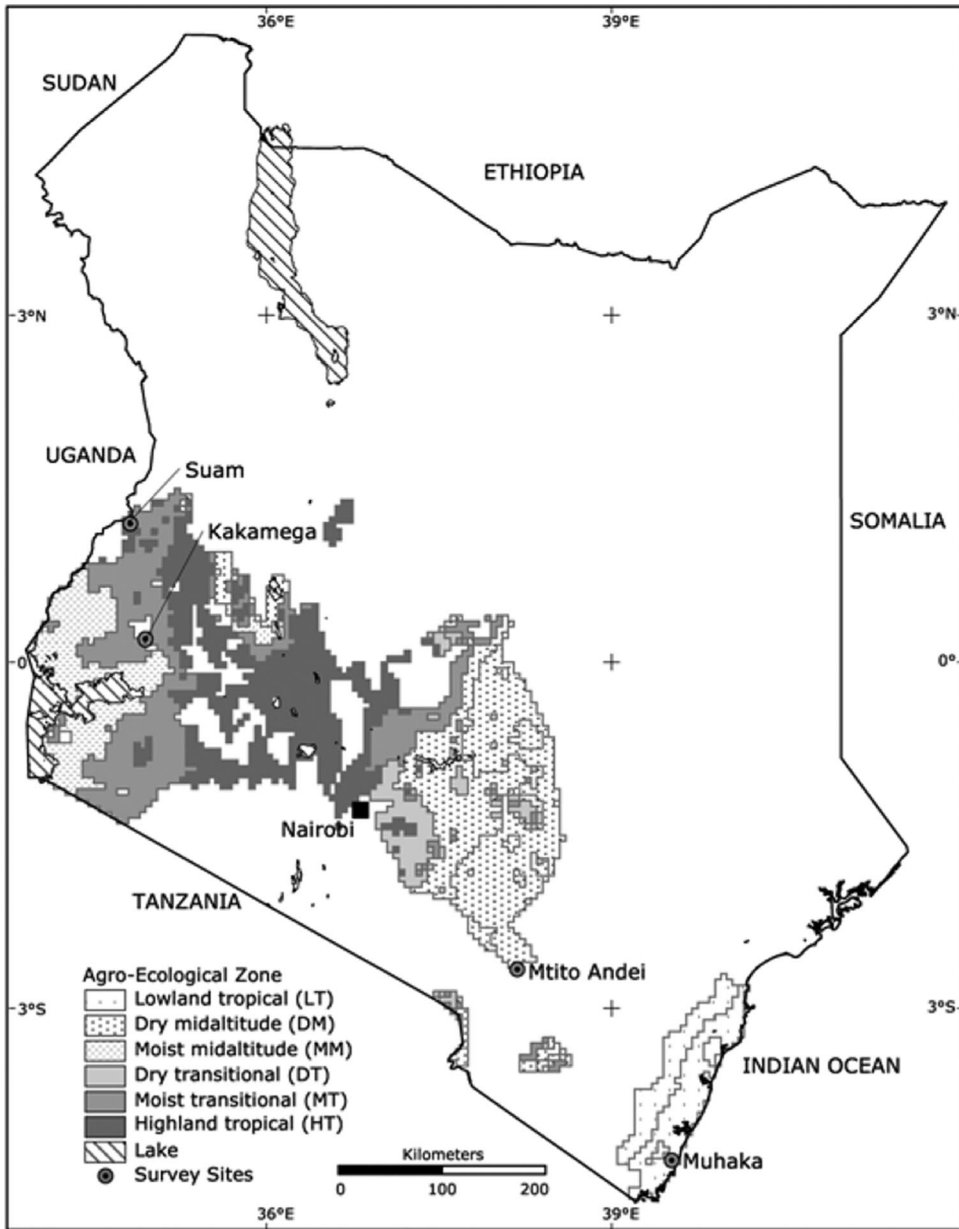


Fig. 1. Surveyed sites in four agroecological zones in Kenya.

**Field Surveys.** Previous studies indicate that stem borer densities were much lower on wild host plants than on adjacent cultivated cereal crops (Gounou and Schulthess 2004, Ndemah et al. 2007, Matama-Kauma et al. 2008). Therefore, to increase the chances of collecting stem borer parasitoids from different habitats, a random sampling scheme was used in cultivated habitats, whereas both random and nonrandom sampling schemes were applied in natural habitats.

**Sampling in Cultivated Habitats.** Based on the sampling plan developed by Overholt et al. (1994) and the proportion of land under cultivation (Guihéneuf 2004,

Goux 2005), we randomly sampled 21, 16, 16, and 10 cereal plots in Kakamega, Mtito Andei, Muhaka, and Suam, respectively. To cover both vegetative and reproductive stages of plant growth, all selected fields were visited at least twice during each rainy and dry season. To estimate stem borer density or richness, depending on the field size and crop availability during different seasons, 50–100 plants were sampled per field. The plants collected were dissected in the field, and stem borer larvae or pupae obtained were reared in the laboratory on artificial diet for subsequent recovery of parasitoids.

**Sampling in Natural Habitats.** *Random Sampling Scheme.* Based on the sampling plan developed by Gounou and Schulthess (2004), grass patches immediately surrounding each cereal field were sampled at regular time intervals as stated above for cultivated habitats. To estimate stem borer parasitoid densities on wild host plants, at each sampling, depending on the availability of host plant species during different seasons or because of disturbances (i.e., livestock overgrazing), 50–100 plants/tillers were randomly sampled per plant species at each site; up to a distance of 50 m from the edge of each cereal field. Each plant/tiller collected was dissected in the field. Stem borer larvae or pupae obtained were reared in the laboratory on artificial diet for subsequent recovery of parasitoids.

*Nonrandom Sampling Scheme.* To estimate parasitoid species diversity on wild host plants, the nonrandom sampling procedure by Le Ru et al. (2006a, b) was applied. During each sampling occasion as described above, wild host plants exhibiting infestation symptoms were sampled where possible at up to 100 m distance of each sampled cereal field. At each sampling site, all known or potential host plants species belonging to the Poaceae, Cyperaceae, Typhaceae, and Junaceae families (Le Ru et al. 2006a, b) were inspected for infestation symptoms. All plants/tillers collected were dissected in the field. Stem borer larvae or pupae recovered were reared in the laboratory on artificial diet for subsequent recovery of parasitoids.

**Stem Borer/Parasitoid Recovery and Identification.** Stem borer larvae recovered were reared on artificial diet developed by Onyango and Ochieng-Odero (1994) in glass vials (2.5 cm diameter by 7.5 cm depth) plugged with cotton wool, which were kept under ambient conditions ( $26 \pm 3^\circ\text{C}$ ;  $65 \pm 5\%$  RH) in the laboratory until pupation or cocoon formation. Each parasitoid puparium or cocoon mass recovered was kept separately in a plastic vial (2.5 cm diameter by 7.5 cm depth) until adult emergence. Adult stem borer or parasitoid specimens were preserved in 70 or 100% alcohol. Identification of stem borers and parasitoids were carried out to species level where possible or otherwise to genera or family levels. Hymenopteran parasitoids were identified by G. Delvare, CIRAD, Montpellier, France. Dipteran parasitoids were identified by D. Barraclough, University of KwaZulu-Natal, Durban, South Africa. Adult stem borers were identified by P. Moyal, IRD, France, and wild host plants were identified by S. Muthenge, East Africa Herbarium, Nairobi, Kenya. Voucher specimens were deposited in the Bio-Systematic Unit Museum, International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya. In addition, temperature and rainfall data were obtained from the AWhere-ACT Database for Africa (2002) and the Spatial Characterization Tool—Africa (Corbett and O'Brien 1997).

**Data Analyses.** Parasitoid and stem borer richness were estimated using the Margalef's richness index ( $D_{mg}$ ) (Magurran 1988). Margalef richness indices were compared between habitats and among localities using analysis of variance (ANOVA) (SAS Institute

2001). Means obtained were separated using the Fisher least significant difference (LSD), with significance set at  $P \leq 0.05$ .

Parasitoid species diversity was estimated using the Shannon diversity index ( $H'$ );  $t$ -tests were further performed to compare parasitoid diversity (Shannon indices) in cultivated and natural habitats (Magurran 1988).

The effects of biotic and abiotic factors or their interactions on parasitoid richness, abundance, and stem borer parasitism were tested for both habitat types using the deviance statistic (Generalized linear model; SAS PROC GENMOD). Poisson regression was used to analyze data on richness, abundance, altitude, rainfall, and temperature, using a Poisson error distribution with a logarithmic link function (McCullagh and Nelder 1989). Additionally, logistic regression was used to analyze stem borer density, using a binomial error distribution with a logistic link function (Collett 1991). Pearson's correlation analysis was performed to assess the relationship between different components of the system. Before correlation analysis, insect counts were  $\log(x + 1)$  transformed and proportion data arcsine-transformed (Zar 1999).

## Results

**General Species Diversity/Richness and Abundance in Different Habitats.** In total, 33 stem borer parasitoid species were recovered, of which 18 and 27 were from cultivated and natural habitats, respectively (Table 1). The species richness and abundance of parasitoids, stem borers, and host plants in cultivated and natural habitats were summarized in Table 2. Across localities, both stem borer and parasitoid richness were in natural habitats. Furthermore, across habitats, parasitoid richness was higher in Kakamega and Muhaka with a bimodal rainfall distribution, whereas parasitoid richness was lower in Mtito Andei and Suam with a single rainfall distribution. Parasitoid diversity ( $H'$ ) for pooled data ranged from 0.43 in Mtito Andei to 1.07 in Suam in cultivated habitats and from 0.99 in Mtito Andei to 2.03 in Kakamega in natural habitats. Parasitoid diversity was significantly higher in natural than cultivated habitats (Suam,  $t = 6.35$ ,  $P < 0.001$ ; Kakamega,  $t = 7.69$ ,  $P < 0.001$ ; Mtito Andei,  $t = 2.60$ ,  $P = 0.05$  and Muhaka,  $t = 7.34$ ,  $P < 0.001$ ).

**Parasitoid Richness.** The effects of biotic and abiotic factors on parasitoid richness are presented in Tables 3 and 4, respectively. Parasitoid richness was positively related to stem borer density and/or its interaction with stem borer richness. However, in each locality, these effects varied with either habitat type or season. Across localities, with the exception of the rainy season in both habitats in Kakamega, parasitoid richness was not affected by stem borer richness. Except for Kakamega, where parasitoid richness was positively correlated with stem borer abundance across seasons in cultivated habitats. Particularly, in natural habitats, this effect was observed mainly during the rainy season. In Suam, parasitoid richness was neither affected by stem borer richness nor abundance. Across local-

**Table 1. List of stem borer parasitoids recovered in cultivated and natural habitats in Kenya**

Order	Parasitoid		Habitat		
	Family	Genus	Cultivated	Natural	
Hymenoptera	Bethyidae	<i>Goniozus</i> sp.	1	1	
		Braconidae	1	2	
			<i>Chelonus</i> sp.	1	1
			<i>Cotesia</i> spp.	2	3
			<i>Dolichogenidea</i> sp.	1	1
			<i>Iphiaulax</i> sp.	—	1
			<i>Macrocentrus</i> sp.	—	1
			<i>Apanteles</i> sp.	—	1
		Ceraphronidae	<i>Aphanogmus</i> sp.	1	—
		Eulophidae	<i>Pediobius</i> sp.	1	1
			<i>Tetrastichus</i> sp.	1	-
		Ichneumonidae	<i>Amouramorpha</i> sp.	-	1
			<i>Dentichasmias</i> sp.	1	—
			<i>Enicospilus</i> spp.	—	2
			<i>Gambroides</i> sp.	1	—
			Ichneumoninae	1	3
			<i>Procerochasmias</i> sp.	1	—
			<i>Pristomerus</i> sp.	—	1
	<i>Syzeuctus</i> sp.		—	1	
	<i>Bathyplectes</i> sp.		—	1	
<i>Venturia</i> sp.	—		1		
<i>Xanthopimpla</i> sp.	1		1		
Diptera	Tachinidae		<i>Linnaemyia</i> sp.	1	1
		<i>Metoposisyrops</i> sp.	1	1	
		<i>Siphona</i> sp.	1	1	
		<i>Sturmiopsis</i> sp.	1	1	

ities and seasons, parasitoid richness was not explained by host plant richness in either habitat type, except for Mtito Andei, where significant effect was observed in natural habitats during the rainy season.

Although parasitoid richness was negatively correlated with rainfall in both habitats, significant effects were only recorded during the rainy season in cultivated habitats. For both habitats and seasons, parasitoid richness was neither affected by altitude nor temperature.

**Parasitoid Abundance.** The effects of abiotic and biotic factors on parasitoid abundance are presented in Tables 4 and 5, respectively. Parasitoid abundance was negatively correlated with altitude and rainfall

during both seasons in cultivated habitats but not in natural habitats. In both habitats, parasitoid abundance was affected by the interactions of altitude and rainfall, as well as rainfall and temperature during the rainy season only.

Across localities and seasons, with the exception of the dry season in Muhaka, parasitoid abundance was positively related to stem borer abundance. Additionally, parasitoid abundance was positively related to stem borer density (and/or its interaction with stem borer richness) and stem borer richness (and/or its interaction with stem borer abundance). However, in some locations, these effects varied with habitat type or season. Across habitats and seasons, Mtito Andei

**Table 2. Richness and abundance of parasitoids, stem borers, and host plants recorded in different seasons and habitats in landscapes of four agroecological zones in Kenya**

Locality and habitat type	Parasitoids				Stem borers			Host plants		
	Season		Margalef's richness index (Dmg)	n	Season		Margalef's richness index (Dmg)	n	Season	
	Rainy	Dry			Rainy	Dry			Rainy	Dry
Suam										
Cultivated	7 (113)	5 (28)	0.88 ± 0.15aA	8	3 (1504)	2 (259)	0.31 ± 0.09aA	8	2	2
Natural	4 (4)	4 (6)	1.74 ± 0.32bA	8	10 (296)	3 (84)	2.14 ± 0.77bA	8	37	34
Kakamega										
Cultivated	7 (128)	2 (27)	1.59 ± 0.09aB	9	5 (733)	3 (268)	0.65 ± 0.10aB	9	2	1
Natural	14 (40)	3 (7)	3.11 ± 0.88bB	9	13 (687)	5 (152)	2.36 ± 1.00bA	9	31	19
Mtito Andei										
Cultivated	10 (128)	2 (27)	0.74 ± 0.13aA	7	2 (489)	2 (494)	0.16 ± 0.08aC	7	2	2
Natural	8 (15)	1 (3)	1.51 ± 0.34bA	7	8 (365)	14 (256)	2.31 ± 0.89bA	7	25	20
Muhaka										
Cultivated	8 (104)	4 (57)	1.38 ± 0.45aB	9	3 (2916)	3 (780)	0.27 ± 0.06aA	9	2	1
Natural	11 (46)	5 (12)	2.19 ± 0.97bC	9	12 (1246)	8 (590)	1.83 ± 0.33bB	9	26	18

Means within columns followed by the same letter are not significantly different at  $P \leq 0.05$  (LSD). Small letters (i.e., a) are comparisons between habitats within each locality, whereas big letters (i.e., A) are comparisons among localities for each habitat type (i.e., cultivated and natural habitats separately).

**Table 3. Biotic factors affecting parasitoid species richness during different seasons in cultivated and natural habitats in four agroecological zones in Kenya**

	Cultivated habitats						Natural habitats					
	Rainy season			Dry season			Rainy season			Dry season		
	Deviance	df	P value	Deviance	df	P value	Deviance	df	P value	Deviance	df	P value
<b>Suam</b>												
Constant	4.96	21		9.13	10		4.46	18		9.95	10	
Borer richness	4.87	1	ns	6.39	1	ns	2.56	1	ns	8.52	1	ns
Borer abundance	4.82	1	ns	7.17	1	ns	1.15	1	ns	8.11	1	ns
Plant richness	4.96	1	ns	9.05	1	ns	4.12	1	ns	9.90	1	ns
Borer richness × abundance	4.36	1	ns	4.85	1	ns	0.89	1	ns	6.13	1	ns
Borer richness × plant richness	4.54	1	ns	6.22	0	ns	0.76	1	ns	7.53	1	ns
Constant	4.68	10		7.91	10		3.36	7		6.53	7	
Borer density	3.61	1	ns	7.37	1	ns	3.25	1	ns	5.94	1	0.0015
Borer richness × density	1.02	1	ns	4.37	1	ns	1.15	1	ns	3.82	1	ns
<b>Kakamega</b>												
Constant	83.54	68		25.95	27		64.08	52		16.75	14	
Borer richness	47.48	1	<0.0001	23.73	1	ns	56.18	1	0.0049	16.25	1	ns
Borer abundance	58.17	1	<0.0001	16.64	1	0.0023	38.53	1	<0.0001	6.89	1	0.0017
Plant richness	62.34	1	ns	25.65	1	ns	63.49	1	ns	12.01	1	ns
Borer richness × abundance	30.40	1	<0.0001	15.88	1	ns	35.92	1	ns	4.67	1	ns
Borer richness × plant richness	46.71	1	ns	23.32	1	ns	52.5	1	ns	12.45	1	ns
Constant	24.80	43		15.96	22		59.98	40		13.04	14	
Borer density	23.59	1	ns	14.79	1	0.0007	58.91	1	<0.0001	12.95	1	0.0575
Borer richness × density	14.02	1	0.0268	9.52	1	0.0243	44.06	1	ns	9.62	1	ns
<b>Mtito Andei</b>												
Constant	9.99	22		5.87	9		13.18	18		7.22	10	
Borer richness	7.31	1	ns	3.83	1	ns	13.08	1	ns	5.56	1	ns
Borer abundance	7.24	1	ns	4.31	1	ns	9.57	1	0.0574	6.01	1	ns
Plant richness	9.95	1	ns	4.99	1	ns	9.61	1	0.0588	5.87	1	ns
Borer richness × abundance	5.64	1	ns	2.13	1	ns	4.36	1	ns	6.11	1	ns
Borer richness × plant richness	5.41	1	ns	3.54	1	ns	3.62	1	ns	5.83	1	ns
Constant	5.31	13		3.61	9		9.53	9		6.01	9	
Borer density	4.98	1	ns	3.51	1	ns	9.37	1	<0.0001	5.87	1	ns
Borer richness × density	3.16	1	0.0141	1.02	1	0.0372	2.95	1	0.4651	4.16	1	ns
<b>Muhaka</b>												
Constant	58.61	58		14.09	23		45.43	52		25.45	26	
Borer richness	57.09	1	ns	11.12	1	ns	43.35	1	ns	24.39	1	ns
Borer abundance	57.37	1	ns	12.36	1	ns	39.75	1	0.0172	25.31	1	ns
Plant richness	58.41	1	ns	14.09	1	ns	45.04	1	ns	25.43	1	ns
Borer richness × abundance	56.74	1	ns	11.04	1	ns	39.29	1	ns	24.26	1	ns
Borer richness × plant richness	57.02	1	ns	11.12	1	ns	42.96	1	ns	23.83	1	ns
Constant	17.95	55		13.75	19		43.40	50		22.52	25	
Borer density	16.96	1	0.0255	13.01	1	0.0197	42.34	1	0.0009	21.62	1	<0.0001
Borer richness × density	7.09	1	ns	11.07	1	ns	33.28	1	ns	13.53	1	ns

All biotic factors were positively (+) correlated with parasitoid species richness.

was the only locality in which parasitoid abundance was significantly related to host plant richness and/or its interaction with stem borer richness.

**Stem Borer Parasitism.** The effects of abiotic and biotic factors on stem borer parasitism are shown in Tables 4 and 6, respectively. Temperature had a significant effect on stem borer parasitism across seasons in cultivated (positively) and natural (negatively) habitats, whereas altitude and rainfall both negatively affected parasitism during the rainy season in either habitat. Additionally, with the exception of natural habitats during the rainy season, the interactions of altitude and rainfall, altitude, and temperature, and also rainfall and temperature, all exhibited significant effects on stem borer parasitism.

Across localities, habitat types, and seasons, stem borer parasitism was significantly positively related to parasitoid richness and abundance. Although, stem borer parasitism was significantly related to the interaction of parasitoid richness and abundance in each

locality, the effects of parasitoid richness and stem borer density as well as host plant richness and stem borer richness interactions on parasitism varied with habitat type and season.

## Discussion

**Parasitoid Richness/Diversity.** Generally higher parasitoid diversity in natural habitats in this study and those of Ndemah et al. (2007) and Matama-Kauma et al. (2008), but higher parasitoid abundance in cultivated habitats (Matama-Kauma et al. 2008, Mailafiya et al. 2009), partially support the “natural enemy” hypothesis (Root 1973). Altogether, these studies indicate that stem borer parasitoid abundance is not necessarily high in natural habitats with high parasitoid species diversity. Considering the high diversity of stem borers recorded in natural habitats (Le Ru et al. 2006a, b) and the fact that most stem borer parasitoids are stenophagous species that exploit two or more host

**Table 4. Environmental variables affecting parasitoid species richness, abundance, and stem borer parasitism during different seasons in cultivated and natural habitats across four agroecological zones in Kenya**

	Cultivated habitats						Natural habitats									
	Rainy season			Dry season			Rainy season			Dry season						
	SC	Deviance	df	P value	SC	Deviance	df	P value	SC	Deviance	df	P value	SC	Deviance	df	P value
<b>Parasitoid richness</b>																
Constant		193.45	149			60.29	65			135.48	119			60.96	56	
Altitude	-	191.18	1	ns	-	59.86	1	ns	+	135.38	1	ns	+	59.09	1	ns
Rainfall	-	185.71	1	0.0054	-	60.29	1	ns	-	135.19	1	ns	-	60.91	1	ns
Temperature	+	191.37	1	ns	+	59.25	1	ns	-	135.45	1	ns	-	57.49	1	ns
Altitude × rainfall		177.68	1	ns		59.39	1	ns		134.76	1	ns		57.52	1	ns
Altitude × temperature		188.53	1	ns		57.57	1	ns		135.05	1	ns		55.84	1	ns
Rainfall × temperature		177.6	1	ns		59.15	1	ns		134.66	1	ns		55.59	1	ns
<b>Parasitoid abundance</b>																
Constant		1093.48	149			239.83	65			271.60	119			86.31	56	
Altitude	-	1068.47	1	<0.0001	-	229.46	1	0.0013	-	271.61	1	ns	-	85.40	1	ns
Rainfall	-	976.04	1	<0.0001	-	220.94	1	<0.0001	-	271.60	1	ns	-	86.12	1	ns
Temperature	+	1082.30	1	0.0008	+	237.99	1	ns	-	271.36	1	ns	-	84.07	1	ns
Altitude × rainfall		844.42	1	0.0003		211.49	1	ns		261.71	1	0.0017		83.50	1	ns
Altitude × temperature		1040.01	1	ns		217.71	1	ns		269.74	1	ns		82.60	1	ns
Rainfall × temperature		871.15	1	<0.0001		218.76	1	ns		262.63	1	0.0031		82.32	1	ns
<b>Parasitism</b>																
Constant		2264.61	149			715.37	65			1185.96	119			535.89	56	
Altitude	-	2231.09	1	<0.0001	-	713.52	1	ns	-	1164.46	1	<0.0001	-	518.04	1	<0.0001
Rainfall	-	2119.82	1	<0.0001	-	715.23	1	ns	-	1175.51	1	0.0012	-	535.63	1	ns
Temperature	+	2246.77	1	<0.0001	+	706.61	1	0.0031	-	1178.49	1	0.0063	-	498.52	1	<0.0001
Altitude × rainfall		1965.35	1	<0.0002		692.05	1	<0.0001		1149.28	1	0.0068		487.20	1	<0.0001
Altitude × temperature		2122.35	1	<0.0001		680.60	1	<0.0001		1139.61	1	ns		484.43	1	0.0593
Rainfall × temperature		1999.17	1	<0.0022		664.99	1	<0.0001		1168.74	1	ns		470.03	1	<0.0001

SC, signs of correlation coefficient; ns, not significant.

species (Zhou et al. 2003, Mailafiya et al. 2009), high parasitoid diversity in natural habitats was probably caused by higher availability of alternative herbivore hosts (Thies et al. 2005). Similarly, Kruess (2003), studying the effects of landscape structure and habitat type on the creeping thistle (*Cirsium arvense* L. Scop.)-insect community, noted higher parasitoid diversity in perennial noncrop habitats (field margin strips and fallow areas) and attributed this to the presence of several alternative hosts compared with crop fields.

In natural habitats, parasitoid richness was lower in Suam and Mtito Andei. This was very likely because of large-scale commercial maize production in Suam and grazing activities coupled with the frequent, severe drought conditions in Mtito Andei. This underlines the negative effect of habitat fragmentation on parasitoids, which are especially sensitive to habitat isolation and destruction (Kruess and Tschamtkke 2000a, Kruess 2003). It also explains the low diversity of parasitoids in cultivated habitats that are regularly disturbed by seasonal crop harvest, intensive tillage, and pesticide/fertilizer application. Such activities often shatter species interactions across different trophic levels, with consequent reduction of farmland agro-biodiversity, thereby requiring periodic recolonization by parasitoids (Tschamtkke and Brandl 2004).

The low parasitoid diversity found in the driest locality Mtito Andei confirms the suggestion by Zhou

et al. (2003) that parasitoid diversity is higher in areas with a higher spatial and temporal continuity of suitable host plants (i.e., areas with bimodal rainfall pattern) that maintain actively feeding stem borers. Sperber et al. (2004), for instance, found that increased herbivore hosts and food/shelter availability caused by increased canopy tree species richness and density in summer increased parasitoid diversity in 16 cacao agro-forestry systems.

**Parasitoid Abundance.** High and low abundance of parasitoids, respectively, in cultivated and natural habitats concurs with the work of Kruess (2003), showing that parasitoid abundance was positively correlated with herbivore abundance. In line with the resource concentration hypothesis (Root 1973) and previous results by Ndemah et al. (2007) and Matama-Kauma et al. (2008), stem borer density was generally low in natural habitats. Low stem borer host abundance in this study coupled with a high density of nonhost plant species in natural habitats existing in the same localities (Otieno et al. 2006, 2008) suggests host finding difficulty of parasitoids in such habitats (Chabi-Olaye et al. 2005). Moreover, parasitoids exhibit low fitness and high mortality on wild host plants, as a consequence of low nutrition (Sétamou et al. 2005) and/or toxic phytochemicals or secondary plant compounds (Ode 2006).

Current results suggest high mortality of stem borer hosts and their associated parasitoids on cultivated

**Table 5. Biotic factors affecting parasitoid abundance during different seasons in cultivated and natural habitats in four agroecological zones in Kenya**

	Cultivated habitats						Natural habitats					
	Rainy season			Dry season			Rainy season			Dry season		
	Deviance	df	<i>P</i> value	Deviance	df	<i>P</i> value	Deviance	df	<i>P</i> value	Deviance	df	<i>P</i> value
<b>Suam</b>												
Constant	59.49	21		24.55	10		6.72	18		11.21	10	
Borer richness	56.17	1	ns	18.65	1	0.0151	3.07	1	0.0558	9.81	1	ns
Borer abundance	32.05	1	<0.0001	13.96	1	0.0011	2.66	1	0.0438	7.21	1	0.0453
Plant richness	58.58	1	ns	24.04	1	ns	6.41	1	ns	10.56	1	ns
Borer richness × abundance	11.40	1	0.0003	9.71	1	0.0046	1.71	1	ns	5.47	1	ns
Borer richness × plant richness	32.29	1	<0.0001	18.38	1	ns	1.07	1	ns	7.51	1	ns
Constant	13.24	10		21.95	10		6.51	7		8.68	7	
Borer density	13.13	1	ns	20.52	1	0.0046	5.11	1	ns	7.32	1	ns
Borer richness × density	9.54	1	<0.0001	11.66	1	0.0017	1.36	1	ns	6.55	1	ns
<b>Kakamega</b>												
Constant	338.99	68		60.32	27		162.69	52		20.79	14	
Borer richness	201.38	1	<0.0001	55.19	1	0.0237	151.47	1	0.0008	20.21	1	ns
Borer abundance	178.91	1	<0.0001	26.90	1	<0.0001	85.11	1	<0.0001	6.82	1	0.0002
Plant richness	238.59	1	ns	53.31	1	ns	161.0942	1	ns	15.22	1	ns
Borer richness × abundance	112.78	1	<0.0001	26.74	1	ns	81.27	1	ns	4.67	1	ns
Borer richness × plant richness	183.62	1	ns	55.18	1	ns	145.529	1	ns	15.61	1	ns
Constant	24.80	43		46.93	22		59.98	40		12.56	14	
Borer density	24.59	1	<0.0001	45.01	1	0.0041	56.09	1	0.0484	12.17	1	0.0303
Borer richness × density	17.78	1	0.0025	36.11	1	0.0056	29.17	1	0.0183	9.58	1	ns
<b>Mtito Andei</b>												
Constant	186.67	22		40.41	9		19.85	18		9.36	10	
Borer richness	130.38	1	<0.0001	28.49	1	0.0006	16.93	1	ns	7.27	1	ns
Borer abundance	48.31	1	<0.0001	21.31	1	<0.0001	9.31	1	0.0012	8.45	1	0.0001
Plant richness	184.43	1	ns	36.32	1	0.0430	9.28	1	0.0011	9.32	1	ns
Borer richness × abundance	32.55	1	0.0162	35.01	1	0.0021	4.28	1	ns	6.57	1	0.0501
Borer richness × plant richness	102.54	1	<0.0001	27.26	0	ns	3.21	1	0.0535	6.31	1	0.0021
Constant	122.24	13		32.76	9		19.07	9		8.62	9	
Borer density	122.02	1	ns	31.92	1	0.0057	18.52	1	ns	8.13	1	ns
Borer richness × density	87.43	1	0.0052	18.15	1	0.0091	11.93	1	0.0018	4.90	1	ns
<b>Muhaka</b>												
Constant	222.56	58		84.29	23		78.21	52		42.83	26	
Borer richness	197.22	1	<0.0001	34.04	1	<0.0001	73.74	1	0.0345	39.45	1	ns
Borer abundance	179.01	1	<0.0001	49.51	1	<0.0001	72.22	1	0.0144	42.17	1	ns
Plant richness	172.11	1	ns	84.29	1	ns	77.39	1	ns	42.72	1	ns
Borer richness × abundance	175.65	1	ns	30.36	1	ns	68.22	1	0.0538	39.31	1	ns
Borer richness × plant richness	159.23	1	ns	34.04	1	ns	72.89	1	ns	39.18	1	ns
Constant	17.95	55		32.62	19		43.40	50		38.00	25	
Borer density	17.31	1	0.0041	32.07	1	ns	42.17	1	ns	37.99	1	<0.0001
Borer richness × density	10.04	1	ns	25.36	1	ns	23.09	1	ns	28.00	1	ns

All biotic factors were positively (+) with parasitoid abundance. ns, not significant.

cereals as a result of heavy rainfall. In natural habitats, stem borer densities were probably too low to allow for density-independent effects such as climate (Hassell 2000). Because rainfall increases with altitudes (Corbett 1998), its negative effects are expected to be more severe at high elevations, especially in areas with bimodal rainfall distribution. Heavy rainfall has been reported to inflict considerable mortality on stem borer populations directly (Schulthess et al. 2001, Ndemah et al. 2003) or indirectly through the disruption of their mating and oviposition activities (Sampson and Kumar 1983). Likewise, in the field, rainfall was observed to be detrimental to immature and adult aphids (Thies et al. 2005) and thrips (Etienne et al. 1990).

**Stem Borer Parasitism.** Our results from both cultivated and natural habitats corroborate the findings of Hawkins and Gross (1992) and Kruess (2003) that parasitism was positively correlated with parasitoid richness and abundance. Higher richness of parasitoids, mainly stenophagous species, implies that more

host species are attacked. Conversely, the decline of both parasitoid richness and abundance, particularly through habitat fragmentation and/or reductions in habitat area, disrupts beneficial community interactions, leading to a decrease in parasitism (Kruess and Tschardt 2000b, Thies et al. 2003).

The relationship of parasitism to temperature, being positive in cultivated habitats, but negative in natural habitats suggests greater sensitivity of parasitoids to extreme temperatures in natural habitats, which could be compounded by environmental disturbances such as bush fires and intensive grazing. The direct effect of extreme temperatures on parasitoids is expected to vary among species based on their adaptation to or capability to escape extreme temperatures and the particular lifestyles exposed (Loxdale and Lushai 1999). On one hand, severe temperatures can directly decimate parasitoid populations (Coley 1998) or accelerate their host's developmental period, thus re-



**Table 6. Biotic factors affecting stem borer parasitism during different seasons in cultivated and natural habitats in four agroecological zones in Kenya**

	Cultivated habitats						Natural habitats					
	Rainy season			Dry season			Rainy season			Dry season		
	Deviance	d.f.	P value	Deviance	d.f.	P value	Deviance	d.f.	P value	Deviance	d.f.	P value
<b>Suam</b>												
Constant	24.36	21		68.51	10		68.29	18		82.76	10	
Parasitoid richness	20.59	1	0.0522	45.02	1	<0.0001	5.92	1	<0.0001	18.56	1	<0.0001
Parasitoid abundance	4.68	1	<0.0001	50.36	1	<0.0001	6.62	1	<0.0001	16.65	1	<0.0001
Borer richness	22.59	1	ns	45.81	1	<0.0001	16.21	1	<0.0001	69.51	1	0.0003
Borer abundance	19.77	1	0.0321	68.04	1	ns	15.97	1	<0.0001	70.52	1	0.0005
Plant richness	24.31	1	ns	66.52	1	ns	50.42	1	<0.0001	82.64	1	ns
Parasitoid richness × abundance	4.54	1	ns	29.35	1	0.0002	2.88	1	ns	23.17	1	<0.0001
Parasitoid richness × borer richness	17.18	1	ns	32.85	1	0.0033	2.56	1	ns	7.38	1	ns
Borer richness × plant richness	10.71	1	0.0006	42.73	1	0.0123	5.65	1	0.0015	19.31	1	ns
Constant	19.44	10		60.77	10		4.93	7		77.31	7	
Borer density	18.94	1	0.0265	58.91	1	0.0054	4.48	1	ns	75.44	1	0.0196
Parasitoid richness × borer density	10.44	1	ns	47.13	1	0.0041	3.08	1	ns	35.31	1	ns
<b>Kakamega</b>												
Constant	1326.86	68		324.38	27		404.11	52		167.20	14	
Parasitoid richness	591.35	1	<0.0001	177.76	1	<0.0001	246.50	1	<0.0001	128.52	1	<0.0001
Parasitoid abundance	774.36	1	<0.0001	212.98	1	<0.0001	306.81	1	<0.0001	139.24	1	<0.0001
Borer richness	985.91	1	<0.0001	296.57	1	<0.0001	365.58	1	<0.0001	115.95	1	<0.0001
Borer abundance	1108.69	1	<0.0001	270.59	1	<0.0001	362.51	1	<0.0001	165.88	1	ns
Plant richness	1326.08	1	ns	310.23	1	0.0510	384.64	1	<0.0001	115.32	1	0.0027
Parasitoid richness × abundance	290.77	1	<0.0001	76.44	1	<0.0001	206.2857	1	<0.0001	35.33	1	<0.0001
Parasitoid richness × borer richness	468.54	1	<0.0001	169.32	1	ns	223.03	1	0.0005	39.44	1	<0.0001
Borer richness × plant richness	947.09	1	ns	279.49	1	0.0021	333.628	1	ns	113.31	1	0.0011
Constant	136.02	43		30.95	22		96.68	40		9.28	14	
Borer density	134.32	1	<0.0001	29.28	1	ns	82.66	1	<0.0001	8.84	1	ns
Parasitoid richness × borer density	110.75	1	0.0112	15.36	1	0.0532	71.18	1	<0.0001	2.03	1	<0.0001
<b>Mtito Andei</b>												
Constant	230.99	22		112.56	9		85.87	18		34.39	10	
Parasitoid richness	76.13	1	<0.0001	51.14	1	<0.0001	80.65	1	0.0224	1.36	1	<0.0001
Parasitoid abundance	126.98	1	<0.0001	86.97	1	<0.0001	73.28	1	0.0004	5.56	1	<0.0001
Borer richness	131.85	1	<0.0001	112.49	1	ns	61.54	1	<0.0001	26.42	1	0.0047
Borer abundance	137.49	1	<0.0001	112.43	1	ns	81.01	1	0.0275	23.54	1	<0.0001
Plant richness	230.90	1	ns	108.66	1	0.0484	79.61	1	0.0123	34.28	1	ns
Parasitoid richness × abundance	20.65	1	<0.0001	51.01	1	0.0001	0.22	1	<0.0001	13.46	1	<0.0001
Parasitoid richness × borer richness	62.21	1	0.0413	3.81	1	ns	22.76	1	<0.0001	5.87	1	<0.0001
Borer richness × plant richness	58.41	1	ns	14.09	1	ns	44.18	1	ns	25.92	1	ns
Constant	65.74	13		24.79	9		10.24	9		11.40	9	
Borer density	64.45	1	0.0005	23.54	1	<0.0001	9.95	1	ns	10.87	1	ns
Parasitoid richness × borer density	32.22	1	0.0032	10.29	1	0.0008	4.79	1	ns	2.01	1	ns
<b>Muhaka</b>												
Constant	518.01	58		184.98	23		566.51	52		220.09	26	
Parasitoid richness	235.74	1	<0.0001	82.01	1	<0.0001	336.47	1	<0.0001	95.89	1	<0.0001
Parasitoid abundance	394.23	1	<0.0001	148.48	1	<0.0001	380.76	1	<0.0001	127.47	1	<0.0001
Borer richness	517.39	1	ns	167.43	1	<0.0001	538.34	1	<0.0001	219.28	1	ns
Borer abundance	508.13	1	0.0017	184.82	1	ns	537.22	1	<0.0001	218.14	1	ns
Plant richness	510.87	1	0.0075	184.98	1	ns	566.45	1	ns	0.0075	1	ns
Parasitoid richness × abundance	163.72	1	<0.0001	25.63	1	<0.0001	268.59	1	<0.0001	16.77	1	0.0008
Parasitoid richness × borer richness	232.17	1	ns	44.78	1	<0.0001	259.85	1	<0.0001	30.32	1	<0.0001
Borer richness × plant richness	510.74	1	ns	167.43	1	ns	529.03	1	ns	208.23	1	0.0025
Constant	150.06	55		62.63	19		79.76	50		90.36	25	
Borer density	149.64	1	ns	61.75	1	<0.0001	78.92	1	0.0219	89.13	1	0.0014
Parasitoid richness × borer density	96.54	1	0.0002	45.93	1	0.0081	67.54	1	<0.0001	77.51	1	ns

All biotic factors were positively (+) correlated with stem borer parasitism. ns, not significant.

ducing their window of vulnerability to parasitization (Coley 1998). However, favorable microclimate conserves adequate humidity that protects parasitoids from desiccation (Willmer et al. 1996), thereby sustaining their feeding and host finding activities. For instance, Alston et al. (1991) reported higher mortality of *Heliothis zea* (Boddie) (Lepidoptera: Noctuidae) larvae caused by parasitism in closed canopy and weedy soybeans than in very open and weed-free soybeans. Additionally, Yarnes and Boecklen (2006)

found that cooler and more humid microclimates resulted in significantly higher parasitism rates of the leaf-miner *Phyllonorycter* sp. because of higher biomass payoff (total biomass divided by density).

In conclusion, our results highlight the importance of natural habitats as refugia for maintaining parasitoid species diversity in the cereal cropping systems in Kenya. Evidence also shows that parasitoid diversity was lower in more fragmented localities. These results further indicate that stem borer parasitism was func-

tionally dependent on parasitoid richness and abundance. However, knowing that parasitoid abundance and dispersal are greatly influenced by landscape spatial complexities (Tschardt and Brandl 2004), the effects of habitat size and fragmentation on parasitism at landscape level needs further studies.

### Acknowledgments

The authors thank D.M. Gwary, N. Gworgwor, E. Essiet, and F. Schulthess for reviewing earlier versions of the manuscript. Our thanks also go to J.-F. Silvain for financial assistance. We are grateful to the entire members of the Noctuid Stem Borer Biodiversity Project (NSBB) and the Biosystematic Unit (BSU) of the International Centre of Insect Physiology and Ecology (ICIPE, Nairobi, Kenya) for assistance with field collections or laboratory work. This research was funded by the German Academic Exchange Service (DAAD) through the African Regional Postgraduate Programme in Insect Science (ARPPIS) at ICIPE in Kenya and the Institut de Recherche pour le Développement (IRD) in Kenya.

### References Cited

- Alston, D. G., J.R. Bradley, Jr., D. P. Schmitt, and H. D. Coble. 1991. Relationship of *Heliothis zea* predators, parasitoids and entomopathogens to canopy development in soybean as affected by *Heterodera glycines* and weeds. *Entomol. Exp. Appl.* 58: 279–288.
- AWhere-ACT Africa database. 2002. Mud Springs Geographers Inc. CD ROM Publication, Temple, TX.
- Bai, Z. G., and D. L. Dent. 2006. Global assessment of land degradation and improvement: pilot study in Kenya. Report 2006/01, ISRIC-World Soil Information, Wageningen, The Netherlands.
- Chabi-Olaye, A., C. Nolte, F. Schulthess, and C. Borgemeister. 2005. Abundance, dispersion and parasitism of the stem borer *Busseola fusca* (Lepidoptera: Noctuidae) in maize in the humid forest zone of southern Cameroon. *Bull. Entomol. Res.* 95: 169–177.
- Coley, P. D. 1998. Possible effects of climate change on plant/herbivore interactions in moist tropical forests. *Clim. Change* 39: 455–472.
- Collett, D. 1991. Modelling binary data. Chapman & Hall, London, United Kingdom.
- Corbett, J. D. 1998. Classifying maize production zones in Kenya through multivariate cluster analysis, pp. 15–25. In R. M. Hassan (ed.), *Maize technology development and transfer: a GIS application for research planning in Kenya*. CAB International, Wallingford, United Kingdom.
- Corbett, J. D. and R. F. O'Brien. 1997. The spatial characterization tool—Africa version 1.0. Report No. 97–03, CD ROM Publication. Texas Agricultural Experiment Station, Texas A&M University System, Blackland Research Center, TX.
- Etienne, J., J. Guyot, and X. Van Waetermeulen. 1990. Effect of insecticides, predation, and precipitation on populations of *Thrips palmi* on aubergine (egg plant) in Guadeloupe. *Fla. Entomol.* 73: 339–342.
- Gounou, S., and F. Schulthess. 2004. Spatial distribution of lepidopterous stem borers on indigenous host plants in west Africa and its implications for sampling schemes. *Afr. Entomol.* 12: 1–8.
- Goux, E. 2005. Caractérisation des habitats sauvages et cultivés des insectes ravageurs des cultures de maïs des localités de Mito Andei et Suam (Kitale), au Kenya. Université Paris, XII Paris, Val de Marne, France.
- Guihéneuf, Y. 2004. Characterisation of wild and cultivated habitats in two ecological areas in Kenya. Mémoire de D.E.S.S., Université de Paris XII, Paris, France.
- Hassell, M. P. 2000. The spatial and temporal dynamics of host-parasitoid interactions. Oxford University Press, New York.
- Hawkins, B. A., and P. Gross. 1992. Species richness and population limitation in insect parasitoid-host systems. *Am. Nat.* 139: 417–423.
- Kruess, A. 2003. Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. *Ecography* 26: 283–290.
- Kruess, A., and T. Tschardt. 2000a. Effects of habitat fragmentation on plant-insect communities, pp. 53–70. In B. Ekbom, M. E. Irwin, and Y. Robert (eds.), *Interchanges of insects between agricultural and surrounding landscapes*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Kruess, A., and T. Tschardt. 2000b. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia* 122: 129–137.
- Landis, D. A., and F. D. Menalled. 1998. Ecological considerations in the conservation of effective parasitoid communities in agricultural systems, pp. 101–121. In P. Barbosa (ed.), *Conservation biological control*. Academic, San Diego, CA.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45: 175–201.
- Le Ru, B. P., G. O. Ong'amo, P. Moyal, E. Muchugu, L. Ngala, B. Musyoka, Z. Abdullah, T. Matama-Kauma, V. Y. Lada, B. Pallangyo, et al. 2006a. Geographic distribution and host plant ranges of East African noctuid stem borers. *Ann. Soc. Entomol. Fr.* 42: 353–361.
- Le Ru, B. P., G. O. Ong'amo, P. Moyal, L. Ngala, B. Musyoka, Z. Abdullah, D. Cugala, B. Defabachew, T. A. Haile, T. Kauma Matama, et al. 2006b. Diversity of lepidopteran stem borers on monocotyledonous plants in eastern Africa and the islands of Madagascar and Zanzibar revisited. *Bull. Entomol. Res.* 96: 1–9.
- Lee, J. C., G. E. Heimpel, and G. L. Leibe. 2004. Comparing floral nectar and aphid honeydew diets on the longevity and nutrient levels of a parasitoid wasp. *Entomol. Exp. Appl.* 111: 189–199.
- Loxdale, H. D., and G. Lushai. 1999. Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype. *Philos. Trans. R. Soc. Lond. B.* 354: 1479–1495.
- Magurran, A. E. 1988. *Ecological diversity and its measurements*. University Press, Princeton, NJ.
- Mailafiya, D. M., B. P. Le Ru, E. W. Kairu, P.-A. Calatayud, and S. Dupas. 2009. Species diversity of lepidopteran stem borer parasitoids in cultivated and natural habitats in Kenya. *J. Appl. Entomol.* 133: 416–429.
- Matama-Kauma, T., F. Schulthess, B. P. Le Ru, J. Mueke, J. A. Ogwang, and C. O. Omwega. 2008. Abundance and diversity of lepidopteran stem borers and their parasitoids on selected wild grasses in Uganda. *Crop Protect.* 27: 505–513.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models*. Chapman & Hall, London, United Kingdom.
- Ndemah, R., F. Schulthess, S. Korie, C. Borgemeister, M. Poehling, and K. F. Cardwell. 2003. Factors affecting infestations of the stalk borer *Busseola fusca* (Fuller) on maize in the forest zone of Cameroon with special reference to Scelionid egg parasitoids. *Environ. Entomol.* 32: 1–70.

- Ndemah, R., F. Schulthess, B. P. Le Ru, and I. Bame. 2007. Lepidopteran cereal stem borers and associated natural enemies on maize and wild grass hosts in Cameroon. *J. Appl. Entomol.* 131: 658–668.
- Ode, P. J. 2006. Plant chemistry and natural enemy fitness: effects on herbivore and natural enemy interactions. *Annu. Rev. Entomol.* 51: 163–85.
- Onyango, F. O., and J.P.R. Ochieng-Odero. 1994. Continuous rearing of *Busseola fusca* (Lepidoptera: Noctuidae) on an artificial diet. *Entomol. Exp. Appl.* 73: 139–144.
- Otieno, N. A., B. P. Le Ru, G. O. Ong'amo, S. Dupas, P.-A. Calatayud, M. Makobe, J. Ochora, and J.-F. Silvain. 2006. Diversity and abundance of wild host plants of lepidopteran stem borers in two different agroecological zones of Kenya. *Ann. Soc. Entomol. Fr.* 42: 371–380.
- Otieno, N. A., B. P. Le Ru, G. O. Ong'amo, P. Moyal, S. Dupas, P.-A. Calatayud, and J.-F. Silvain. 2008. Diversity and abundance of wild host plants of lepidopteran stem borers in two agro-ecological zones of Kenya. *Int. J. Biodivers. Sci. Manage.* 4: 1–12.
- Overholt, W. A., K. Ogedah, and P. Lammers. 1994. Distribution and sampling of *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) in maize and sorghum at Kenya Coast. *Bull. Entomol. Res.* 84: 367–378.
- Risch, S. J., D. Andow, and M. A. Altieri. 1983. Agroecosystem diversity and pest control: data, tentative conclusions and new research directions. *Environ. Entomol.* 12: 625–629.
- Root, R. B. 1973. Organization of plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleraceae*). *Ecol. Monogr.* 43: 95–124.
- Sampson, M. A., and R. Kumar. 1983. Population dynamics of the stem-borer complex on sugar-cane in southern Ghana. *Insect Sci. Appl.* 4: 25–32.
- SAS Institute. 2001. PROC user's manual, version 6th ed. SAS Institute, Cary, NC.
- Schulthess, F., A. Chabi-Olaye, and G. Goergen. 2001. Seasonal fluctuations of noctuid stem borers egg parasitism in southern Benin with special preference to *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae) and *Telenomus* species (Hymenoptera: Scelionidae) on maize. *Biocontrol Sci. Technol.* 11: 745–757.
- Seshu Reddy, K. V. 1998. Maize and sorghum: East Africa, pp. 25–27. In A. Polaszek (ed.), African cereal stem borers: economic importance, taxonomy, natural enemies and control. CAB International, Wallingford, Oxon, United Kingdom.
- Sétamou, M., N. Jiang, and F. Schulthess. 2005. Effect of the host plant on the survivorship of parasitized *Chilo partellus* Swinhoe (Lepidoptera: Crambidae) larvae and performance of its larval parasitoid *Cotesia flavipes* Cameron (Hymenoptera: Braconidae). *Biol. Control* 32: 183–190.
- Sperber, C. F., K. Nakayama, M. J. Valverde, and F. S. Neves. 2004. Tree species richness and density affect parasitoid diversity in cacao agroforestry. *Basic Appl. Ecol.* 5: 241–251.
- Thies, C., I. Steffan-Dewenter, and T. Tscharntke. 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101: 18–25.
- Thies, C., I. Roschewitz, and T. Tscharntke. 2005. The landscape context of cereal aphid-parasitoid interactions. *Proc. R. Soc. B.* 272: 203–210.
- Tscharntke, T., and R. Brandl. 2004. Plant-insect interactions in fragmented landscapes. *Annu. Rev. Entomol.* 49: 405–430.
- Tscharntke, T., R. Bommarco, Y. Clough, O. Crist, D. Kleijn, T. A. Rand, J. M. Tylianakis, S. Van Nouhuys, and S. Vidal. 2007. Conservation biological control and enemy diversity on landscape scale. *Biol. Control* 43: 294–309.
- Willmer, P. G., J. P. Hughes, J.A.T. Woodford, and S. C. Gordon. 1996. The effects of crop microclimate and associated physiological constraints on the seasonal and diurnal distribution patterns of raspberry beetle (*Byturus tomentosus*) on the host plant *Rubus idaeus*. *Ecol. Entomol.* 21: 87–97.
- Yarnes, C. T., and J. R. Boecklen. 2006. Abiotic mosaics affect seasonal variation of plant resources and influence the performance and mortality of a leaf-miner in Gambel's oak (*Quercus gambelii*, Nutt.). *Biomed. Life Sci.* 21: 157–163.
- Zar, J. H. 1999. Biostatistical analysis, 4th ed. Prentice Hall, Upper Saddle River, NJ.
- Zhou, G., W. A. Overholt, and S. W. Kimani-Njogu. 2003. Species richness and parasitism in assemblage of parasitoids attacking maize stem borer in coastal Kenya. *Ecol. Entomol.* 28: 109–118.

Received 14 July 2009; accepted 11 September 2009.