Species diversity of lepidopteran stem borer parasitoids in cultivated and natural habitats in Kenya

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Abstract

Field surveys were conducted during 2005 to 2007 to assess the species diversity of stem borer parasitoids in cultivated and natural habitats in four agroecological zones in Kenya. In total, 33 parasitoid species were recovered, of which 18 parasitized six stem borer species feeding on cereal crops, while 27 parasitized 21 stem borer species feeding on 19 wild host plant species. The most common parasitoids in cultivated habitats were *Cotesia flavipes* Cameron, *Cotesia sesamiae* (Cameron), *Pediobius furvus* Gahan and the tachinid *Siphona* sp., whereas in natural habitats, *Siphona* sp. was the most common. The majority of parasitoids were stenophagous species; only five species – *Cotesia* sp., *Enicospilus ruscus* Gauld and Mitchell, *Pristomerus* nr. *bullis*, *Sturmiopsis parasitica* (Curran) and *Syzeuctus ruberrimus* Benoit – were monophagous. In both cultivated and natural habitats, parasitoid species diversity was highest on the most dominant stem borers *Busseola* spp. and *Chilo* spp. On cereal crops, parasitoid diversity was highest on maize and among wild host plants, it was highest on *Setaria* spp. The ingress-and-sting attack method was the most common strategy used by parasitoids in both habitats. In all agroecological zones, parasitoid species diversity was significantly higher in natural than in cultivated habitats. Furthermore, the majority of parasitoid species were common to both cultivated and natural habitats. It was concluded that natural habitats surrounding cereal crops serve as refugia for sustaining the diversity of stem borer parasitoids from adjacent cereal fields.

Introduction

In sub-Saharan Africa, cereal crops are mainly grown at subsistence level by resource-poor farmers. The bulk of cereal fields are usually small and surrounded by patches of natural habitats that habour wild host plants (i.e. grasses and sedges) of cereal stem borer pests. Lepidopteran stem borers, among others, are the major biotic constraints to increased cereal production (Polaszek 1998) and have been reported to cause losses ranging between 5% and 73% of potential crop yield (Seshu Reddy and Walker 1990; De Groote 2002; De Groote et al. 2003). In Kenya, species diversity of stem borer parasitoids has been intensively studied in cultivated habitats. Thus far, 85 species of parasitoids have been reported attacking seven species of stem borer pests on maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* L.) (Mohyuddin and Greathead 1970; Bonhof et al. 1997; Zhou et al. 2003). Despite the high diversity of stem borer species on wild host plants (Le Ru et al. 2006a,b), only 10 species of parasitoids have been reported attacking six other species of stem borers on 10 species of wild host plants (Khan et al. 1997; Overholt et al. 1997; Polaszek and Khan 1998; Conlong 2000; Songa et al. 2002). In view of the high diversity of stem borers in natural habitats, parasitoid diversity has likely been underestimated.

Although lepidopteran stem borers have been an important subject of study for the past 50 years (Polaszek 1998), there is no general theory that predicts the role of natural habitats on stem borer parasitoid perpetuation or effectiveness. Currently, some researchers suggest that stem borer parasitoids can persist and increase their populations across season in natural habitats (Khan et al. 1997; Schulthess et al. 1997; Bonhof et al. 2001; Muturi et al. 2005), arguing that wild host plants adjacent to cultivated crops provide important refugia and food resources such as pollen and nectar for parasitoids to sustain their populations during different seasons.

Knowing that parasitoids develop and function in a multitrophic context (Landis et al. 2000, 2005; Wilkinson and Landis 2005; Bianchi et al. 2006), it is crucial to understand the diversity and ecology of stem borer parasitoids in the context of both cultivated and natural habitats. Moreover, future design of successful sustainable stem borer pest management strategies would require sufficient knowledge of not only parasitoid species diversity, but their host ranges and multitrophic interactions in cultivated and natural habitats too. In this paper, we present results of a study that was carried out during 2 years in four different agroecological zones (AEZs) in Kenya. Our focus was: (i) to provide a catalogue of parasitoid species and their stem borer or host plant ranges in cultivated and natural habitats; (ii) to describe the diversity of stem borer parasitoids on different stem borer and host plant genera or families; and (iii) to assess the diversity of stem borer parasitoids in cultivated and natural habitats in different agroecological zones, as well as during different seasons.

Materials and Methods

Survey sites

Field surveys were conducted in four AEZs in Kenya from December 2005 to December 2007: Kakamega (Kakamega District) in the moist transitional (MT) AEZ, Mtito Andei (Makueni District) in the dry mid-altitudes (DM), Muhaka (Kwale District) in the lowland tropics (LT) and Suam (Trans-Nzoia District) in the highland tropics (HT) (fig. 1). Kakamega (0°13′N, 34°56′E) is 1655 metres above sea level (m a.s.l.) 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 1570 mm and 21°C, respectively. Local vegetation mosaic is of the typical Guineo-Congolian rain forest type. Mtito Andei (2°39′S, 38°16′E, 760 m a.s.l.) has a single cropping season lasting from November to January. Average annual rainfall and temperature are 665 mm and 23°C, respectively. Typical vegetation is Somalia–Masai *Acacia–Commiphora* deciduous bushland and thicket. Muhaka (4°18′S, 39°31′E, 40 m a.s.l.) 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 1210 mm and 26°C, respectively. Local vegetation is East African coastal grassy and woody mosaic bordering the undifferentiated Zanzibar-Inhambane forest type. Suam (1°11′N, 34°47′E, 1995 m a.s.l.) has a single cropping season that lasts from March to November. Average annual rainfall and temperature are 1190 mm and 19°C, respectively. Local vegetation is characterized by a mosaic of both rainforest and secondary grassland.

Field survey

Previous studies suggest that stem borer densities were much lower on wild host plants than on adjacent cultivated cereal crops (Nye 1960; Gounou and Schulthess 2004; Le Ru et al. 2006a,b; Ndemah et al. 2007; Matama-Kauma et al. 2008). Therefore, to increase the chances of collecting stem borers and their parasitoids from both habitats, we used the random sampling scheme in cultivated habitats and non-random sampling scheme 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. Cereal fields of the same farmer were sampled at regular intervals, once every 2 months, to include both vegetative and harvest stages of cereal crops. Hence, the same site was visited at least twice during the long rainy period, short rainy period and dry season throughout the study period. To estimate stem borer/parasitoid diversity, depending on crop

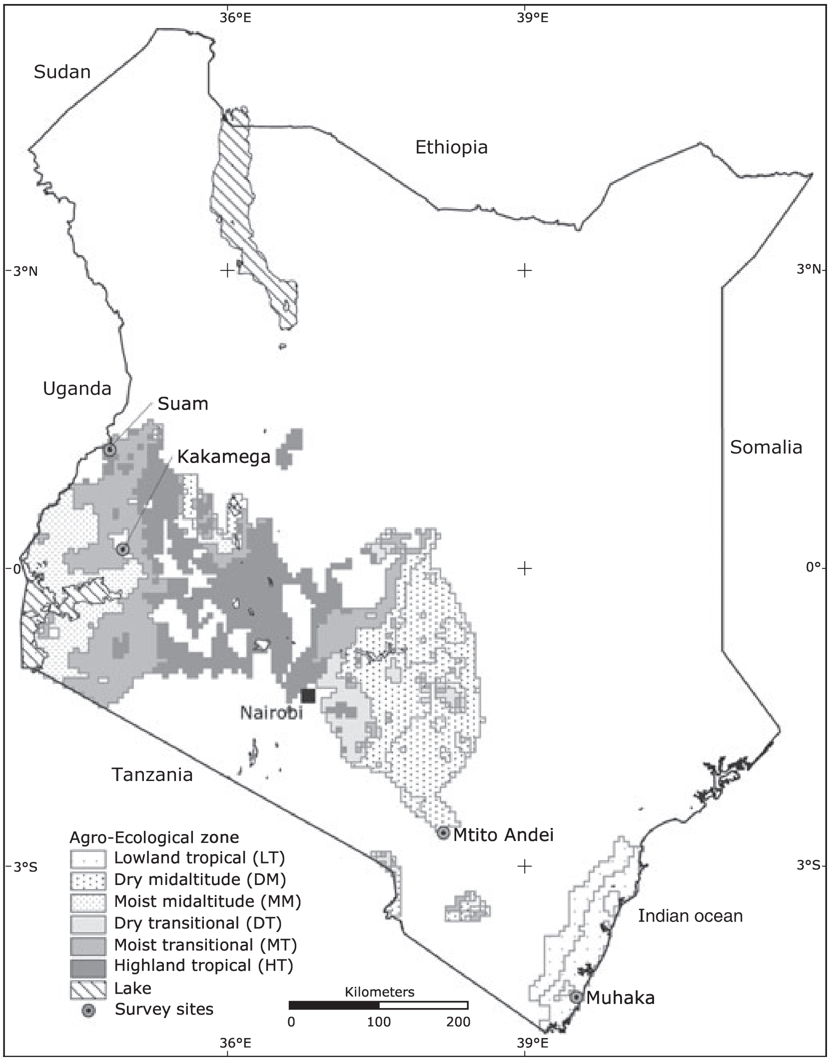

Fig. 1 Map of Kenya showing surveyed sites in four agroecological zones.

availability across seasons, we sampled 50 to 100 plants per plot. Each plant selected was dissected thoroughly in the field, and stem borer larvae or pupae collected were transported to the laboratory for rearing and subsequent recovery of parasitoids.

Sampling in natural habitats

To estimate stem borer or parasitoid species diversity on wild host plants, stem borers were collected using a slight modification of the non-random sampling procedure applied by Le Ru et al. (2006a,b). During each sampling occasion as described above, wild host plants exhibiting infestation symptoms were sampled within 100 m of each sampled cereal plot, including grass patches found along road sides, open forest grass patches, on the banks of streams, dams or rivers and in swamps. At each sampling site, all known or potential host plants belonging to the Poaceae, Cyperaceae and Typhaceae families (Khan et al. 1997; Le Ru et al. 2006a,b) were checked for infestation symptoms such as scarified leaves (window panes and pin holes), dry leaves and shoots (dead hearts), bored (entrance or exit) holes and frass. All plants/tillers selected were thoroughly dissected in the field, and stem borer larvae or pupae collected were transported to the laboratory for rearing and 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 × 7.5 cm depth) plugged with cotton wool, and maintained under ambient conditions in the laboratory until pupation (26 ± 1°C; 65 ± 5% relative humidity).

Parasitoid puparia or cocoons recovered from stem borer larvae or pupae were kept separately in plastic vials (2.5 cm diameter × 7.5 cm depth) until emergence. Adult stem borer or parasitoid specimens were preserved in 70% or 100% alcohol. Identification of stem borers and parasitoids was conducted to the 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). Wild host plants were identified by S. Muthenge (East Africa Herbarium, Nairobi, Kenya). Details of all identified species were used to prepare a catalogue of parasitoid species (table 1). In addition, parasitoid species were described according to their feeding site (Smith et al. 1993; Polaszek 1998), progeny allocation (Smith et al. 1993; Polaszek 1998), attack method (Smith et al. 1993) and interaction with host as either idiobiont or koinobiont (Askew and Shaw 1986; Polaszek 1998; Zhou et al. 2003).

Data analyses

Because of the scarcity of data for some species, parasitoid data obtained from various stem borer and host plant species were pooled according to their respective genera for appropriate analysis or presentation. The Shannon diversity index (H'), which takes into account the number of species (species richness) and their relative abundance (equitability), was used to compute parasitoid species diversity in cultivated and natural habitats (Magurran 1988):

$$H' = -\sum P_i \ln P_i$$

where i is the parasitoid species, P_i is the proportional abundance of the ith species and ln is the natural logarithm.

Because the Shannon diversity index is inappropriate for estimating species diversity when species richness is extremely low, the index was used only in cases where parasitoid species richness was ≥5; t-tests were performed to examine differences in parasitoid species diversity in cultivated and natural habitats on different stem borer or host plant genera and families (pooled data) in each locality (pooled data) and during different seasons (pooled data) (Magurran 1988). Significance was set at $P \leq 0.05$. However, this test was not performed for host plant genera or families that did not occur in both habitats.

Additionally, differences in parasitoid species composition in cultivated and natural habitats was compared by calculating the Morista-Horn index (C_{mH}):

$$C_{mH} = \frac{2\sum (n_{ia} n_{ib})}{(d_a + d_b) N_a N_b}$$

where N_a and N_b are the total number of individuals in cultivated and natural habitats, respectively; n_{ia} and n_{ib} are number of individuals of a particular species i in cultivated and natural habitats, respectively; $d_a = \sum n_{ia}^2 / N_a^2$ and $d_b = \sum n_{ib}^2 / N_b^2$. Increasing values of C_{mH} indicate increasing similarity between the two habitats, with a maximum of 1.

Results

Parasitoid species composition

During the 2 years of field surveys, 7443 and 3676 stem borers were collected from cultivated and natural habitats, respectively. A total of 33 parasitoid species were recovered (table 1). In cultivated habitats, 18 species of parasitoids (11 larval and seven pupal parasitoids) were recovered from six species of stem borers feeding on maize and cultivated sorghum, while in natural habitats, 27 species (24 larval and three pupal parasitoids) were recovered from 21 species of stem borers feeding on 19 species of wild host plants. Not a single parasitoid was recovered from an additional 11 species of stem borers obtained from 19 other wild host plant species. Only four species of dipteran parasitoids were recovered from stem borers in both cultivated and natural habitats. The number of endoparasitic species was three and four times higher than ectoparasitic species in cultivated and natural habitats, respectively. In cultivated habitats, ingress-and-sting (59%) attack was the most common strategy utilized by parasitoids, followed by planidial ingress (23%), drill-and-sting (12%) and direct attack (6%) methods. However, more attack methods were utilized by parasitoids in natural habitats, with ingress-and-sting (43%) method being the most common strategy, followed by planidial ingress (24%), drill-and-sting (14%), direct attack (9%), probe-and-sting (5%) and wait-and-sting (5%) methods. About 52% and 39% of parasitoid species found in cultivated and natural habitats, respectively, were strictly solitary species, while 22% and 28% other species were both solitary and gregarious in cultivated and natural habitats, respectively.

Table 1 Parasitoids of lepidopteran stem borers feeding on cereal and wild host plants in four AEZs in Kenya, 2005–2007

Parasitoid species	H	L	Season	Stem borer	Host plant	BS	IB	FS	PA	AS
Hymenoptera										
Bethylidae										
Goniozus indicus Ashmead	C	Su	Ds	Bf (1)	Zm	L	i	Ec	G	IS
	C	Ma	Sr	Cp (1)	Zm					
	N	Mu	Sr	Em (1)	Re					
Braconidae										
Bracon sp.	N	Ma	Sr	Sn (1)	Cs	L	i	Ec	G	DS
Bracon sesamiae Cameron	C	Ka	Sr	Bp (1)	Zm	L	i	Ec	G	DS
	N	Ka	Lr	Bnsp1 (1)	Sm					
	N	Su	Lr	Sc (1)	Si					
Chelonus curvimaculatus Cameron	C	Ma	Sr	Cp (4)	Sb, Zm	L	k	En	S	DA
	N	Ka	Sr	Bnsp1 (1)	Sm					
	N	Mu	Sr	Cp (2)	Pp					
Cotesia flavipes Cameron	C	Ma	Ds, Sr	Cp (121), Sc (7)	Sb, Zm	L	k	En	G	IS
	C	Mu	Lr, Sr	Cp (117), Sc (18)	Sb, Zm					
	N	Ma	Sr	Cp (1)	Sa					
	N	Mu	Lr, Sr	Cp (16)	Sa					
Cotesia sesamiae (Cameron)	C	Ka	Ds, Lr, Sr	Bf (76), Bp (12), Sc (7)	Sb, Zm	L	k	En	G	IS
	C	Su	Lr	Bf (90), Sc (2)	Sb, Zm					
	N	Ka	Sr	Bp (1)	Pm					
	N	Su	Lr	Bf (1)	Sa					
Cotesia sp.	N	Ka	Lr	Snsp9 (3)	Cp	L	k	En	G	IS
Dolichogenidea polaszeki Walker	C	Su	Lr	Bf (5)	Zm	L	k	En	S	IS
	N	Ka	Lr	Snsp9 (1)	Cp					
	N	Ma	Sr	Cp (1)	Sa					
Iphiaulax pilisoma van Achterberg	N	Mu	Sr	Em (1)	Re	L	i	Ec	S	WS
Macrocentrus sp.	N	Mu	Ds	Tr (1)	Cr	L	k	En	S/G	PS
Apanteles fuscivorus (Walker)	N	Ka	Sr	N (1)	Pp	L	k	En	G	IS
Ceraphronidae										
Aphanogmus fijiensis (Ferrière)	C	Su	Lr	Bf (3)	Sb	L	i	Ec	S	IS
	C	Mu	Sr	Cp (1)	Zm					
Eurytomidae										
Pediobius furvus Gahan	C	Su	Lr	Bf (1)	Zm	P	i	En	G	IS
	C	Mu	Sr	Cp (2), Sc (1)	Zm					
	N	Ka	Lr	Snsp9 (2)	Cp					
	N	Ma	Sr	Sn (1)	Td					
Tetrastichus sp.	C	Su	Ds	Bf (1)	Zm	P	i	En	G	IS
Ichneumonidae										
Amouramorpha sp.	N	Ka	Lr	Tr (1)	Cd	L	i	Ec	S	PS
Dentichasmias busseolae Heinrich	C	Ma	Sr	Cp(1)	Zm	P	i	En	S	IS
Enicospilus ruscus Gauld & Mitchell	N	Ka	Sr, Lr	Snsp9 (17)	Cp, Sm	L	k	En	S	?
Enicospilus antefurcalis Szépligeti	N	Ka	Ds	Bnsp1 (1)	Sm	L	k	En	S	?
Gambroides nimbipennis Seyrig	C	Mu	Lr	Cp (1)	Zm	P	i	En	S	PS?
Ichneumoninae 1	N	Ka	Lr	Bnsp1 (1)	Sm	L	?	En	S	?
Ichneumoninae 2	N	Ka	Lr	? (1)	Sm	P	?	En	S	?
Ichneumoninae 3	N	Su	Sr	C (1)	Ec	L	?	En	S	?
Ichneumoninae 4	C	Su	Lr	Bf (1)	Zm	P	?	En	S	?
Procerochasmias nigromaculatus Cameron	C	Su	Ds, Lr	Bf (3)	Zm	P	i	En	S	IS
Pristomerus nr. bullis Fitton	N	Mu	Lr	Em (5)	Re	L	k	En	S	PS
Syzeuctus ruberrimus Benoist	N	Mu	Ds, Lr, Sr	Co (18)	Pm	L	k	En	S	PS
Unidentified Genera nr. *Bathyplectes*	N	Su	Lr	Scn (1)	Pt	L	?	En	S	?
Venturia sp.	N	Su	Lr	C (1), Scn (1)	Ec, Pt	L	k	En	S	PS
Xanthopimpla stemmator (Thunberg)	C	Ma	Ds	Cp (2)	Sb	P	i	En	S	DS
	C	Mu	Lr, Sr	Cp (4)	Zm					
	N	Mu	Lr, Sr	Co (1), Em (1), Mn (1)	Pm, Re					

Table 1 (*Continued*)

Parasitoid species	H	L	Season	Stem borer	Host plant	BS	IB	FS	PA	AS
Diptera										
Tachinidae										
Linnaemyia sp.	C	Ka	Sr	Bf (3)	Zm	L	k	En	S	PI
	C	Su	Lr	Bf (1)	Zm					
	N	Ka	Ds, Lr, Sr	Bnsp1 (4), Bp (4)	Sm, Pm					
	N	Su	Lr	Bf (1), Scp (1)	Sa, Pc					
Metoposisyrops sesamiae Mesnil	C	Ma	Sr	Cp (2)	Zm	L	k	En	S	PI
	N	Ma	Sr	Co (1), Cp (2), Em (1), Sn (4), Sp (2)	Ci, Cs, Pm, Re, Sa, Td					
Siphona sp.	C	Ka	Ds, Lr, Rs	Bf (16), Bp (6), Sc (29)	Sb, Zm	L	k	En	S/G	PI
	C	Su	Lr	Bf (34)	Sb, Zm					
	C	Mu	Sr	Cp (3), Sc (1)	Zm					
	N	Ka	Ds, Lr, Sr	Bnsp1 (1), Bp (2), Msp (1), Scn (1), Scp (2)	Em, Pc, Pm, Pp, Sm					
	N	Su	Lr	Bf (1), Scn (2)	Pt, Sa					
	N	Mu	Lr	Scnsp3 (1)	Eh					
Sturmiopsis parasitica (Curran)	C	Mu	Lr	Cp (6)	Zm	L	k	En	S/G	PI
	N	Mu	Sr	Co (4), Csp (1)	Cr, Pm					

H, habitat; C, cultivated; N, natural; L, locality; Ka, Kakamega; Ma, Mtito Andei; Mu, Muhaka; Su, Suam; Ds, dry season; Lr, long rainy period; Sr, short rainy period.

Bf, *Busseola fusca*; Bnsp.1, *Busseola* s.l. nov. sp.1; Bp, *Busseola phaia*; C, Crambidae; Co, *Chilo orichalcociliellus*; Cp, *Chilo partellus*; Csp, *Chilo* sp.; Em, *Ematheudes* sp.; Ichneumoninae 1/2/3/4; Mn, *Manga nubifera*; Msp., Manga sp.; N, Noctuidae; Sc, *Sesamia calamistis*; Scn, *Sciomesa nyei*; Scnsp.3, *Sciomesa* nov. sp.3; Scp, *Sciomesa piscator*; Sn, *Sesamia nonagrioides*; Snsp.9, *Sesamia* nov. sp.9; Sp, *Sesamia poephaga*; Tr, Tortricidae.

Ca, *Cynodon aethiopicus*; Cd, *Cyperus dichroostachyus*; Ci, *C. involucratus*; Cs, *C. distans*; Cv, *C. dives*; Cp, *C. papyrus*; Cr, *C. rotundus*; Ec, *Eleusine corocana*; Eh, *Echinochloa haploclada*; Em, *Euclaena mexicana*; Pm, *Panicum maximum*; Pc, *Pennisetum macrourum*; Pp, *P. purpureum*; Pt, *P. trachyphyllum*; Re, *Rottboellia exaltata*; Sa, *Sorghum arundinaceum*; Sb, *S. bicolor*; Si, *Setaria incrassata*; Sm, *S. megaphylla*; Td, *Typha domingensis*; Zm, *Zea mays*; BS, borer growth stage; L, Larva; P, pupa; IB, interaction with borer; i, idiobiont; k, koinobiont; FS, feeding site; Ec, ectoparasite; En, endoparasite; PA, progeny allocation; G, gregarious; S, solitary; AS, attack strategy; DA, direct attack; DS, drill-and-sting; IS, ingress-and-sting; PI, planidial ingress; PS, probe-and-sting; WS, wait-and-sting.

Numbers of specimens recovered are given in parentheses.

Based on seasons, 5% and 7% of parasitoid species were found during the dry season in cultivated and natural habitats, respectively. In total, 67% of species collected were restricted to a particular AEZ, and only one species was recovered from all four AEZs.

Parasitoid diversity on stem borers, host plants, and according to localities and season

Noctuidae and Crambidae were the only families that were heavily parasitized (table 2). For these two families, parasitoid diversity was significantly higher in natural than in cultivated habitats (table 2). *Chilo* spp., *Busseola* spp. and *Sesamia* spp. were the major stem borer genera found in both cultivated and natural habitats (table 3). For these genera, parasitoid diversity was significantly higher in natural than in cultivated habitats (table 3).

Only host plants belonging to the family Poaceae occurred in both cultivated and natural habitats, and parasitoid diversity was significantly higher in natural than in cultivated habitats (table 4). In addition, on the same plant family, parasitoid species and individuals utilizing the ingress-and-sting attack method were more than those utilizing other attack strategies. Among host plant genera, only *Sorghum* spp. occurred in both cultivated and natural habitats. However, parasitoid diversity on *Sorghum* spp. was not significantly different in both habitats (table 5).

Within each and across all localities, parasitoid diversity was significantly higher in natural than in cultivated habitats (table 6). Based on season, parasitoid diversity was significantly highest in natural habitats during the cropping season (table 7). In a similar trend, with the exception of Kakamega, parasitoid diversity was significantly higher in natural than in cultivated habitats during the cropping season in all localities (table 8). In general, parasitoid species composition was different in the two habitats on various stem borer and host plant families or genera, and in different localities, but mainly during the cropping season (tables 2–8).

Table 2 Diversity of parasitoids recovered from four stem borer families in cultivated and natural habitats in Kenya, 2005–2007

	Noctuidae		Crambidae		Pyralidae		Tortricidae	
	C	N	C	N	C	N	C	N
Stem borers/Parasitoids	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)
Stem borers	4 (3601)	22 (1809)	2 (3897)	5 (1911)	1 (23)	3 (240)	0	1 (19)
Parasitoid order/family								
Hymenoptera	9 (232)	16 (40)	8 (260)	7 (46)	1 (2)	5 (10)	0	2 (2)
Braconidae	4 (221)	7 (12)	2 (243)	3 (22)	1 (2)	1 (1)	0	1 (1)
Ichneumonidae	1 (3)	8 (25)	3 (10)	4 (24)	0	3 (8)	0	1 (1)
Others	4 (8)	1 (3)	3 (7)	0	0	1 (1)	0	0
Diptera/Tachinidae	2 (90)	3 (27)	3 (11)	2 (8)	1 (1)	1 (1)	0	0
Total parasitoids								
Species richness (*S*)	11	19	11	9	2	6	0	2
No. individuals (*N*)	322	67	271	54	2	11	0	2
H′	1.19	2.37	0.62	1.61	NC	1.42	NC	NC
t-value	8.72		6.58		–		–	
P-value	< 0.001		< 0.001		–		–	
C_{mH}	0.24		0.53		–		–	

C, cultivated; N, natural habitats; SR, species richness; A, abundance; NC, not computed; *H′*, shannon diversity index; t, test; C_{mH}, morista-horn index.

Table 3 Diversity of parasitoids recovered from three stem borer genera in cultivated and natural habitats in Kenya, 2005–2007

	Busseola spp.		*Sesamia* spp.		*Chilo* spp.		Other spp.	
	C	N	C	N	C	N	C	N
Stem borers/parasitoids	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)
Stem borers	2 (2626)	4 (465)	1 (959)	8 (636)	2 (3897)	3 (1900)	1 (16)	15 (812)
Parasitoid order/family								
Hymenoptera	8 (196)	8 (12)	4 (36)	7 (24)	8 (259)	5 (44)	1 (2)	10 (17)
Braconidae	3 (187)	4 (5)	2 (34)	5 (7)	2 (242)	3 (22)	1 (2)	2 (2)
Ichneumonidae	1 (3)	4 (7)	0	1 (14)	4 (14)	2 (22)	0	7 (14)
Others	4 (6)	0	2 (2)	1 (3)	2 (3)	0	0	1 (1)
Diptera/Tachinidae	2 (60)	2 (13)	1 (30)	1 (6)	3 (11)	2 (8)	1 (1)	3 (9)
Total parasitoids								
Species richness (*S*)	10	10	5	8	11	7	2	13
No. individuals (*N*)	256	25	66	30	270	52	2	26
H′	0.91	1.93	1.13	1.59	0.62	1.47	NC	2.21
t-value	4.54		2.56		6.13		–	
P-value	< 0.001		0.02		< 0.001		–	
C_{mH}	0.26		0.01		0.54		–	

C, cultivated; N, natural habitats; SR, species richness; A, abundance; NC, not computed; *H′*, shannon diversity index; t, test; C_{mH}, morista-horn index.

Discussion

Prior to this study, only ten species of stem borer parasitoids had been reported from natural habitats in Kenya (Khan et al. 1997; Overholt et al. 1997; Polaszek and Khan 1998; Conlong 2000; Songa et al. 2002), in contrast to 27 species in the present study, of which the tachinid *Siphona* sp. was the most common. In cultivated habitats, corroborating results by Ogol et al. (1998) and Zhou et al. (2003) from western and coastal Kenya, respectively, *C. flavipes*, *C. sesamiae* and *P. furvus* were found to be the dominant

Table 4 Diversity of stem borer parasitoids recovered from three host plant families in cultivated or natural habitats in Kenya, 2005–2007

Stem borers/ Parasitoids	Poaceae		Cyperaceae	Typhaceae
	C	N	N	N
	SR (A)	SR (A)	SR (A)	SR (A)
Stem borers				
Species richness	7 (7446)	29 (3178)	11 (343)	2 (131)
Parasitoid order/family				
Hymenoptera	13 (493)	19 (73)	8 (24)	1 (1)
Braconidae	5 (465)	7 (29)	5 (7)	0
Ichneumonidae	4 (13)	11 (43)	2 (15)	0
Others	4 (15)	1 (1)	1 (2)	1 (1)
Diptera/Tachinidae	4 (102)	4 (31)	2 (3)	1 (2)
Total parasitoids				
Species richness (*S*)	17	23	10	2
No. individuals (*N*)	595	104	27	3
H′	1.43	2.59	1.70	NC
t-value	11.24		–	
P-value	< 0.001		–	
C_{mH}	0.45		–	
Parasitoid attack strategy				
Direct attack	1 (4)	2 (7)	0	0
Drill-and-sting	2 (7)	2 (5)	1 (1)	0
Ingress-and-sting	10 (482)	7 (60)	5 (21)	1 (1)
Planidial ingress	4 (102)	4 (31)	2 (3)	1 (2)
Probe-and-sting	0	0	1 (1)	0
Wait-and-sting	0	1 (1)	0	0

C, cultivated; N, natural habitats; SR, species richness; A, abundance; NC, not computed; *H′*, shannon diversity index; t, test; C_{mH}, morista-horn index.

species in addition to *Siphona* sp. These results further confirm the establishment of the exotic species *C. flavipes* in Kenya (Omwega et al. 2006), as it was recovered from its old association host *Chilo partellus* (Swinhoe) in both cultivated and natural habitats.

The richness of pupal parasitoids was quite high on cultivated cereals, perhaps because, on cereal crops, stem borers frequently pupate inside plant stems, whereas on wild host plants, stem borers seldom pupate within plant stems, but rather on the outside, often at the bottom of plants close to the roots in the soil. As such, it is most probable that pupal parasitoids are underestimated in natural habitats. Another possible explanation is that many more stem borers survived to the pupal stage in cultivated grasses either due to high nutritive value (Ofomata et al. 2000) or low predation rates of both parasitized and unparasitized larvae or pupae (Bonhof et al. 1997). Although *Xanthopimpla stemmator* (Thunberg) was not released in Kenya, the pupal parasitoid is being reported for the first time parasitizing stem borers in both cultivated and natural habitats. Considering that *X. stemmator* was released in Ethiopia, Eritrea, Tanzania, Uganda and Zanzibar (C. Omwega, personal communication), it was assumed that the parasitoid got established in Kenya after crossing borders from neighbouring countries.

Similar to our results, Ndemah et al. (2007) in Cameroon and Matama-Kauma et al. (2008) in Uganda reported a high diversity of stem borer parasitoids on wild host plants. However, in contrast, Zhou et al. (2003) in coastal Kenya reported a much higher diversity of parasitoids on cultivated crops. In addition to the fact that parasitoid diversity is not static, as it changes considerably over time as densities of herbivore hosts change (Menalled et al. 2003), differences in species diversity between these studies was attributed to study duration and the numbers of stem borers collected.

The results of Bonhof et al. (1997) and Zhou et al. (2003), in conjunction with those presented here showed that the majority of species recovered are common to both cultivated and natural habitats, whereas only an unknown *Cotesia* sp. was exclusive to natural habitats. In concordance with the definition by Smith et al. (1993), in this study, ‘stenophagous parasitoids’ referred to those parasitoids that were reared from a narrow range of host species while ‘monophagous parasitoids’ are those that were reared from only one host species. Most of the species recovered were stenophagous, and only four species – *Cotesia* sp., *Enicospilus ruscus*, *Pristomerus* sp. and *Syzeuctus ruberrimus* – were monophagous. It is very likely that low host and habitat specificity in most of these parasitoids, and the availability of alternative herbivore hosts in natural habitats allowed for their exchange between habitats (Askew 1994; Hoffmeister and Vidal 1994). Furthermore, for both habitats, more than half of the parasitoids collected were restricted to a particular AEZ, indicating variability in parasitoid species composition among different AEZs. Possibly due to differences in herbivore species composition or the local ecological conditions (Askew and Shaw 1986; Hawkins and Sheehan 1994; Shaw 1994; Sheehan 1994; Tscharntke and Brandl 2004). Altogether, these imply that rare species were probably near the edge of their distribution and do not necessarily survive in high numbers in natural habitats to occasionally spill over onto cereal stem borers.

Table 5 Diversity of stem borer parasitoids recovered from six host plant genera in cultivated or natural habitats in Kenya, 2005–2007

	Sorghum spp.		*Zea* spp.	*Cyperus* spp	*Panicum* spp.	*Pennisetum* spp.	*Setaria* spp.	Other spp.
	C	N	C	N	N	N	N	N
Stem borers/parasitoids	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)
Stem borers								
Species richness	5 (776)	6 (495)	6 (6665)	10 (231)	10 (1382)	12 (267)	4 (398)	19 (879)
Parasitoid order/family								
Hymenoptera	5 (62)	3 (19)	14 (432)	8 (24)	3 (24)	4 (7)	6 (10)	8 (13)
Braconidae	3 (57)	3 (19)	5 (408)	5 (7)	1 (1)	2 (5)	2 (3)	1 (1)
Ichneumonidae	1 (2)	0	5 (12)	2 (15)	2 (23)	2 (2)	4 (7)	5 (10)
Others	1 (3)	0	4 (12)	1 (2)	0	0	0	2 (2)
Diptera/Tachinidae	1 (8)	3 (4)	4 (93)	2 (3)	4 (11)	2 (8)	2 (5)	2 (5)
Total parasitoids								
Species richness (*S*)	6	6	18	10	7	6	8	10
No. individuals (*N*)	70	23	525	27	35	15	15	18
H′	1.27	0.98	1.44	1.70	1.35	1.58	1.88	2.03
t-value	1.13		–	–	–	–	–	–
P-value	0.20		–	–	–	–	–	–
C_{mH}	0.71		–	–	–	–	–	–
Parasitoid attack strategy								
Direct attack	1 (1)	0	1 (3)	0	0	2 (5)	1 (1)	1 (1)
Drill-and-sting	1 (2)	0	2 (5)	1 (1)	1 (2)	0	1 (2)	1 (1)
Ingress-and-sting	3 (59)	3 (19)	10 (431)	5 (21)	1 (1)	1 (1)	2 (5)	2 (2)
Planidial ingress	1 (8)	3 (4)	4 (93)	2 (3)	3 (11)	2 (8)	2 (5)	2 (5)
Probe-and-sting	0	0	0	1 (1)	0	0	0	0
Wait-and-sting	0	0	0	0	0	0	0	1 (1)

C, cultivated; N, natural habitats; SR, species richness; A, abundance; *H′*, shannon diversity index; t, test; C_{mH}, morista-horn index.

Table 6 Diversity of stem borer parasitoids recovered in cultivated and natural habitats in four AEZs in Kenya, 2005–2007

	Suam		Kakamega		Mtito Andei		Muhaka		Total	
	C	N	C	N	C	N	C	N	C	N
Stem borers/ parasitoids	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)
Stem borers	3 (1763)	9 (380)	5 (1001)	13 (839)	2 (983)	13 (621)	3 (3696)	11 (1836)	7 (7443)	32 (3676)
Parasitoid order/family										
Hymenoptera	8 (109)	5 (6)	3 (99)	12 (33)	5 (138)	4 (4)	6 (148)	8 (54)	14 (494)	23 (97)
Braconidae	2 (99)	2 (2)	2 (98)	6 (9)	2 (132)	3 (3)	1 (136)	4 (22)	5 (465)	10 (36)
Ichneumonidae	2 (4)	3 (4)	0	5 (22)	2 (4)	0	3 (6)	3 (31)	5 (14)	11 (57)
Others	4 (6)	0	1 (1)	1 (2)	1 (2)	1 (1)	2 (6)	1 (1)	4 (15)	2 (4)
Diptera (Tachinidae)	2 (35)	2 (5)	2 (55)	2 (15)	1 (2)	1 (10)	2 (10)	2 (6)	4 (102)	4 (36)
Parasitoids										
Species richness (*S*)	10	7	5	14	6	5	8	10	18	27
No. individuals (*N*)	144	11	154	48	140	14	158	60	596	133
H′	1.07	1.85	0.81	2.03	0.43	0.99	0.65	1.76	1.44	2.75
t-value	6.35		7.69		2.00		7.34		14.15	
P-value	< 0.001		< 0.001		0.05		< 0.001		< 0.001	
C_{mH}	0.38		0.19		0.11		0.48		0.36	

C, cultivated; N, natural habitats; SR, species richness; A, abundance; *H′*, shannon diversity index; t, test; C_{mH}, morista-horn index.

Low species diversity of parasitoids in cultivated habitats was very likely due to low stem borer and host plant species diversity. In addition, regular disturbances experienced in modified habitats through agricultural practices such as land tillage, pesticides or fertilizer applications and crop harvest often alter

Table 7 Diversity of stem borer parasitoids recovered during cropping and non-cropping seasons in cultivated and natural habitats in Kenya, 2005–2007

	Season			
	Cropping season		Non-cropping season	
	C	N	C	N
Stem borers/parasitoids	SR (A)	SR (A)	SR (A)	SR (A)
Stem borers	5 (5642)	7 (2594)	2 (1801)	28 (1082)
Parasitoid order/family				
Hymenoptera	13 (366)	20 (80)	8 (128)	8 (15)
Braconidae	5 (347)	8 (30)	2 (118)	4 (6)
Ichneumonidae	5 (10)	10 (46)	2 (4)	4 (11)
Others	3 (9)	2 (4)	4 (6)	0
Diptera (Tachinidae)	4 (89)	4 (23)	1 (13)	3 (13)
Total parasitoids				
Species richness (*S*)	17	24	9	11
No. individuals (*N*)	455	103	141	30
H′	1.47	2.69	1.20	2.15
t-value	12.09		6.73	
P-value	< 0.001		< 0.001	
C_{mH}	0.37		0.24	

C, cultivated; N, natural habitats; CS, cropping season; NCS, non-cropping season; SR, species richness, A, abundance; *H*′, shannon diversity index; t, test; C_{mH}, morista-horn index.

or reduce species interactions across different trophic levels, causing parasitoids to re-colonize crop fields each growing season (Levins and Wilson 1980; Tylianakis et al. 2007). High parasitoid diversity in natural habitats might have been supported by high stem borer species diversity (Le Ru et al. 2006a,b; Ndemah et al. 2007; Matama-Kauma et al. 2008), which in turn provided several alternative hosts to parasitoids the perennial habitats (Kruess 2003). Nevertheless, for both habitats, parasitoid diversity was much higher during the cropping than non-cropping seasons, most probably due to high host plant richness and abundance that enhanced the diversity and abundance of stem borer hosts.

These results and those of Ndemah et al. (2007) and Matama-Kauma et al. (2008), that reported a high diversity of parasitoids on the dominant wild host plant species with high stem borer infestation levels in different ecological regions, suggest that parasitoid species diversity on wild host plants not only varied with host plant species composition occurring among localities, but is also likely to be higher on dominant wild host plant species harbouring relatively higher stem borer diversity and abundance than on other host plant species. For natural habitats, the abundance of parasitoids from wild host plants was quite low, probably due to three reasons. First, most of the parasitoids recovered from wild host plants were solitary compared to the higher number of gregarious species recorded on cultivated cereals. Since clutch size is positively correlated with host size (Ode 2006; Jervis et al. 2008), it is very likely that gregarious species in natural habitats revert to a solitary status by lowering their clutch size (Waage 1989; Godfray 1994) in response to the small size of stem borers encountered in wild host plants (Haile and Hofsvang 2002; Sétamou et al. 2005). Secondly, low fitness of parasitoids on wild host plants as a result of poor hosts (both herbivores and plants) quality (Setamou et al. 2005; Ode, 2006; Jervis et al. 2008). Thirdly, low host availability owing to low stem borer densities (Ndemah et al. 2007; Matama-Kauma et al. 2008), high larval mortality (Sétamou et al. 1993) and host-finding difficulties in natural habitats (Vinson 1976; Takabayashi et al. 1991; Gauld and Gaston 1994). By contrast, cultivated crops supply more abundant herbivore hosts of much higher quality because of their high nutritious content and very low levels of toxic allelochemicals rather than wild host plants (Shanower et al. 1993; Benrey et al. 1998; Ofomata et al. 2000), thereby supporting higher parasitoid survival and abundance.

Considering that the ingress-and-sting attack method was the most common attack strategy utilized by parasitoids on both cereals and wild host plants, these results contradict earlier suggestions

Table 8 Diversity of stem borer parasitoids recovered during cropping and non-cropping seasons in cultivated and natural habitats in four localities in Kenya, 2005–2007

	Kakamega				Suam				Mtito Andei				Muhaka			
	CS		NCS		CS		NCS		CS		NCS		CS		NCS	
	C	N	C	N	C	N	C	N	C	N	C	N	C	N	C	N
Stem borers/parasitoids	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)	SR (A)
Stem borers	5 (338)	13 (205)	3 (128)	5 (44)	3 (598)	10 (124)	2 (107)	3 (13)	2 (241)	8 (237)	2 (261)	14 (187)	3 (1144)	12 (255)	3 (298)	8 (152)
Parasitoid order/family																
Hymenoptera	2 (82)	11 (32)	2 (17)	1 (1)	6 (83)	4 (4)	4 (26)	2 (2)	4 (110)	4 (4)	3 (28)	0	5 (91)	6 (40)	4 (57)	5 (14)
Braconidae	2 (82)	7 (10)	1 (16)	0	2 (76)	1 (1)	1 (23)	1 (1)	2 (107)	3 (3)	1 (25)	0	1 (82)	2 (17)	1 (54)	3 (5)
Ichneumonidae	0	3 (20)	0	1 (1)	3 (3)	3 (3)	1 (1)	1 (1)	2 (2)	0	1 (2)	0	3 (5)	3 (22)	1 (1)	2 (9)
Others	0	0	1 (1)	0	1 (1)	0	2 (2)	0	1 (1)	1 (1)	1 (1)	0	1 (4)	1 (1)	2 (2)	0
Diptera (Tachinidae)	2 (44)	2 (9)	1 (11)	2 (6)	2 (33)	1 (1)	2 (2)	2 (4)	1 (2)	1 (7)	0	1 (3)	2 (10)	2 (6)	0	0
Total parasitoids																
Species richness (S)	4	13	3	3	8	5	6	4	5	5	3	1	7	8	4	5
No. individuals (N)	126	41	28	7	116	5	28	8	112	11	28	3	101	46	57	14
H′	NC	1.97	NC	NC	1.08	1.48	0.71	NC	0.38	1.16	NC	NC	0.79	1.69	NC	1.33
t-value	–		–		2.25		–		2.74		–		5.61		–	
P-value	–		–		0.05		–		0.02		–		0.001		–	
C_{mH}	–		–		0.01		–		0.14		–		0.81		–	

CS, cropping season; NCS, non-cropping season; C, cultivated; N, natural habitats; SR, species richness; A, Abundance; NC, not computed; H′, shannon diversity index; t, test; C_{mH}, morista-horn index.

(Hawkins et al. 1987; Muturi et al. 2005) that the drill-and-sting attack method would be more common on wild host plants because of the ease of accessing stem borer hosts within thin-stemmed wild host plants. Differences observed in these studies might have been due to the number of parasitoid and host plant species studied. Both Hawkins et al. (1987) and Muturi et al. (2005) conducted investigations on a single parasitoid species, and on not more than two species of wild host plants, while 33 parasitoids and 38 wild host plant species were considered in this study.

In conclusion, these results showed that stem borer parasitoid species diversity is much higher in natural than in cultivated habitats. Most parasitoid species found were stenophagous and parasitized stem borer hosts in both cultivated and natural habitats. Natural habitats surrounding cereal crops appeared to serve as refugia for sustaining the diversity of stem borer parasitoids from adjacent cereal fields. However, to gain further insight into the role of the natural habitats in the management of cereal stem borer pests, more studies are necessary to elucidate the influence of trophic interactions or environmental factors on parasitoid richness and abundance, the relationship between parasitoid richness and parasitism rates, as well as specific interactions or suitability of stem borer species found in natural habitats to the dominant parasitoid species found in cultivated habitats.

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