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Host–parasitoid community model and its potential application in biological control of cereal stemborers in Kenya

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Abstract A two-host–two-parasitoid model was con-structed to assess the effects of the introduced larval parasitoid, the braconid *Cotesia flavipes*, on its primary target host, the invasive crambid *Chilo partellus*, and on secondary host species, in inter-specific competition with *Cotesia sesamiae*, the main native parasitoid species of stemborers in Kenya. The model assumed that: (1) there was no host discrimination by either parasitoid species; (2) *Cotesia flavipes* was the superior competitor that out-com-peted *Cotesia sesamiae* when the host was suitable; and (3) *Cotesia flavipes* could only develop in an unsuitable host if it had been previously parasitized by *Cotesia sesamiae*. Model parameters were estimated from surveys conducted in Kenya and from laboratory experiments. Different sce-narios of host and parasitoid species composition and host suitability occurring in the different ecological zones in Kenya were analyzed. Results indicated that: (1) the coex-istence of stemborer host populations are determined by their population growth rates, the degree of aggregation of the parasitoids and their searching efficiency; (2) in the regions where both the invasive and the predominant native host species were suitable to either parasitoid species, stemborer densities would be reduced to and controlled at low densities, and *Cotesia flavipes* would become the dominant parasitoid species. However, the extinction or predominance of the native stemborer species depends on the ratio of the growth rates of exotic and native stemborers and their relative searching efficiencies; and (3) if the native host species was acceptable but unsuitable to *Cotesia flav-ipes*, the parasite would not become established.

Keywords Ecological zones ·
Exotic and native host species · Inter-specific competition ·
Pyralid and noctuid borer species ·
Suitable and unsuitable host species ·
Two-host–two-parasitoid model

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Introduction

The crambid *Chilo partellus* (Swinhoe) was accidentally introduced into eastern Africa sometimes before the 1930s (Tams 1932). It has become the most serious pest of cereals in the lowlands of the region and is now expanding its distribution to higher elevations (Kfir 1997; Overholt et al. 2000; Zhou et al. 2001a). Kenya has a wide range of ecological zones, which vary in their stemborer species compositions. There are several native stemborer species in the region, whose importance vary with agro-ecozone, such as the noctuids *Sesamia calamistis* Hampson and *Busseola fusca* (Fuller), the crambid *Chilo orichalcociliellus* Strand

and the pyralid *Eldana saccharina* (Walker). Evidence showed that, in some regions, *Chilo partellus* is displacing native stemborer species (Bate et al. 1991; Overholt et al. 1994a; Kfir 1997). For example, in the past 40 years, there is evidence that *Chilo partellus* is increasingly displacing the native crambid stemborer *Chilo orichalcociliellus*, whose relative importance decreased from 66 to 14% (Mathez 1972; Zhou et al. 2001a).

The most common native larval parasitoid, *Cotesia sesamiae* (Cameron) (Hymenoptera: Braconidae), is closely related to the gregarious larval endoparasitoid *Cotesia flavipes* Cameron, which was introduced into Kenya in 1991 from Asia and released in the coastal area in 1993 (Overholt et al. 1994a). *Cotesia sesamiae* was not able to control the invasive pest, and its parasitism typically never exceeded 5% (Sallam et al. 1999). By contrast, *Cotesia flavipes* reduced pest infestations by 57% and increased maize yields by 10–15% by 2000 (Zhou et al. 2001b). It has now become the major mortality factor of stemborers at the coast (Zhou et al. 2001b), and its parasitism had increased linearly to about 20–30% (Jiang et al. 2006). Since then, this parasitoid was released and became permanently established in nine more countries in East and Southern Africa (Omwega et al. 2006).

Suppression of cereal stemborers in Africa normally involves two or three host species and two oligophagous gregarious parasitoid species. The success of *Cotesia flavipes* not only depends on its adaptation to new abiotic conditions and on the suitability of potential hosts, but also on inter-specific competition with native parasitoid species (Mackauer 1990). However, multiple parasitism can lead to a displacement of one species by another, which may happen when an exotic parasitoid is introduced into a new area. Laboratory studies found that both *Cotesia flavipes* and *Cotesia sesamiae* would accept all four borer species

(Table 1) (Overholt et al. 1997), but eggs of *Cotesia flavipes* are encapsulated in *B. fusca* as a result of physiological incompatibility (Ngi-Song et al. 1995). However, if *B. fusca* was parasitized by both *Cotesia sesamiae* and *Cotesia flavipes*, only *Cotesia flavipes* emerged from those hosts parasitized by *Cotesia sesamiae* first (Ngi-Song et al. 2001). Inter-specific competition between the two parasitoid species with either *Chilo partellus* or *S. calamistis* larvae indicated that *Cotesia flavipes* out-competed *Cotesia sesamiae* (Sallam et al. 2002). *Chilo orichalcociliellus* occupies a similar niche as *Chilo partellus* (Ofomata et al. 1999), and is susceptible to parasitism by both *Cotesia sesamiae* and *Cotesia flavipes* (Ngi-Song et al. 1995). *Eldana saccharina* is unsuitable to either parasitoid species (Hailemichael et al. 1997; Overholt et al. 1997), even in a multi-parasitism situation.

To explore the regulatory mechanisms of host–parasitoid interactions, the Nicholson–Bailey's model is considered to be the basic model (Nicholson and Bailey 1935). It has been used to study one-parasitoid–one-host systems (Holling 1959; Hassell and Varley 1969; Royama 1971; Rogers 1972; Hassell and May 1973; Allen 1975; May 1978; Hassell and Godfray 1992), multi-parasitoid–one-host systems (May and Hassell 1981; Shimada and Fuji 1985; Shimada 1999), and one-parasitoid–multi-host systems (Comins and Hassell 1976, 1987; Holt and Lawton 1993; Bonsall and Hassell 1999). Wilson et al. (1996) studied the community stability of a food web of two hosts and their specialist parasitoid with the invasion of a generalist parasitoid. By comparing foraging efficiencies and within-host competition behavior, Schellhorn et al. (2002) showed that an introduced parasitoid reduced the native parasitoid population on aphids in the greenhouse. In general, studies on the effect of foraging efficiency of parasitoids on the coexistence of host and parasitoid species and their

Table 1 Variables of the stemborer host and parasitoid species used in the model system, and host acceptability and suitability for each parasitoid species

Species	P_{EX}		P_{NA}	
	Cotesia flavipes		*Cotesia sesamiae*	
	Acceptability	Suitability	Acceptability	Suitability
H_{EX} *Chilo partellus*	+++	+++	+++	++
H_{NA} *Sesamia calamistis*	+++	++	+++	+++
H_{NA} *Chilo orichalcociliellus*	+++	++	+++	++
H_{NA} *Busseola fusca*	+++	–	+++	+
H_{NA} *Eldana saccharina*	+	–	+	–

H_{EX}, H_{NA} denote the exotic and native stemborer species population

P_{EX}, P_{NA} denote the population density of the exotic and native parasitoid species, respectively

– Not suitable

The number of plus signs represents the degree of preference of host suitability of a borer species by a parasitoid

dynamics in the system are of utmost importance, especially in view of the short life span of *Cotesia* spp. under field conditions.

In this paper, a two-host–two-parasitoid model was developed, which focused on the system coexistence characteristics of different degrees of suitability of host species to parasitoids and their host searching abilities. We tried to answer the following questions. What will be the effect of different stemborer and parasitoid species compositions occurring in different ecological zones in Kenya on the stability of the system? Will *Cotesia flavipes* eventually suppress *Chilo partellus* populations? If it does, will populations of other secondary stemborer species increase? Would the introduced parasitoid replace the native parasitoid? We attempted to model the performance of parasitoids in the field and then discussed the conditions for coexistence of stemborer and parasitoids in the context of summarized field data collected in Kenya. Thus, insight gathered here may also be useful for predicting the success rate of biological control for other countries in East and Southern Africa with similar ecological conditions and stemborer species compositions. This will help to modify the release strategy in order to make future releases more cost efficient.

Materials and methods

Stemborer species compositions in the study regions and cropping system

Figure 1 shows the regions under study in Kenya and Table 2 provides the species composition (Zhou et al. 2001a) and environmental conditions for each region. *Chilo partellus* is the dominant stemborer of maize in the lowlands (Region A) (Overholt et al. 1997), while *S. calamistis* is common in some mid-altitude areas (Region B). *Busseola fusca* is widely distributed in the mid-altitudes and highlands (Region C) (Kfir and Bell 1993; Ogedah 1999). Secondary native stemborer species of lesser importance include *Chilo orichalcociliellus*, mainly found in the coastal regions (Region A), and *E. saccharina*, which is relatively common in the Lake Victoria area (Region D) (Zhou and Overholt 2001).

The lowlands and mid-altitudes allow for two cropping seasons while in the highlands there is only one. In the lowlands, maize maturity is reached at 3–4 months, in the mid-altitudes at 4–5 months, and in the highlands at > 6 months (Hassan et al. 1998). Oviposition by *Chilo* spp. and the noctuid borer species starts from 2–3 weeks of crop emergence and continues to the tasseling stage (Alghali 1985; Bate et al. 1991; Sémeglo 1997; Ndemah et al. 2001). *Eldana saccharina*, on the other hand, oviposits
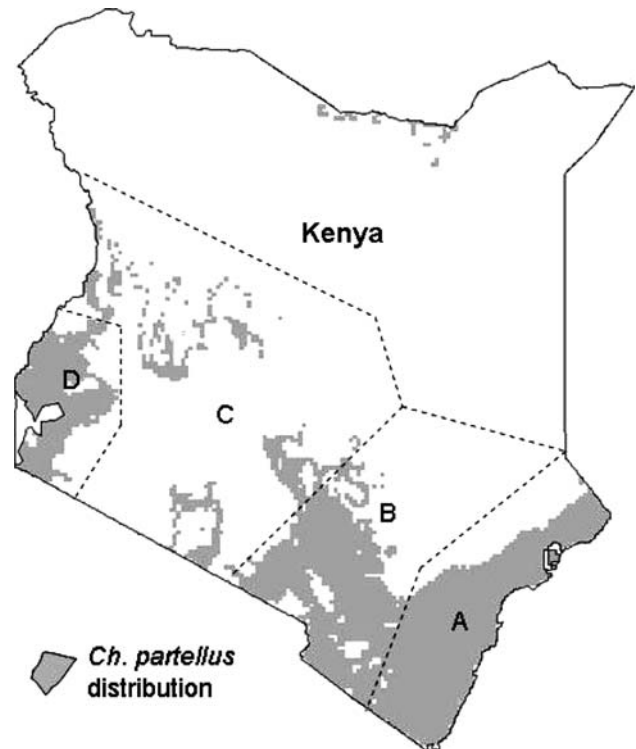
Fig. 1 Ecological zones of stemborer distributions in Kenya. Detailed distribution of stemborers referred to Zhou et al. (2001b)

only on tasseling and older plants (Atachi et al. 2005). Thus, the duration of plant growth stages suitable for oviposition is relatively short and overlapping generations are not common. During the off-season, when conditions are unfavorable, *Chilo partellus* and *B. fusca* diapause in the larval stage.

The stemborer–parasitoid model

For simplification, only two borer species were considered in the model, namely *Chilo partellus* and the most important native species in a given region (see Table 2).

Stemborer populations

$$H_{EX}^{t+1} = \lambda_{H_{EX}} H_{EX}^t f_{H_{EX}}(P_{EX}^t) f_{H_{EX}}(P_{NA}^t) \qquad (1-1)$$

$$H_{NA}^{t+1} = \lambda_{H_{NA}} H_{NA}^t f_{H_{NA}}(P_{EX}^t) f_{H_{NA}}(P_{NA}^t) \qquad (1-2)$$

H_{EX}^t and H_{NA}^t denote population densities of exotic and the native host species, respectively, at time t. $\lambda_{H_{EX}}$ and $\lambda_{H_{NA}}$ are the growth rates of the two hosts. $f_{H_{EX}}(P_i)$ and $f_{H_{NA}}(P_i)$ ($i =$ EX, NA) represent the probabilities of the exotic or native host escaping from parasitism by the introduced or the native parasitoid, respectively. The intra- and inter-specific competitions of the hosts are ignored as intra-specific competition is seldom identified as a key source of mortality (Cornell and Hawkins 1995), and inter-specific

Table 2 The geographic and climatic conditions, and the importance of pyralid and noctuid borer species in the study regions

Region	Altitude (10^3 m)	Rainfall (10^3 mm)	T_{max} (°C)	T_{min} (°C)	Bf	Co	Cp	Es	Sc
A (Coast)	L (< 0.5)	1.0–1.2	29.4	20.0	–	++	+++	–	++
B (East)	L (0.5–1.2)	0.5–1.0	28.6	16.4	+	–	+++	–	+
C (West)	H (> 1.5)	0.8–2.5	23.0	10.0	+++	–	+	–	++
D (Lake)	M (1.0–1.5)	1.0–2.0	23.3	13.4	++	–	+++	+	–

Bf Busseola fusca, *Co* Chilo orichalcociliellus, *Cp* Chilo partellus, *Es* Eldana saccharina, *Sc* Sasamiae calamistis; *L, H, M* low and high lands, mid-altitude

– Absence of a species

The number of plus signs represents the importance of a borer species in a region

competition is not common for inside tunnel feeding borers.

Parasitoid populations

Three situations based on different degrees of host suitability and inter-specific competition of parasitoid species were formulated.

a) If both stemborer hosts are suitable,

$$P_{EX}^{t+1} = \gamma_{11}H_{EX}^t\left(1 - f_{H_{EX}}\left(P_{EX}^t\right)\right) + \gamma_{12}H_{NA}^t\left(1 - f_{H_{NA}}\left(P_{EX}^t\right)\right)$$
$$(2-1a)$$

$$P_{NA}^{t+1} = \gamma_{21}H_{EX}^t f_{H_{EX}}\left(P_{EX}^t\right)\left(1 - f_{H_{EX}}\left(P_{NA}^t\right)\right)$$
$$+ \gamma_{22}H_{NA}^t f_{H_{NA}}\left(P_{EX}^t\right)\left(1 - f_{H_{NA}}\left(P_{NA}^t\right)\right) \quad (2-2a)$$

$$f_{H_i}(P_{EX}) = \left(1 + \frac{a_{H_i}P_{EX}}{k_{EX}(c + a_{H_i}\gamma_{11}(1 - a_H)H_i)}\right)^{-k_{EX}}$$

$$f_{H_i}(P_{NA}) = \left(1 + \frac{b_{H_i}P_{NA}}{k_{NA}(c + b_{H_i}H_i)}\right)^{-k_{NA}} (i = EX, NA)$$

P_{EX}^t and P_{NA}^t represent the population densities of females of the introduced and the native parasitoid species, respectively. γ_{ij} ($i, j = 1, 2$) is the number of female progeny of parasitoids that successfully emerged from a parasitized host (Table 3), which depends on specific combinations of host species, multi-parasitism and parasitoid species. $f_{H_{EX}}(P_i)$ and $f_{H_{NA}}(P_i)$ are described by a negative binomial function (May and Hassell 1981) with a type II functional response (Mills 2001), where a_{H_i} and b_{H_i} are the searching efficiencies of introduced and native parasitoid species for a specific host species, and c is the attack capacity or maximum number of hosts that the parasitoids attack in a lifetime; it is assumed to be the same for both parasitoid species. k_i is the degree of clumping in parasitoid attacks (May and Hassell 1981). Equation 2–2a indicated that the exotic parasitoid P_{EX} always out-competes the native parasitoid with either native or exotic

hosts, and the native parasitoid P_{NA} can develop only if any host escapes from parasitism by P_{EX} (Sallam et al. 2002).

b) If H_{NA} is an unsuitable host for P_{EX},

$$P_{EX}^{t+1} = \gamma_{11}H_{EX}^t\left(1 - f_{H_{EX}}\left(P_{EX}^t\right)\right)$$
$$+ \gamma_{12}H_{NA}^t\left(1 - f_{H_{NA}}\left(P_{NA}^t\right)\right)\left(1 - f_{H_{NA}}\left(P_{EX}^t\right)\right)$$
$$(2-1b)$$

$$P_{NA}^{t+1} = \gamma_{21}H_{EX}^t f_{H_{EX}}\left(P_{EX}^t\right)\left(1 - f_{H_{EX}}\left(P_{NA}^t\right)\right)$$
$$+ \gamma_{22}H_{NA}^t\left(1 - f_{H_{NA}}\left(P_{NA}^t\right)\right) \quad (2-2b)$$

In this case, the exotic parasitoid P_{EX} can only develop in a native host if it is parasitized by the native parasitoid P_{NA} first, otherwise it will be encapsulated (Eq. 2–1b) (Ngi-Song et al. 2001).

c) If H_{NA} is not suitable to either parasitoid, it is a special case where γ_{12} and γ_{22} are both 0.

Parameter estimation

The nominal parameters of the model were estimated or assigned from field and laboratory experiments and references (Table 3). The growth rates of the stemborer populations ($\lambda_{H_{EX}}$ and $\lambda_{H_{NA}}$) are the multiplication of fecundity, sex ratio and survivorship of the species. For all stemborer species, sex ratio is assumed to be 0.5. The survivorship was estimated at less than 10% (Oloo 1989; Ogedah 1999; Jiang and Schulthess 2005; Sétamou et al. 2005). Data on fecundity and egg viability of each species were obtained from Usua (1968), Kumar and Saxena (1985), Unnithan (1987), Berger (1989), Gebre-amlak (1989), Unnithan and Paye (1990), Shanower et al. (1993), Ofomata et al. (2000) and Ratnadass et al. (2001).

Degree of aggregation of parasitoids (k_{EX}, k_{NA}) were estimated from the ratio of the variance (V) to the mean number of parasitized stemborer hosts (m) estimated from monthly field sampling in coastal, eastern and central Kenya from 1996 to 1998, respectively (Songa 1999; Zhou et al. 2001a). Its standard error was estimated by bootstrap

Table 3 Nominal parameters of Eqs. 1 and 2 for model simulation of each regions of Kenya

Parameters	Description	Regions			
		A	B	C	D
$\lambda_{H_{EX}}$	Growth rate of H_{EX} (generation)	30	35	20	30
$\lambda_{H_{NA}}$	Growth rate of H_{NA}	12	30	33	50
γ_{11}	Female progeny of one parasitized H_{EX} larva by P_{EX} (number/parasitoid)	21.9 ± 9.5	20.1 ± 9.5	7.9 ± 5.1	19.4 ± 8.6
γ_{12}	Female progeny of one parasitized H_{NA} larva by P_{EX}	19.5 ± 15.2	22.4 ± 15.2	6.0 ± 0.3	16.3 ± 0.3
γ_{21}	Female progeny of one parasitized H_{EX} larva by P_{NA}	19.2 ± 11.6	17.2 ± 11.6	7.0 ± 9.4	16.8 ± 9.4
γ_{22}	Female progeny of one parasitized H_{NA} larva by P_{NA}	17.9 ± 5.6	25.9 ± 7.2	5.2 ± 1.2	12.3 ± 4.1
$a_{H_{EX}}$	Searching efficiency of P_{EX} to H_{EX}	0.0065			
$a_{H_{NA}}$	Searching efficiency of P_{EX} to H_{NA}	0.0037			
$b_{H_{EX}}$	Searching efficiency of P_{NA} to H_{EX}	0.0020			
$b_{H_{NA}}$	Searching efficiency of P_{NA} to H_{NA}	0.0023			
C	Maximum number of hosts that the parasitoid can attack	6			
k_{EX}	Aggregation degree of P_{EX}	1.29 ± 0.23	1.01 ± 0.15	1.95 ± 0.64	N/A
k_{NA}	Aggregation degree of P_{NA}	1.70 ± 0.55	0.53 ± 0.03	2.02 ± 0.17	N/A

method using R language (Venables et al. 2007). However, the survey in Western Kenya did not use random sampling, and the data were not used. It was assumed that there was no difference in k for the different hosts by either parasitoid species as there was no host discrimination by either species (Sallam et al. 2002). The searching efficiency parameters $(a_{H_{EX}}, a_{H_{NA}}, b_{H_{EX}}, b_{H_{NA}})$ were estimated from the functional response of *Cotesia flavipes* at different host densities of *Chilo partellus* and *S. calamistis* (Sallam 1998). It was found that *Cotesia flavipes* had a higher searching efficiency for *Chilo partellus* than *Cotesia sesamiae*, but there was no difference in the searching efficiency for native borer species among the parasitoids (Sallam et al. 1999). Therefore, in the model, it is assumed that $\frac{a_{H_{EX}}}{a_{H_{NA}}} > 1$ and $\frac{b_{H_{EX}}}{b_{H_{NA}}} < 1$. Number of female progeny (γ_{11}, $\gamma_{12}, \gamma_{21}, \gamma_{22}$) and sex ratio of *Cotesia sesamiae* and *Cotesia flavipes* were estimated by Ngi-Song et al. (1995, 1998, 2001), Mbapila (1997) and Sallam (1998). Their progeny in different eco-regions were estimated by Weibull model of temperature dependence (Weibull 1951).

There was no estimate available for the maximum numbers of hosts that a parasitoid attacks in a lifetime. *Cotesia* adults have a life span of a maximum of 3 days. It enters from the exit hole to search for the host and is often killed by the host inside the tunnel (Potting et al. 1997; Takasu and Overholt 1997). Therefore, the number of hosts than can be parasitized is limited. In the model, the number of host encounters was estimated from the multiplication of average progeny of 30 and the parasitism of 20%, which was a maximum of 6.

For the two-host and two-parasitoid system, since both parasitoid species are not specific, the model equations become non-algebraic. Therefore, we used numeric simulation methods. The persistence criterion is that all species should have a population density greater than 1.0E−6 after 500 iterates, all starting from the same initial density of population.

Results

Before the introduction of the exotic parasitoid, only the native parasitoid species was present. In this two-host–one-parasitoid system, there was no 'apparent competition' (Holt 1977; Bonsall and Hassell 1999) as the parasitoid had no choice of host; the host lives cryptically inside the stem tunnel and the parasitoid appears to have no means of determining the host species before entering the tunnel (Ngi-Song et al. 1996; Potting et al. 1997). The relationship between the degree of aggregation of the parasitoid k_{NA} and the stemborer growth rate ratio $\frac{\lambda_{H_{EX}}}{\lambda_{H_{NA}}}$ indicated that the exotic stemborer easily out-competed the native species, as H_{EX} has a higher growth rate than H_{NA} (Sallam et al. 2001), unless P_{NA} had a highly aggregated distribution (Fig. 2). An increase in the searching efficiency ratio of the native parasitoid $\frac{b_{H_{EX}}}{b_{H_{NA}}}$ would be favorable for the existence of H_{NA} (Fig. 2). If $k_{NA} > 1$, both stemborer populations outbreak.

Coastal region (A)

In region A (Fig. 1), *Chilo partellus* and *Chilo orichalcociliellus* are the dominant exotic and native stemborer species, respectively (Table 2), and the growth rate of *Chilo partellus* is higher than that of *Chilo*
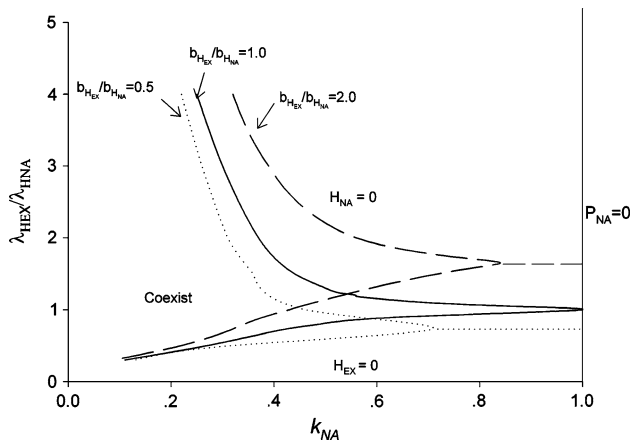
Fig. 2 The regions of parameter space representing the two-host–one-parasitoid system, where the system is observed for given parameter values. The X-axis reflects the aggregation degree of native parasitoid, low values of k_{NA} imply high aggregation. The Y-axis is the relative host population growth rate $\left(\frac{\lambda_{H_{EX}}}{\lambda_{H_{NA}}}\right)$. The species that will go extinction is mentioned in the figure

orichalcociliellus $\left(\frac{\lambda_{H_{EX}}}{\lambda_{H_{NA}}} > 1\right)$ (Mbapila 1997; Table 3). Before the introduction of *Cotesia flavipes*, *Chilo partellus* was dominant and increasingly displaced *Chilo orichalcociliellus* (Fig. 2). After its introduction, the model predicted that the coexistence of four species was only possible when both k were very small (Fig. 3a). Otherwise, it would cause extinction of the native stemborer; *Cotesia sesamiae* could survive at low densities if k_{EX} was smaller than 0.65. In this case, *Chilo partellus* populations could be controlled at low density. An increase in k_{EX} would increase the risk of extinction of both the native stemborer and the native parasitoid species. The inter-specific competition between exotic and native parasitoids helped to stabilize the system; otherwise outbreaks of both stemborers would occur.

Using parameters in Table 3, the model showed that the native stemborer species was at risk to decline to extinction before the release of the exotic parasitoid (Fig. 2). After its release, both the native stemborer and the native parasitoid species were at risk of decline, as values of k_{EX} and k_{NA} in the coast of around 1 (Fig. 3a). *Cotesia flavipes* populations would stabilize with time and reduce *Chilo partellus* to low densities. Survey data from 1965 to 1969 (Mathez 1972) showed that *Chilo orichalcociliellus* (H_{NA}) was 66.4% of the total stemborers collected, *Chilo partellus* (H_{EX}) was 28.5%, while the remainder were *S. calamistis*. Thereafter, density of *Chilo orichalcociliellus* decreased and between 1995 and 1998, it accounted for only 8.66–18.6% of all host species (Zhou et al. 2001a). Concomitantly, the relative importance of *Chilo partellus* increased and accounted for 67% by 1998 and 87% by 2004 (Jiang et al. 2006).
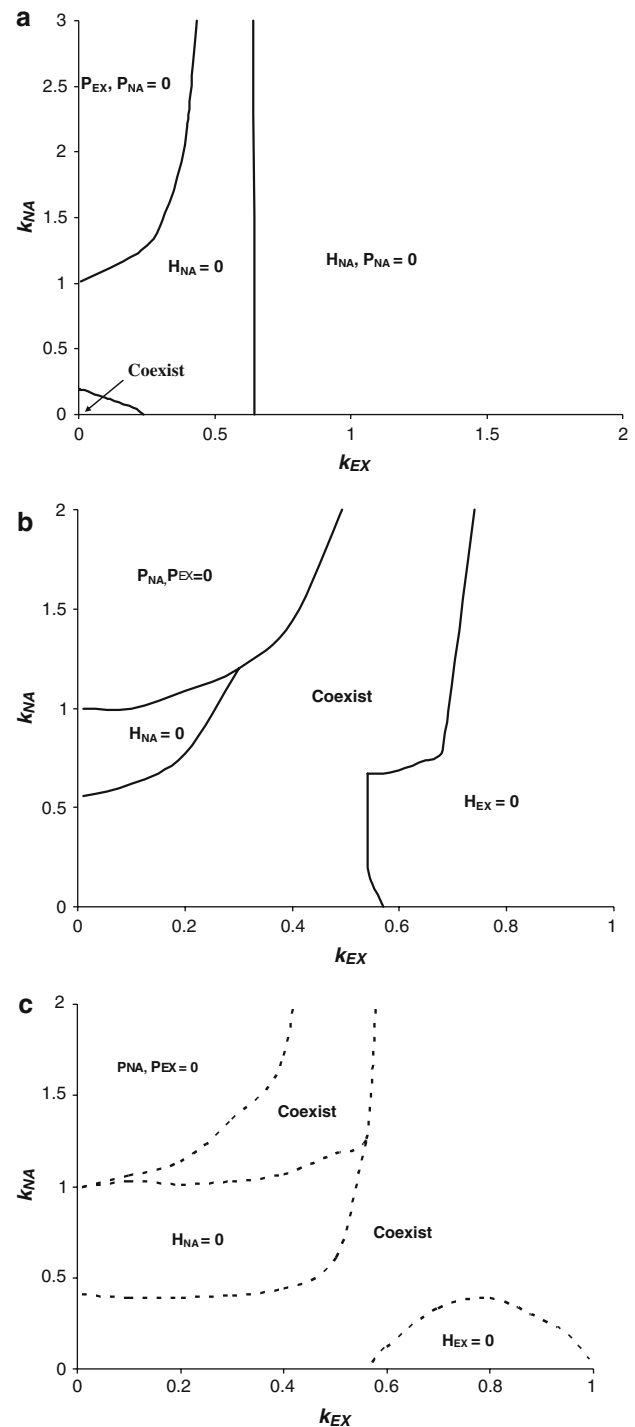
Fig. 3 The regimes of parameter space representing the two-host–two-parasitoid system, when both hosts are suitable for parasitoids. The X- and Y-axis reflects the aggregation degree of exotic and native parasitoids, respectively; low values of k imply high aggregation $\left(\frac{a_{H_{EX}}}{a_{H_{NA}}} = 1.76 \text{ and } \frac{b_{H_{EX}}}{b_{H_{NA}}} = 0.87\right)$. The species that will be extinct is mentioned in the figure; **a** Coastal Kenya (Region A), $\frac{\lambda_{H_{EX}}}{\lambda_{H_{NA}}} = 2.5$; **b** Eastern Kenya (Region B) $\frac{\lambda_{H_{EX}}}{\lambda_{H_{NA}}} = 1.17$; **c** Parameters are the same as in **b**, except for $\frac{b_{H_{EX}}}{b_{H_{NA}}} = 0.5$

After the release of *Cotesia flavipes* in 1991, *Chilo partellus* densities declined by 57% with an increase in parasitism by *Cotesia flavipes* to 12% in 1997 (Zhou et al. 2001b). Parasitism increased further to 20–30% between 2004 and 2005 with a decrease in pest populations of an additional 20% (Jiang et al. 2006). However, parasitism of *Cotesia sesamiae* remained at only about 2%. Therefore, the field results support the dominance of exotic stemborer and decline of the native stemborer and native parasitoid with the introduction of exotic parasitoid.

Eastern Kenya (B)

In region B (Fig. 1), the model assumed that *Chilo partellus* had a higher growth rate than *S. calamistis* $\left(\frac{\lambda_{H_{EX}}}{\lambda_{H_{NA}}} > 1\right)$. Before the introduction of *Cotesia flavipes*, the system was similar to the situation at the coast, namely that *Chilo partellus* was the dominant stemborer species. The model with the parameters in Table 3 predicted that, after release of *Cotesia flavipes*, the coexistence of stemborer and parasitoid species is mainly dependent on k_{EX} (Fig. 3b), and that in the situation of species coexistence, *Cotesia flavipes* would dominate over *Cotesia sesamiae*. The native stemborer would become extinct if k_{EX} was small, and if k_{NA} was between 0.5 and 1. If k_{EX} was greater than 0.55, the exotic stemborer would become extinct. The stemborer populations would outbreak if either native or exotic parasitoid was randomly distributed ($k_{EX} > 1$) (Fig. 3b). The decrease of $\frac{b_{H_{EX}}}{b_{H_{NA}}}$ or the increase of $\frac{a_{H_{EX}}}{a_{H_{NA}}}$, which meant that either the native and exotic parasitoid had a higher searching efficiency for their old than the new association host species, would increase the possibility of coexistence where the upper region of coexistence is stable and the second is periodic. However, it reduces the region of extinction of exotic stemborer (Fig. 3c). Coexistence is possible if k_{EX} is greater than 1.

Field data of k_{EX} and k_{NA} in region (B) in most cases are less than 1, and k_{NA} is smaller than 0.5, therefore the model coexists or the exotic stemborer population declines. Survey data from 1996–1997 to 2002–2004 showed that *Chilo partellus* was dominant averaging about 83.5% of the total species, but densities decreased from 1997 to 2004 (J.M. Songa, unpublished data). *Cotesia flavipes* was released in this region in 1997 on-station and in 2003 on-farm, and it became firmly established in the area (Songa et al. 2007). Since the release of *Cotesia flavipes* had been relatively recent, the survey data reflected the scenario before establishment of the exotic parasitoid, thus the exotic stemborer dominated (Fig. 2). Data in Eastern Kenya between 2002 and 2005 indicated a decrease of the relative importance of *Chilo partellus* from 80 to 30% (J.M. Songa,

unpublished data), which indicates the decline of exotic stemborer. However, coexistence is possible if the relative searching efficiency of parasitoids decreased. The model predicted that *Cotesia flavipes* would establish successfully in this region, and that *Chilo partellus* densities would be reduced.

Highland (C)

In region C (Fig. 1), the dominant native stemborer species was *B. fusca*, which is not a suitable host for *Cotesia flavipes*. The model assumed a lower growth rate of *Chilo partellus* compared to *B. fusca* $\left(\frac{\lambda_{H_{EX}}}{\lambda_{H_{NA}}} < 1\right)$. Without *Cotesia flavipes* in the system, H_{EX} could coexist with H_{NA} when either k_{NA} or $\frac{b_{H_{EX}}}{b_{H_{NA}}}$ was small (Fig. 2). The native
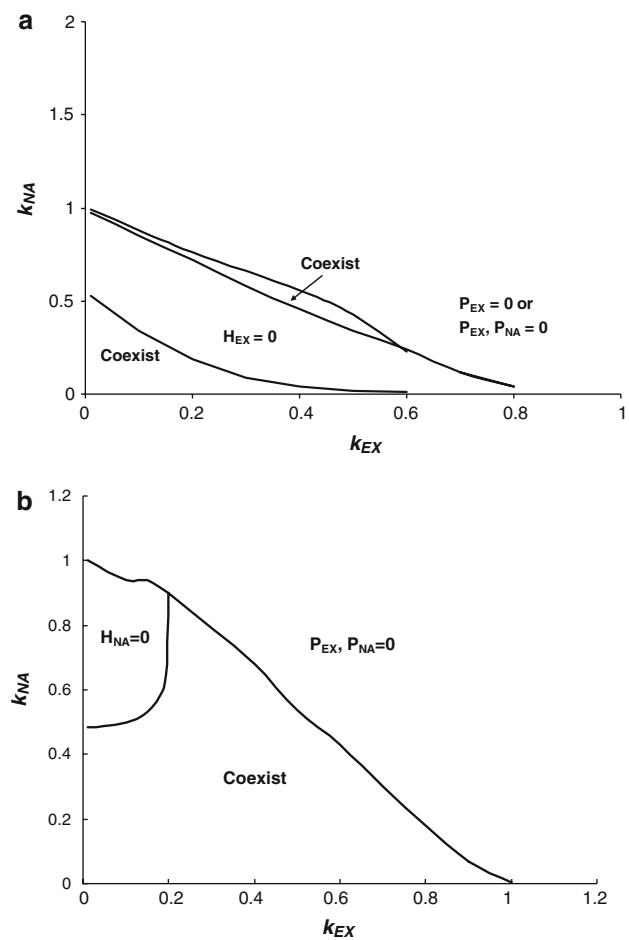
Fig. 4 The regimes of parameter space representing the two-host–two-parasitoid system, when both hosts are unsuitable for parasitoids. The *X*- and *Y*-axis reflects the aggregation degree of exotic and native parasitoids, respectively; low values of *k* imply high aggregation $\left(\frac{a_{H_{EX}}}{a_{H_{NA}}} = 1.76 \text{ and } \frac{b_{H_{EX}}}{b_{H_{NA}}} = 0.87\right)$. The species that will be extinct is mentioned in the figure. **a** Highland Kenya (Region C), $\frac{\lambda_{H_{EX}}}{\lambda_{H_{NA}}} = 0.61$; **b** Lake Victoria (Region D), $\frac{\lambda_{H_{EX}}}{\lambda_{H_{NA}}} = 1.5$

stemborer species dominated and *Chilo partellus* would become extinct with higher values of k_{NA}. If *Cotesia flavipes* was included, the four species could coexist if the degree of aggregation of the parasitoid species were low or if both were around 0.5 (Fig. 4a), which in the lower region is stable and in the second is periodic oscillations. Otherwise, with an increase in degree of aggregation of either parasitoid species, the decrease of stemborer densities caused a decrease of parasitoid populations, and the possibility of both surviving stemborer hosts escaping from parasitism was close to 1; this would cause the extinction of the exotic and native parasitoids and eventually there would be outbreaks of both stemborer populations. Hence, the model predicts that *Cotesia flavipes* would not easily establish in this region, and that *Chilo partellus* would become extinct in areas where the parasitoids are aggregated. Multiparasitism by *Cotesia flavipes* of native hosts would not significantly change the character of the system.

The mean temperature in the highlands is low compared to other regions, which allows for low growth parameters of hosts and parasitoids (Table 3). *Cotesia flavipes* has not yet been released in this region. *B. fusca* constituted 92.7% of all stemborer species, followed by *Chilo partellus* with 3.8%, and *S. calamistis* with 2.8%. Moreover, Ogedah (1999) and G. Zhou (unpublished data) found high parasitism by *Cotesia sesamiae* at concomitant high densities of *B. fusca*. The model predicted a dominance of the native stemborer species in most cases before the release of exotic parasitoid (Fig. 2). If *Cotesia flavipes* was released in this area, with the values of k_{EX} and k_{NA} close to 2, the exotic or native parasitoid cannot establish or stay in the system, respectively. With the high parasitism of both parasitoid populations, there is a high risk that both parasitoid populations under very low level become extinct. Since *Chilo partellus* is not widely distributed and of low importance in this region, there is no need to release extra *Cotesia flavipes*.

Lake Victoria (D)

In this region, *Chilo partellus* and *B. fusca* are the major stemborer species and the former has a higher growth rate than the latter, because high temperatures favor *Chilo partellus* over *B. fusca* $\left(\frac{\lambda_{H_{EX}}}{\lambda_{H_{NA}}} > 1\right)$. Thus, without the release of the parasitoid, the model predicted that *Chilo partellus* would dominate (Fig. 2). If *Cotesia flavipes* was released, the native stemborer would become extinct if k_{EX} was small (Fig. 4b). The system allowed for host–parasitoid species to coexist if both k_{EX} and k_{NA} were less than 1. Otherwise, there would be outbreaks of both borer species. A decrease in $\frac{b_{H_{EX}}}{b_{H_{NA}}}$ would enhance the dominance of *Chilo partellus*, while an increase of $\frac{a_{H_{EX}}}{a_{H_{NA}}}$ would be favorable for

Cotesia sesamiae. Therefore, the success of *Cotesia flavipes* relies on the specific searching ability of the parasitoid for its old association host.

For areas where the unsuitable host *E. saccharina* is the key native stemborer species, the model predicted that *Cotesia sesamiae* would become extinct, because *Cotesia flavipes* would out-compete it in situations where *Chilo partellus* was the only suitable host, and *E. saccharina* would eventually dominate over *Chilo partellus*.

This area is highly populated and a major agricultural zone. Survey data showed that *Chilo partellus* is the dominant borer with 57.8%, followed by *B. fusca* with 25.5% and *E. saccharina* with 7.3% (G. Zhou, unpublished data). Though it has never been released in the area, *Cotesia flavipes* was found in surveys in 1995 (Omwega et al. 1997). *Chilo partellus* has been replacing *B. fusca* near Lake Victoria since the 1950s (Nye 1960), which could be attributed to the higher searching efficiency of *Cotesia sesamiae* for *B. fusca*, which is as an old-association host. A similar trend was observed in Eastern Uganda near Lake Victoria, where *Chilo partellus* became the dominant species (Matama-Kauma et al. 2007). The model predicted that, before the release of *Cotesia flavipes*, the coexistence of the native and exotic stemborer was possible, and *Chilo partellus* would dominate. With the introduction of *Cotesia flavipes*, it would out-compete *Cotesia sesamiae* on *Chilo partellus*. However, if *Cotesia sesamiae* became extinct, due to the unsuitability of the native stemborer species for the exotic parasitoid, there would be outbreaks of the stemborer populations. Therefore, in this region, even though field data indicated the establishment of *Cotesia flavipes*, long-term observations of the native parasitoid populations are needed to ensure firm establishment and coexistence of the parasitoid species.

In general, the model suggests that *Cotesia flavipes* should not be released in regions where the native stemborer species are important but not suitable. In regions where the native host species is suitable for *Cotesia flavipes*, the exotic stemborer can be controlled, although the degree depends on the growth rate of the native stemborer species.

Discussion

We examined the effect of different host and parasitoid species compositions on the success of biological control of maize stemborers and consequences to the stemborer communities in eastern Africa. Here, we have analyzed a complicated community consisting of two hosts and their parasitoids, with host species composition varying with ecozone, and have attempted to predict their effects on

biological control. The model has some important features that were absent from previous models: the system was composed of native and exotic hosts and native and exotic parasitoid species; the two parasitoid species attack both host species, irrespective of whether they are suitable or not, and have different foraging behaviors and degree of aggregation. In particular, based on field and laboratory results, it was assumed that the exotic parasitoid was the superior competitor and more efficient at locating hosts than the native parasitoid. The model indicated that the growth rate ratio of exotic and native stemborer is important for the dominance of the stemborer species; as shown with long-term field data, due to its higher growth ratio the exotic borer would eventually displace the native borer species in the system. Moreover, the host's rate of increase could be a key constraint to the efficiency of a host-limited parasitoid (Mills 2001). Furthermore, the coexistence of the different borer and parasitoid species depends on the degree of aggregation of the exotic parasitoid. However, from a study of a two-host, and two specific and one generalist parasitoid community, Wilson et al. (1996) concluded that the searching efficiency of parasitoids and their interactions with the host is important for the community structure, which support our current findings.

Since our model was designed to predict the effects of the competition between exotic and native parasitoids on the coexistence of the different borer and parasitoid species in the system rather than population densities, we used lumped parameters, which did not include age-structure of the population. In our analysis, the relationship between the ratios of host population growth rates, the relative searching efficiency of the parasitoids, together with the degrees of aggregation of the parasitoids mainly stressed the competition strength of the hosts and parasitoids and its effects on the species coexistence in the system. However, stemborer host stage and quality were found to be important for the development of *Cotesia flavipes* larvae, and the host continues to feed and grow until parasitoid cocoon formation (Jiang et al. 2004; Sètamou et al. 2005). Thus, for the predictions on changes in population density, a physiological simulation model based on individual levels including the effect of temperature on growth rates would be required (Goudriaan and van Roermund 1993), as the number of suitable hosts and parasitoid progeny will be affected.

In the model, we also ignored the density dependent effects of host populations. The relationship between population abundance and intra-specific competition is affected by the aggregation of a species (Maurer and Taper 2002). If the exponent (b) of Taylor's power law of the population (Taylor and Woiwood 1982) was between 1 and 2, which is common for stemborers (Schulthess et al. 1991; Overholt et al. 1994b; Songa 1999; Ndemah et al. 2001), regions with

high abundance have local populations that are more resilient but have weak intra-specific competition. The spatial heterogeneity of stemborer distributions has a direct influence on the searching efficiencies of parasitoids. *Cotesia sesamiae* and *Cotesia flavipes* are attracted by volatiles from frass produced by feeding stemborer larvae (Ngi-Song and Overholt 1997b), but they appear not to be able to discriminate between frass produced by the different host species (Ngi-Song and Overholt 1997a). As *Cotesia* spp. use the 'ingress-and-sting' method to attack the host inside the stem (Smith et al. 1993), the parasitoid has to enter the tunnel in order to discriminate between species. Therefore, a parasitoid has a spatial density dependent relationship with the host, but the chances to encounter a specific host species is random. On the other hand, both *Cotesia sesamiae* and *Cotesia flavipes* are gregarious with a limited life span of 2–3 days in the field and a finite egg-load, and they are not being affected by direct spatial density dependence (Walde and Murdoch 1988). In our model, the negative binomial function of parasitoids (May 1978) was used as it is suitable for gregarious parasitoid with a limited number of eggs oviposited inside the host, and it is one of the mechanisms for stabilizing the host–parasitoid system (Walde and Murdoch 1988). Therefore, the impact of parasitoid fecundity was ignored in our model. Moreover, other theoretical studies also indicated that fecundity contributed less than searching efficiency to a reduction of host densities (Kean et al. 2003).

The success of the establishment of an introduced parasitoid for biological control of insect pests in a target region is affected by many factors, including climate (DeBach 1958), host strain suitability, and availability of alternative hosts (Mills 2001). In the present study, the dynamics of stemborer–parasitoid systems in different regions was mainly driven by biological parameters, which were influenced by climatic conditions prevalent in the different ecozones. Similarly, Tuda et al. (2006) showed that biological control of the arrowhead scale by two parasitoids in Japan was affected by both climatic and intertrophic effects. A spatial and temporal synchrony between the major stemborer and parasitoid species was found in coastal Kenya (Jiang et al. 2006). Therefore, the introduction of *Cotesia flavipes* changed the regional synchrony of *Chilo partellus* and other native stemborer species; the effect of rainfall and temperature was either direct or indirect by affecting the plant habitats of borers and parasitoids.

Because of the simplification of the model, other minor native host species could be ignored, especially for the regions were the native stemborer was not suitable to the exotic parasitoid and which could not be considered as a reservoir for the parasitoid during the off-season, when the crop was not present. In our model, we only considered the

maize mono-crop system. However, in eastern Africa, farmers usually practice mixed-cropping and, moreover, the fields are surrounded by wild grasses, some of which are hosts of maize stem borers (Mbapila 1997; Sétamou et al. 2005; Le Rü et al. 2006). Some of these plant hosts help to stabilize the system for the *Cotesia sesamiae* population, which should therefore not get extirpated by the introduction of the exotic *Cotesia flavipes*. However, the effect of diversity of agro-ecosystem needs more information, and studies as their consequences on pest control appears to be inconsistent (Andow 1991; Potting et al. 2005).

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