UC Berkeley
UC Berkeley Previously Published Works

Title

A coffee agroecosystem model: III. Parasitoids of the coffee berry borer (Hypothenemus hampei)

Permalink

https://escholarship.org/uc/item/9hc9c6jc

Authors

Rodríguez, Daniel
Cure, José Ricardo
Gutierrez, Andrew Paul
et al.
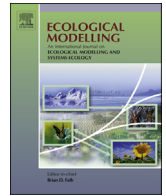
Publication Date

2017-11-01

DOI

10.1016/j.ecolmodel.2017.08.008

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, availalbe at https://creativecommons.org/licenses/by/4.0/

Peer reviewed

A coffee agroecosystem model: III. Parasitoids of the coffee berry borer (*Hypothenemus hampei*)

Daniel Rodríguez [a,b,*], José Ricardo Cure [a,b], Andrew Paul Gutierrez [b,c], José Miguel Cotes [d]

[a] Facultad de Ciencias Básicas y Aplicadas, Universidad Militar Nueva Granada, Cr. 11 No. 101-80, Bogotá, Colombia
[b] Center for the Analysis of Sustainable Agricultural Systems, USA[1]
[c] College of Natural Resources, University of California, Berkeley, USA
[d] Facultad de Ciencias Agropecuarias, Universidad Nacional de Colombia, Sede Medellín, Calle 59A No 63-20, Medellín, Colombia

ARTICLE INFO

ABSTRACT

Parasitoids native to tropical Africa have been released in the Americas for the biological control of the coffee berry borer (CBB), but their establishment has been checkered. A tritrophic distributed maturation time model for the coffee plant – CBB – three parasitoids (*Phymastichus coffea*, *Cephalonomia stephanoderis*, *Prorops nasuta*) system was proposed by Gutiérrez et al. (1998). Based on this pioneering work, and improved models for coffee and CBB (Rodríguez et al., 2011, 2013), we present an updated version of the parasitoid models. The new elements in this analysis include:

1. New data on the biology and behavior of the parasitoids are added.
2. A fourth parasitoid (*Cephalonomia hyalinipennis*) is added to the system.
3. Interspecific competitive interactions among parasitoids (e.g., dyadic contests, intra-guild predation and hyperparasitism) and their effects on the control of CBB are explored.

Because field data on the effectiveness of the parasitoids on CBB control is sparse, we assessed the efficacy of the parasitoids for control of CBB heuristically. The results are compared to prior analyses, and are related to field observations. Specifically, we found:

1. Control of CBB by betilid parasitoids (*Cephalonomia stephanoderis*, *Cephalonomia hyalinipennis* and *Prorops nasuta*) is ineffective because of their low reproductive capacity relative to CBB, their host-feeding behavior, and phenological mismatches with CBB life stages.
2. Of the parasitoids, the eulophid *P. coffea* has the greatest potential to suppress CBB infestation levels, though the fungal pathogen *B. bassiana* and insecticides are reported to have detrimental effects on its establishment and dynamics.

© 2017 Elsevier B.V. All rights reserved.

1. Introduction

Coffee (*Coffea arabica*) is native to Ethiopia and was introduced to the Americas in 1723 (Ferré, 1991). The coffee berry borer (CBB = *Hypothenemus hampei*) (Curculionidae: Scolytinae) is native to West Africa (Hopkins, 1915) and is the most destructive pest of coffee worldwide (International Coffee Organization, 2007; Vega et al., 2009; CABI, 2011). It was first found in Brazil in 1922 (Costa-Lima, 1924), spread to Central America and Mexico between 1971 and 1978 (Carrillo and Campos 1991; Muñoz-Hernández, 1991; Villanueva-Marrufo, 1991), and was first found in Colombia in 1988 (Bustillo, 2006).

Like other Scolytinae, CBB females form galleries for the development of progeny (Vega and Hoffstetter, 2014). In coffee, a female CBB bores into the calyx end of a single berry and forms galleries in the seed. At maturity, new CBB adults leave the host berry to infest other berries. Considerable effort has occurred to develop strategies for control of CBB, including classical and augmentative biological control using introduced parasitic wasps (parasitoids), nematodes

and entomo-pathogens. Here we focus on the biological control of CBB using parasitic wasps. Three parasitoids species were released in the Americas: two betilids *Cephalonomia stephanoderis* (Abraham et al., 1990; Barrera, 1994; Aristizábal et al., 1996; Aristizábal et al., 1997; Aristizábal et al., 1998) and *Prorops nasuta* (Hempel, 1933; Hempel, 1934; Abraham et al., 1990; Infante, 1998), and the eulophid *Phymastichus coffea* (Infante et al., 1994; Aristizábal et al., 2004; Castillo et al., 2004a; Castillo et al., 2004b; Castillo, 2005; Jaramillo et al., 2005; Jaramillo et al., 2006).

In Colombia, *C. stephanoderis, P. nasuta* and *P. coffea* were released (ICA, 1999; Orozco, 2000; Salazar et al., 2007), but only *P. nasuta* established (Maldonado and Benavides, 2007). In Brazil *C. stephanoderis* and *P. nasuta* were established (Benassi, 2007), and *P. coffea* was introduced in 1999 (Cantor et al., 1999) but its establishment is unknown.

A third betilid, *Cephalonomia hyalinipennis* was reviewed as a possible control agent, but research suggests it could have a detrimental effect on control of CBB because of its negative interaction with the other betilids (Pérez-Lachaud et al., 2002; Batchelor et al., 2006), and hence has not been released in the Americas. The braconid *Heterospilus coffeicola* is reported from CBB in Africa (Toledo and Pinto da Fonseca, 1935; Kucel et al., 2004), but it has not been reared successfully for field releases in South America (Vega et al., 2009), and it is not considered in this study.

Good quantitative field data on the efficacy of these parasitoid species is lacking, and hence we model the biology of the three betilids and the eulophid parasitoid to examine heuristically their potential as biological control agents of CBB. In the text and figures, we use the convenient notation *Cs = C. stephanoderis, Ch = C. hyalinipennis, Pn = P. nasuta, Pc = P. coffea.*

1.1. Modeling parasitoid biology

Gutierrez et al. (1998) developed a tritrophic coffee-CBB-three parasitoid demographic system model based on the distributed maturation time demographic model proposed by Manetsch (1976) and Vansickle, (1977). Rodríguez et al. (2011, 2013) updated the models for coffee and CBB with new laboratory data, and tested them against field data. Here, we update the parasitoid models, and add the parasitoid *C. hyalinipennis* to the system. All the models use the physiologically based demographic modeling approach (PBDM) developed by Gutierrez and Baumgärtner (1984) (see Gutierrez 1996). We first review the biology of the parasitoids.

1.2. Biology of the eulophid P. coffea

P. coffea is an endoparasitoid of CBB adult females, and attacks them as they are beginning gallery formation. In Colombia, the development time of the immature parasitoid stages is about 45 days, while adult longevity is approximately 3 days, and the sex ratio (female: male) is 1:1.5 under field conditions (Vergara-Olaya et al., 2001) and 1:1 in the laboratory (Castillo et al., 2004b). The reproductive strategy of *P. coffea* is deuterotokous parthenogenesis wherein virgin females produce females and males (Feldhege, 1992). *P. coffea* females normally lay two eggs per CBB adult, one in the abdomen and the other in the head, and commonly yield a female and a male parasitoid, but superparasitism may also occur (Jaramillo et al., 2006). Because *P. coffea* attacks only the adult stage, Espinoza et al. (2009) suggested that its action would complement the action of betilid parasitoids in control of CBB.

1.3. Biology of the betilid parasitoids

Adult females of *C. stephanoderis* and *P. nasuta* enter one CBB gallery during their life time where they host-feed on CBB adults and immature stages, and oviposit in mature larvae and pupae (Hempel, 1934; Barrera et al., 1989; Abraham et al., 1990; Ticheler, 1961; Benassi, 2007). The sex ratio of *C. stephanoderis* decreases with temperature being 25 females: one male at 17 °C and 7.3:1 at 32 °C. The sex ratio of *P. nasuta* increases from 4.5:1 to 5.8:1 over the same range of temperature (Benassi, 2007). The reproductive strategy of *C. stephanoderis* (Lauzière et al., 2000) and *P. nasuta* (Abraham et al., 1990) is characterized by sibling-mating. At maturity, new adult parasitoid females leave host berries in search of CBB infested berries. Superparasitism by both parasitoids has been observed under laboratory conditions, but not in the field (Benassi, 2007), and intraguild predation between *C. stephanoderis* and *P. nasuta* occurs (Infante et al., 2001).

C. hyalinipennis is a facultative predator and hyperparasite of *C. stephanoderis* and *P. nasuta* immature stages, and in the laboratory super parasitizes CBB larvae and hyperparasitizes conspecifics. A female invades only one infested berry, sibling mating is the norm, and it has not been observed attacking CBB adults (Pérez-Lachaud et al., 2004).

Dyadic contest was defined by Pérez-Lachaud et al. (2002) as direct competition by females of different betilid species for the resources of a CBB infested berry. Triadic contest has not been observed in the field, and it is not considered in this study.

2. Methods

2.1. Study sites

Table 1 provides coordinates and climatic details of the five locations simulated in this study, but the simulation results reported in the figures are for Buenavista (Colombia) and Londrina (Brazil). The studies were conducted using weather data for the period 1990–1995 for Colombia and 1982–1986 for Londrina, PR, Brazil. Daily maximum and minimum temperatures (°C), relative humidity (%), precipitation (mm), and hours of sunshine for Colombia were obtained from data published in the Anuario Meterológico Cafetero (Cenicafé, 1990–1995). Daily solar radiation (MJ m^{-2} day^{-1}) was estimated from recorded hours of sunshine using the relationship developed by Prescott (1940). Weather data for Londrina, Brazil were obtained from the Instituto Agronômico do Paraná. To assess the effects of weather on system dynamics, the six years of weather data were shuffled across the four Colombian localities to increase the number of weather scenarios.

2.2. Population models

The coffee system model consists of 14 linked age-structured population sub models on a per tree basis. The coffee plant model consists of seven sub models for the different organs: mass of leaves {n = 1}, stem {2}, branches {3}, and root {4}, number of flowers {5}, and the mass and number of berries {6, 7}. The models for CBB consist of two dimensional age structured models for immature stages developing inside fruits that are also aging {8}, dispersing adult females outside fruits {9} and females in colonized berries {10}. The parasitoids model consists of the population submodels for *Cephalonomia stephanoderis* {11}, *Cephalonomia hyalinipennis* {12}, *Prorops nasuta* {13} and *Phymastichus coffea* {14}. The developmental biology of each species and the linkages of between them and their trophic interactions are illustrated in Fig. 1.

Completion of development by a cohort of poikilotherms born at the same time is distributed over a range of developmental times even if they experience the same environmental conditions (stochastic development; Di Cola et al., 1998). To capture this biology for each species/stage, we used the time-invariant

Table 1
Summary of the climate data sets from all localities included in simulations.

Locality	Location	Altitude (m)	Annual Rainfall (mm)	Daily average temperature (°C)
COLOMBIA				
Buenavista	75°44′ W 4°24′ N	1250	2060	21.97 ± 1.32[b]
Chinchiná[a]	75°39′ W 4°59′ N	1400	2516	21.37 ± 1.21
Marquetalia[a]	75°00′ W 5°19′ N	1450	3781	20.45 ± 1.24
Ciudad Bolívar[a]	76°01′ W 05°51′N	1342	2766	21.53 ± 1.56
BRAZIL				
Londrina	51° 9′ W 23° 18′ S	566	1622	22 °C ± 1.34

[a] Used only for simulations under multiple climatic conditions (see below).
[b] Mean ± standard deviation.

Erlang distributed maturation-time dynamics model proposed by Manetsch (1976) (Eq. (1)).

$$\frac{dN_i}{dt} = \frac{k\Delta x(T(t))}{\Delta}\left[N_{i-1}(t) - N_i(t) - \mu_i(t)N_i(t)\right] \tag{1}$$

N_i is the density of the cohort (numbers or mass) of a stage/species, k is the number of age classes, Δ is the mean developmental time, and $\mu_i(t)$ is the age specific proportional net loss rate due to all causes affecting the population at time t. The distribution of maturation times of a cohort of N is determined by the number of age classes k, the mean developmental time of the species/stage (Δ), and the variance of maturation times (var) (e.g., $k = \Delta^2/var$). The numerical solution by Gutierrez (1996) using Euler's integration is used in this study. Time and age (x) in the model are in physiological time units (Table 2).

2.2.1. Physiological time

The developmental rate of all of the species are nonlinear functions of temperature ($R(T(t))$), and in our study we use the developmental rate model (Eq. (2)) proposed by Lactin et al. (1995).

$$R(T(t)) = \lambda + \exp(\rho T(t)) - \exp\left[\rho T_m - \frac{T_m - T(t)}{T_u}\right] \tag{2}$$

The parameter λ forces the curve to intercept the x-axis providing an estimate of the lower thermal threshold (see Table 2), ρ can be interpreted as a compounded Q_{10} (van't Hoff's law) which measures the sensitivity of the rate of development to temperature, T_m is the maximum temperature threshold (see Table 2), and T_u is the approximate upper temperature range (Sigsgaard, 2000). $R(t(T))$ is the proportion development at temperature T at time t with completion of stage of development occurring when $\int R(T(t))dt = 1$ (Stinner et al., 1974).

For use by biologist, developmental times constants of each species (Δ) were estimated in the favorable mid-range of temperatures using the linear day-degree rule (dd, see Rodríguez et al., 2012a). For aging, daily increments of degree-days ($\Delta dd(T(t))$) at temperature T at time t were corrected for the nonlinear effects of temperature on development as $\Delta dd(T(t)) \cong \Delta \cdot R(T(t))$ with development completed when $\sum \Delta dd(T(t)) = \Delta$. The simulation results are plotted either on days (d) after planting or on cumulative dd for coffee.

2.2.2. CBB attack biology

CBB attacks different age berries with varying preferences (Rodríguez et al., 2013), and hence CBB life stages in these berries age in two dimensions – the berry time scale and CBB time scale. Using the method of Stone and Gutierrez (1986), new CBB infested berries were transferred to the same age fruit in a 2-dimension distributed maturation time model matrix wherein the CBB larvae age in fruit that are also ageing. Specifically, movement due to temperature in the column dimension represent ageing of host berries, and movement in the rows represent ageing of CBB life stages. New CBB eggs enter at age zero in the row for fruit age. This 2-d matrix provides a realistic method for modeling the attack behavior of betilid

females on CBB in infested berries, and of the eulophid *P. coffea* that parasitizes CBB females as they begin gallery formation.

2.2.3. Parasitoid functional response

Organisms in all tropic levels are consumers, and the functional response model estimates the resource acquisition rate as a function of resource density (e.g., Beddington et al., 1976), and determines their growth and reproductive rates (Gutierrez, 1996). The functional response model includes the demand for resources and the attack behavior. We first describe the attack behavior of the eulophid *P. coffea* and then the more complicated attack behavior of the betilid parasitoids. The biological parameters of the parasitoid species are summarized in Table 2 (see also Fig. 1b–d).

Phymastichus coffea – The Fraser and Gilbert (1976) parasitoid functional response model Eq. (3) is used to estimate the parasitism rates by *P. coffea* females because it allows super parasitism and the attack of more than one CBB adult per day (Gutierrez, 1996).

$$S(t) = B_a(t)\left\{1 - \exp\left[\frac{D(t)A(t)\left[1 - \exp\left[-\frac{\alpha B_a(t)}{D(t)A(t)}\right]\right]}{B_a(t)}\right]\right\} \tag{3}$$

$S(t)$ is the number of CBB females parasitized at time t, $B_a(t)$ is the number of CBB females attacking berries corrected for preference that varies with maturation stage of the berry (Jaramillo et al., 2002). Specifically, *P. coffea* preference for CBB females attacking stage 1 = 0.0, stage 2 = 0.6, stage 3 = 0.8 and stage 4 = 0.31. The parameter α is the search rate of the parasitoid, $D(t)$ is the per capita demand for hosts per female per dd (see Table 2) at time t, and $A(t)$ is the number of adult parasitoid females seeking CBB females (see parameters in Table 2). The ratio $0 <$ supply/demand $= S(t)/D(t)A(t) < 1$ is an estimate of *P. coffea* parasitization success at time t (Gutierrez, 1996).

Betilid parasitoids – Betilid females (e.g., *C. hyalinipennis, C. stephanoderis* and *P. nasuta*) enter only one CBB infested berry during their life and attack the CBB life stages and those of competing parasitoid species. Colonization by betilid parasitoids is a two-stage process: the 1st stage involves finding CBB infested berries and the 2nd stage occurs within the berry when the parasitoid female attacks CBB life stages either for host-feeding or parasitism. Both stages of attack are estimated using the predator form of the Gutierrez-Bäumgartner functional response model (Eq. (4); Gutierrez, 1996):

$$S_k(t) = D_k(t)A_k(t)\left\{1 - \exp\left[-\frac{\alpha_k B_{a,k}(t)}{D_k(t)A_k(t)}\right]\right\} \tag{4}$$

In the 1st stage of attack, $S_k(t)$ is the number of CBB infested berries successfully colonized by the kth betilid species. $B_{a,k}(t)$ is the number of CBB infested berries with CBB stages suitable for parasitization and host-feeding by the population of the kth species of betilid females ($A_k(t)$); α_k is the parasitoid search rate for berries; and $D_k(t)$ is the parasitoid demand for CBB infested berries (i.e. 1 per female). *C. hyalinipennis* requires a longer time to colonize a berry than the other betilids (Batchelor et al., 2006), and this attack
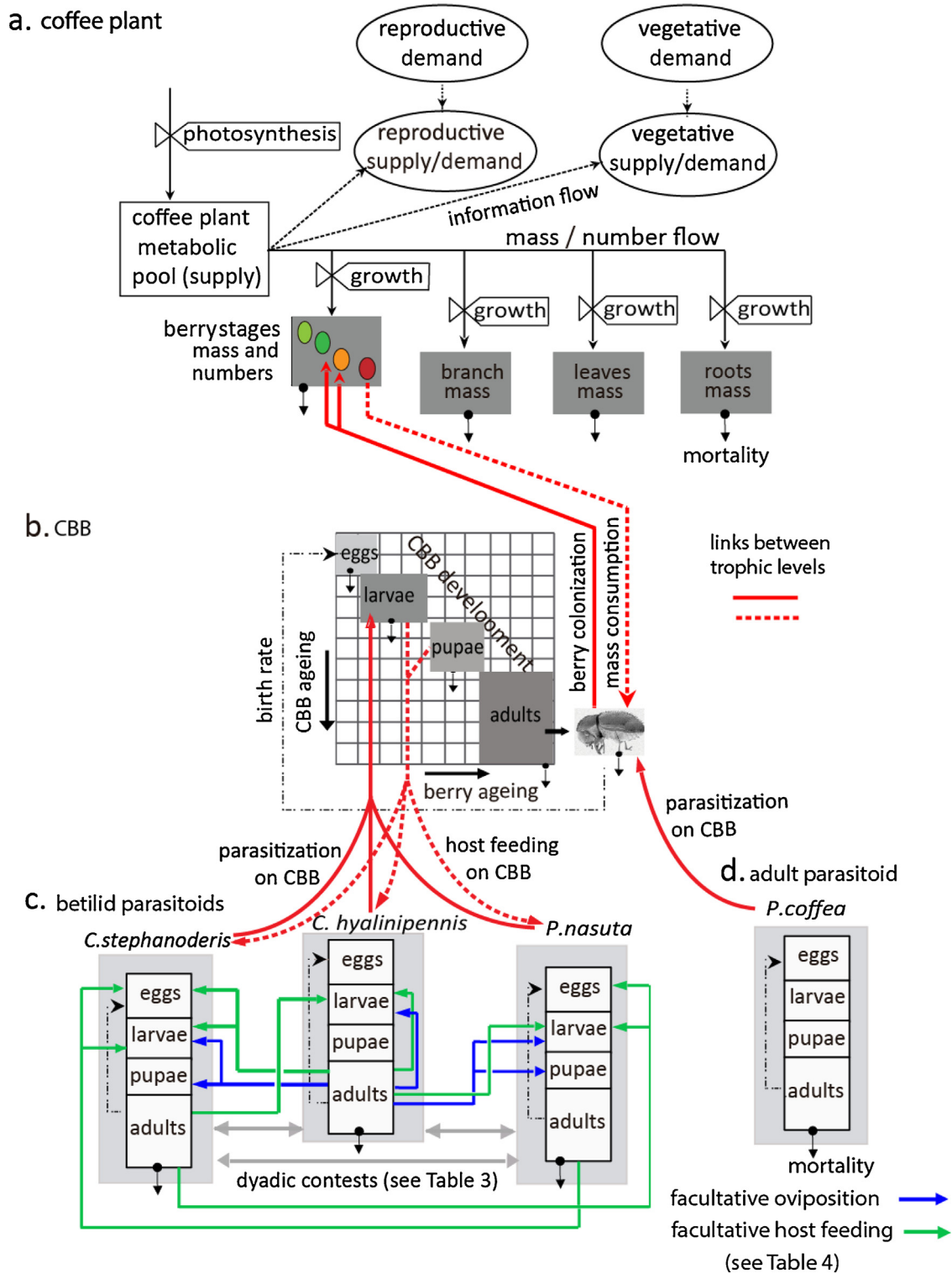
Fig. 1. Tritrophic system showing links between species and trophic levels: (a) coffee plant and berry dynamics (1st trophic level); (b) coffee berry borer (CBB) ageing dynamics inside coffee berries (2nd trophic level); (c) CBB betilid parasitoids (3rd trophic level) – *Cephalonomia stephanoderis*, *C.hyalinipennis* and *Prorops nasuta* – dynamics, trophic relationships and their interspecific interactions (i.e. dyadic contexts, facultative host feeding and facultative oviposition); (d) CBB eulophid adult parasitoid *Phymastichus coffeae* (3rd trophic level).

biology is reflected in the lower search rate α_k. Specifically, α_k for *C. hyalinipennis* is 0.5, and that for *C. stephanoderis* and *P. nasuta* is 0.9.

In the 2nd stage of attack, the same functional response Eq. (4) is used to capture the biology of the betilid species' attack on CBB life stages. $A_k(t)$ is the population of female of the kth parasitoid attack-

ing CBB stages, $B_{a,k}(t)$ is the number of CBB available for parasitism or host-feeding corrected for preference, $\alpha_k = 1$ is the search rate of betilids inside the berry, and $D_k(t)$ is the temperature dependent per-capita demand for parasitism and host-feeding. *C. hyalinipennis* females superparasitize conspecifics and other betilid species, and lays 1–3 eggs per host (Pérez-Lachaud and Hardy, 1999). Eggs

Table 2
Biological parameters for the parasitic wasps.

| Parameters | Parasitoids | | | |
	C. stephanoderis	*C. hyalinipennis*	*P. nasuta*	*P. coffea*
Thermal Thresholds				
Minimum	14.99	14.99	14.27	16.02
Maximum	37.45	37.45	33.18	33.64
reference	(Benassi, 2007)	(Benassi, 2007)	(Benassi, 2007)	(*)
Linear developmental rate model				
a	−0.06966	−0.06966	−0.05508	−0.06486
b	0.004648	0.004648	0.003858	0.004048
Non linear (Lactin et al., 1995) developmental rate model				
λ	−0.00448	−0.00448	−0.0338	−0.0317
ρ	0.1706	0.1706	0.1602	0.1607
Tm	37.4583	37.4583	33.18	33.64
Δ	5.8601	5.8601	6.2334	6.2185
reference	(Benassi, 2007)	(Benassi, 2007)	(Benassi, 2007)	(*)
Developmental time (dd)				
Egg	0–20.35	0–20.35	0–35.19	0–29.9
Larva	20.35–108.76	20.35–108.76	35.19–122.54	29.9–167.44
Pupa	108.76–276.22	108.76–276.22	122.54–312.41	167.44–257.14
Pre-oviposition	276.22–621.65	276.22–621.65	312.41–520.91	
Post-oviposition	1409.72–1675.85	1409.72–1675.85	1135.64–1346.35	
reference	(Benassi, 2007)	(Benassi, 2007)	(Benassi, 2007)	(Vergara-Olaya et al., 2001)
Intrinsic mortality (individuals/dd)				
Egg	0.001798	0.001798	0.0036	0.0001
Larva	0.002671	0.002671	0.0033	0.0001
Pupa	0.0003468	0.0003468	0.00093	0.0001
reference	(Benassi, 2007)	(Benassi, 2007)	(Infante, 2000)	
Young Adult	0.00097136	0.00089437	0.0009075	0.04258
Old Adult	0.00097136	0.00089437	0.0009075	0.04258
reference	(Infante et al., 1992)	(Pérez-Lachaud and Hardy, 1999)		(Castillo et al., 2009)
Mortality rate of seeking females				
	0.01189	0.01189	0.02625	
reference	(Damon et al., 1999)	(assumed equal to *Cs*)	(Damon et al., 1999)	
CBB stage attacked—age in dd (preference)				
old larvae	64.92–108.76 (1.0)		64.92–122.54 (1.0)	–
pupae	108.76–276.22 (1.0)		122.54–312.41 (1.0)	–
CBB adult females tunneling the berry				257.14–275.08
CBB stage for host-feeding— age in dd (preference)				
Eggs	0–20.35 (1.0)	0–20.35 (0.6)	0–35.19 (1.0)	no
Young Larvae	20.35–64.92 (1.0)	20.35–64.92 (0.6)	35.19–64.92	no
Host-feeding demand (immatures/dd)				
	0.052	0.052	0.052	
	(Gómez et al., 2012)	(Gómez et al., 2012)	(assumed equal to *Cs*)	
Sex ratio (female:male)				
	$SR = 1-0.0063Temp^*$	0.788	$SR = 0.77-0.0027Temp^*$	0.6
reference	(Benassi, 2007)	(Pérez-Lachaud and Hardy, 1999)	(Benassi, 2007)	(Vergara-Olaya et al., 2001)
Oviposition demand rate (eggs/dd)				
	0.076	0.071	0.055	0.56
	(Benassi, 2007)	(Pérez-Lachaud and Hardy, 1999)	(Benassi, 2007)	(Feldhege, 1992)
Search rate for berries				
	0.9	0.5	0.9	0.95
Search rate inside berries	1.0	1.0	1.0	–

[*]Estimated from a set of rough data provided by F. Cantor. [*]*SR* = Sex ratio, *Temp* = average temperature of the last 30 days used to calculate the sex ratio.

oviposited by parasitoid females enters to population submodels {11}, {12}, {13} and {14} as $N_0(t)$ (Eq. (1)).

2.3. Competitive interactions between parasitoids

Competition between individual parasitoids of two different species (dyadic contest) occurs in coffee berries when a betilid female enters a berry previously colonized by a female of another species (Batchelor et al., 2005). This behavior is more likely to occur when CBB infested berries are scarce. In the model, dyadic contest occurs at a rate dependent on the shortfall of CBB infested berries attacked (*i.e.* 1-(*S(t)*/*D(t)*) > 0) (Table 2).

Direct competition occurs only among the betilids species, while indirect competition occurs with *P. coffea*. Gutierrez et al. (1998) considered symmetric competition among the betilids, but new data enables parametrization of asymmetric competition in dyadic contests the success rate of which depends on their biol-

Table 3
Proportions of total contests won by each parasitoid in dyadic contests (δ) (modified from Batchelor et al., 2005). Previous experience of the parasitoids considered by Batchelor et al. (2005) was not distinguished here.

| Contest (dyadic) | | |
Owner	Intruder	δ
C. stephanoderis	*C. hyalinipennis*	0.09
	P. nasuta	0
C. hyalinipennis	*C. stephanoderis*	0.48
	P. nasuta	0.15
P. nasuta	*C. stephanoderis*	0.69
	C. hyalinipennis	0.8

ogy (Batchelor et al., 2005, Table 3). The different success rates are included in the model via the parameter δ (Table 3), which weights the proportion of contest that are successful for the dif-

ferent combinations of species. No information is available on rare triadic interactions, and hence is not considered in our analysis.

When a second species of a betilid parasitoid enters a berry previously colonized by another parasitoid species, it attacks the immature stages of both CBB and the first parasitoid. Facultative oviposition and host-feeding interactions between betilid species are summarized in Table 4 (see also Fig. 1c).

2.4. Simulation of parasitoid control of CBB and parasitoid interactions

Simulations for Colombia had a five year time horizon corresponding to the normal crop cycle (Arcila et al., 2007). In Brazil, the crop cycle is four years. In Colombia, two coffee harvests occur per year, a main one in September-November and a minor harvest in April-June (Arcila and Jaramillo, 2003). At Londrina PR (Brazil), only one coffee harvest occurs per year that may occur during June through September (Vieira, 2008).

The ratio of parasitoid released was 1 per 1 CBB infested berry. In Colombia, the first berries colonized by CBB females appear around 5300 *dd* after planting (425 days), and at 7500 *dd* (640 days) in Brazil. The times of berries first appear are reference times for parasitoid release. In Colombia, an initial release of 11 adults/plant of each betilid species occurs at 6790 *dd* and corresponds to a ratio of 1:1 parasitoid adults to CBB infested berries. For *P. coffea*, the initial release was 5 adults/plant corresponding to a ratio of 1:1 parasitoid females to CBB infested berries at time 5678 *dd*.

For Brazil, the initial release of each of the betilid parasitoids at 8500 *dd* is 4 adults/plant corresponding to a 1:1 ratio of adult females of each betilid species to CBB infested berries. For *P. coffea*, 6 adults were released at 7500 *dd* for a 1:1 ratio of parasitoids to CBB infested berries.

Single and multiple parasitoid releases during the crop cycle were also evaluated. Two strategies for multiple releases were evaluated: the first consisted of one release at the start of each coffee production cycle when CBB attack begins and the second in had releases at the start and end of each production cycle. The release rates were one female parasitoid per infested berry. The season-long damage reduction for each scenario is computed as the ratio of CBB infested berries with control/CBB infested berries without control, while the proportion of parasitoid colonization rate by each species was computed as the ratio of CBB infested berries with parasitoid/total CBB infested berries.

A constant immigration rate of 0.25 CBB females per day and plant was used in the model, while no immigration was assumed for the parasitoids. Dyadic contests, facultative host-feeding and facultative hyperparasitism as appropriate for each species were examined for all combinations of parasitoid species interactions (see Tables 3 and 4). The effects of interspecific competition were analyzed using the number of adult parasitoids of each species produced per plant as affected by the presence of competing parasitoid species.

2.5. Simulations under multiple climatic conditions

The effects of weather at five locations on the coffee agroecosystem were analyzed (see Table 1) for the $2^4 = 16$ combinations of the four parasitoids including the null set (Walpole et al., 2007). The different combinations in the model were characterized using Boolean presence (1), absence (0) values. The efficacy of each parasitoid species on CBB control was further evaluated using permutations of the years of weather data from the five locations obtained using the allPerms procedure of the "permute" package in the statistical software *R* (Simpson, 2016). For Colombia, this resulted in a random subset of 24 combinations of yearly weather data and 16 combinations of parasitoids (i.e. 384 parasitoid x weather scenar-

ios). A similar procedure was used to generate 128 scenarios for Brazil.

2.6. Statistical analysis of simulation data

Negative binomial mixed regression models (O'hara and Kotze, 2010) were fit to simulation outputs. This method accounts for over dispersion and skewness in the data, satisfies the assumptions of the parametric analysis, and allows interpretation of the stochastic effect of the combinations of years of weather obtained by the shuffling procedure. In the analysis, the Boolean variables are the independent variables, while the cumulative number of CBB infested berries·year^{-1} (IB) in the simulation runs are the dependent variables. The effects of species-specific biology such as facultative host-feeding, facultative hyperparasitism and dyadic contests were critical underlying factors affecting the output of the model (see Tables 3 and 4). The simulation runs were used to estimate the effects of parasitoid species on CBB infestation levels and on each other. Akaike's information criteria (Akaike, 1973) was used to select the final model for the different combinations of parasitoids, and chi-square (X^2) goodness of fit tests were used to assess the significance level.

3. Results

3.1. Control of CBB by single species

3.1.1. Colombian study

The dynamics of CBB infested berries in the absence of the parasitoids are depicted in Fig. 2a and predict CBB infestation of berries of 64.67%. Because parasitoid releases at the beginning and at the end of each harvest period for each species acting alone gave only slightly better control than the single release strategy (not shown), only the results for single releases are illustrated in Fig. 2.

A single release of *C. stephanoderis* at 10 CBB infested berries/plant resulted in a 21.06% reduction of CBB infested berries on the plant and an 11.35% reduction in infestetation in shed berries on the ground. Compared to *C. stephanoderis*, a single release of *C. hyalinipennis* resulted in a 16.93% reduction in infestation on the plant and 8.23% reduction in infestation in shed berries, whilst a release of *P. nasuta* yielded 16.83% and 7.59% reductions respectively. In contrast, a single release of the eulophid *P. coffea* resulted in a 47.38% reduction in CBB infested berries on the plant and a 46.85% reduction in infestation in shed berries. Operating singly, the order of effectiveness of the parasitoids is *P. coffea* >> *C. stephanoderis* > *C. hyalinipennis* = *P. nasuta* (Fig. 2g), but none of the parasitoids provided high levels of control.

Simulation of CBB infested berries available for attack by the betilid species shows asynchrony between seeking adult parasitoids (Fig. 2b–d) and the low availability of CBB infested berries (Fig. 2a). The low level of control by single releases of the betilids (Fig. 2g) is the consequence of the lag between the peaks of colonization of CBB infested berries attacked by the betilids and the late emergence of searching betilid females at the end of the ripening season (vertical dotted lines in Fig. 2).

Regressions of CBB infested berries·year^{-1} (IB) on the presence of the parasitoid species under multiple climatic conditions (Eq. (5)) shows that only *P. coffea* has a significant impact in reducing CBB infestation levels (i.e., 40.48%), a level of control that is clearly insufficient.

$$IB = \exp\left(10.93 - 0.51\,Pc\right) \quad \left(x^2 = 273.14, p < 0.01\right) \tag{5}$$

The subscript for χ_1^2 is the degrees of freedom.

Table 4
Facultative oviposition and host-feeding interactions between betilid species. Stages of the three parasitoid species attacked by each of the betilids for oviposition (ovip) and/or host-feeding were estimated from Infante et al. (2001) and Pérez-Lachaud et al. (2004).

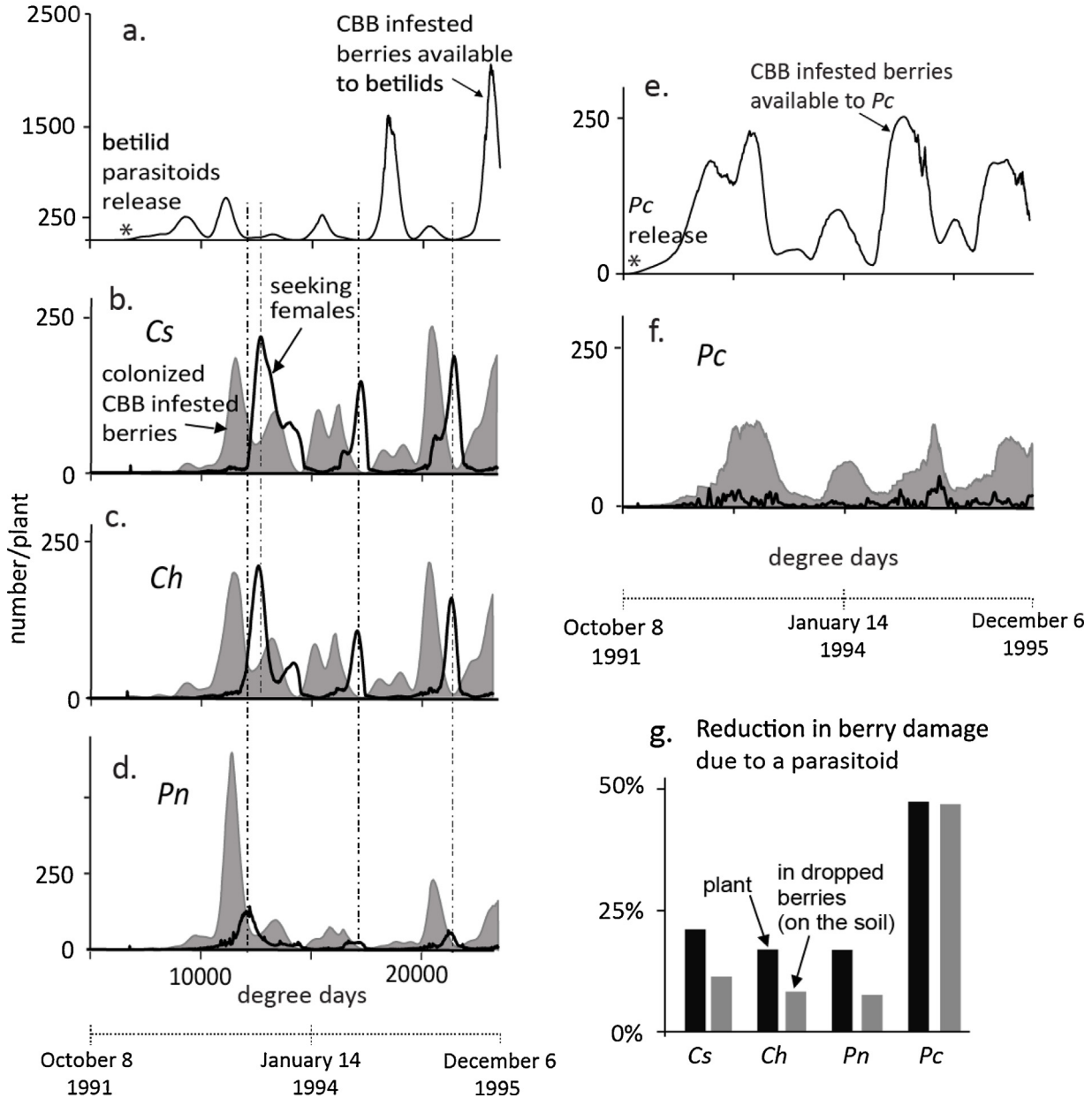| Attacking parasitoid →	*Cephalonomia stephanoderis* (*Cs*)		*Cephalonomia hyalinipennis* (*Ch*)		*Prorops nasuta* (*Pn*)	
	facultative oviposition	facultative host-feeding	facultative oviposition	Facultative host-feeding	facultative oviposition	Facultative host-feeding
host species ↓			stages attacked			
Cs	–	–	larvae and pupae	eggs and larvae	–	eggs and larvae
Ch	–	larvae	larvae	larvae	–	–
Pn	–	eggs and larvae	larvae and pupae	larvae	–	–

Fig. 2. Simulation results for Colombia (Buenavista) for single releases (*) of each parasitoid species (*Cs* = *C. stephanoderis*, *Ch* = *C. hyalinipennis*, *Pn* = *P. nasuta*, and *Pc* = *P. coffea*) acting alone at the beginning of the berry-ripening period: (a) simulation of CBB infested berries available for attack by the betilid species with the vertical dotted lines indicating asynchrony between seeking adult parasitoids and the low availability of CBB infested berries; (b, c, d) simulation dynamics of the CBB infested berries colonized by betilid parasitoids (gray areas) and of seeking females (continuous lines); (e) CBB adults available to attack by *P. coffea* (i.e., sub fig. f); and (g) summarizes the percentage reduction in berry infestation levels on the plant (black) and in shed berries on the ground (gray) when each parasitoid species acts alone. (*) indicates the time of parasitoid releases (see text in section 2.4). Plots are based on one climate scenario.
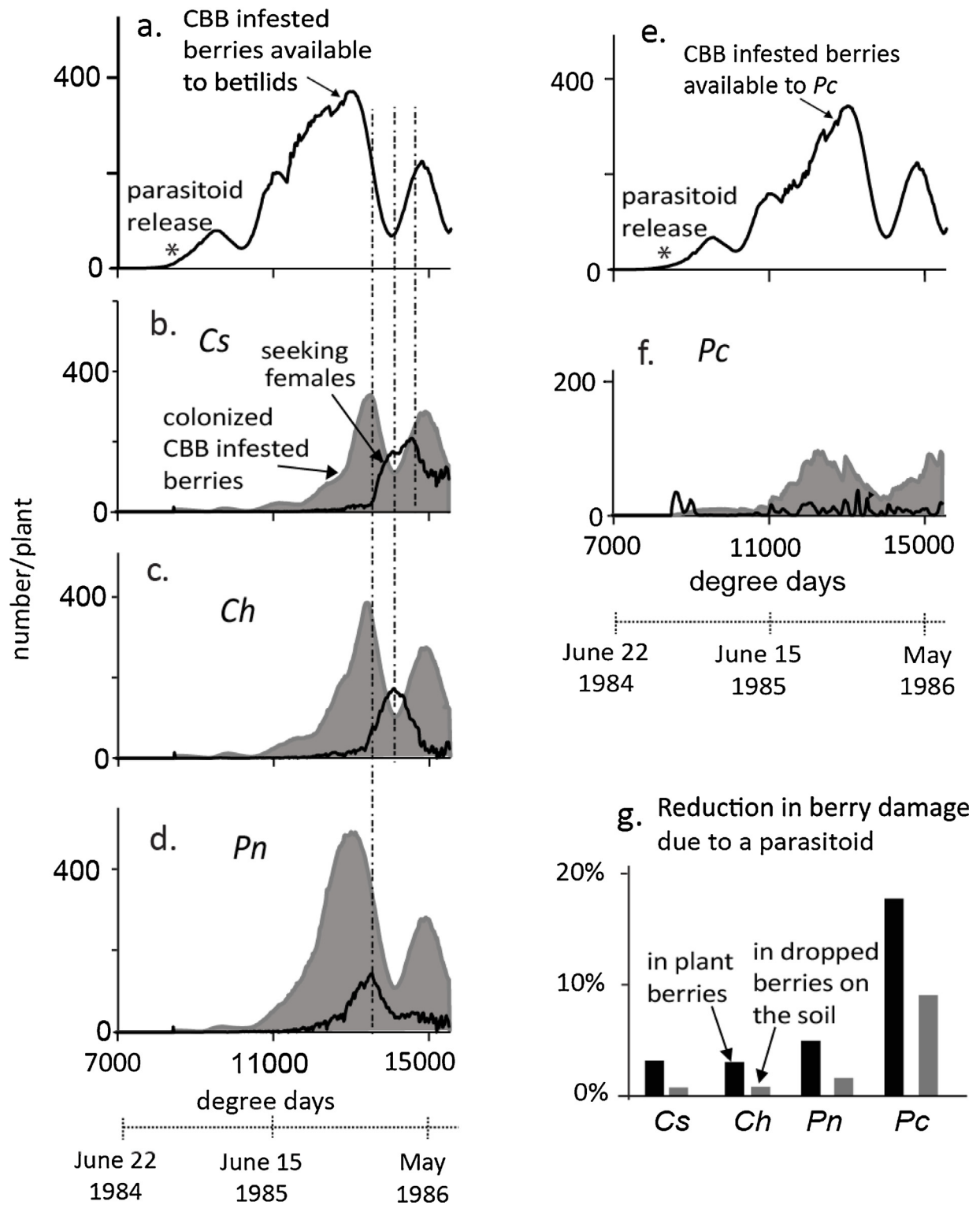
BRAZIL

Fig. 3. Simulation results for Brazil (Londrina) for single releases (*) of each parasitoid species (*Cs* = *C. stephanoderis*, *Ch* = *C. hyalinipennis*, *Pn* = *P. nasuta*, and *Pc* = *P. coffea*) acting alone at the beginning of the berry-ripening period: (a) simulation of CBB infested berries available for attack by the betilid species with the vertical dotted lines indicating asynchrony between seeking adult parasitoids and the low availability of CBB infested berries; (b, c, d) simulation dynamics of the CBB infested berries colonized by betilid parasitoids (gray areas) and of seeking females (continuous lines); (e) CBB adults available to attack by *P. coffea* (i.e., sub fig. f); and (g) summarizes the percentage reduction in berry infestation levels on the plant (black) and in shed berries on the ground (gray) when each parasitoid species acts alone. (*) indicates the time of parasitoid releases see text in section 2.4. Plots are based on one climate scenario.

3.1.2. Brazilian study

In the absence of parasitoids, the level of CBB infestation was 73.75%. Compared to Colombia, higher percentages of colonization of CBB infested berries by betilid parasitoids occurred (e.g., *C. stephanoderis* (24.40%), *P. nasuta* (39.92%), and *C. hyalinipennis* (26.86%)). However, their effectiveness in reducing CBB berry infestation compared to infestation levels without parasitoids was very low: 3.17%, 4.96% and 3.05% respectively (see Fig. 3g), and still lower in shed berries (i.e., 0.76%, 1.62% and 0.83%). This suggests that the numerical response of the betilids is too low for CBB control because their reproductive rates are about six times lower than that of CBB. Accordingly, even high levels of fruit colonization by betilids do not represent satisfactory control of CBB. As was observed in Colombia, mismatches between the emergence of betilids (Fig. 3b–d) and availability of suitable fruits that limits the resource for parasitoids (Fig. 3a) were also observed in Brazil (vertical dotted lines in Fig. 3). Compared to CBB infestation levels without control, the percentage of CBB infested berries colonized by *P. coffea* was 15.62% resulting in a reduction of 17.74% infested berry on the plant and 9.07% in shed berries.

As in Colombia, the regression analysis of CBB infested berries·year^{-1} on the presence of the parasitoid species under multiple climatic conditions (Eq. (6)) shows that only *P. coffea* markedly reduced CBB infestations, but the average reduction was much lower than in Colombia (14.44% vs.40.48%).

$$IB = \exp(11.83 - 0.16Pc) \quad x_1^2 = 207.54, p < 0.01 \tag{6}$$

3.2. Control of CBB by multiple parasitoid species

3.2.1. Colombian study

Fig. 4a shows the dynamics of the three species of betilid when acting alone, while the effects on their dynamics when interacting are shown in Fig. 4b. The interaction reduces the levels of all three parasitoids (Fig. 4a vs. b), but control of CBB is not markedly improved (not shown). The action of *C. stephanoderis* alone reduces berry damage 21.06%, while only a 19.48% reduction accrues from the action of the three betilids acting together. When *P. coffea* is introduced to the system (Fig. 4c), the densities of the betilid parasitoids are reduced 2–3 fold. This reduction occurs because *P. coffea* attacks the adult stage greatly decreasing the supply of hosts for the betilid parasitoids. However, the combined action of the four parasitoids reduces CBB attacks only 49.43% compared to 47.38% with *P. coffea* acting alone. None of the scenarios results in effective biological control of CBB.

3.2.2. Brazilian study

Acting alone (Fig. 4d) or together (Fig. 4e), the dynamics of the betilids are similar, but in the latter case the densities of the three betilids are approximately halved. When *P. coffea* is added to the system, the dynamics of the betilid parasitoids are altered and their densities are halved still again (Fig. 4f). Compared to the situation without parasitoids, the action of all parasitoids reduces CBB infested berries 22.50% compared to 16.03% with *P. coffea* acting alone (Fig. 3g). In all scenarios, the biological control of CBB is insufficient.

3.3. Competition among parasitoid species under multiple climatic conditions

3.3.1. Colombia

The percentage reductions per year (*y*) of adult parasitoids in fruit due to competition in the different parasitoid scenarios are summarized in Table 5, and show that scenarios including *P. coffea* have the highest effect in reducing betilid densities, but *P. coffea* is not affected by any of the betilids. The multiple regression models

of competitive interactions between parasitoids are summarized below Eqs. (7)–(9).

(1.) *C. stephanoderis* is affected by *P. coffea* and to a lesser extent by *P. nasuta*: (x_2^2=238, p < 0.01):

$$Csy^{-1} = \exp(7.60 - 0.39Pn - 2..76Pc) \tag{7}$$

(2.) *P. nasuta* is negatively affected by the other parasitoids (x_3^2=177.58, p < 0.01):

$$Pny^{-1} = \exp(4.60 - 0..89Cs - 1.32Ch - 2.52Pc) \tag{8}$$

(3.) *C. hyalinipennis* is affected by *C. stephanoderis* and *P. coffea* (x_2^2=249.24, p < 0.01):

$$Chy^{-1} = \exp(6.73 - 1.39Cs - 3.06Pc) \tag{9}$$

3.3.2. Brazil

The percentage reductions in the number of adult betilid parasitoids predicted by the simulation models are summarized in Table 6. The multiple regression models evaluating of the competitive interactions of the parasitoids in Brazil parallel those from Colombia and are summarized below. Again, *P. coffea* affects all the betilids (see above), but it is not affected by them, Eqs. (10)–(12):

$$Csy^{-1} = \exp(11.76 - 0.47Pn - 0.26Cs - 0.77Pc)(x_3^2 = 169.44, p < 0.01) \tag{10}$$

$$Pny^{-1} = \exp(12.42 - 0.77Cs - 0.70Ch - 0.64Pc)(x_4^2 = 281.64, p < 0.01) \tag{11}$$

$$Chy^{-1} = \exp(11.55 - 0.87Cs - 0.45Pn - 0.81Pc)(x_3^2 = 176.33, p < 0.01) \tag{12}$$

3.4. Effect of host-feeding on betilid efficacy

Population dynamics theory predicts that host-feeding parasitoids are unable to depress host population equilibria as strongly as non-host-feeders (Jervis and Kidd, 1999). To examine this, we evaluated the hypothetical absence of host-feeding in *C. stephanoderis* to determine its effect on its population dynamics and on the reduction in CBB infested berries (Fig. 5) in Buenavista (Colombia). Absent host-feeding, the number of parasitoids females seeking hosts and their colonization of infested fruits increases (Fig. 5b and c), and compared to the scenario with host feeding (Fig. 5a) results in only a further 12.06% reduction in CBB berry infestation. On a practical level, Gómez et al. (2012) proposed that feeding honey to adult betilid females before augmentative release reduced host feeding, but the small gain posited here would tend to negate the usefulness of this practice.

4. Discussion

From a human perspective, control of coffee berry borer (CBB) using effective augmentative and/or classical biological control is desirable, but this outcome appears not to be possible in Central and South America using the three commonly introduced parasitoids (*C. stephanoderis*, *P. nasuta* and *P. coffea*). Of these parasitoids, only *P. nasuta* established in Colombia (Maldonado and Benavides, 2007), and only *C. stephanoderis* and *P. nasuta* established in Brazil (Benassi, 2007). A fourth parasitoid, *C. hyalinipennis* was considered for introductions, but laboratory studies revealed it is a facultative predator and hyperparasite on immature stages of the other betilids and conspecifics, it super parasitism of CBB larvae, and it does not attack CBB adults (Pérez-Lachaud et al., 2002; Batchelor et al., 2006). Our simulation results confirm the impact of these detrimental effects.
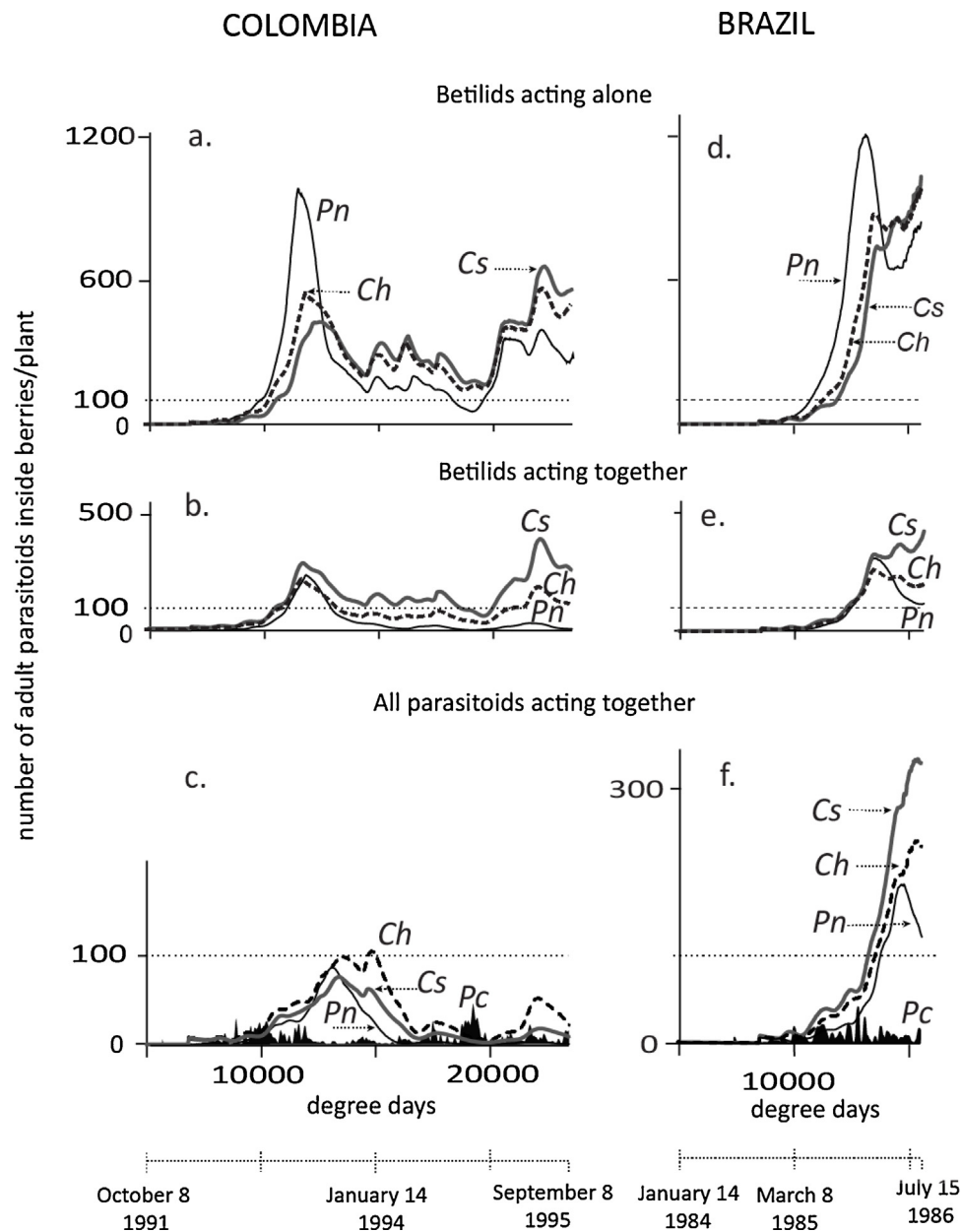
COLOMBIA   BRAZIL

Fig. 4. Simulated number of adult parasitoids in berries, alone or in combinations, for Colombia (Buenavista) (a,b,c) and Brazil (Londrina) (d,e,f). The results shown are for single releases of each parasitoid (see text and Table 4). (Cs = C. stephanoderis, Ch = C. hyalinipennis, Pn = P. nasuta, Pc = P. coffea (black filled area). Plots are based on one climate scenario.

4.1. Review of simulation results

4.1.1. Establishment of parasitoids

We sought to determine why the establishment of the parasitoid species in the face of high CBB infestations in Colombia and Brazil has been difficult, and why no combination of the parasitoids shows promise for effective control of CBB. We first review the simulation results and then relate them to ecological theory.

In sharp contrast to what is observed in the field, we assumed that all of the parasitoids established in the field and are attacking CBB and interacting with each other. This discrepancy with the facts suggests deficiencies in our knowledge of the biology of the species, and the omission in the model of the limiting effects of harvesting, crop management and cultural controls, and alternate hosts. For these reasons, our analysis of the parasitoids for control of CBB must be viewed as heuristic. Earlier simulation results by Gutierrez et al. (1998) and here suggest that only the eulophid adult

endo-parasitoid (*P. coffea*) can reduce CBB populations significantly but not sufficiently.

Unlike the betilids, *P. coffea* attacks multiple CBB females as they are boring into coffee berries and effectively stops CBB reproduction. Furthermore, *P. coffea* does not host-feed on siblings, allowing rapid growth of its populations during the berry-ripening period. Studies with *P. coffea* in Costa Rica and Mexico using sleeve and field cages support our simulation results. In Costa Rica, Espinoza et al. (2009) released a 1:10 ratio of *P. coffea* adults to CBB infested berries in entomological sleeves and obtained 95% parasitization of CBB adults and a 3 − 5.6 fold decrease in berry damage. In a similar study in México, Infante et al. (2013) obtained *P. coffea* parasitism rates of 79%. Unfortunately, cage results cannot be compared with open field releases such as those of Castillo et al. (2006) who obtained a very low progeny from the original number of female adults liberated. In a two year survey of CBB parasitoids in Western Kenya, only 17 *P. coffea* adults were reared from 69,500 CBB infested

Table 5
Percentage reduction in the number of adult betilid parasitoids (first column) with two, three and four species interactions in Colombia. Only significant relationships were included in regressions (ns = not significant) (*Cs* = *Cephalonomia stephanoderis*, *Ch* = *Chyalinipennis*, *Pn* = *Prorops nasuta*, *Pc* = *Phymastichus coffea*).

Two species interactions				
Parasitoids	Cs	Pn	Ch	Pc
Cs	–	32.21	ns	93.67
Pn	59.13	–	73.50	91.99
Ch	75.12	ns	–	95.33

Three species interactions						
Parasitoids	Cs + Ch	Cs + Pn	Cs + Pc	Ch + Pn	Ch + Pc	Pn + Pc
Cs	–	–	–	ns	ns	95.71
Pn	89.17	–	96.73	–	97.88	–
Ch	–	ns	98.83	–	–	ns

Four species interactions				
Parasitoids	Cs + Ch + Pn	Cs + Ch + Pc	Cs + Pn + Pc	Ch + Pn + Pc
Cs	–	–	–	ns
Pn	–	99.13	–	–
Ch	–	–	ns	–

Table 6
Percentage reduction in the number of adult betilid parasitoids (first column) with two, three and four species interactions in Londrina, PR, Brazil. Only significant relationships were included in the regressions (**ns** = not significant) (*Cs* = *Cephalonomia stephanoderis*, *Ch* = *Chyalinipennis*, *Pn* = *Prorops nasuta*, *Pc* = *Phymastichus coffea*).

Two species interactions				
	Cs	Pn	Ch	Pc
Cs	–	37.49	23.10	53.81
Pn	53.55	–	50.29	47.23
Ch	58.19	36.53	–	55.43

Three species interactions						
Parasitoids	Cs + Ch	Cs + Pn	Cs + Pc	Ch + Pn	Pn + Pc	Ch + Pc
Cs	–	–	–	51.93	71.13	64.48
Pn	82.20	–	75.49	–	-	73.77
Ch	–	73.46	81.36	–	71.71	–

Four species interactions				
Parasitoids	Cs + Ch + Pn	Cs + Ch + Pc	Cs + Pn + Pc	Ch + Pn + Pc
Cs	–	–	–	77.80
Pn	–	90.61	–	–
Ch	–	–	88.17	–

berries (Jaramillo et al., 2009b). These differences in the field studies suggest that crop management, harvest intensity, weather and other unexplored factors must play large roles that will be explored in a forthcoming report.

4.1.2. Low reproductive capacity of the betilid parasitoids relative to CBB

Gutierrez et al. (1998) found that the betilids released singly or in combination assuming high immigration and search rates gave poor control of CBB. They attributed the result to a low numerical parasitoid response relative to CBB as each betilid female colonizes only one berry and only partial mortality of the available hosts may occur. Our results confirm this interpretation. Further, the oviposition rate of betilids estimated from field data (Benassi, 2007) ranged from 0.055 to 0.076 eggs·female^{-1}·dd^{-1} which is about six fold lower than the oviposition rate of 0.348 eggs CBB female^{-1}·dd^{-1} (Jaramillo et al., 2009a). In addition, host-feeding by betilid adults on CBB eggs and larvae is common and reduces the future availability of preferred stages for parasitism. Under laboratory conditions, *C. stephanoderis* females fed honey had 80% greater longevity and decreased host feeding, and this practice has been proposed to

improve the survival in the field after release and to improve control of CBB, especially when preys are scarce (Gómez et al., 2012). Our simulation results suggest this practice would not significantly reduce CBB infestations (Fig. 2).

4.1.3. Phenological mismatches with CBB life stages

In Colombia, high densities of betilid females emerge at the end of the berry ripening seasons when CBB infested berries are in short supply. Thus, despite predicted high parasitization rates, a bottleneck occurs between harvests that reduces adult betilid densities to levels that are slow to rebuild in the face of rapidly increasing CBB populations. This result was verified by Benassi (2007) in the states of Espiritu Santo and São Paulo, Brazil who observed that low densities of wasps at the beginning of the harvest period required several months to increase significantly. Benavides et al. (1994, 1998) suggested that parasitoid releases should be made during the middle of the ripening season, but high CBB damage rates normally occur by this time.
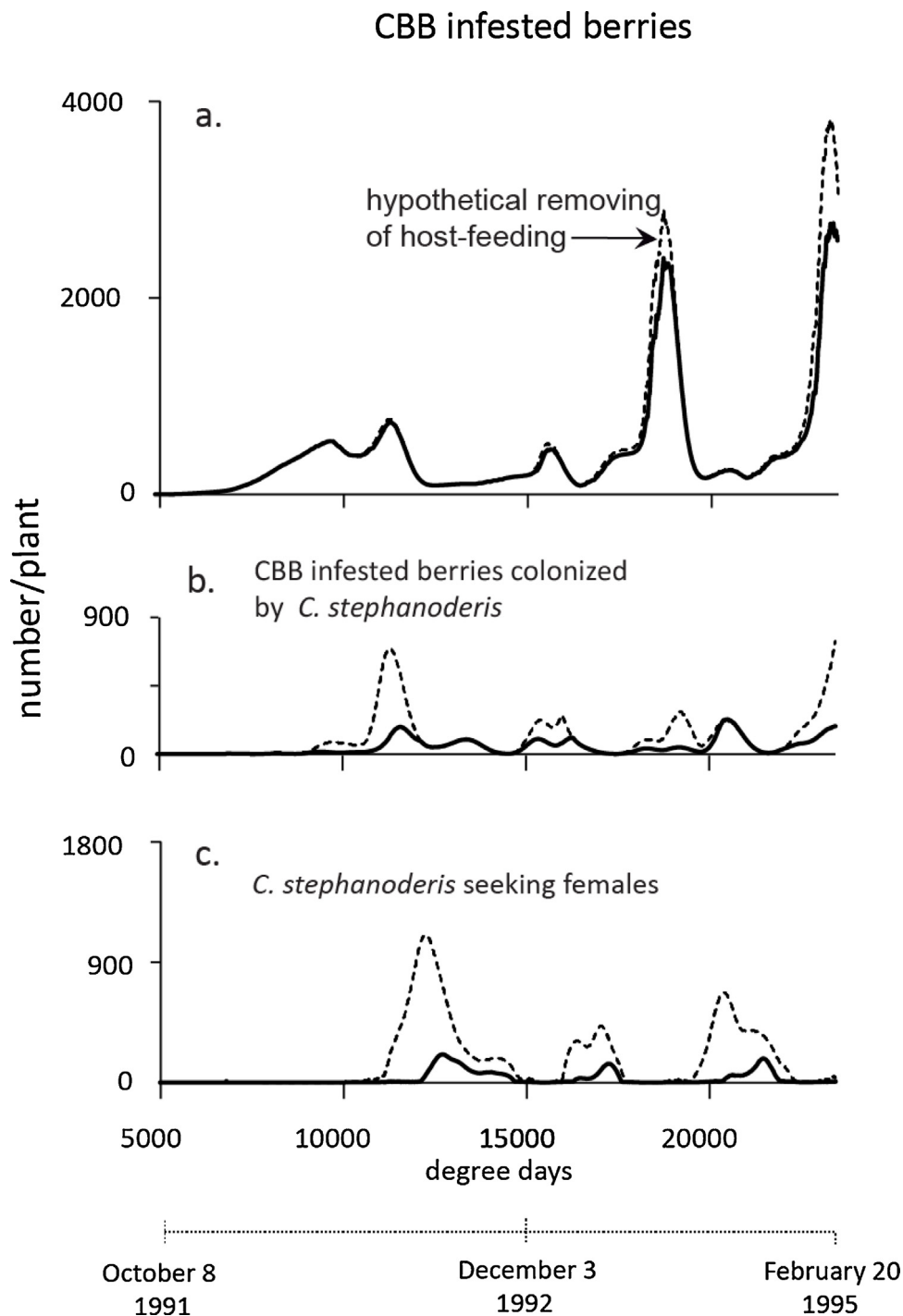
CBB infested berries

Fig. 5. Compared simulated effects of host feeding (———) vs. hypothetical removing of host-feeding (– – – –) by *C. stephanoderis*: (a) number of CBB infested berries; (b) number of CBB infested berries colonized, and (c) number of adult parasitoid females seeking hosts.

4.1.4. Negative effects of intra guild competition among betilid parasitoids

Laboratory studies by Infante et al. (2001), Pérez-Lachaud et al. (2002, 2004) and Batchelor et al. (2005, 2006) suggest that the net effect of competitive interactions between betilid parasitoids is antagonistic rather than synergistic. This was confirmed by Gutierrez et al. (1998) and our studies. Espinoza et al. (2009) proposed a complementary effect between the action of the betilids and *P. coffea*, but Gutierrez et al. (1998) and our results suggest the opposite as *P. coffea* greatly reduces the supply of hosts for the betilids by killing CBB females before they can reproduce

4.1.5. Factors affecting P. coffea establishment

Simulation results suggest that the eulophid *P. coffea* is potentially the most effective parasitoid for the control of CBB. However, in the field its efficacy can be strongly reduced by the fungal pathogen *Beauveria bassiana* (Castillo et al., 2009) and by insecticide use that appears to have a negative effect on the ongoing efforts to maintain high field populations of *P. coffea* in México (Barrera, 2005; Gómez et al., 2011). In Colombia, *P. coffea* population levels rapidly decreased in all farms after initial releases (Aristizábal et al., 2004; Salazar et al., 2007), and it is not known whether the parasitoid is established.

4.2. Ecological theory

Whatever strategy a species evolves, it must assure its continuity in time, and hence its traits must assure "adaptedness" to the biotic and abiotic conditions to minimize the likelihood of extinction (*sensu* Ayala, 1969). Further, Gutierrez and Regev (1983, 2005) proposed that evolved strategies may have little to do with maximizing the commonness of the species in the environments. Rather, adapted individuals and the species they comprise must via their genetics, take a long-term view of their resource management problem, and that tradeoffs are based on sufficiency or constrained optimization behavior rather than maximization rules. On the theoretical r-K continuum (Pianka, 1970), coffee and CBB have r-selected strategies, while the parasitoids have intermediate ones.

The well-documented biology of coffee, CBB and its parasitoids suggests that poor control of CBB is not unexpected because coffee is a long-lived shrub that produces high numbers of fruit, and few seeds need survive CBB attack to provide replacements (*c.f.,* Gutierrez and Regev, 1983). Furthermore, CBB is polyphagous in its home range in Africa with coffee being but one of its hosts (Vega et al., 2012). Similarly, the linkages of the parasitoids to CBB are not particularly tight (Vega et al., 2012) because the parasitoids also have other hosts (Pérez Lachaud and Hardy, 2001) and CBB and the parasitoids spread the risk of extinction through polyphagy (*c.f.,* Boer, 1968). As a result, little by way of regulation of CBB occurs resulting in high infestation levels in coffee in the Americas and in its native range in Africa. According to Kucel et al. (2008), severe infestation of up to 80% of berries occurs in Uganda and Ivory Coast, and 96% in Congo and Tanzania. In Kenya, Jaramillo et al. (2009b) reported infestations ranging between 60 and 91% of berries on the plant and 44–84% of shed berries on the ground. Given the lack of control of CBB by parasitoids, cultural controls need to be developed to control CBB infestation levels as explored in a forthcoming paper.

5. Conclusions

CBB in coffee is not effectively regulated by the action of parasitoids, the establishment of which in new world coffee has often proven difficult. In our studies, the interactions of coffee system components were captured using the physiologically based demographic modeling (PBDM) approach (Gutierrez and Baumgärtner, 1984; Gutierrez et al., 1998). Control of CBB by augmentative releases of parasitoids (e.g., *C. stephanoderis*, *P. nasuta* and *P. coffea*) in the Americas is neither effective nor stable, and the introduction of the additional betillid parasitoid *C. hyalinipennis* is predicted to be detrimental. *P. coffea* can provide substantial but insufficient control in zones with narrow flowering periods that concentrate the harvests period (e.g., Londrina, PR, and Brazil). Furthermore, the *P. coffea* is highly susceptible to the fungal pathogen *Beauveria bassiana* and insecticide, and its establishment is uncertain. Hence, cultural controls appear to be the only viable option for control of CBB, and will be explored in a forthcoming paper.

Acknowledgements

References

Abraham, Y.J., Moore, D., Goodwing, G., 1990. Rearing and aspects of biology of *Cephalonomia stephanoderis* and *Prorops nasuta* (Hymenoptera:Bethylidae) parasitoid of the coffee berry borer *Hypothenemus hampei* (Coleoptera: scolytidae). Bull. Entomol. Res. 80, 121–128.

Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov, V.N., Csaki, F. (Eds.), Second International Symposium on Information Theory. Academiai Kiado, Budapest, pp. 267–281.

Arcila, J., Jaramillo, R.A., 2003. Relación entre la humedad del suelo, la floración y el desarrollo del fruto del cafeto. Avances Técnicos Cenicafé 311, 1–7.

Arcila, J., Farfán, V.F., Moreno, B.A., Salazar, G.L.F., Hincapié, G.E., 2007. Sistemas de producción de café en Colombia. Cenicafé, Colombia.

Aristizábal, A.L.F., Baker, P.S., Orozco, H.J., Orozco, G.L., 1996. Determinación de las horas del día convenientes para la liberación del parasitoide *Cephalonomia stephanoderis* (Betrem) (Hymenoptera: bethylidae). Rev. Colomb. de Entomol. 22, 99–104.

Aristizábal, A.L.F., Baker, P.S., Orozco, S.J., Chaves, C.B., 1997. Parasitismo de *Cephalonomia stephanoderis* Betrem sobre una población de *Hypothenemus hampei* (Ferrari) con niveles bajos de infestación en campo. Rev. Colomb. Entomol. 23, 157–164.

Aristizábal, A.L.F., Bustillo, A.E., Orozco, H.J., Chaves, C.B., 1998. Efecto del parasitoide *Cephalonomia stephanoderis* (Hymenoptera: bethylidae) sobre las poblaciones de *Hypothenemus hampei* (Coleoptera: scolytidae) durante y después de la cosecha. Rev. Colomb. de Entomol. 24, 149–155.

Aristizábal, A.L.F., Salazar, E.H.M., Mejía, M.C.G., Bustillo, P.A.E., 2004. Introducción y evaluación de *Phymastichus coffea* (Hymenoptera: eulophidae) en fincas de pequeños caficultores, a través de investigación participativa. Rev. Colomb. Entomol. 30, 219–234.

Ayala, F.J., 1969. An evolutionary dilemma: fitness of genotypes versus fitness of populations. Can. J. Genet. Cytol. 11, 439–456.

Barrera, J.F., Gómez, J., Infante, F., Castillo, A., De la Rosa, W., 1989. Biologie de *Cephalonomia stephanoderis* Betrem (Hymenoptera:Bethylidae) en laboratoire. I. cycle biologique, capacité d'oviposition et emergente du fruit du caféier. Café, Cacao, Thé 33, 101–108.

Barrera, J.F., Dynamique des populations du scolyte des fruits du caféier, *Hypothenemus hampei* (Coleoptera: Scolytidae), et lutte biologique avec le parasitoide *Cephalonomia stephanoderis* (Hymenoptera: Bethylidae), au Chiapas, Mexique. Ph.D. Thesis. Université Paul Sabatier, Toulouse III. France, 1994.

Barrera, J.F., 2005. Investigación sobre la broca del café en México: Logros, retos y perspectivas. In: Barrera, J.F. (Ed.), Situación actual y perspectivas de la investigación y manejo de la broca del café en Costa Rica, Cuba, Guatemala y México, Symposium. El colegio de la Frontera Sur, México, pp. 1–13.

Batchelor, T.P., Hardy, I.C.W., Barrera, J.F., Pérez-Lachaud, G., 2005. Insect Gladiators II: Competitive interactions within and between parasitoids species of the coffee berry borer *Hypothenemus hampei* (Coleoptera: scolytidae). Biol. Control 33, 194–202.

Batchelor, T.P., Hardy, I.C.W., Barrera, J.F., 2006. Interactions among bethylid parasitoid species attacking the coffe berry borer, *Hypothenemus hampei* (Coleoptera:Scolytidae). Biol. Control 36, 106–118.

Beddington, J.R., Hassell, M.P., Lawton, J.H., 1976. The components of arthropod predation: II. The predator rate of increase. J. Anim. Ecol. 45, 165–185.

Benassi, V.L.R.M., 2007. Biologia em diferentes temperaturas e ocorrência de *Prorops nasuta* Wat. e *Cephalonomia stephanoderis* Betr. (Hymenoptera:Bethylidae) parasitando *Hypothenemus hampei* (Ferr.) (Coleóptera:Scolytidae). Thesis. Universidade Estadual Paulista-Câmpus de Jaboticabal, Brasil.

Benavides, M.P., Bustilo, P.A.E., Montoya, E.C., 1994. Avances sobre el uso del parasitoide *Cephalonomia stephanoderis* para el control de la broca del café, *Hypothenemus hampei*. Rev. Colomb. Entomol. 20, 247–253.

Benavides, P., Bustillo, A.E., Orozco, J., Cháves, B., 1998. Efecto del parasitoide *Cephalonomia stephanoderis* (Hymenoptera: bethylidae) sobre las poblaciones de *Hypothenemus hampei* (Coleoptera: scolytidae) durante y despúes de la cosecha. Rev. Colomb. Entomol. 24, 149–156.

Boer, P.J., 1968. Spreading of risk and stabilization of animal numbers. Acta Biotheor. 18 (1–4), 165–194.

Bustillo, A.E., 2006. Una revision sobre la broca del café, *Hypothenemus hampei* (Coleoptera: curculionidae: Scolytinae), en Colombia. Rev. Colomb. Entomol. 32, 101–116.

CABI, 2011. Stopping the Coffee Berry Borer in Its Tracks (Accessed on: 01 January 2011. http://www.cabi.org/default.aspx?site=170&page=1017&pid=2734).

Cantor, R.F., Vilela, E.F., Bustillo, A.E., 1999. Primeira introdução no Brasil do endoparasitoide *Phymastichus coffea* (La Salle) (Hymenoptera; Eulophidae), para o controle biologico da broca do café *Hypothenemus hampei* (Ferrari) (Coleoptera; Scolytidae). In: Riede, C.R., Sera, T., Soccol, C.R., Roussos, S. (Eds.), Proceedings of the 3rd International Seminar on Biotechnology in the Coffee Agroindustry. UFPR-AIAPR-IRD, Londrina, Brasil, p. 305.

Carrillo, E., Campos, O., 1991. La broca del café en Guatemala. In: Barrera, J.F., Castillo, A., Gómez, J., Malo, E., Infante, F. (Eds.), I Reunión Intercontinental Sobre Broca Del Café. CIES, Tapachula, México, p. 4.

Castillo, A., Infante, F., Vera-Graziano, J., Trujillo, J., 2004a. Host-discrimination by *Phymastichus coffea*, a parasitoid of the coffee berry borer (Coleoptera: scolytidae). BioControl 49, 655–663.

Castillo, A., Infante, F., López, G., Trujillo, J., Kirkendall, L.R., Vega, F.E., 2004b. Laboratory parasitism by *Phymastichus coffea* (Hymenoptera: eulophidae): upon non-target bark beetles associated with coffee plantations. Florida Entomol. 87, 274–277.

Castillo, A., Espinoza, J.C., Valle, M.J., Infante, F., 2006. Dispersión del parasitoide africano *Phymastichus coffea* La Salle (HYMENOPTERA:EULOPHIDAE) en un nuevo agroecosistema. Folia Entomol. Mexicana 45 (3), 319–327.

Castillo, A., Gómez, J., Infante, F., Vega, F.E., 2009. Susceptibilidad del parasitoide *Phymastichus coffea* LaSalle (Hymenoptera: eulophidae) a *Beauveria bassiana* en condiciones de laboratorio. Neotrop. Entomol. 38, 665–670.

Castillo, A., 2005. Análisis Post-introductorio Del Parasitoide Africano *Phymastichus Coffea* LaSalle (Hymenoptera: Eulophidae) a México Thesis. Colegio de Postgraduados, México, pp. 2005.

Cenicafé, Anuario Meteorológico Cafetero 1990–1995. Chinchiná, Colombia: Centro Nacional de Investigaciones del Café Pedro Uribe Mejía.

Costa-Lima, A.M., 1924. Sobre a broca do café (*Stephanoderes coffea*, Hag.). Chacaras e Quintais 30, 413–416.

Damon, A., Segura, P.H., Valle, M.J., Santiesteban, A., 1999. Effect of *Euphorbia hirta* nectar and its component sugars, upon the survival of bethylid parasitoids of the coffee berry borer. Southw. Entomol. 24, 49–59.

Di Cola, G., Gilioli, G., Baumgärtner, 1998. Mathematical models for age-structured population dynamics. In: Huffaker, C.B., Gutierrez, A.P. (Eds.), Ecological Entomology. John Wiley & Sons, Inc, USA, pp. 503–531.

Espinoza, J.C., Infante, F., Castillo, A., Pérez, J., Nieto, G., Pinson, E.P., Vega, F.E., 2009. The biology of *Phymastichus coffea* LaSalle (Hymenoptera: eulophidae) under field conditions. Biol. Control 49, 227–233.

Feldhege, M.R., 1992. Rearing techniques and aspects of biology of *Phymastichus coffea* (Hymenoptera: Eulophidae), a recently described endoparasitoid of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). Café, Cacao, Thé 36, 45–54.

Ferré, F., 1991. La aventura del café. Altamir Ediciones, Colombia.

Fraser, B.D., Gilbert, N., 1976. Coccinelids and aphids: a quantitative study of the impact of adult ladybirds (Coleóptera:Coccinelidae) preying on field populations of pea aphids (Homoptera: aphididae). J. Entomol. Soc. Br. Columb. 73, 33–56.

Gómez, R.J., Santos, O.A., Valle, M.J., Montoya, G.P.J., 2011. Determinación del establecimiento de parasitoides de la broca del café *Hypothenemus hampei* (Coleoptera: curculionidae: Scolytinae) en cafetales del Soconusco Chiapas, México. Entomotrópica 25, 25–36.

Gómez, J., Barrera, J.F., Liedo, P., Valle, J., 2012. Influence of age and diet on the performance of *Cephalonomia stephanoderis* (Hymenoptera, Bethylidae) a parasitoid of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: curculionidae). Rev. Brasil. Entomol. 56, 95–100.

Gutierrez, A.P., Baumgärtner, J.U., 1984. Multitrophic level models of predator-prey energetics: II: A realistic model of plant-herbivore- parasitoid-predator interactions. Can. Entomol. 116, 933–949.

Gutierrez, A.P., Regev, U., 1983. The economics of fitness and adaptedness: the interaction of sylvan cotton (*Gossypium hirsutum* L.) and the boll weevil (*Anthonomus grandis* Boh.): An example. Acta Oecol. Oecol. Generalis 4 (3), 271–287.

Gutierrez, A.P., Regev, U., 2005. The bioeconomics of tritrophic systems: applications to invasive species. Ecol. Econ. 52, 382–396.

Gutierrez, A.P., Villacorta, A., Cure, J.R., Ellis, C.K., 1998. Tritrophic analysis of the coffee (*Coffea arabica*) − coffee berry borer [*Hypothenemus hampei* (Ferrari)] − parasitoid system. Annais da Sociedade Entomologica do Brasil 27 (3), 357–385.

Gutierrez, A.P., 1996. Applied Population Ecology: A Supply-Demand Approach. John Wiley & Sons, United States.

Hempel, A., 1933. Combate à broca do café por meio da Vespa de Uganda. Bol. Agric. Zoot. Vet. 6 (9), 551–555.

Hempel, A., 1934. A *Prorops nasuta* Waterston no Brasil. Arquivos do Instituto Biológico 5, 197–212.

Hopkins, A.D., 1915. Classification of the Cryphalinae with descriptions of new genera and species. United States Department of Agriculture, Report 99., pp. 1–75.

ICA-Instituto Colombiano Agropecuario, 1999. Protección sanitaria del cultivo del cafeto. Convenio ICA-FNC. Informe 1998. ICA, Bogotá, pp. 1–48.

Infante, F., Luis, J.H., Barrera, J.F., Gómez, J., Castillo, A., 1992. Thermal constants for preimaginal development of the parasitoid *Cephalonomia stephanoderis* Betrem (Hymenoptera:Bethylidae). Can. Entomol. 124, 935–941.

Infante, F., Murphy, S.T., Barrera, J.F., Gómez, J., De la Rosa, W., Damon, A., 1994. Cría de *Phymastichus coffea*, parasitoid de la broca del cafí y algunas notas sobre su historia de vida. Southw. Entomol. 19, 313–315.

Infante, F., Mumford, J., Baker, P.S., Barrera, J., Fowler, S., 2001. Interespecific competition between *Cephalonomia stephanoderis* and *Prorops nasuta* (Hym., Bethylidae), parasitoids of the coffee berry borer, *Hypothenemus hampei* (Col., Scolytidae). J. Appl. Entomol. 125, 63–70.

Infante, F., Castillo, A., Pérez, J., Vega, F., 2013. Field-cage evaluation of the parasitoid *Phymastichus coffea* as a natural enemy of the coffee berry borer *Hypothenemus hampei*. Biol. Control 67, 446–450.

Infante, F., 1998. Biological Control of *Hypothenemus Hampei* (Coleoptera:Scolytidae) in Mexico, Using the Parasitoid *Prorops Nasuta* (Hymenoptera:Bethylidae) Thesis. Imperial College, University of London.

Infante, F., 2000. Development and population growth rates of *Prorops nasuta* (Hym., Bethylidae) at constant temperatures. J. Appl. Entomol. 124, 343–348.

International Coffee Organization, 2007. Accessed on: 15 January 2011. Coffee berry borer-The need for a review of the status and knowledge of a serious coffee pest. Project Proposal. http://www.ico.org/show_document. asp?id=2098.

Jaramillo, S.J., Bustillo, P.A.E., Montoya, R.E.C., 2002. Parasitismo de *Phymastichus coffea* sobre poblaciones de *Hypothenemus hampei* en frutos de café de diferentes edades. Revista Cenicafé 53, 317–326.

Jaramillo, J., Bustillo, A.E., Montoya, E.C., Borgemeister, C., 2005. Biological control of the coffee berry borer *Hypothenemus hampei* (Coleoptera: curculionidae) by *Phymastichus coffea* (Hymenoptera: eulophidae) in Colombia. Bull. Entomol. Res. 95, 1–6.

Jaramillo, J., Borgemeister, C., Setamou, M., 2006. Field superparasitism by *Phymastichus coffea*, a parasitoid of adult coffee berry borer, *Hypothenemus hampei*. Entomol. Exp. Appl. 119, 231–237.

Jaramillo, J., Chabi, O.A., Kamonjo, C., Jaramillo, A., Vega, F.E., Poehling, H.M., Borgemeister, C., 2009a. Thermal tolerance of the coffee berry borer Hypothenemus hampei: predictions of climate change impact on a tropical insect pest. PLoS One 4, e6487, http://dx.doi.org/10.1371/journal.pone.0006487.

Jaramillo, J., Chabi-Olaye, A., Borgemeister, C., Kamonjo, C., Poehling, H., Vega, F., 2009b. Where to sample? Ecological implications of sampling strata in determining abundance and impact of natural enemies of the coffee berry borer, *Hypothenemus hampei*. Biol. Control 49, 245–253, http://dx.doi.org/10.1016/j.biocontrol.2008.12.007.

Jervis, M.A., Kidd, N.A.C., 1999. Parasitoid adult nutritional ecology: implications for biological control. In: Hawkins, B.A., Cornell, H.V. (Eds.), Theoretical Approaches to Biological Control. Cambridge University Press, United Kingdom, pp. 131–151.

Kucel, P., Murphy, S.T., Orozco-Hoyos Day, J.R., 2004. Developing mass rearing procedures for the parasitoid H. coffeicola Schmeid for control of the coffee berry borer Hypothenemus hampei Ferrari. In: ASIC (Ed.), 20th Proceedings of the International Conference on Coffee Science. Bangalore. India, pp. 1235–1242.

Kucel, P., Kangire, A., Egonyu, J.P., 2008. Status and Current Research Strategies for Management of the Coffee Berry Borer (*Hypothenemus Hampei* Ferr) in Africa. National Crop Resources Research Institute, Uganda, pp. 1–9.

Lactin, D.J., Holliday, N.J., Johnson, D.L., Craigen, R., 1995. Improved rate model of temperature dependent development by arthropods. Environ. Entomol. 24, 68–75.

Lauzière, I., Pérez-Lachaud, G., Brodeur, J., 2000. Behavior and activity pattern of *Cephalonomia stephanoderis* (Hymenoptera: bethylidae) attacking the coffee berry borer, *Hypothenemus hampei* (Coleoptera: scolytidae). J. Insect Behav. 13 (3), 375–395.

Maldonado, L.C.E., Benavides, M.P., 2007. Evaluación del establecimiento de *Cephalonomia stephanoderis* y *Prorops nasuta*, controladores de *Hypothenemus hampei*, en Colombia. Revista Cenicafé 58, 333–339.

Manetsch, T.J., 1976. Time-varying distributed delays and their use in aggregate models of large systems. IEEE Trans. Syst. Man Cybernet. 6, 547–553.

Muñoz-Hernández, R., 1991. Estrategias de manejo de la broca del café en los países de Promecafé. In: Barrera, J.F., Guerra, A.A., Menn, J.J., Baker, P.S. (Eds.), II Reunión intercontinental sobre broca del café. A.R.S-CABI Bioscience-Ecosur, Tapachula, México, p. 82.

O'hara, R.B.O., Kotze, D.J., 2010. Do not log-transform count data. Methods Ecol. Evol. 1, 118–122.

Orozco, H.J., 2000. Programa de introducción de parasitoides en la zona cafetera. In: Cenicafé (Ed.), Informe anual de actividades de la Disciplina de Entomología, Octubre de 1999–Septiembre de 2000. Chinchiná, Colombia.

Pérez Lachaud, G., Hardy, I.C.W., 2001. Alternative hosts for bethylid parasitoids of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: scolytidae). Biol. Control 22, 265–277.

Pérez-Lachaud, G., Hardy, I.C.W., 1999. Reproductive biology of *Cephalonomia hyalinipenis* (Hymenoptera:Bethylidae) a native parasitoid of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: scolytidae), in Chiapas, México. Biol. Control 14, 152–158.

Pérez-Lachaud, G., Hardy, I.C.W., Lachaud, J.P., 2002. Insect gladiators: competitive interactions between three species of bethylid wasps attacking the coffee berry borer, *Hypothenemus hampei*, (Coleoptera: scolytidae). Biol. Control 25, 231–238.

Pérez-Lachaud, G., Batchelor, T.P., Hardy, I.C.W., 2004. Wasp eat wasp: facultative hyperparasitism and intra-guild predation by bethylid wasps. Biol. Control 30, 149–155.

Pianka, E.R., 1970. On r and K selection. Am. Nat. 104 (940), 592–597.

Prescott, J.A., 1940. Evaporation from water Surface in relation to solar radiation. Trans. R. Soc. Aust. 64, 114–118.

Rodríguez, D., Cure, J.R., Cotes, J.M., Gutierrez, A.P., Cantor, F., 2011. A coffee agroecosystem model: I. Growth and development of the coffee plant. Ecol. Model. 222, 3626–3639.

Rodríguez, D., Cotes, J.M., Cure, J.R., 2012a. Comparison of eight degree-day estimation methods in four agroecological regions in Colombia. Bragantia 71, 299–307.

Rodríguez, D., Cure, J.R., Cotes, J.M., Gutierrez, A.P., Cantor, F., 2013. A coffee agroecosystem model: II. Dynamics of coffee berry borer. Ecol. Model. 248, 203–214.

Salazar, E.H.M., Mejía, M.C.G., Aristizábal, A.L.F., Jiménez, Q.M., Cantor, R.F., 2007. Introducción de *Phymastichus coffea*, parasitoide de la broca, en fincas de caficultores experimentadores. Avances Técnicos Cenicafé 358, 1–8.

Sigsgaard, L., 2000. The temperature-dependent duration of development and parasitism of three cereal aphid parasitoids, *Aphidius ervi, A. rhopalosiphi* and *Praon volucre*. Entomologia. Experim. et Appl. 95 (2), 173–184.

Simpson, G.L., 2016. Permute: Functions for Generating Restricted Permutations of Data. R Package Version 0. 9-0.

Stinner, R.E., Gutierrez, A.P., Butler Jr., G.D., 1974. An algorithm for temperature-dependent growth rate simulation. Can. Entomol. 106, 519–524.

Stone, N.D., Gutierrez, A.P., 1986. A field oriented simulation of pink bollworm in southwestern desert cotton. Hilgardia 54, 1–24.

Ticheler, J., 1961. Etude analitique de l'épidemiologie du scolyte des graines de café *Stephanoderes hampei* Ferr, vol. 61. Mededelingen Landbouwhogeschool Wageningen, Cote d'Ivoire, pp. 1–49.

Toledo, P.S., Pinto da Fonseca, J., 1935. *Heterospillus coffeicola* Schmied parasita da broca do café, *Stephanoderis hampei* (Ferr.), vol. 6. Arquivos do Instituto Biológico, pp. 179–199.

Vansickle, J., 1977. Attrition in distributed delay models. IEEE Trans. Syst. Man Cybernet. 7, 635–638.

Vega, F.E., Hoffstetter, R.W., 2014. Bark Beetles: Biology and Ecology of Native and Invasive Species. Academic Press, United Kingdom.

Vega, F.E., Infante, F., Castillo, A., Jaramillo, J., 2009. The coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera:Curculionidae): A short review, with recent findings and future research directions. Terres. Arthropod. Rev. 2, 129–147, http://dx.doi.org/10.1163/187498209x12525675906031.

Vega, F.E., Davis, A., Jaramillo, J., 2012. From forest to plantation? Obscure articles reveal alternative host plants for the coffee berry borer, *Hypothenemus hampei* (Coleoptera: curculionidae). Biol. J. Linn. Soc. 107, 86–94.

Vergara-Olaya, J.D., Orozco-Hoyos, J., Bustillo, P.A.E., Cháves-Córdoba, B., 2001. Biología de *Phymastichus coffea* en condiciones de campo. Revista Cenicafé 52, 97–103.

Vieira, H.D., 2008. Coffee: the plant and its cultivation. In: Souza, R. (Ed.), Plant-Parasitic Nematodes of Coffee. Springer.

Villanueva-Marrufo, A.E., 1991. Investigaciones del Inmecafé sobre la broca del café. In: Barrera, J.F., Castillo, A., Gómez, J., Malo, E., Infante, F. (Eds.), I Reunión Intercontinental Sobre Broca Del Café. CIES, Tapachula, México, p. 13.

Walpole, R.E., Myers, R.H., Myers, S.L., Ye, K., 2007. Probability and Statistics for Engineers and Scientists. Pearson Education International, United States.